Littoral Zonation in Two Caves in the Auckland District

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Abstract

IN two caves, at Red Beach and Stanmore Bay, on the east coast mainland of the Hauraki Gulf, zonation of marine organisms is described. Consideration of the incidence of direct sunlight and indirect daylight indicates that the latter is probably the more important factor ecologically. Cave-dwelling species are classified into eury- and steno-photic, light and shade preferring groups.

INTRODUCTION

Apart from the work of Lami (refs. in Chapman, 1946) and Grubb and Martin (1937), the amount of information on cave fauna and flora in different parts of the world is rather scarce. The obvious factors regulating growth of organisms which may be classed as cave-dwellers are light and humidity (Chapman, *loc. cit.*, p 637). Lami (1939, 1940) records maximum and minimum light values, pH and relative humidity for a number of "cavernicole" algae. He distinguishes three groups of algae according to the degree of their light tolerance: firstly those which can grow only under intense illumination; secondly those which have a moderately wide range in both well- and dimly-lit habitats; and lastly those which are confined to caves and shaded clefts.

Within the Waitemata Sandstone area on the east coast mainland of the Hauraki Gulf, caves are encountered at frequent intervals, often coincident with a fault line at the junction of cliff bases and intertidal platforms. Many are no deeper than a metre or two—mere concave hollows which harbour a seepage or high spring tide community of *Lichina, Enteromorpha* or *Rhizoclonium*. Others are hollowed out to form caverns more than 30 metres deep and several metres high. Two caves were selected for observation, one at Red Beach, the other at Stanmore Bay. Both places are in the southern sweep of Whangaparaoa Bay, about 17 miles north of Auckland City (see Chapman, 1950, Fig. 1, for location of the Stanmore Bay cave). Zonation of the dominant species on each wall was recorded by the first author early in February, 1950, at Red Beach, while that at Stanmore Bay was recorded in midwinter of the same year (2.7.50). The caves were re-examined by both authors some two years later (30 12.52) when a detailed topographic survey was made, and daylight penetration measured with a Weston photo-electric meter. Each meter reading was taken from the surface of a sheet of white unglazed paper held against the wall, 2 metres above the floor of the cave, and at such an angle that maximum deflection of the meter was obtained. The day was a clear, sunny one, and all light readings were taken within an hour of noon. Although the light intensity values as shown in Figure 1 will have no absolute significance except for the time of observation, it is believed that they will indicate reasonably well the gradient of indirect illumination in the caves at most times when direct

