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THE INTERTIDAL ECOLOGY OF THE MONTEMAR AREA, CHILE

by

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(With 20 Text Figures, 3 Plates and 4 Tables)

ABSTRACT

A description is given of the zonation at Montemar, near Valparaiso, on the Chilean coast. The zonal pattern is a barnacle-algal type with the Infralittoral fringe dominated by large brown algae. The Supralittoral fringe is poorly developed, littorines forming a part of the barnacle belt.

1. INTRODUCTION

The salient feature of the Chilean coastline is its great length, extending from the Subantarctic region at Cape Horn (lat. 55° 58′) through a distance of over 2,600 miles to the Tropics at Arica (lat. 18° 20′ S.). The nature of the coastline changes several times within this distance. In the south the coast is exposed to extremely heavy wave action, but numerous islands give local sheltered conditions. This type of coast is replaced at Chiloë Is. (lat. 42° S.) by an exposed coast with few sheltered bays but with rocky headlands and surf beaches. The rainfall gradually diminishes towards the north and the beaches become smaller and less frequent until the desert coast is reached in about lat. 30° S.

Several expeditions have made brief calls along the Chilean coast to make collections and these have been described in the various reports of the expeditions concerned. However, it is still true to say that the standard reference work for Chilean zoology is Gay's (1847) History of Chile. As recently as 1953 Ekman pointed out that there is a very poor literature from Chile and that the faunal changes are insufficiently recorded.

A start has been made in recent years on the systematics of the Chilean fauna. Yanez (1949a and b) has reviewed the marine birds of Chile and Riveros (1950, 1951) has catalogued two families of molluscs. The algae are not being ignored, as Etcheverry (1955) lists the species found on a restricted part of the Chilean coast and gives general notes on the distribution of the species. The Lund University Expedition to Chile is the most important marine expedition to visit Chile, the collections being made on most of the accessible parts of the Chilean coast, but with particular reference to the south. The reports of the expedition, which are now appearing, will do much to extend our knowledge of Chilean zoology.

This paper is concerned with the survey of the major ecological features of a restricted part of the Chilean coast and is the first of a series of three papers dealing with the important zonal features of that coastline. One of the later papers will describe the zonation encountered on other restricted parts of the Chilean coast and the final paper will compare the conditions found over all of the northern parts of that coast betwen latitudes 35° S. and 18° S. In all of these papers, partly in the interests of space, non-zonal organisms will be dealt with only in a general fashion, but their ecology will form the topic of the final paper.

Since the systematics of the Chilean marine fauna is so poorly understood, it follows that the distribution of many of the marine animals is not known. This lack of knowledge may be extended to include all aspects of marine ecology in Chile, and there is no literature dealing with the ecology of any one intertidal area. There are several papers dealing with the bio-geography of the Chilean coasts in the widest sense and these will be discussed in the relevant paper.

2. NOMENCLATURE

The nomenclature used is that of Stephenson and Stephenson (1949) and Guiler (1953). The author of each species is cited only once.

3. GEOGRAPHIC LOCATION AND TOPOGRAPHY

Montemar, approximate latitude 32° 57′ S., longitude 71° 33′ W., is situated on the west coast of South America some sixteen kilometres to the north of Valparaiso. It is the site of the Marine Station of the University of Chile. Montemar is a small seaside resort, but has the disadvantage that there is a considerable influx of daily visitors in the summer.

The Marine Station is situated on a small point which is exposed to the full effect of the oceanic swell and sea breezes. The coastline to the north is rocky, but to the south, towards Valparaiso, there are several sandy beaches of varying extent. However, the effect of sand scouring at Montemar can be regarded as minimal.

4. METHODS

Collections were made at various places on the rocks at different levels of the shore in the immediate vicinity of the Marine Station. The specimens were provisionally identified and samples were sent to systematic experts for determination. Comparative examinations were carried out on the shore both to the north and the south of Montemar.

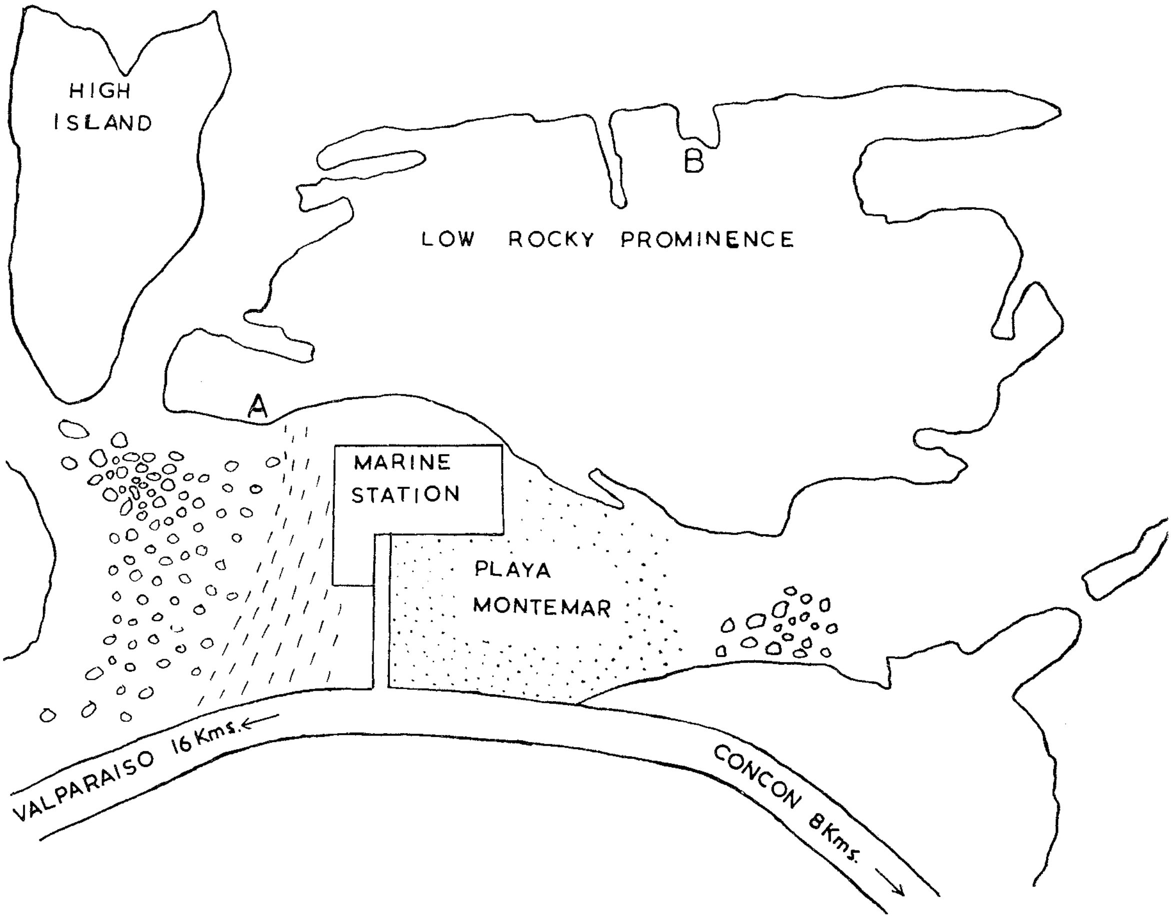

FIG. 1.—Sketch of the Montemar area. The location of sand is shown by stippling, broken lines indicate coarse sand, while gravel and boulders are shown by circles. The letters A and B show the position of the exposed and sheltered transects.

5. TIDAL DATA

Details of the tides, based on actual recorded data, are not available and the only information which I have been able to obtain are the tidal tables prepared by the Chilean Navy (1954). The Lund University Expedition made tidal observations at all their collecting stations and the leaders of the expedition point out that errors exist in the predictions prepared by the Navy and that these errors are greatest in the south (Brattstrom and Dahl, 1951). However, in the absence of any data, I have used the predictions as prepared by the Chilean Navy, but the reader must bear in mind that these figures may be subject to a small error.

The tidal datum line is a level established at Valparaiso and is 0.9 metres below mean sea level.

The tides show the typical oceanic form (fig. 2) and I propose to follow Chapman (1938) and call the tides "high high", "high low" and "low low". Terms widely used in many countries, both in Europe and elsewhere, are all related to certain tidal levels, e.g., mean high water springs. Zanefeld (1937) recognized no fewer than 10 different tidal levels covering a total tidal range of 2.56 metres. This principal is one which is followed in most countries where there is a large tidal range.

In Chile and certain other countries there is a small tidal range. The effects of barometric pressure and prevailing winds are relatively great and it is not possible to recognize, with certainty, any other than the four basic levels noted above. Further, on coasts which are exposed to very heavy wave action, such as much of the Chilean coastline, there appears to me to be little point in attempting to recognize many tidal levels since the spray and wave action factors make detailed tidal calculations somewhat inaccurate and meaningless.

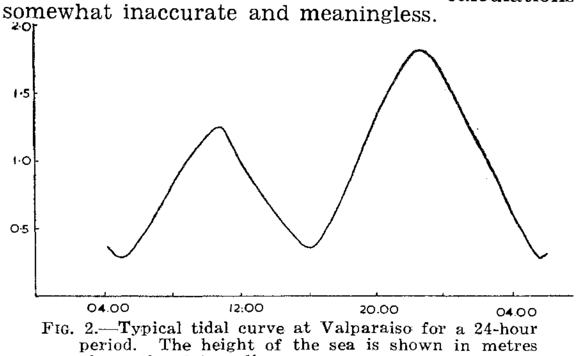

FIG. 2.—Typical tidal curve at Valparaiso for a 24-hour period. The height of the sea is shown in metres above the datum line.

TABLE 1.—*Tidal Data calculated from the Tide Tables published by the Chilean Navy (1954). The heights are expressed in metres above Chart Datum. The Abbreviations used are H.H.W., high high water; L.H.W., low high water; H.L.W., high low water; L.L.W., low low water; M.S.L., mean sea level.*

Average Monthly Data during 1954.

H.H.W.	1.58	1.56	1.53	1.50	1.53	1.56	1.56	1.51	1.48	1.49	1.53	1.60
L.H.W.	1.18	1.25	1.24	1.22	1.16	1.13	1.16	1.20	1.23	1.18	1.15	1.16
H.L.W.	0.54	0.52	0.50	0.47	0.47	0.48	0.49	0.48	0.47	0.48	0.49	0.52
L.L.W.	0.45	0.45	0.43	0.39	0.36	0.37	0.38	0.40	0.39	0.38	0.37	0.39
M.S.L.	0.937	0.945	0.925	0.895	0.88	0.885	0.897	0.897	0.892	0.882	0.885	0.942
Greater Rise	1.13	1.07	1.07	1.04	1.80	1.12	1.10	1.06	1.02	1.04	1.07	1.10
Lesser Rise	0.70	0.78	0.80	0.85	0.79	0.73	0.73	0.78	0.83	0.76	0.75	0.72
Greater Fall	1.08	1.12	1.08	1.13	1.17	1.18	1.13	1.11	1.08	1.09	1.13	1.11
Lesser Fall	0.65	0.75	0.72	0.76	0.71	0.66	0.68	0.75	0.79	0.70	0.69	0.65

Mean Annual M.S.L. .... 0.905.

The average heights of the tides have been calculated from the figures given in Chilean Navy Tide Tables and are shown in Table 1. In this Table the expressions "greater rise, lesser rise, greater fall and lesser fall" are used. Reference to figure 2 shows that there are two high tides during a tidal day. Each of these tides rises by a different height from a different level than the other. The maximum rise is called the greater rise and the other is known as the lesser rise. The meaning of greater and lesser fall is derived by the same method. The figures given in Table 1 are graphed on Figures 3 and 4.

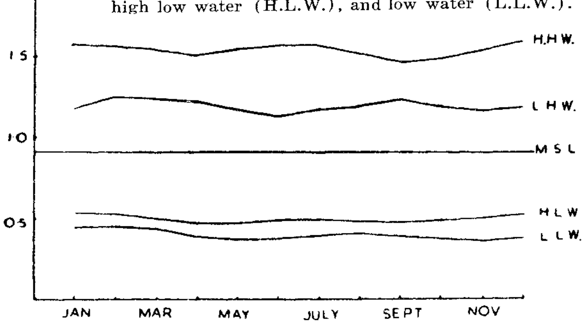

FIG. 3.—Average monthly tidal levels at Valparaiso of high water (H.H.W.), low high water (L.H.W.), high low water (H.L.W.), and low water (L.L.W.).