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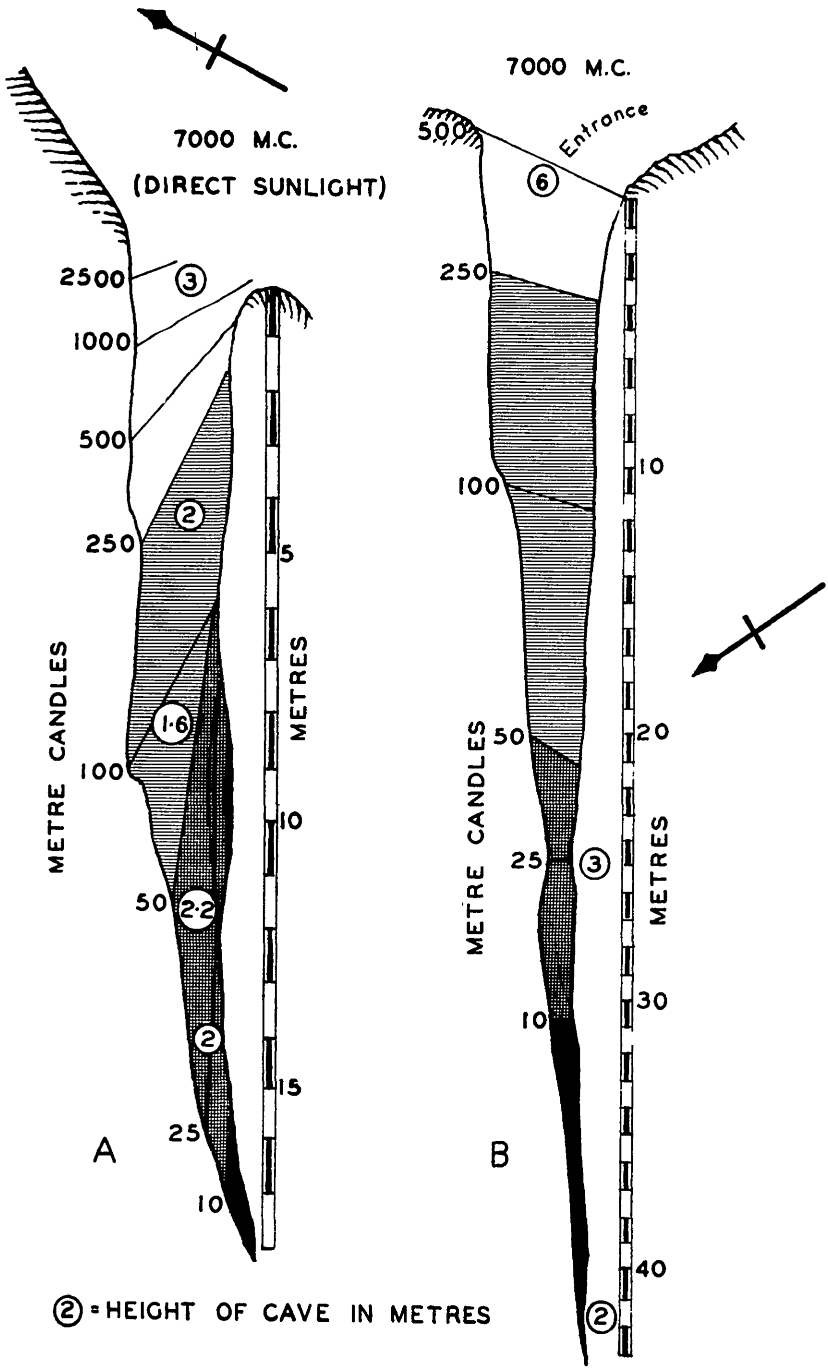

FIGURE 1.—Ground plan of caves in relation to penetration of indirect daylight
A, Red Beach Cave B, Stanmore Bay Cave.

sunlight is absent. The principal difference between the two in this respect appears to be that, while opposite walls of the Stanmore Bay cave are very nearly equally illuminated, at Red Beach the north-western wall receives more light than the south-eastern

The penetration of direct sunlight has been estimated from a table of azimuth and apparent elevation of the sun* for midsummer (December 22) and mid-winter (June 21). The isopleths in Figure 2 indicate the number of hours' exposure to direct sunlight at a level 2 metres (Stanmore Bay) or 1 metre (Red Beach) above the cave floor The most significant feature indicated by the figure is that, while the Stanmore Bay cave receives the majority of its direct sunlight in summer, the reverse is the case at Red Beach This is due to the fact that the two caves face respectively the mid-summer (N 60° E.) and mid-winter (S 60° E.) sunrises. Maximum light penetration can only occur when the sun is relatively low and virtually all direct light is intercepted by the cave roof for elevations greater than 10 degrees

When the above data are compared with the distribution of the cave-dwelling organisms, it will be seen from the ensuing description and illustrations that the biological pattern follows more closely the penetration of indirect daylight. No obvious correlation can be inferred between zonation and direct sunlight because, although one cave receives nearly all its direct sunlight in summer and the other in winter, there is no great difference in the pattern of distribution of the dominant plants and attached animals between the two caves.

(a) *Red Beach Cave.*

The cave at Red Beach measures 18 metres from mouth to vertex, and 3 metres at the highest part of the entrance. The floor is 1–2 metres wide, its lowest level being slightly above E (H)L W N. (Figure 1A). As mentioned before, it faces approximately N. 60° E Relative humidity (measured by using a whirling psychrometer) at 2 0 p m. on 6 2 50 was 75% inside the cave, as against 57% outside in broad daylight (air temperature 23 0° C.) Unlike the situation in the caves examined by Lami, there was no appreciable difference in humidity measurements in different sectors Overarching of the south-east wall at the entrance to meet up with the north-west wall, which is more or less vertical, is responsible for cutting off direct sunshine from it during mid-summer. The north-west wall, in spite of receiving less direct sunlight than the south-east wall in winter, is more strongly lit than the latter by continuous, diffuse daylight. The light gradually loses intensity until in the ultimate recesses the meter fails to register and it is almost completely dark. The fact that *Sabellaria* penetrates a greater distance on the north-west wall may be correlated with the greater degree of penetration of indirect daylight on that wall (cf Figures 3, 4). By contrast, at upper levels on the south-east wall *Nodularia* and *Rhodochorton* each occupy a narrow belt, but *Rhodochorton* is absent from a corresponding position on the north-west wall. *Tethya*, too, is confined to darker crannies, though nearer E.(H.)L W N. On both walls *Hildenbrandtia* gradually assumes complete dominance at all levels beyond 10 metres in from the mouth The more recent visit in December, 1952, revealed the presence of *Mitella spinosa*, a dark brown, stalked barnacle on the south wall at 10 metres, in almost total

* These figures were computed by Mr I. L Thomsen, director of the Carter Observatory, whose assistance is gratefully acknowledged by the authors.

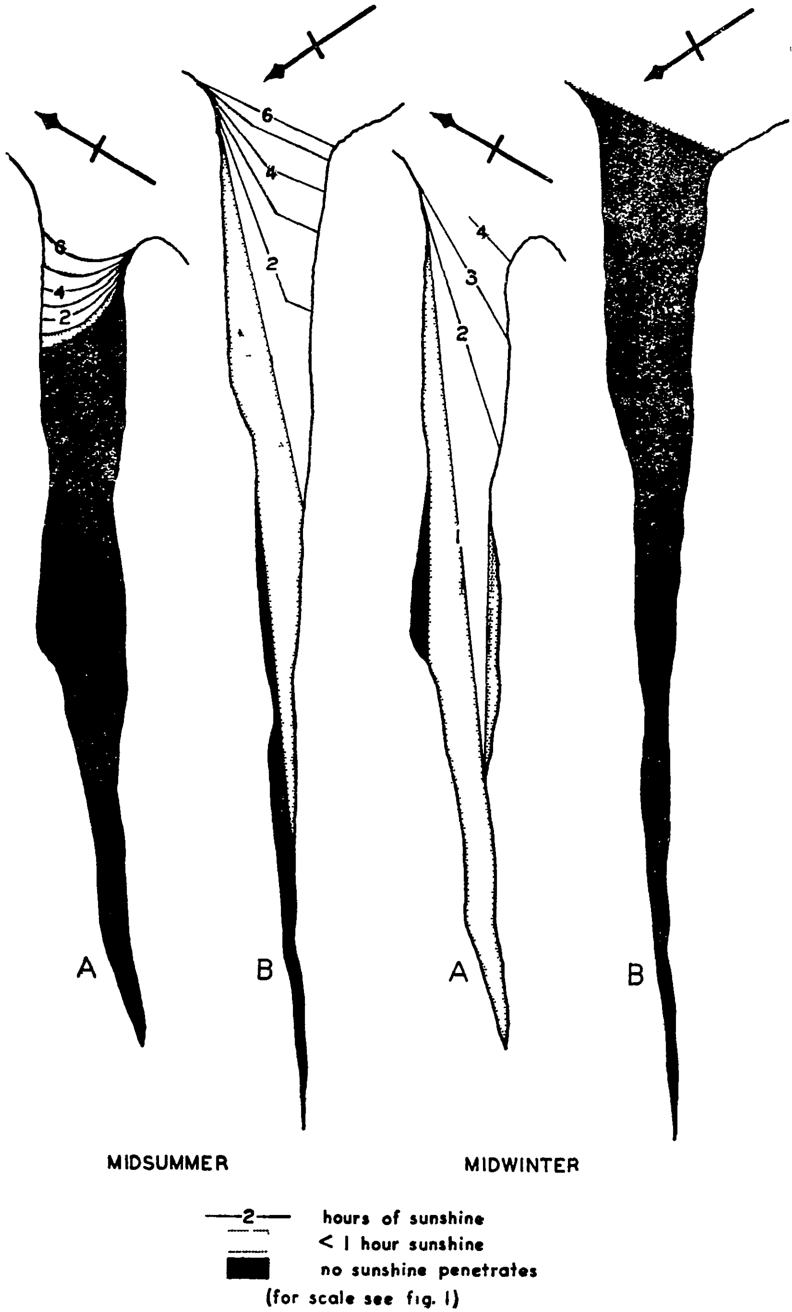

FIGURE 2.—Penetration of direct sunshine, summer and winter into—A, Red Beach Cave and B. Stanmore Bay Cave.