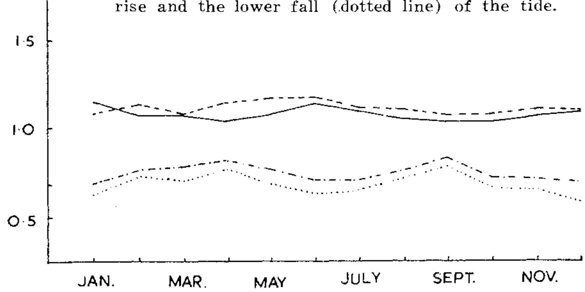

FIG 4.—Average monthly rise and fall of the tides at Valparaiso. The upper pair of curves show the maximum fall (broken line) and the maximum rise of the tide and lower pair of curves shows the lower rise and the lower fall (dotted line) of the tide.

The effect of the tides as an ecological factor has not been examined in detail by any of the few workers who have, to date, worked on the shores of Chile. Studies on the effect of the rise and fall of the tides on intertidal organisms have been carried out in many countries and, although this is not the place to review this work, it is necessary to draw attention to the work of Colman (1933), who stressed the importance of "critical levels" at which the number of species found on the shore changes sharply. Many papers have been published since Colman's work, all of the later workers finding an exposure curve which is similar in form to that described by Colman. Doty (1946), applying Colman's technique to tides exhibiting diurnal inequality found that at certain levels on the shore there were sudden increases in the time per day that organisms were exposed to the atmosphere. Guiler (1948), working in Tasmania, noted a sudden decrease in the number of species occurring at these levels and proposed that these levels be known as "lethal" levels. In this paper I have noted that the effect of low tidal amplitudes on the appearance of the shore is not only to lessen the vertical range of the organisms but also to give the shore a very bare appearance above mean sea level. On places which are exposed to heavy wave action the intertidal population has a greatly increased range of vertical distribution and this may rather obscure the bare appearance of the upper shore. The tides in Tasmania are semi-diurnal in nature, but this observation can be held to be true for Chile, where the tides are of the same behaviour. The mean annual tide amplitude at Montemar is 0.92 metres.

The exposure curve for each month of a twelve-month period has been calculated. The number of hours that certain levels of the shore were exposed per month was obtained graphically and these figures, expressed as a percentage, were plotted against Chart Datum level giving the graphs shown in Figures 5 to 16. These graphs show the considerable difference each month in the percentage exposure at any one level on the shore, e.g., at a height on the shore 1.0 metres above Chart Datum the percentage exposure ranges from 53% in

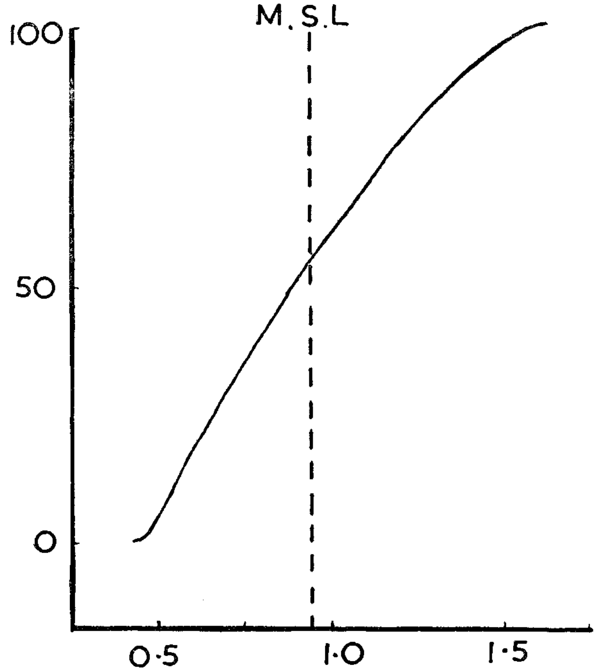

FIG. 5.—Percentage exposure to the air at different levels on the shore at Montemar in January.

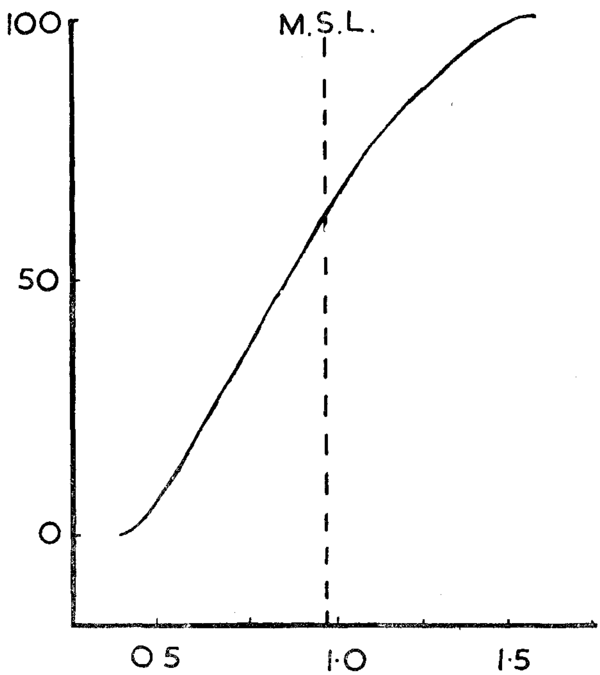

FIG. 6.—Percentage exposure to the air at different levels on the shore at Montemar in February.

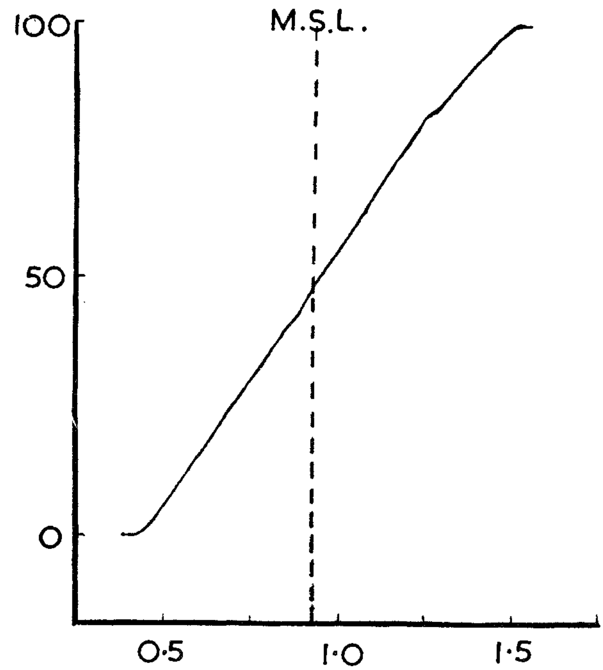

FIG. 7.—Percentage exposure to the air at different levels on the shore at Montemar in March.

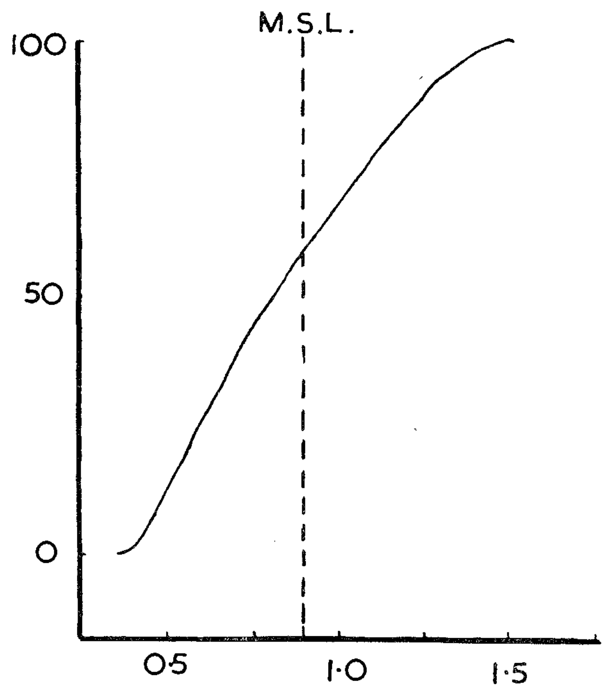

FIG. 8.—Percentage exposure to the air at different levels on the shore at Montemar in April.

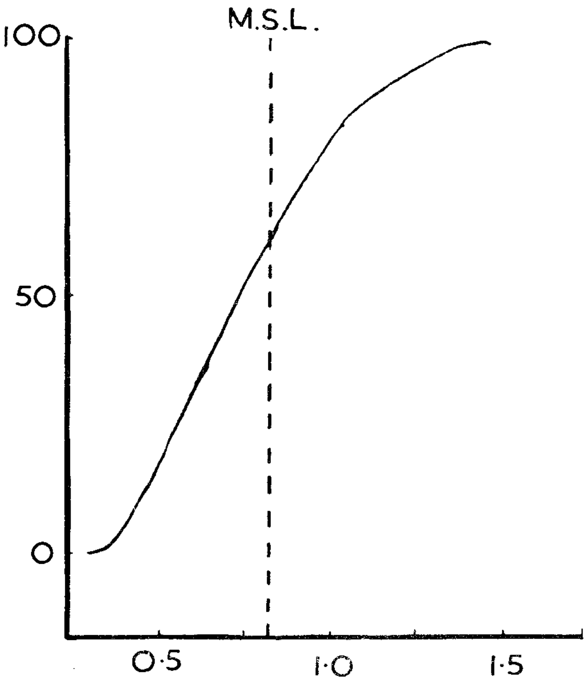

FIG. 9.—Percentage exposure to the air at different levels on the shore at Montemar in May.

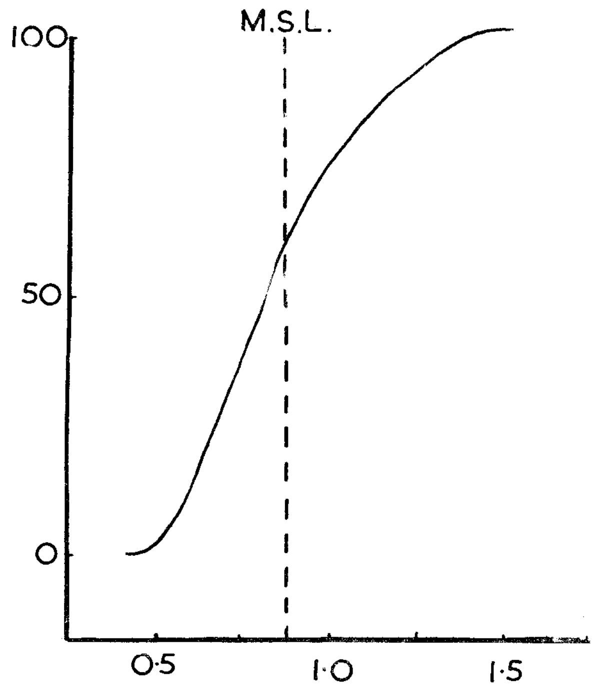

FIG. 11.—Percentage exposure to the air at different levels on the shore at Montemar in July.

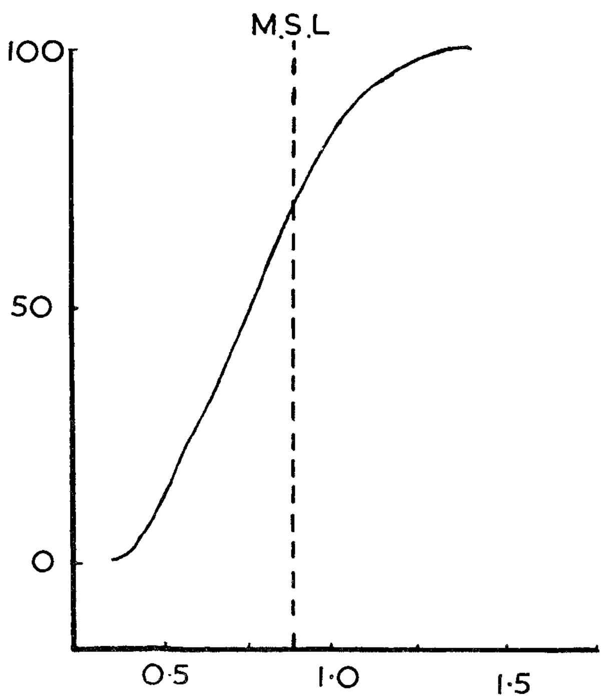

FIG. 10.—Percentage exposure to the air at different levels on the shore at Montemar in June.

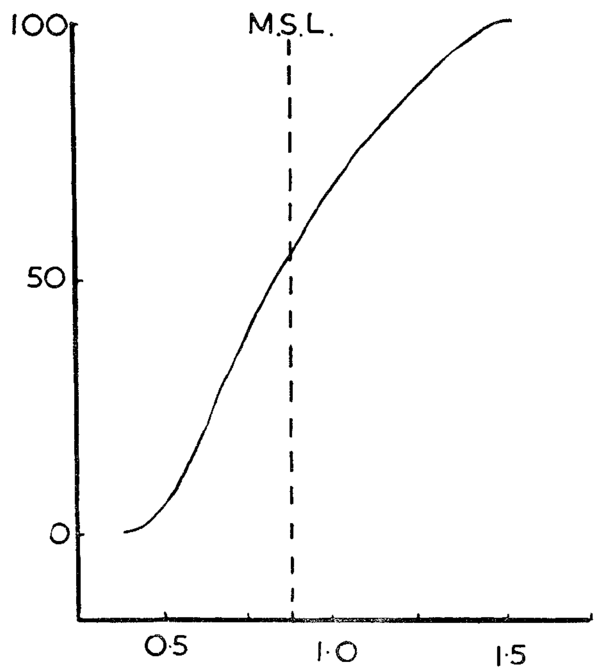

FIG. 12.—Percentage exposure to the air at different levels on the shore at Montemar in August.

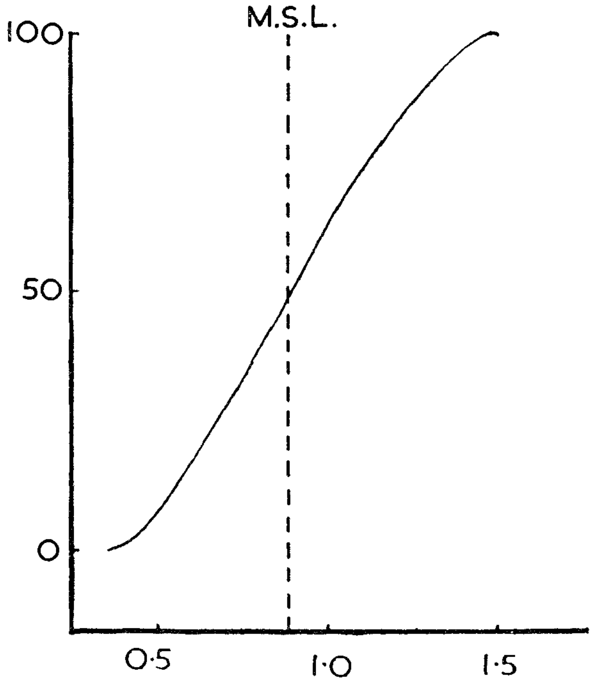

FIG. 13.—Percentage exposure to the air at different levels on the shore at Montemar in September.

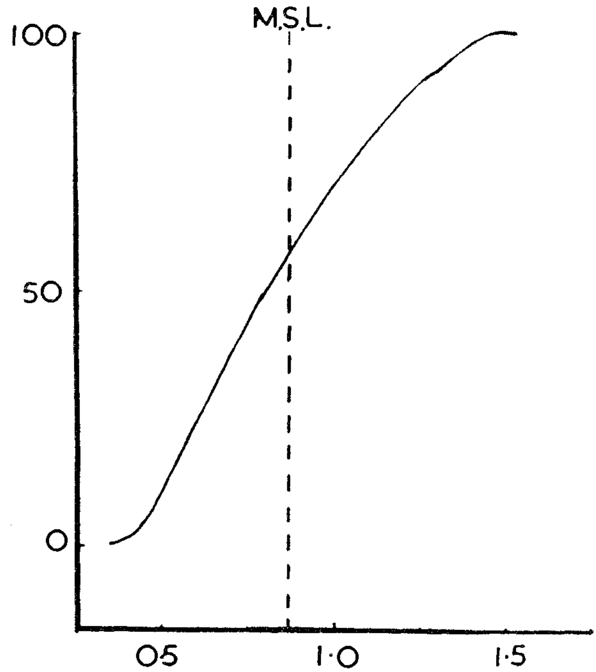

FIG. 15.—Percentage exposure to the air at different levels on the shore at Montemar in November.

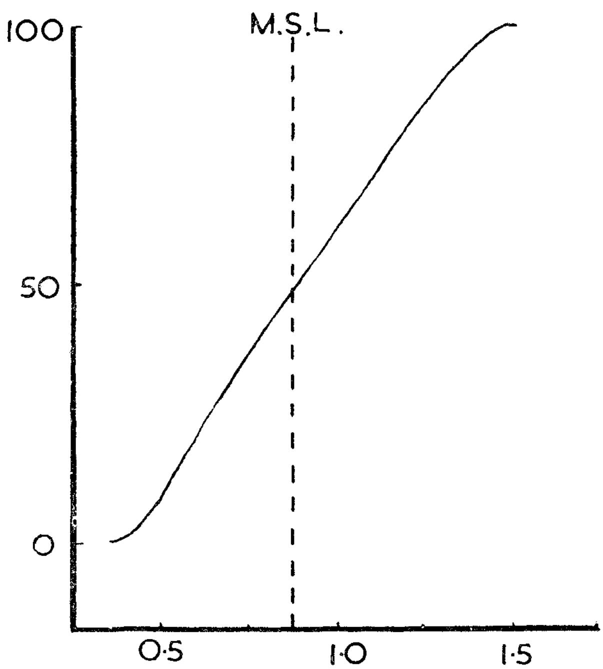

FIG. 14.—Percentage exposure to the air at different levels on the shore at Montemar in October.

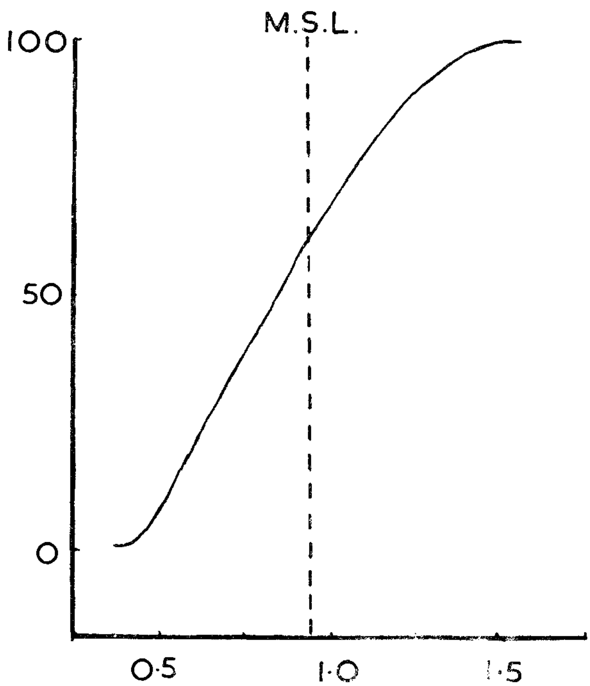

FIG. 14.—Percentage exposure to the air at different levels on the shore at Montemar in December.

February to 82% in May. It is also found that the monthly Mean Sea Level (M.S.L.) also varies in its position on the shore (Fig. 17) and the Mean Sea Level is at its highest and lowest levels respectively during these two months.

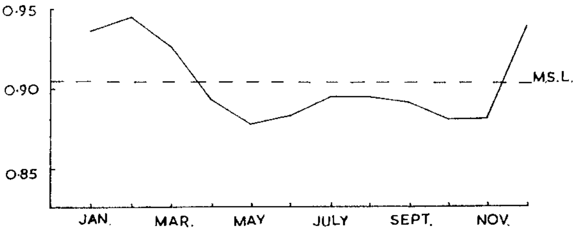

FIG. 17.—Monthly variations in Mean Sea Level at Valparaiso. The mean annual sea level is shown as a broken line.

Patulio, et al (1955), found that the seasonal oscillation in sea level on the Chilean coast departs from the estimated monthly mean by as much as 5 cm. with a standard deviation of 1.0-1.2 cm. Between January and June the level is higher than estimated and for the remainder of the year the levels are lower (fig. 17). The coastline which is being examined is very exposed and a difference of 5 cm. in the level of the sea is not significant in determining the zonal pattern, particularly when, as at Montemar, the wave action causes spray to splash on rocks 20 metres above sea level. For the purpose of the present study, there is little practical point in correcting for this error.

6. OCEANOGRAPHICAL AND HYDROLOGICAL DATA

A brief examination of a chart of the Chilean coast north of Chiloë Island (lat. 42° S.) shows the almost complete absence of a Continental Shelf, though there is a narrow shelf of shallow water, usually 10-15 kilometres in width, but rarely more than 30 kilometres wide. The 200 metre contour passes close to Point Curuamilla, south of Valparaiso, while the 1,000 metre contour is some 20 kilometres offshore. The Fosse de Haeckel, 5,600 metres in depth, is about 100 kilometres to the west of Valparaiso.

The absence of a Continental Shelf is reflected in the amount of heavy and continuous wave action encountered on the coast. The prevailing winds are on-shore, so there is no respite from the incessant battering received from the waves. Although continuous, the wave action in the Montemar area is not as heavy as that encountered in some other coasts in the southern hemisphere, but is heavy enough to render collecting in the Infralittoral Fringe a hazardous and wet business. It is possible only to collect in this belt when low water spring tides combine with the minimum of wave action. It is worth noting that there are no beds of *Macrocystis* to diminish the effect of the waves.

(1) *Sea Temperatures*

Graphs of the sea temperatures at Montemar were published by Cubilios (1955). I am indebted to Sra. Cubillos for the information upon which her temperature graphs were based (Table 2).

TABLE 2.—*Mean Monthly Superficial Sea Temperatures (in degrees Centigrade) at Montemar for the Period May,* 1947, *to August,* 1954.

	Time	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1947	08.00	....	....	....	....	11.89	12.23	11.95	11.85	11.49	11.81	12.77	12.86
	20.00	....	....	....	....	12.15	12.36	11.93	12.17	11.58	12.47	13.04	12.70
	Mean	....	....	....	....	12.02	12.29	11.94	12.01	11.53	12.14	12.90	12.75
1948	08.00	14.45	13.77	13.66	12.71	12.78	12.04	11.90	10.75	11.99	12.78	12.84	14.59
	20.00	14.33	14.22	13.97	12.98	12.94	12.10	12.20	11.36	12.28	13.53	13.40	15.67
	Mean	14.39	13.99	13.81	12.84	12.86	12.07	12.05	11.05	12.13	13.15	13.12	15.13
1949	08.00	16.05	16.24	13.22	13.16	13.03	12.15	11.13	11.32	11.50	12.49	13.20	14.56
	20.00	17.88	17.09	13.85	13.46	13.47	12.36	12.24	11.91	12.32	13.52	13.00	15.41
	Mean	16.96	16.66	13.53	13.31	13.25	12.25	11.68	11.61	11.91	12.95	13.10	14.98
1950	08.00	16.00	14.40	13.75	13.38	12.52	12.74	12.26	11.16	12.30	12.20	13.33	13.64
	20.00	16.95	14.93	14.59	14.69	13 00	13.15	13.00	12.34	13.79	13.39	15.16	15.96
	Mean	16.47	14.66	14.17	14.03	12.71	12.94	12.63	11.75	13.04	12.79	14.24	14.80
1951	08.00	14.75	13.97	12.98	13.32	13.23	12.29	13.40	12.20	11.69	12.24	13.04	15.05
	20.00	16.98	17.80	15.40	14.88	14.87	13.34	14.20	13.57	13.86	14.05	13.89	15.74
	Mean	15.86	15.88	14.19	14.10	14.05	12.81	13.80	12.88	12.77	13.14	13.46	15.39
1952	08.00	16.47	15.77	13.99	13.20	13.86	11.70	11.75	11.70	12.30	12.60	13.60	14.87
	20.00	17.37	16.58	14.62	14.20	14.30	12.04	12.30	12.20	12.79	13.60	15.16	15.89
	Mean	16.92	16.17	14.30	13.70	14.08	11.87	12.02	11.95	12.54	13.10	14.38	15.38
1953	08.00	15.35	....	....	....	....	....	....	11.60	12.48	11.40	12.60	14.26
	20.00	16.70	....	....	....	....	....	....	12.04	13.08	12.20	14.26	15.75
	Mean	16.02	....	....	....	....	....	....	11.82	12.78	11.80	13.43	15.00
1954	08.00	13.10	14.10	14.00	12.75	12.00	12.40	11.56	11.41	....	....	....	....
	20.00	15.72	15.90	15.67	13.96	12.50	12.86	12.15	12.23	....	....	....	....
	Mean	14.41	15.00	14.83	13.35	12.25	12.63	11.85	11.82	....	....	....	....

During the period May, 1947, to August, 1954, the coldest temperature recorded at 08.00 hours was 8.9° C., and the warmest at the same time of day is 19.4° C. At 20.00 hours the coldest temperature recorded is 9.2° C., and the warmest 20.2° C. The warmest monthly average of the mean daily temperature is 16.96° in January, 1949. The coldest mean monthly average of the mean daily temperatures is 11°55 C. in August, 1948.