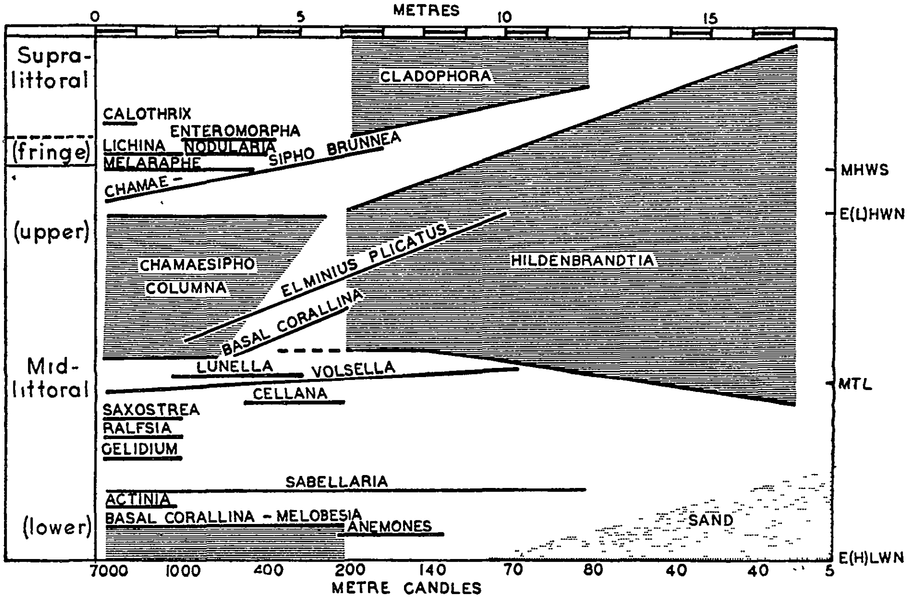

FIGURE 3.—Schematic diagram of zonation on north-west wall of Red Beach Cave—summer. Vertical scale = twice horizontal.

darkness. It was noticed that the pattern of distribution mapped in February, 1950, had altered considerably. Populations of most of the cave dwellers were seriously depleted, apart from encrusting species. The lack of accumulation of sand in the innermost recesses pointed to a recent scour by an easterly gale, which no doubt had removed some of the organisms. A continuous study of the duration and rate of establishment of each species would provide more valuable information

(b) *Stanmore Cave.*

The Stanmore Bay cave, which opens directly to the south-east, is more impressive in its depth, dampness, and darkness. It is 38 metres long, 6 metres wide across its diagonal entrance, and up to 6 metres high (Fig 1B). Boulder fragments are strewn across the entrance and for several metres inside, after which the floor is permanently wet by a pool. The cave floor is approximately 1 foot below E.(H.)L.W.N. In contrast with its total lack of winter sunshine, this cave is lit by summer rays for nearly 20 metres down the south wall. But no direct correlation can be inferred with the distribution of any of the dominant organisms, except perhaps *Ptilothamnion* (Fig. 5). However, other factors must also be concerned, including reduced salinity and topography, since this alga is confined to upper sides of flat ledges below seepage cracks at high levels on the southern cave face.

No psychrometer was available at the time the Stanmore cave was examined; but higher humidity values are to be expected, owing to the greater length and dimensions, the continual seepage from above, and to the large pool on the cave floor.

North and south walls join at a wide angle 6 metres above the entrance (Fig. 1B). Between 20 and 24 metres from the mouth the aperture narrows