Further figures for this part of the coast are available from the U.S. Coast and Geodetic Survey (1952) and comparison of the results from the two sets of observations shows that those taken at Montemar are usually lower than those taken by the Survey at Valparaiso, except in the summer months when they tend to be higher. The differences, of up to 1° C. in magnitude, can be explained by the methods of sampling employed at the two stations. Basically, the methods used at both places are the same, namely a bucket is filled with sea water and the temperature of the water in the bucket is taken with a thermometer. However, at Montemar, the bucket is filled off the rocks beside the place marked B on Fig. 1, whereas the U.S. Coast and Geodetic Survey made their observations on the inshore side of the Molo de Abrigo at Valparaiso, in deep water. The temperatures taken at Montemar are thus subject to the cooling or heating influence of the rocks, while the Valparaiso temperatures are a truer record of the temperature of the sea. However, for the purpose of the present work, the Montemar temperatures are used, being the temperatures actually experienced by intertidal organisms.

7. CLIMATIC DATA

All the information quoted has been kindly supplied to me by the Oficina Meteorologica de Chile.

(*a*) *Temperature*

Temperature records have been made at Valparaiso from 1899 and the mean monthly temperatures are given in Table 3.

TABLE 3.—*Mean Monthly Temperatures in degrees Centigrade at Valparaiso for the Period* 1899-1946.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
18.0	17.9	16.7	14.9	13.5	12.3	11.8	12.1	12.9	14.1	15.8	17.3

Annual Average Temperature 14.8° C.

The above table shows that the air temperature at Valparaiso is very equable with no great extremes of temperature. The relative humidity is also fairly constant (Table 4).

TABLE 4.—*Mean Monthly Relative Humidity at Valparaiso for the Period* 1899-1946.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
72%	74%	76%	76%	80%	78%	80%	79%	78%	75%	17%	70%	76%

The rainfall shows a very marked seasonal variation with a maximum in June and the winter months all having considerable rainfall. The summer months are dry with the minimum rainfall occurring in February. These conditions are typical of the Mediterranean type of climate.

It was noted above that the intertidal region at Montemar experiences the greatest air exposure during May. This means that organisms living there are exposed to the second heaviest rainfall of the year (95.4 mms.), a cold temperature and the high relative humidity of 80%. During February, when the air exposures on the shore are at the minimum, the shore-dwelling organisms are protected from the heat (17.9° C.), low humidity (74%) and little rainfall (2.0 mms.). Examination of the tide tables reveals that the " low low " tides during the winter most frequently occur during the period 12.00-23.58 hours which, in itself, acts as a further protection for shore-living forms, since they are not exposed to the full effect of cold nights. During the same time of the year the " high high " tide usually occurs between midnight and midday, thus frequently immersing organisms during the coldest part of the day.

In the summer the reverse holds good, the " high high " tide occurring during the midday-midnight period, thus often immersing intertidal organisms during the heat of the day, while " low low " water takes place during the midnight-midday period. Frequently during the summer mornings, the coast is shrouded in mist so that the full effect of the insolation during the " low low " tide period may not be felt on the shore.

Comparison Tables 2 and 3 show that with the exception of June, July and August the mean monthly sea temperature is below the mean monthly air temperature. Even during the three months when the air is cooler than the sea, there is less than 1° C. difference between the temperatures of the two media. In other words, the greatest cold to which intertidal organisms are liable to be exposed is that of the sea.

It has already been deduced that the air exposure in winter and atmospheric conditions combine to give animals and plants living on the shore the maximum protection from climatic factors. It would thus appear that the minimum sea temperatures play the more important part in the distribution of intertidal plants and animals during the winter.

In the summer the continuous wave action keeps the lower tidal belts cool and wet but the upper shore levels can become very hot. The extreme of this is to be seen on a very hot day when spray falls on the highest parts of the shore and steam forms from the very rapid evaporation of the water. As will be seen later, there are very few organisms inhabiting this part of the shore and these few are all well adapted against the heat or cold so that it can be said that, with the possible exception of the upper part of the shore, sea temperatures in summer are again the controlling factor.

In general, it can be concluded that the sea temperature is very important in controlling the distribution of the intertidal organisms at Montemar and they outweigh the atmospheric factors in importance. However, it must be remembered that the effects of extremes of climate may be locally catastrophic to intertidal animals and plants.

8. ZONATION AT MONTEMAR

The zonation of the exposed rocks at Montemar is as shown below.

Situation: On sloping dolerite rocks N.E. of Marine Station.

Supralittoral:
- Usually bare, often with bird excreta.

Supralittoral Fringe:
- Vacant.

Midlittoral:
- *Chthamalus cirratus*.
- *Chthamalus cirratus* + *Porphyra columbina* Mont.
- *Littorina peruviana*.
- *Chthamalus* + *Porphyra columbina* Mont.
- *B. laevis laevis* + *B. flosculus* + *Chthamalus*.
- *Iridaea laminarioides* Bory + *Brachidontes purpuratus* Lam. + *Ulva lactuca* L.
- *Centroceras clavulatum* (C. Ag.) Mont. + *Corallina chilensis* Dec. + *Gelidium filicinum* Bory.

Infralittoral Fringe:
- *Lessonia nigrescens* Bory with a few *Durvillea antarctica* (Cham.) Hariot.
- ? *Lithothamnia*.

As is usual on these coasts which experience heavy wave action, it is difficult to decide on the lower limits of the Midlittoral. At low tide the *Lessonia* belt is always exposed but it is constantly inundated by waves and surf. However, the level of low water as calculated from the available data occurs below the level of *Lessonia*, thus showing that the *Lessonia* belt is in the Infralittoral Fringe.

The next lowest belt, that of *Lithothamnion*-like weeds, can more likely be included in the Infralittoral zone. The rocks are covered by these algae but they are only exposed in the trough of the swell. The *Lithothamnia* do extend into the Infralittoral Fringe where they grow around the holdfasts of *Lessonia*, but they are very soon replaced either by other weeds or by the very dense growth of *Lessonia*.

At low water of very low spring tides there is no doubt that the *Lithothamnion* belt is exposed. During periods when there is a minimum of swell, the *Lithothamnion* belt is exposed for periods of up to minutes at a time but the belt is always inundated before becoming dry. If it were not for this inundation it is unlikely that the *Lithothamnia* would survive for long. It is on sheltered coasts or in sheltered positions that some idea of the true ecological position of these algae can be gained. The *Lithothamnion* belt on a sheltered section at Montemar is found growing at such a level that it is never exposed at low water, thus indicating quite clearly that these algae are of the Infralittoral zone rather than of the Infralittoral Fringe.

The zonation as noted in the table above is very general at Montemar throughout all of the shore where the wave action is strong, except in situations where intense sand scouring takes place. *Iridaea* and the other algae appear to be able to withstand a considerable amount of scouring, but are more critically affected by wave action, since in places they disappear. Where the wave action is diminished they are not replaced by any other algal species.

The vertical heights of the belts at any one place depends entirely on the wave action and the conformity of the rocks at that place. At places where the dolerite has weathered into clefts, the waves here surge back and forth and, consequently, organisms extend far up these clefts. This leads to animals and plants of the Infralittoral Fringe being found very far up the shore.

The relative absence of lichens from this coast is a very surprising feature. The rocks of the Supralittoral are spray swept and one might expect lichens to occur in great numbers, both in species and in individual colonies. However, this is not the case. In places, the rocks are smeared with bird excreta, largely of the gull *Larus dominicanus* Lichtenstein, *Phalacrocarox* spp. and the night-heron *Nycticorax nycticorax obscurus* Bonaparte, and this may act as a limiting factor to the successful spread of lichens. The richest growth of lichen occurs in the northerly, i.e., sun-exposed, aspect of rocks beside the Marine Station. Yet other rocks of similar aspect close by are not populated by lichens. It may well be that the majority of the rocks at Montemar are too near sea level to support a lichen population on account of wave drenching. A small island to which access can be gained at low tide, immediately adjoining the Marine Station, shows very rich lichen growth but at a height considerably above the height of the rocks at Montemar in general. The lichen on this island growes at heights of three metres and more above the highest of the rocks at the Marine Station.

On the rocks, often in places not readily accessible, above the height usually reached by the waves in normal weather, are numerous empty Patelloid shells. These shells are probably collected and brought there by the gull *L. dominicanus*. Matthews (1929) notes the natural food of this species is S. Georgia as " limpets picked off the rocks at low tide ". The oyster catcher *Ostralegus ostralegus L.* has been noted by Murphy (1936) as also catching limpets, so that this group of molluscs suffers considerable predation from birds.

THE BARNACLE BELT

This belt is the most extensive on the shore at Montemar. The barnacles are of three species and all are most numerous where surf surges over the rocks, or where the rocks are spray drenched. The density of population of this belt is shown in fig. 18.

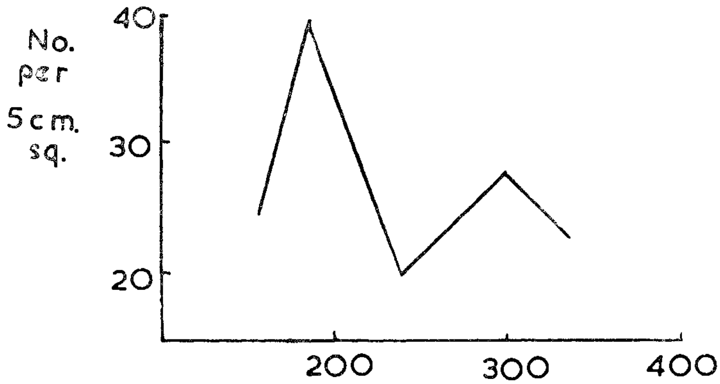

FIG. 18.—The density of population of *Chthamalus cirratus* on the exposed shore at Montemar. The heights are expressed in cms. above M.S.L.

The top of the barnacle belt is occupied by *Chthamalus cirratus* Darwin. This species is easily the most numerous barnacle on the shore, forming dense colonies covering much of the rock surface (Photo 1). The individuals of the species are small in size and form the usual *Chthamalus*-type aggregations.

The barnacles, particularly *Chthamalus*, favour living in the dolerite-granite junction where the rock is much cracked and fissured. Numerous counts and examinations were made in places where the dolerite and granite respectively were populated by barnacles, living at the same height above reference level and with the same sun and wave aspect. It was found that in some places dolerite supported the greater population of cirripedes but in other places the larger number of barnacles lived on the granite. Undoubtedly, the barnacles prefer the rock junction on account of the larger number of clefts which favour larval settlement and also serve to retain water, but beyond that there would appear to be no preference for either type of rock. Visscher (1928) found that cypris larvae were negatively phototropic so that the colour of the rocks, dolerite being darker than granite, may influence the larval settlement.

Included in the barnacle belt are two sub-belts, which may locally form a prominent feature on the shore. The Littorinid belt, populated by *Littorina peruviana* is almost continuous on the shore, though in places where the rock is vertical with little spray, the littorinid population may be so low as to be almost absent. The Littorines favour places where there is heavy and continuous spray (Photo 2) or else where there is residual water, e.g. the dolerite-granite junction where *Littorinas* are numerous together with *Chthamalus*. Around the edges of ponds is another favoured position. *Littorina* seeks sun-sheltered positions and will congregate in greater numbers on rocks with no sun and little spray, than on rocks with more spray but also with more sun.

The *Porphyra* belt, normally occurring below the *Littorina* belt, is sporadic and discontinuous. The alga *P. columbina* Mont. is not very common, and is subject to considerable seasonal fluctuation in density of colonization. The species is most numerous in the spring and early summer when it forms a very well developed band at or near the top of the barnacle belt. The summer sun dries the weed and it is collected by Chileans, who utilise it for food. By the autumn the band is practically non-existent. The seasonal nature of the occurrence of the genus *Porphyra* is well known. This alga, like the mollusc *Littorina peruviana*, also lives around the edges of ponds. In this position in the summer it shows an interesting gradation of colours which reflects the seasonal changes. Early in the spring *Porphyra* is a rich dark purple-brown in colour, and in summer weeds of this colour are to be seen around the top of the pools at water level. As the summer progresses the weed becomes progressively more yellow-brown in colour, eventually becoming a yellow remnant which dries crisp between tides, but recovers on wetting. The various colour stages are to be seen the further away from the pool the weed is found.