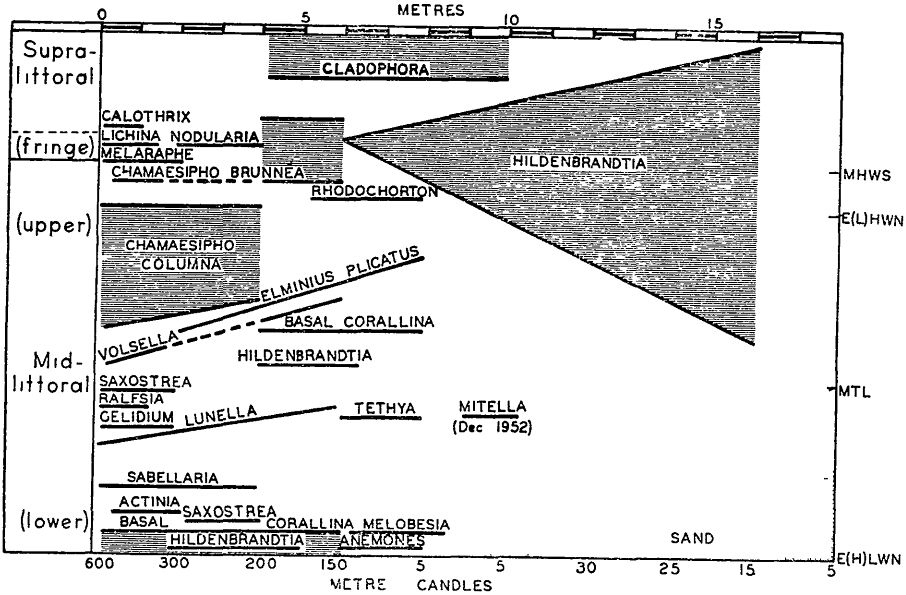

FIGURE 4.—Schematic diagram of zonation on south-east wall of Red Beach Cave—summer Vertical scale = twice horizontal

considerably owing to a curve of the west wall so far in towards the centre of the aperture that there is scarcely room to squeeze sideways into the innermost recesses. The south wall is tiered in a series of terraces 0 2–0 5 metres wide from above E.H.W S. to about M T.L for the first 10 metres, the wall then becoming steep and more or less vertical. This portion is continually moist, probably through seepage from the cliffs above, and the moisture is responsible for reflecting a certain amount of light across to the more seaward facing north wall. Differential indirect lighting effects between walls are less pronounced than in the Red Beach cave; however, the flat ledges between M H.W N. and E H.W S on the south wall, together with the more constant moisture, encourage growth of certain algae—e g., *Bostrychia arbuscula* and *Ptilothamnion pectinatum,* which are absent from the vertical northern side

The absence of *Peyssonelia* from the south wall could conceivably be related to the occurrence of direct summer sunshine on that wall, but this seems unlikely in view of the fact that the same species is known to occur in sunlit pools in the open midlittoral Among the crustose red algae *Peyssonelia* and basal *Corallina* seem less shade-tolerant than *Hildenbrandtia,* which is the last algal survivor as far in as 24 metres. extending from the cave roof to just below high water mark. as far as could be judged. At this depth it was necessary to shine a torch or light a match to examine the walls in mid-winter. Beyond the narrow crack was found a scattered assemblage of tiny *Micrelenchus dilatus,* a univalve with an opalescent shell typically living among kelp at extreme low water Such a population may be expected to range over almost any part of the cave according to its immediate preference or requirements The same applies to *Melaraphe, Lepsiella* (and *Onchidella*), the ranges on the charts being those at the time of observation Shells of *Elminius plicatus* show a marked difference in shape from those of individuals growing on exposed midlittoral rocks (Cf. Cranwell and Moore, 1938, p. 387) Cave-dwellers are wider at the base than the apex, with a more conical outline than usual for this species.

In summarising this section, the cave-inhabiting organisms found in the above districts are classed as:

(I.) Euryphotic (Table I) Species with a wide range of light and shade tolerance

1. Shade-tolerating species of a light-exposed shore;
2. Shade-preferring species which can tolerate a certain amount of light;

(II) Stenophotic (Table I) Species with a narrow range of light and shade tolerance

TABLE I—*Cave-dwelling Organisms, Red Beach and Stanmore Bay*

	Euryphotic Species	Stenophotic Species
Light Preferring	*Chamaesipho brunnea*	*Lichina pygmaea*
	Chamaesipho columna	*Calothrix scopulorum*
	Elminius plicatus	*Ralfsia verrucosa*
	Saxostrea glomerata	
	Pomatoceros coeruleus	
	basal *Corallina officinalis*	
	Volsella neozelanicus	
Shade Preferring	*Melaraphe oliveri*	*Microelenchus dilatatus*
	Melaraphe cincta	*Actinia tenebrosa*
	Cellana ornata	*Tethya fissurata*
	Lunella smaragda	anemones
	Sabellaria kaiparaensis	†*Rhodochorton* sp.
	Lepsiella scobina	†*Ptilothamnion pectinatum*
	Hildenbrandtia crouanii	*Bostrychia arbuscula*
	Melobesia sp.	*Bostrychia mixta*
	Peyssonelia sp	*Gelidium pusillum*
		Nodularia harveyana
		Cladophora sp
		Oscillatoria nigroviridis
		Mitella spinosa

DISCUSSION

In considering the zonation features as a whole, there emerges the fact that differences in general pattern between the two caves are only slightly greater than those between opposite walls of the same cave. These can be summarised as follows —

(a) Differences between walls (excluding mobile animals).