The common shore crab, *Leptograpsus variegatus* (Fabr.), lives in clefts in the barnacle belt as well as further up the shore, even extending into the bare rock zone. This species is extremely numerous, and narrow clefts are frequently found to have an unbroken row of *Leptograpsus* living in them. The crabs often come out during the day, moving slowly and cautiously across the rocks. The slightest movement sends them scampering for cover. At night they are easier to capture, especially in ponds. This species has a very wide toleration of stagnant water, as it will readily enter and hide in stagnant ponds half-filled with rotting algae.

In some places, particularly the more sheltered and those where the direct wave action is not too strong, such as the spray zone on exposed rocks, the upper part of the barnacle belt is populated by a tiny red acarine, a *Microtrombidium* sp. In some places this population is very numerous.

The barnacle belt changes in species composition lower down the shore, *Chthamalus* being replaced to a large extent by *Balanus laevis laevis* Brug. and to a much lesser extent by *Balanus flosculus* Darwin. Figure 18 shows the density of population of the barnacle belt at various heights on the shore.

The crevice fauna of the barnacle belt is not numerous in species but there are often considerable numbers of individuals living in clefts. The crab *L. variegatus*, has been noted above as occurring in the upper part of the belt and the chitons *Chiton cumingsi* Frembly and *Chaetopleura peruviana* (Lam.) form a thick incrustation in clefts in the rocks.

On the shore, the *Iridaea-Brachidontes* belt is the most conspicuous one above the *Lessonia* belt, *Iridaea laminarioides* being a light-greenish yellow in colour. The belt, except in places where it is found in clefts, is not of a great vertical height and it does not occur on parts of the rocks which do not receive considerable wave action. *Iridaea* often uses the valves of the mussel as a substratum. *Ulva lactuca* is also found on this belt, and occurs over most of the shore from the top of the barnacle belt to the lower *Centroceras* belt but it is most common in the *Iridaea-Brachidontes* band. In some places *Ulva* is sufficiently dense to form a band, usually immediately above the *Iridaea*, though this is a very local feature, often associated with surf action.

The *Brachidontes* band is well developed, but the mussels are small in size and do not offer much shelter to other animals. However, in the mussel-*Iridaea* band the number of species found on the shore increases sharply and it continues to increase in the next band, that of the mixed algae of the genera *Centroceras-Gelidium-Corallina*. Etcheverry (1955) records 40 species of algae from these two bands .

Living on the mussels are barnacles, *B. flosculus* Darwin and *Chthamalus scabrosus* Darwin, a small anemone, and several species of limpets. *Porphyra* is very common on the mussels. Living below the mussels are crabs, *Pilumnoides perlatus* (Poepping) and *Acanthocyclus gayi* H. M.-Edw. & Lucas, the worm *Pseudonereis gallapagensis* Kinberg, amphipods, &c. The identity of *Chthamalus scabrosus* is unconfirmed, the specimens being lost in the mail from Chile to Dr. Henry.

The *Centroceras* belt is continuous with the *Iridaea-Brachidontes* belt. The dominant weeds in this belt are *Gelidium filicinum* Bory, *Centroceras clavulatum* (C. Ag.) Mont., *Porphyra columbina*, *Corallina chilensis* Decaisne. These weeds are often attached to *Pyura chilensis* Molina, small individuals of this species often forming densely aggregated sheets on the rocks. *Colpomenia sinuosa* (Roth.) Derby & Sol. is commonly found in this band, as well as in the *Iridaea-Brachidontes* belt, living attached to either the mussels or the rock. The alga also favours ponds on the shore, especially those which receive fresh supplies of surf water.

Limpets of at least four species are found in clefts in this band, accompanied by other species. All places, many of them inaccessible, which are more or less continually deluged with spray, support a number of large limpets of the species *Nacella magellanica*. At no place do these Patelloids form a well-defined belt though they may attain a local dominance on spray-soaked areas. Other smaller species of limpets are found with the large species. These will be described in a later paper dealing with the ecology of special groups.

The cleft fauna of this belt is enriched by the presence of Fissurelids and chitons as well as the limpets noted above. These species are *Fissurella costata* Lesson, *F. crassa* Lam., *Chiton cumingsi*, *C. granosus* Frembly and *C. latus* Sow.

A large chiton, *Enoplochiton niger* Barnes, forms a conspicuous feature on the shore at this level. Although common and large (8 cms. long), this species does not form a belt. This chiton is a dark red-brown colour with the valves often showing heavy erosion. The girdle has sparsely-distributed scales. Individuals of this species may reach as much as 8 cms. in length. Frequently associated with *Enoplochiton* is another chiton, *Acanthopleura echinata* (Barnes). The latter species, although not as numerous as *Enoplochiton*, is more conspicuous on account of the very prominent black girdle which bears a number of strong, projecting spines. *Acanthopleura* is particularly numerous around the holdfasts of *Lessonia* as well as below extreme low water mark. Dall (1909) notes that these two species are characteristic of the Peruvian province. Although the Lund University Expedition found *Acanthopleura* at Montemar, they did not record *Enoplochiton* (Leloup, 1956).

The lowest belt on the shore, the *Lessonia* belt, is wide but difficult to examine on account of the prevalent surf. The *Lessonia* fronds are often very badly battered by the waves and measure less than 0.3 metres in length. Although *Lessonia* is the dominant plant on this part of the shore, scattered individual plants of *Durvillea antarctica* (Cham.) Hariot form a conspicuous feature. The latter species is readily identified, having long fleshy fronds over a metre in length. Even in the most exposed position these fronds are not shortened by wear against the rocks. *Durvillea* is yellowish-brown in colour, which contrasts sharply with the dark chocolate-brown of *Lessonia* (Photos 3 and 4).

Durvillea is harvested by fishermen and by visitors to the beach, the weed being dried in the sun and then sold for human consumption. The continual removal of *Durvillea* cannot fail to affect the numbers of this weed, and under undisturbed conditions it is likely that this species would be of greater ecological significance.

The *Lessonia* belt forms a very suitable habitat for animals, and the fauna found there is varied. Living on the rock between the holdfasts are very large barnacles, *Balanus psittacus* Darwin, and the chitons, *Enoplochiton niger* and *Acanthopleura echinata*. Fissurelids are very common in this belt, the large species, *F. crassa* Lam., being very frequent. *F. crassa*, which often has a small limpet attached to the shell, is also numerous. *Pyura chilensis* is often found in this belt, though it is not continuous around the shore.

A Thaid, *Concholepas concholepas* Bruguiere, is found in clefts in the *Lessonia* belt. This mollusc known as " Loco ", is very popular as food and it is extensively hunted. In spite of this predation, the species is common on exposed coasts. Also found in clefts are a thaid, *Thais chocolata* Duclos, *Chiton granosus*, *Fissurella crassa*, *Enoplochiton niger* and *Turbo niger*.

The holdfasts of the weed offer shelter to a number of forms. Prominent amongst these are small crabs, of which there are four species, *Petrolisthes spinifrons* (H. M.-Edw.), *Pachycheles grossimanus*

(Guerin), *Pilumnoides perlatus* (Poepping), and *Taliepus dentatus* (H. M.-Edw.). Adult specimens of *Petrolisthes spinifrons* are found in the weed holdfasts, also the snapping shrimp *Synalpheus spinifrons* (H. M.-Edw.).). The "snapping" of this species can be heard at low tide. Small molluscs also frequent the holdfasts. *Pseudonereis gallapagensis* Kinberg is found amongst the roots of the holdfast.

Specimens of the Majid crab, *Pisoides edwardsii* (Bell) can be found crawling among the *Lessonia* fronds. These crabs have a very strong carapace and also have powerful legs so that they can hold very tightly to the weed and withstand wave action. These crabs are parasitized by a leech which lives around the bases of the thoracic appendages. This leech, according to Miss Ingram, may well belong to a new genus.

Two other species of crab lead a roving existence among the *Lessonia* stipes and fronds. These are *Acanthocyclus hassleri* Rathbun and *A. gayi* H.M.-Edw. & Lucas. Both of these species have a very strong calcified integument and can exert a most powerful grip with their claws. Although *A. gayi* was collected on the rock as well as on *Lessonia, A. hassleri* was found only on *Lessonia.*

Where the *Lessonia* belt extends into gullies there are species of small algae which form tufts on the rock with limpets. In semi-sheltered places which also receive some shelter from wave action the alga *Codium dimorphium* Svedeleus forms a thick continuous cover over the rock. This alga grows only on vertical rock faces.

Also found on vertical or steeply-sloping rock faces, particularly in gullies, in the rocks, is a most remarkable fish, *Sicyases sanguineus* Muller & Troschel (Gobiesocidae). This fish clings by means of its ventral sucker to the rock and, where the surf has receded, it can be seen feeding with its incisor teeth on the minute algae growing on the rock. The fish clings on to the rock in spite of the heaviest surf, allowing its tail to swing with the flow of the water. The fish, which is effectively protectively coloured, grows to about 0.4 metres in length and quite large fishes can be seen clinging to the rocks. These fishes can tolerate some insolation, having been seen fully exposed to the summer sun for a period of up to three minutes. When a fish wishes to change position it partially relaxes its sucker and slithers down the rock or else is swims quickly to a new resting place when it is submerged by a wave during the very brief period when the water is nearly stationary before the wave recedes.

The fish is parasitized by a species of leech probably belonging to the genus *Platybdella,* the leeches being found in the operculum and sucker regions. Miss Ingram tells me that neither this leech, nor the one from *Pisoides,* has been recorded previously from South America.

Sicyases is subject to some hunting, being caught with long-handled dip nets. It offers but poor food.

A large actinian, *Phymactis clematis,* M. Edw., is found mainly in this zone. This species occurs in three colour phases, a red, a green, and a bright-blue. The red individuals occur highest on the shore, but still in the Infralittoral Fringe or in ponds, and in light-exposed places. The green specimens are found at slightly lower levels, not in small ponds and in places where there is shelter from the light, while the blue individuals occur in semi-cryptic places with no direct illumination. Often associated with this anemone is a Porcellanid crab, *Petrolisthes angulosus* (Guérin). Also occurring with blue variety of *Phymactis clematis* are the large chitons *Enoplochiton niger* and *Acanthopleura echinata,* the Sagartid, *Sagartia chilensis,* and the echinoid *Loxechinus albus* (Molina).

The echinoid is very common in rock pools of the lower Midlittoral, particularly those which continuously receive surf. In several pools this species is so common that all the algae have been eaten out of the pond. A feature of this browsing is the very sharp cut off of the upper limit of feeding. *Loxechinus* is collected and sold for human consumption. It is parasitized by *Pinnotheres chilensis* M. Edw., the latter species being regarded as an epicurean delight.

The weed, *Chaetomorpha aerea* (Dilwyn) often hangs over the entrance to clefts, forming a thin screen. It also occurs in other semi-cryptic places. *Dendrymenia flabellifolia* (Bory) Skottsb. often forms a thick carpet in sun-shaded places, frequently using *Pyura* as a substratum.

Lessonia is subject to the attacks of a limpet *Scurria scurra* (Lesson). This species burrows into the stipe of the weed, causing a considerable wound (Photo 3) which in time develops into a point of weakness at which the stipe breaks. I have seen stipes which have been broken by this limpet and the limpet has remained on the stipe, forming an apical hollow in which it lives and feeds. Another species of *Scurria* burrows up into the holdfast of *Lessonia,* forming another source of weakness to the wave action. There is a very interesting parallel to this in the stages of *Patina laevis* (L.) attacking *Laminaria digitata* (Huds.) Lamour in the British Isles and Europe. It is worthy of note that the Chilean limpets do not attack *Durvillea,* which grows in amongst the *Lessonia* plants. The ecologically and phylogenetically related *Sarcophycus potatorum* (Labill.) Kutz also is not attacked by limpets in Australia.

The *Lithothamnion* belt is surprisingly devoid of life other than the continuous coating of the algae. Although it has not been possible to collect in this belt, I have been able to observe it closely on many occasions. The chiton *Acanthopleura echinata,* which grows to a length of more than 15 cms., is a most obvious inhabitant of the zone. The population of this species is not dense, one or two individuals being found at about 3 or 4 metres distance apart. The gastropod *Thais chocolata* is also sparsely distributed in the belt, though it is sometimes more numerous than *Turbo niger.* This species is difficult to observe since the shell is often coated with *Lithothamnion.* It usually favours small crevices or niches in the rocks, since it cannot hold on against wave action as strongly as *Thais.* In these places it is sometimes very numerous.

Two asteroids are common in these clefts, namely the large blue *Meyenaster gelatinosus* (Meyer) and *Stichaster striatus* Müller and Troschel.

It is difficult to account for the paucity of numbers of animals in this region of the shore. One might reasonably expect Patelloids, more numerous chitons and some more algae to occur, but they are not present. The most likely reason is that the incessant thrashing of the fronds of *Lessonia* tends to brush away the animals.

ZONATION IN SHELTERED POSITIONS

Since the whole of the coast of Montemar falls into the category of an exposed coast it must be understood that by a sheltered position I mean a place which is sheltered from the main force of the waves. There are no islands or bays which give sheltered waters such as may be encountered in other parts of the world, or on the southern Chilean coast.

Two localities at Montemar are sheltered from the maximum wave action. These are the beach, Playa Montemar to the north-east of the Marine Station, and a beach to the south-west. This latter beach is not as completely sheltered from the waves as is the Playa, the shore hereabouts consisting of shingle and coarse sand with stones in the lower parts of the Midlittoral and the Infralittoral Fringe.

The South-West Beach

The true zonation on most of this beach is obscured because the beach is much broken up by stones, forming ponds and areas of running water. It is possible, however, to obtain a picture of the zonation in the rocks at the western side of the beach.

Substratum: Granite without dolerite dykes.
Zonation: Bare rock.
Barnacles.
Barnacles + *Mytilus* + very few *Ulva lactuca* plants.
Tegula atra (Lesson) + *Adenocystis utricularis* (Bory) Skottsb.
Lessonia nigrescens.

The zonation is very simple and without any complex variations. The barnacle belt is practically pure, there being very few *Littorina peruviana* present, the few being mostly confined to rock clefts.

The limpets are scarce, being confined to clefts.

Telgula atra is very numerous. The species is most conspicuous against the rock because all the shells are covered with *Lithothamnion*.

The transition from exposed conditions to sheltered is very rapid, occurring as a horizontal distance of less than one metre. The most notable differences from exposed conditions is the very sudden drop in the numbers of animal and plant species and the equally sudden lessening of the vertical height of the zones on the shore. Figure 19 shows the vertical distribution of the principal belt-forming organisms on both exposed and sheltered coasts at Montemar.

In this figure, the point of reference on the shore cannot be that of any intertidal organism, but it must be a tidal level, the height of which it reaches on both types of shore being noted simultaneously. This level was observed and used as the reference point for all measurements. The effect of wave action is shown in the raising of all of the belts of the intertidal region on the exposed shore. It is particularly significant that Mean Sea Level on the exposed coast is below the level of the species normally considered as being characteristic of the Infralittoral Fringe, namely *Lessonia nigrescens*.

The boulder region just below the shingle beach furnishes the richest collecting. Most of the forms are semi-cryptic or cryptic in habit. All of this area is subject to considerable wave action during heavy winter storms and although many of the boulders are very large and have been wedged together by the waves, it is possible to collect the area fairly effectively.

The most noteworthy feature of the fauna dwelling below the boulders is the poverty of the Poriferan fauna. Sponges were not collected anywhere on the exposed coast, except in the " roots " of *Lessonia*. The only sponges collected here were a yellow-coloured *Haliclona sordida* Thiele and *Halichondria panicea* (Pallas). The latter specimen resembles *H. prostrata* Thiele, previously recorded from Tumbes, but the spicules are longer than for *prostrata* and Dr. Burton believes that the specimen can be assigned to *panicea*. Many places which appear to be suitable for colonization by sponges, both on sheltered and exposed coasts, are not populated by representatives of this phylum. *Codium dimorphum*, to some extent, occupies a typical encrusting poriferan habitat.

The snapping shrimp *Synalpheus spinifrons* is common below stones on this part of the shore as is *Betaeus emarginatus* (H. M.-Edw.). The Decapod crustacean fauna on this part of the shore is very rich in numbers and species. The most numerous decapod is the hermit crab *Pagurus edwardsii* (Dana) which lives in the vacated shells of *Tegula* spp. The population of this species often reaches a local density of 5 per cm. square. The asteroid *Patiria chilensis* (Lutken) a small *Patiriella*-like species, is common below stones on this shore.

The Porcellanid *Petrolisthes angulosus* (Guérin) is also very numerous in the typical Porcellanid habitat below loose stones and rocks and *Gaudichaudia gaudichaudii* (H. M.-Edw.) is also numerous living buried in the shingle at low water. This species ranges in colour from brownish-red to a blue-red.

Other common crabs are *Paraxanthus barbiger* (Poepping), *Petrolisthes spinifrons* (H. M.-Edw.), *Pachycheles grossimanus* (Guérin), *Pilumnoides perlatus* (Poepping), *Taliepus dentatus* (H. M.-Edw.), and juvenile *Acanthocyclus gayi*. The Majid *Pisoides edwardsii* is uncommon and is always found crawling in *Lessonia* fronds. *Leptograpsus variegatus* is absent from this part of the shore because the area, having an immersion factor tolerated by this species, is formed of coarse sand unsuited to *Leptograpsus*, which lives on rocky places.

The prawn, *Rhynchocinetes typus* H. M.-Edw., is very common and is found swimming in ponds and still water left among the rocks by the receding tide. These animals are of the common transparent yellow shrimp colour with red and white markings and yellow spots.

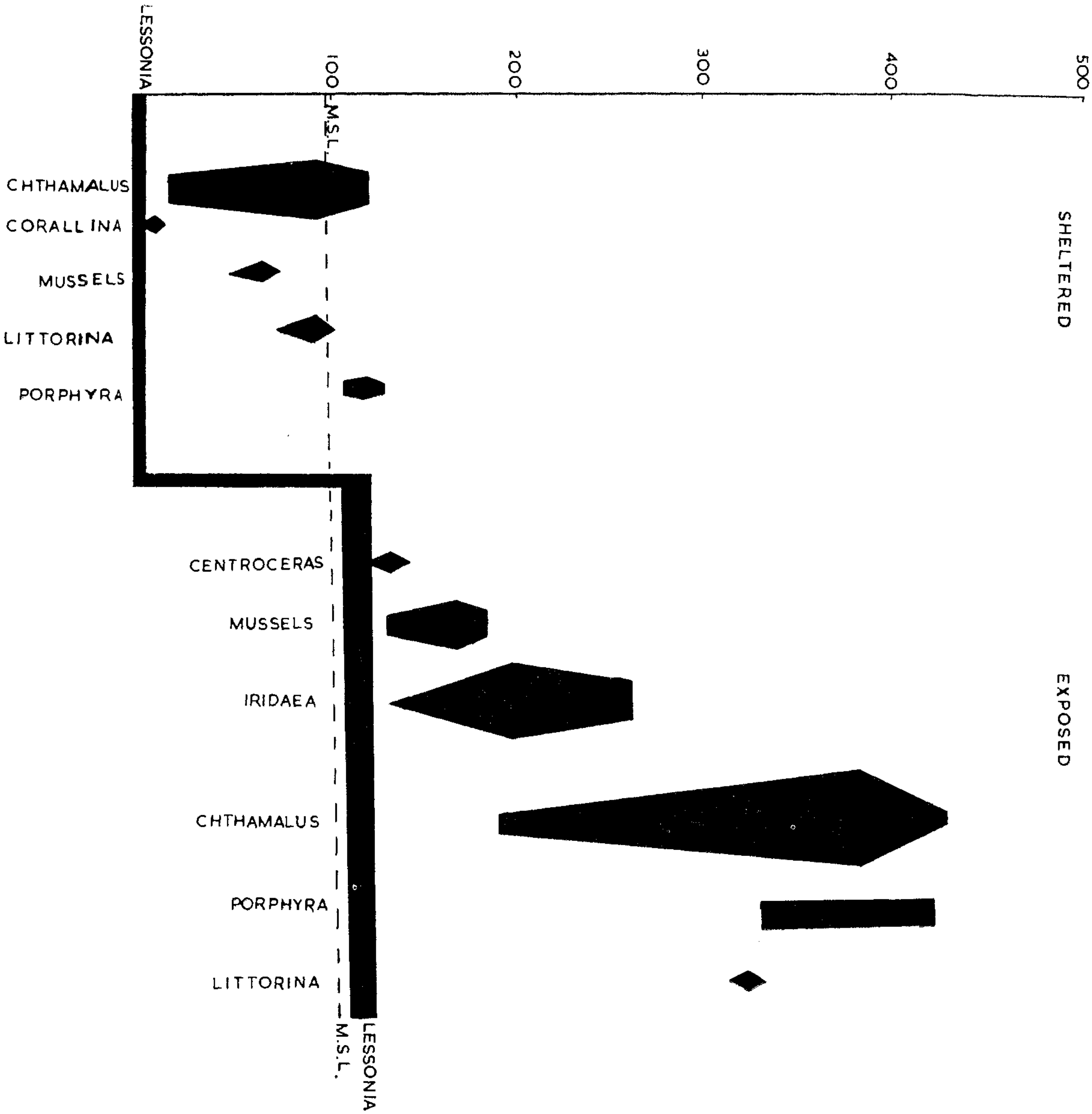

FIG. 19.—The heights of the main intertidal zones on exposed and sheltered shores at Montemar.

Although the fauna and flora of intertidal ponds is outside the scope of this work, there are certain features of the pond habitat which must be mentioned. All the ponds at the high levels of the shore are polluted by decaying debris or by the decaying food left by picnic parties. In spite of what is, in some case, a very high degree of pollution, *Leptograspus variegatus* runs in and out of these ponds.

The ponds at the lower levels on the shore are populated by forms usually found living even further down the shore than the ponds themselves. This generalization is found to be true throughout the region and sometimes this feature is very noticeable so that it is surprising to find *Betaeus emaginatus*, a large olive-brown form, living in considerable numbers in a pond on Concon Island at the level of extreme high water.

The deep ponds are frequented by young fish. The most common of these is the "vieja negra", *Graus negra* Philippi. A small Clinid fish is also frequent. Mann (1952) observes that this family in Chile is very confused and no satisfactory identification could be undertaken.

The sheltered stony shore is primarily occupied by animals, the plants being secondary in importance. The only large plants found are *Lessonia nigrescens, Codium dimorphium, Adenocystis utricularis* (Bory) Skottsberg, *Colpomenia sinuosa* and *Scytosiphon lomentarius* (Lyng.) J. Ag. Although these algae are common, only *Lessonia* is a prominent feature on this part of the shore.

The upper surfaces of the large boulders on the shore are usually fairly densely populated by the barnacle *Chthamalus cirratus*. It is noticeable that the dolerite rocks weather to a more rounded shape than the granite, which always has a rough surface. This rough surface presents a more suitable substratum for the settlement of barnacle larvae and there is a resultingly larger barnacle population on the granite. This is strikingly in contrast to the situation on the exposed shore, where, as noticed above, there appears to be no detectable difference between the populations of the two types of rock.

The rocks are embedded in a shelly sand which shelters numbers of a holothurian. *Meyenaster gelatinosus* is also found below the stones, though it is not embedded in the sand. Certain of the belt-forming algae are subject to seasonal variations in their numbers. *Porphra columbina* has been noted above as being seasonal in occurrence.

Iridaea also shows some degree of seasonal variation. About the middle of January the plants growing in the upper part of the *Iridaea* belt wither, die, and turn white in colour. This part of the *Iridaea* belt then is dominated by barnacles and so becomes the lower part of the barnacle belt.

Ulva also becomes scarcer in the summer, plants in the high rock ponds dying, as do those in the upper parts of the mussel beds.

Similar seasonal variation in *Porphyra* and *Ulva* have been noted in Tasmania (Guiler, 1950).

The area described above is a popular holiday beach, many people spending a day there. It is difficult to assess the damage done to the density of intertidal populations by human interference. Chileans are very fond of seafood and collect considerable numbers of animals and plants from the rocks. The species taken for food are *Ulva lactuca, Porphyra columbina, Durvillea antarctica, Pyura chilensis, Concholepas concholepas, Turbo niger, Teluga,* spp., *Thais chocolata* and the large chitons. *Iridaea* also may be collected, being mistaken for *Porphyra*. With one exception, *Durvillea,* little damage has been done to the main features of the zonation which is the same as that seen along many kilometres of coastline. The possible human effect on the distribution of *Durvillea* is discussed below. The smaller crustacean groups are well represented but have not been collected in any numbers with the exception of the Caprellidae which will be the topic of a separate systematic paper.

The annelids are well represented on this shore, but a surprising feature of the species composition of this phylum on the sheltered beach is the absence of the larger species of Serpulid. *Spirorbis* sp. is present, often coating the underside of rocks or living on the stipes or holdfasts of *Lessonia,* but there are no species of *Galeolaria, Pomatoceros, Pomatoleios* or similar genera.