(i) Red Beach Cave

Restriction of *Rhodochorton, Tethya* and *Mitella* to more shaded, south east wall, more vigorous development of *Sabellaria, Volsella* and *Hildenbrandtia* on more brightly illuminated north-west wall *Enteromorpha* is restricted to this wall

(ii) Stanmore Bay cave

Restriction of *Ptilothamnion* and *Bostrychia* to south wall, and of *Oscillatoria* and *Peyssonelia* to north wall.

* Cf Feldmann, Tr Doty, 1951, p 324

† Species apparently confined to caves in the Hauraki Gulf, though further search may reveal them elsewhere.

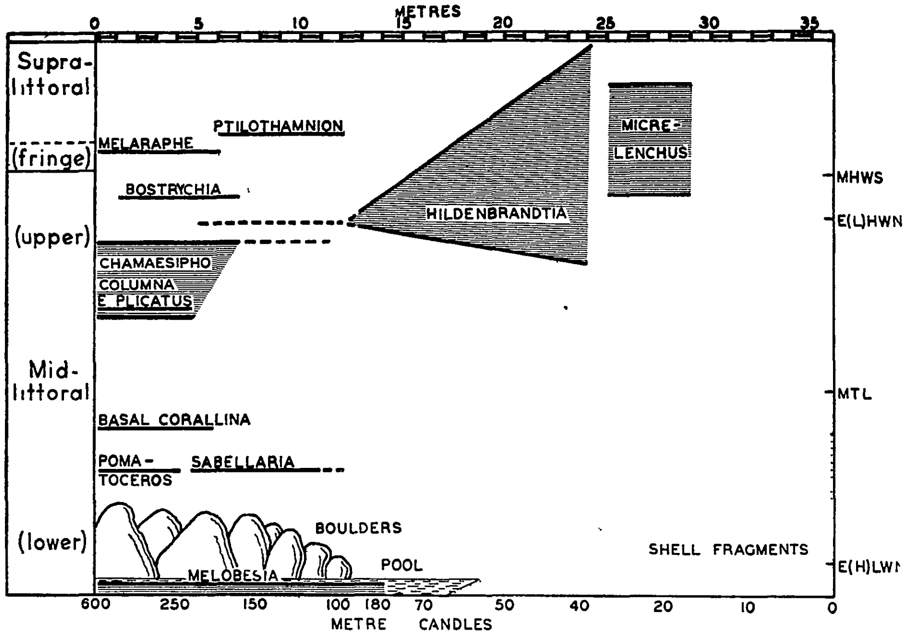

FIGURE 5—Schematic diagram of zonation on south wall of Stanmore Bay Cave—winter. Vertical scale = four times horizontal.

(b) Differences between caves.

(i) Absence of *Oscillatoria, Peyssonelia, Bostrychia* and *Ptilothamnion* from Red Beach.

(ii) Absence of *Lichina, Nodularia, Calothrix, Enteromorpha, Rhodochorton, Volsella, Tethya, Mitella, Actinia* and anemones from Stanmore.

It has been mentioned already that direct sunlight appears to play a subsidiary role to indirect daylight in regulating the distribution of cave-dwellers By contrast a much more direct correlation can be inferred between the zonation of the cave biota and the relative incidence of indirect daylight, which, though altered in intensity by the degree of sunlight outside each cave, is a more consistent and therefore a more easily measurable factor. These statements will now be examined more fully in conjunction with Figures 1–6.

(a) Direct summer sunshine.