A sabellarian, *Phragmatopoma moerchi* Kinberg, is very common below stones, living in a tube formed of shingle fragments, usually pieces of mollusc shells. *Potamilla* sp., (Fam. Sabellidae), is frequently encountered living below rocks. Another common species also found below rocks is the tubicolous *Platynereis magalhaensis.* Other species found below rocks are a species of *Euphrosine* (Fam. Sabellidae), *Lumbrineris tetraura* (Schmarda), *Demonax* sp. (Fam. Sabellidae), and a Terebellid *Thelepus concinnatus* (Fabr.).

The dominant fauna living in the sand at the north-eastern end of the rocky area at Montemar is annelidan. Apart from the Anomuran *Emerita analoga* (Stimpson), the only other common macroscopic organisms found are annelids, namely, *Nerides* sp., *Lumbrineris* sp., *Scoloplos* (Leodamos), *ohlini* (Ehlers), *Lumbrineris? tetraura* (Lumbrineridae) (these last two species being extremely common), *Marphysa? sanguinea* (Eunicidae) *Hemipodus simplex* (Grube) (Glyceridae) *Cirriformia* sp. (Cirratulidae) and a Spionid. All of these species are very common in sand washings obtained at low water level.

9. COMPARISON WITH NEARBY AREAS

(a) Laguna Verde and Pt. Curaumilla

Twenty-two kilometres to the south of Valparaiso there is a beach known as Laguna Verde. This beach is not a very widely used holiday resort and so the zonation there is less spoilt by human interference. Point Curaumilla is ten kilometres further south than Laguna Verde and is only accessible by walking or by transport over a very rough road.

The beach at Laguna Verde is about one mile in length with an electricity power station at the southern end, followed by a rocky coastline. At the northern end of the beach the shore line changes abruptly to high vertical cliffs.

(i) *The Zonation at the Northern End of the Beach*

Due to the topography of the coastline it is not possible to carry out examinations of much of the shore hereabouts. However, examination of the accessible area did show some important variations from the zonation at Montemar.

The most significant feature is that *Littorina peruviana* forms the highest belt on the shore. This is in accordance with the expected littorinid habitat in other parts of the temperate and even semi-tropical regions of the world, where one species or another of this family forms the first belt of marine organisms encountered below the trrestrial realms.

The littorinid belt is replaced by a *Porphyra* belt which, in turn, is replaced by *Iridaea*. The latter is followed by the *Centroceras-Gelidium-Corallina* belt. The surprising feature is the complete absence of barnacles, *Chthamalus cirratus*. This species does not form a belt nor does it occur as individuals. The absence of the barnacles is associated with the intense sand scouring.

There may well be seasonal variation in the form of the zonation. The above condition was observed in February and March.

It was noted on a later visit to this beach that the level of the coarse sand on the rocks had fallen about 5 cms. In spite of the heavy scouring which must take place during the sand movement, *Lessonia*, *Porphyra* and *Iridaea* were still present on the rocks and showed little apparent effects.

Movements of sand will, of course, have some effect on the organisms which live in the sand, though these creatures are usually fairly mobile and, unless storm conditions prevail, can usually look after themselves. The organisms living on nearby rocks must, to survive, be able to withstand periodical burial under sand for varying periods.

Below the mixed algal belt is the conspicuous *Lessonia nigrescens,* with which are associated *Lithothamnia* and *Pyura*. *Acanthopleura* and *Enoplochiton* do not occur in places where there is strong sand scouring.

In this place there are very few limpets, only one species being there.

(*ii*) *At the Southern End of the Bay on the Rocks Beyond the Power Station*

The zonation here is strikingly different from that seen at the northern end of the bay. The littorinid belt is still found and the barnacle belt is absent, *Porphyra* and *Iridaea* being the zonal organisms in this part of the shore.

The *Centroceras-Geldidium* belt is also absent, being replaced by an *Ahnfeltia durvillaei* (Borg.) J. Ag.-*Gymnongrus-Laurencia chilensis* Forti and Howe association with *Dendrymenia flabellifolia* (Bory) Skottsb. in sun-shaded places. This is, in turn, replaced, though in shaded places it is overlapped by a very rich *Codium dimorphum* belt, by *Lithothamnion* at the lowest tidal levels.

The most striking feature is, of course, the absence of either of the large Phaeophyceae, *Durvillea* or *Lessonia*. Other species which are characteristic of the Phaeophycean zone are present, e.g., *Acanthopleura echinata* and *Turbo niger*. This feature, combined with the changed species composition and slightly modified appearance of the algal belt immediately above it, makes the shore most strikingly different from any other part of the coast.

About one kilometre to the south of the Power Station the zonation changes sharply, the upper parts of the shore returning to a condition more resembling that at Montemar. The littorinid belt is present and quite well developed, the barnacle belt is present, and so is the *Centroceras-Gelidium* belt. However, in the Infralittoral Fringe the *Lessonia* belt is replaced by a belt of pure *Durvillea antarctica*. *Lessonia nigrescens* is present in slightly sheltered positions in this area. It is found living in places which suffer from slightly less to considerably less wave action than those situations occupied by *Durvillea*. *Lessonia* plants collected here show a considerable difference in form from those found on exposed shores, the stipe being very short and the fronds broader. (Photo 5). The identity of a specimen of this alga was kindly checked for me by Professor Etcheverry.

Durvillea becomes very common towards Point Curaumilla and completely replaces *Lessonia* on this coastline, but only in places where there is considerable wave action. In more sheltered places *Lessonia* is still the dominant alga of the Infralittoral Fringe. In some places *Lessonia* forms beds on rocks in shallow water in sheltered inlets similar to those formed by *Macrcystis* (see below). These beds must exert a considerable effect in lowering the strength of wave action and in forming a shelter for other forms.

To the south of Point Curaumilla the dominant alga is again *Durvillea.*

The full significance of the change in zonal species is apparent whenever the distribution of *Durvillea* is considered in relation to wave exposure. This alga occurs on the southern side of Point Curaumilla as well as on the more exposed places on the northern side of the Point. The prevailing swell is from the south-west so that it is obvious that this alga has a very strong preference for places of strong wave action. At Las Ventanas, to the north of Montemar, *Durvillea* almost reaches the status of the dominant species in places where the wave action is most strong. At Pichidanqui, however, *Lessonia* is the dominant species and also at Coquimbo.

Why, then, is this species almost absent from the Laguna Verde-Montemar-Quintero area? Is it possible that Point Curaumilla acts as a breakwater and diminishes the waves to such an extent that Durvillea cannot flourish until Ventanas is reached? This hypothesis can hardly be held correct, since the wave action on the sheltered northern side of Point Curaumilla is appreciably less than at Montemar, even allowing for "bending" of the swell around the point.

The influence of fresh water throughout this area is negligible though it can have important local effects as at Concon (p. 181). In general, however, this part of the coast can be considered to be washed by the same type of water as the areas immediately to the north and south.

The only factor which offers any explanation of this peculiarity in the distribution of *Durvillea* is the effect of human interference. As noted above, *Durvillea* is in considerable demand for food. It is collected by fishermen, dried and sold for human consumption, under the name of "cuchoyuyo". Considerable quantities are collected, the stipe being cut just above the holdfast, the latter being left on the rock. In areas where there is a permanent fishing population with readily accessible *Durvillea*, this harvesting continues throughout the summer, i.e., the growing period. There cannot fail to be some considerable effect on the abundant *Durvillea*. Is this effect great enough to reduce the *Durvillea* from the status of dominant to that of subdominant, or, in extreme cases, even making the species rare? I consider that this is so, especially in view of the fact that *Durvillea* significantly is more common in inaccessible places. The continual harvesting of *Durvillea* has cleared the shore for population by *Lessonia* which, although not as ideally suited to the exposed coast Infralittoral Fringe as is *Durvillea*, is, nevertheless, able to survive there quite well in the absence of competition from the larger weed. It is significant in this regard that *Lessonia* on exposed coasts tends to consist largely of stipe and holdfast with a few very lateral fronds, whereas specimens of the same species from sheltered places have a small stipe but a large, broad healthy-looking frond. In this case it is likely that there is intense interspecific competition between these two algae, each being slightly more suited to one habitat than the other. I consider that *Lessonia* is the more adaptable species, being found in a greater variety of habitats than the wave action loving *Durvillea*. This is abundantly clear from the field observations, especially since *Durvillea* is absent from sheltered places.

It may not be significant that I did not see any beds of *Macrocystis* in the area Point Curaumilla to Quintero, though there are beds at Las Ventanas and Quintero. The absence of this species may be correlated with a sandy floor along this coastline.

(b) Quintero and Ventanas

These two places are on the coast to the north of Montemar, lat. 32° 45′ S. Although Quintero is about five kilometres from Ventanas, it is convenient to consider them together as one ecological unit. The position of these two places in relation to the prevailing swell is shown in fig. 20.

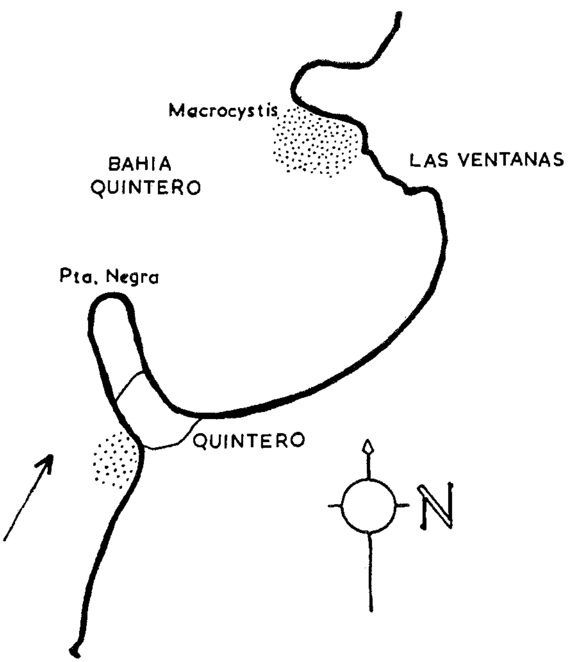

FIG. 20.—Outline sketch of the Quintero area. The stippled areas show the location of the beds of Macrocystis.

At Ventanas the most salient feature, one which is very different from any conditions seen near Montemar, is the presence of an area of *Macrocystis* which is exposed at low water spring tides. This species, *M. integrifolia* Bory, favours places where there is just less than the maximum wave exposure (Photo 6).

Macrocystis also occurs in beds offshore, the fronds of the plants being visible floating on the surface of the water. These beds are not extensive in area and cannot be considered as forming a continuous breakwater, though they must have some local effect.

The algae of the Infralittoral fringe on the fully exposed coast at Ventanas are *Lessonia* and *Durvillea*. The latter species is fairly common, there being more plants than at Montemar, but it does not reach the status of the dominant alga of the Infralittoral Fringe.

Iridaea is present at Ventanas in the barnacle band, but at Quintero the zonation is slightly changed. The shore at Quintero is more sheltered than any other part of the coast examined. This is especially true of the area on the northern side of Quintero, which is sheltered from the prevailing northerly swell of the headland. In this area *Iridaea* is absent as is *Lessonia* from the very sheltered places. *Porphyra* is very scarce but the barnacle belt is present with a very well developed *Littorina* belt.

Macrocystis does not occur in the sheltered waters but is found in rocky bays suffering just less than maximum exposure. The sandy bay on the exposed side of Quintero, which has rocky outcrops in the Infralittoral, is richly covered with *Macrocystis*.

The principal interest and significance of this area lies in the absence of *Iridaea* from the sheltered coast and the presence of *Macrocystis* in the Infralittoral Fringe on nearly exposed coasts. It is also of not considerable importance to note that on the sheltered coast of Quintero there is no Infralittoral Fringe alga replacing *Lessonia*.

(c) Concon

Concon lies nine kilometres to the north of Montemar.

The Concon bay area (lat. 32° 56′ S.) is of interest because the River Aconcagua enters the sea at this town, and so some estimate can be made of the effect of fresh water on the intertidal zonation. No attempt was made to examine the animals and plants of the fresh water.

The River Aconcagua flows from the Cordillera to the sea and is very seasonal in its volume of flow. In the summer the water entering the sea is all contained in a channel about six metres in width and about three metres deep at its deepest point. However, in winter and during the melting of the snows on the mountains the river becomes greatly swollen and is almost one kilometre in width.

The flow from the river enters a broad bay at its southern end. The shoreline of all of the northern part of the bay is composed of sandy beaches. To the south between Concon and Montemar there are rocks and cliffs, and it is on these rocks near the River Aconcagua that the examination was carried out.

The rocks nearest the river mouth are devoid of all forms of macroscopic life. The first zonal organism encountered is *Enteromorpha intestinalis* (L.) Link. This alga forms a green covering over most of the rocks which are just outside the mouth of the river. The rocks in this area are fine-grained sandstone, but this type of substratum alters after a few metres to the typical rocks of the area, namely, granite pierced by dolerite dykes.

The first evidence of truly marine forms occurs halfway between a bridge, La Calietilla, and the mouth of the river. At this place, *Porphyra columbina* occurs. Barnacle tests without living animals are very frequent on this part of the shore. It is probable that the barnacles were all killed during very heavy flooding by the river during the winter of 1954.

The first living barnacles occur about six metres further along the shore from La Calletilla. The majority of the barnacles are dead but there are a few living specimens. The live specimens are of about the same size as the dead tests. This may indicate that they are of the same year group and, therefore, survivors of the 1954 flood or, on the other hand, they may be of a different year group and no similar conclusion can be drawn.

Some 10 metres from the first appearance of barnacles, the facies becomes decidely marine, with the sudden appearance of *Iridaea laminarioides, Brachidontes purpuratus, Siphonaria laeviuscula* Sow. and the proportion of live barnacles increases very greatly.

An examination carried out a further 10 metres along the shore shows that nearly all the barnacles are living, and that the mussels have become very numerous and extend down into the Infralittoral Fringe, forming dense sheets covering the rocks. *Porphyra* is very plentiful and the grapsid crab, *Leptograpsus variegatus*, is first seen here. *Littorina peruviana* is common on sun-sheltered rocks, and *Corallina chilensis* appears hereabouts in rock pools but not as a belt-forming species.

Lessonia first appears just to the south of a small prominence, also *Acanthopleura echinata*, "Lithothamnia", *Turbo niger* and *Centroceras clavulatum*. The cling fish *Sicyases sanguineus* is also noted to be here. In some places *Littorina peruviana* is sufficiently numerous to form a distinct band in the upper parts of the barnacle belt.

The Littorinids hereabouts are of two species. The most common is *L. peruviana* (= *L. zebra*), but *L. araucana* d'Orb. is also frequent, being larger in size and occurring slightly higher on the shore than *L. peruviana*.

10. DISCUSSION

At this stage I do not propose to discuss the distribution, habits and general biology of any of the non belt-forming species. This will be dealt with in a later contribution, but here I will confine myself to a few general remarks concerning the zonally-significant species.

One of the most surprising features at Montemar is the absence of a Supralittoral Fringe in the immediate vicinity of the Estacion de Biologia Marina. This has been attributed to a combination of excessive nitrogenation, combined with an immersion factor which does not permit the development of a characteristic fringe of Littorinids. *Littorina peruviana* occurs within the barnacle belt and does not form the characteristic strip above the barnacles. This feature is not only confined to Montemar but also is found at all other parts of the neighbouring coast with the exception of near the Rio Aconcagua where *L. araucana* is the dominant species and forms a well-developed band above the barnacles. The top of the barnacle belt is dominated by *Chthamalus cirratus*. This species is known from Peru to Chiloë Island (Darwin, 1854, and Pilsbury, 1910). *Chthamalus cirratus* extends as far down the shore as the Infralittoral Fringe, being collected on *Balanus psittacus* by Coker. The lower part of the *Chthamalus* belt also has individuals of *Chth. scabrosus* Darwin. This species was recorded by Darwin as often with *Chth. cirratus* and *Balanus flosculus*. The latter species is the more common barnacle on the lower part of the shore, being found on *Concholepas, Brachidontes,* on *Mytilus*, rocks or on *Balanus psittacus*. *Chth. scabrosus* is more common at the lower shore levels with *B. flosculus* than with *Chth. cirratus*. The lower part of the belt is also occupied by three other barnacles, *Balanus laevis* Bruguiere, *B. psittacus* (Molina), *Verruca laevigata* Sowerby. *B. psittacus* is the most conspicuous of these, being the largest of the family. I measured a specimen 18 cms. in height and Darwin records the species as being "more than nine inches in length". It is of interest that he doesn't record the species as intertidal. Darwin noted *B. psittacus* adhering to *Concholepas*, but I did not see any such association.

The character of the zonal organisms changes at the bottom of the *Chthamalus* belt, algae becoming the dominant organisms. *Iridaea* is generally distributed throughout the Montemar area, except in places with strong sand scouring and this, in turn, is replaced by a mixed algal association, in turn yielding to the large brown *Lessonia* of the Infralittoral Fringe. *Iridaea, Centroceras* and *Gelidium* all utilise mussels of either of the genera *Mytilus* or *Brachidontes* as a substratum, *Brachidontes* being found at a slightly higher level on the shore than *Mytilus*. I am not sure of the permanence of the mussel beds as a zonal feature at any one place. I have found in Tasmania that the mussel beds at any one place change in extent from time to time and even may be absent for short periods. However, it is important to note that mussels, particularly *Brachidontes*, are of considerable ecological significance in this region, since the presence of these organisms on exposed coasts has been found to be of biogeographical importance elsewhere (Bennett and Pope, 1953).

The influence of wave action on the vertical distribution of organisms is shown in fig. 18. Several authors have investigated this problem, notably Burrows, Conway, Lodge and Powell (1954). These authors investigated the Law of Widar Brenner (Du Reitz, 1940), which states that the high-water line of the sheltered shore has its ecological equivalent on the exposed shore, not in the high-water line of the exposed shore, but in the upper limits of the reach of the storm waves.

Burrows, *et al*, found that the absence of a climatic factor limited the applicability of the Law because they found that the fogs and mist of Fair Isle assisted the upward extension of the limits of the algae. They go further and point out that the wetting power of a wave is dependent upon the drying power of the atmosphere. In warmer climates than Fair Isle an important part of the drying power of the atmosphere must be the heat of the substratum, for example, at Montemar, during the summer, spray deposited on the shore evaporates very rapidly, almost as soon as it is deposited.

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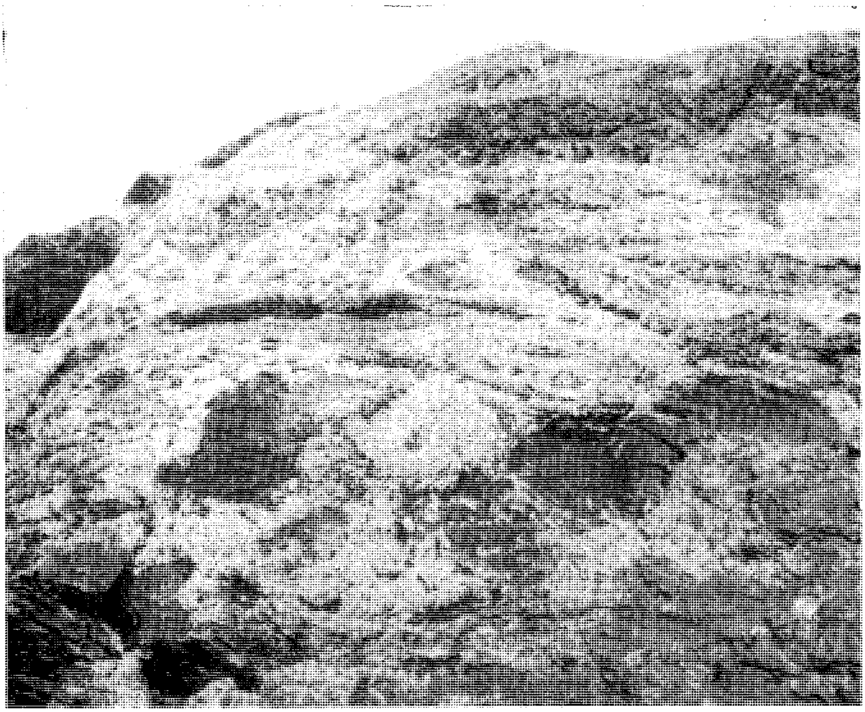

Photo 1.—*Chthamalus cirratus* belt on the exposed coast at Montemar, February, 1955.

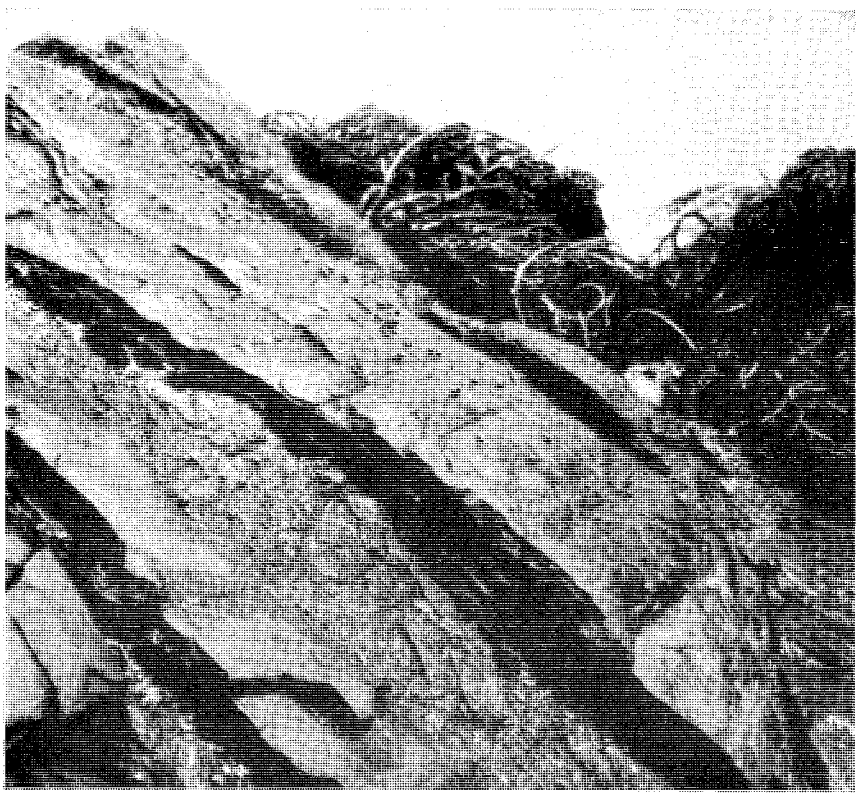

Photo 2.—*Littorina* on a spray-soaked, sun-exposed rock, Montemar, January, 1955. Note the absence of a barnacle belt in this area.

Photo 3.—The Infralittoral Fringe near Montemar, March, 1955. The *Lessonia* plant in the foreground shows the typical scars caused by the limpet *Scurria*.

Photo 4.—*Durvillea antarctica* at Montemar, January, 1955.

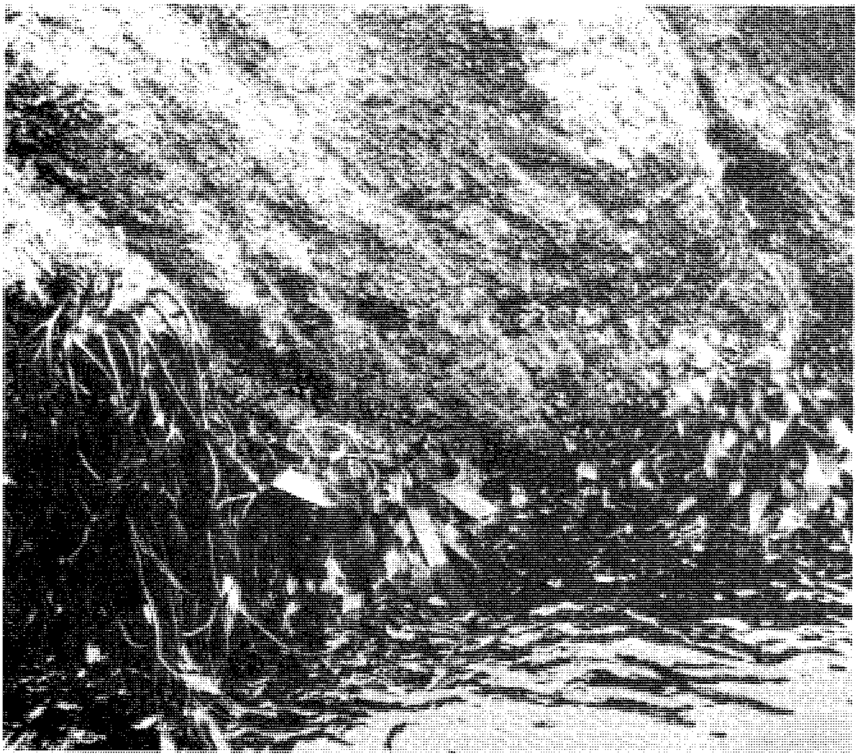

Photo 5.—The sheltered coast form of *Lessonia nigrescens* at Laguna Verde, March, 1955.

Photo 6.—*Macrocystis integrifolia* at Las Ventanas, February, 1955.