If sunlight were to operate as a presence or absence factor, then one would expect certain species to occur only on rocks which receive direct illumination from the sun's rays. Examination of the first two horizontal metres on the north wall of the Red Beach cave (cf. Figs. 2A, 3) fails to show the presence of a single species which does not occupy a comparable position on the opposite wall The south wall at Stanmore on the other hand, receiving direct sunlight on early mornings in summer to a distance of 30 metres, shows one or two discrepancies with its opposite face—namely, in the presence of *Bostrychia** spp and *Ptilothamnion,** and absence of *Elminius plicatus.* It is possible that summer sunlight affects the reproductive cycle of the red algae—a hypothesis that needs checking

* Known to occur in this spot both winter and summer.

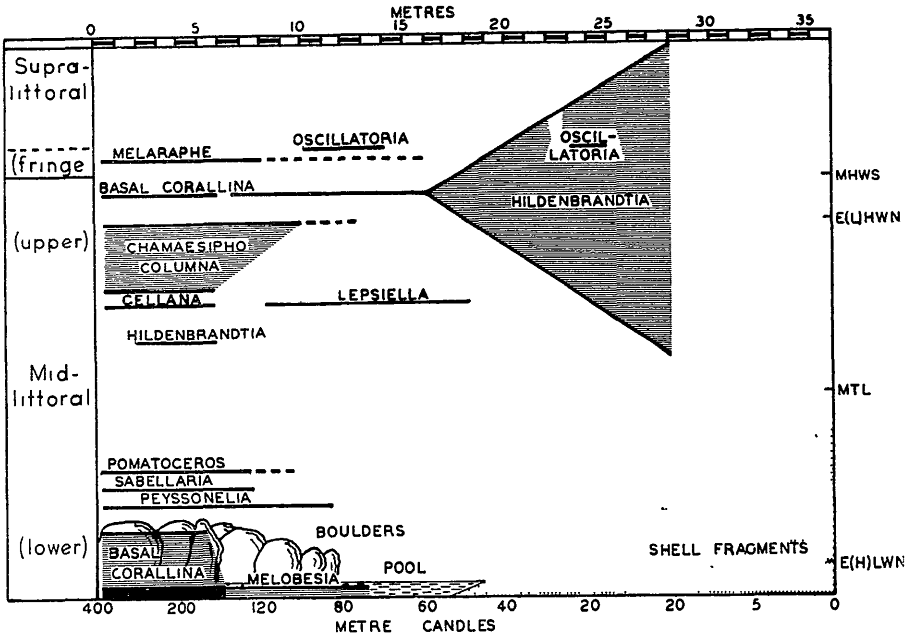

FIGURE 6.—Schematic diagram of zonation on north wall of Stanmore Bay Cave—winter. Vertical scale = four times horizontal.

from more frequent collections of these species. Mention has already been made, however, that angle of substrate, and perhaps salinity, seem to affect their distribution as markedly as light. Absence of *Elminius plicatus* from the south wall is less easy to explain, for this barnacle is a characteristic cave-dweller, in its modified growth form.

(b) Direct winter sunshine, affecting only the south-east wall of the Red Beach cave.

Again no direct effect can be observed from the zonation pattern; but the possibility must be envisaged that life cycles and seasonal abundance of red algae such as *Rhodochorton* are influenced in some degree

(c) Indirect daylight penetration.

A glance at Figure 1 and then at Figures 3–6 indicates at once that the pattern of zonation follows quite closely the gradient of indirect daylight. At Red Beach on both walls, regardless of varying amounts of direct summer and winter sunshine, there is an abrupt cessation of *Calothrix, Lichina* and *Ralfsia,* classed in Table I as stenophotic, light-demanding species. There is a more gentle gradient of indirect daylight in the Stanmore cave, because of its wider mouth This allows a more gradual transition from one dominant to another. Moreover, all the stenophotic light demanders are absent about the entrance to this cave.

Between 500 and 100 metre candles (approx.) there is a transition zone or ecotone where euryphotic, shade-tolerating species such as *Chamaesipho columna, C. brunnea, Sabellaria* and basal *Corallina* overlap with wider ranging shade-lovers like *Peyssonelia* and *Hildenbrandtia.* The greater penetration of *Sabellaria,*

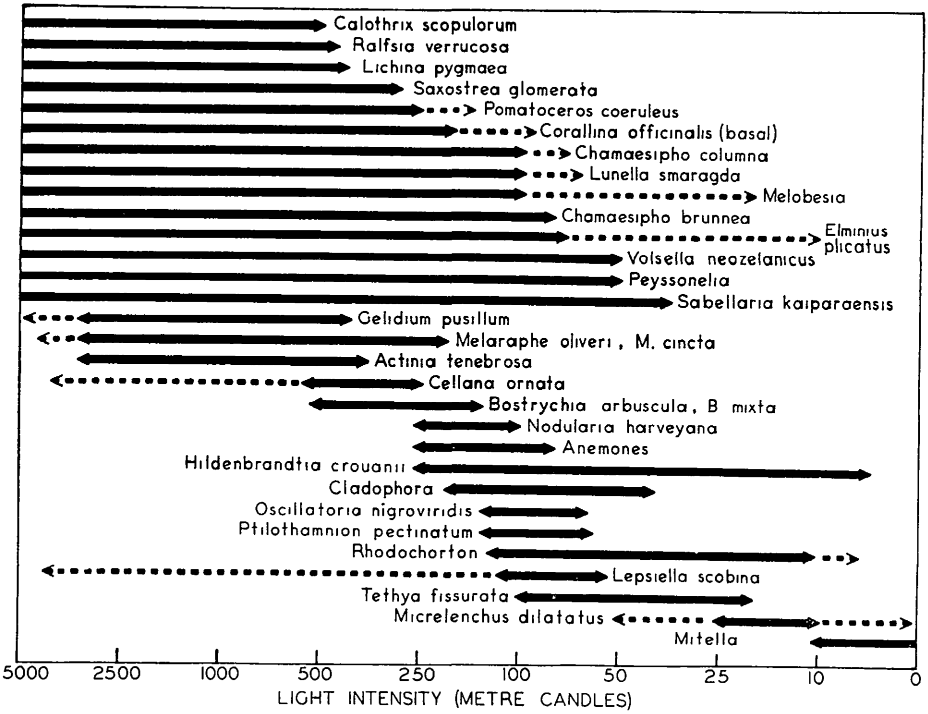

FIGURE 7.—Range of tolerance of organisms to variation in intensity of indirect daylight within caves at Red Beach and Stanmore Bay.

Volsella and *Elminius plicatus* on the Red Beach north-west wall is probably a direct response to the brighter indirect daylight as far in as 10 metres, at which level the south wall is in almost total darkness. Stenophotic forms are included within and confined to this ecotone—e g., *Nodularia* and *Bostrychia* Rather surprising is the abrupt termination of *Gelidium pusillum* not far in from the mouth of the Red Beach cave, for it is so often confined in the open midlittoral to moist and shady clefts.

Below 100 metre candles the truly shade-demanding species come into prominence in both caves. In this category may be listed *Ptilothamnion, Rhodochorton. Hildenbrandtia, Tethya* and *Mitella*

In Figure 7 an attempt has been made to summarize the relative ranges of tolerance to the variations in daylight observed and recorded in mid-summer, 1952 When this chart is correlated with Table I, it may appear anomalous to regard *Calothrix, Ralfsia* and *Lichina* as stenophotic, seeing that their ranges in Figure 7 are as wide as others classed as euryphotic. The classification into eury- and stenophotic light and shade preferring species in Table I has been made not only from the facts arising out of the cave survey, but through the writers' knowledge of their behaviour in the littoral. The "normal" daylight range may be quite wide but there is, in the case of *Lichina, Calithrix* and *Ralfsia* a sharp lower limit beyond which they cannot penetrate. This limit is high in comparison with most other species, except possibly *Saxostrea* Similarly other shade preferring forms—e g, *Bostrychia* and *Tethya,* have a sharply regulated upper limit of light tolerance Other organisms, however, do not fit so easily into any one category—e.g., *Actinia tenebrosa,* which from its name one would expect to find in dark recesses, yet which has a relatively high lower limit

The importance of other factors responsible for determining the distributional limits of cave-dwellers cannot be minimised The fact that the tidal complex of factors is obviously still operative for some distance within the caves is evident from the restriction of most organisms to their usual tide level Once the transition zone is reached the pattern starts to become modified until the stage where the gradient of indirect daylight exerts a threshhold effect by eliminating the tide-regulated bands of organisms altogether Minor space adjustments between one species and the next are very likely due to variations in response to a secondary factor or group of factors (cf Doty and Archer, 1950, p. 463), e.g., the effects of reduced salinity, topography preferences, competition and ability of the species to reproduce under the existing conditions

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