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INTERTIDAL BELT-FORMING SPECIES ON THE ROCKY COASTS OF NORTHERN CHILE

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(With 22 Text Figures and 2 Plates)

ABSTRACT

The zonation at four places in northern Chile is described. The general pattern of zonation throughout the Chilean coast is remarkably uniform with the important exception of Antofagasta where *Pyura chilensis* replaces algae in the Infralittoral fringe. The physical environment is described in some detail and the major intertidal features of Chile are compared with those of eastern Australia and South-West Africa to which they bear a close resemblance.

(1) INTRODUCTION

The only paper dealing with the intertidal ecology of restricted parts of the coast of Chile has been published earlier (Guiler, 1959). The present contribution describes the zonation at Iquique and Arica. These results are compared with each other and with the physical environment and the features of the Chilean coast as a whole is given. The relation of the fauna and flora of this coast to that of the Australian and South African coasts is shown. The present study does not include details of the distribution of the Chilean fauna and flora.

General observations on the geographic regions of Chile are made by Ekman (1953), who states that the southern limit of the tropical-subtropical fauna of the west coast of South America is very close to the Equator at either Punta Aguja (lat. 6° S.) or the Gulf of Guayaquil (3° S.). Ekman goes on to suggest that it is difficult to decide on location of the southern limit of the warm temperate fauna and suggests that there may not be two independent components—the warm temperate and the cold temperate. He later states that it is probable that there are two elements in the fauna and that the transition zone is at or near Chiloe Island (lat. 43° S.) since the cold water with a summer surface temperature of 8° C. commences thereabouts. Ekman further points out that the upwelling of cold water and the Humbolt Current are the two factors responsible for keeping the sea off the west coast of South America at a low temperature.

Oceanographic surveys have been made off the Chilean coast, Sverdrup (1931), Gunther (1936), and Deacon (1937) describing the results of these surveys, Deacon's work being concerned with only the extreme south of the continent. Schott (1935) gives much oceanographic and general information on the western coast of South America, while Murphy (1926, 1936) gives further oceanographic data as do Sverdrup, Johnson and Fleming (1942).

Mann (1954) describes the biogeographical regions of Chile, especially the northern parts. Koepcke and Koepcke (1951) give information on the ecological divisions of the Peruvian coast which has a direct bearing on the present study, and Petersen (1949) gives a small amount of ecological information in his study of the River Zuraumilla in Peru. However, none of these works makes any attempt to describe in detail the ecology of any one area or to compare the ecology of two different places.

During the summer of 1955 I was permitted to accompany an oceanographic expedition to the north of Chile. The expedition was organized by the Corporacion de Fomento in conjunction with the Estacion de Biologia Marina of the University of Chile. The expedition was transported on board the Chilean corvette *Papudo* and short stays were made at four of the northern ports.

The climate of the coast of Chile to the north of Coquimbo becomes very dry and, ultimately, in the provinces of Tarapaca and Atacama, results in the desert coast of northern Chile. The seaports are the only human settlements on this coast and it is nearly impossible, on account of inaccessibility, to make examination of the shore at places other than the ports. I have noted earlier (Guiler, 1959) that the Chileans are very fond of seafood and their gathering of animals and plants is restricted to the vicinity of the seaports by the same geographical factors as limit the collection of scientific material. Thus, some degree of human interference with the zonal organisms is to be expected, particularly with those species which are edible.

The places visited and described in this paper are Coquimbo (Lat. 29° 59′ S.), Antofagasta (Lat. 23° 40′ S.), Iquique (Lat. 20° 15′ S.), and Arica (Lat. 18° 20′ S.). I do not propose to detail the zonation and physical environment at these ports in this paper, but will do this in a later contribution. I have considered these ports together for the purpose of describing the zonation because the zonal pattern is so similar and also on account of the great amount of repetitive information that would be necessary if a description of each area were made the topic of a separate paper. Only the belt forming species are considered, the other ecologically significant species forming the topic of another paper.

(2) NOMENCLATURE

In the earlier paper describing the intertidal ecology of Chile I used the nomenclature put forward by Stephenson and Stephenson (1949) without any comment, but since this scheme has not been previously used in South America it seems desirable to have some discussion on the applicability of the scheme to Chilean coasts in general.

The Supralittoral Fringe

The limits of the Supralittoral Fringe furnish one of the major problems encountered in Chilean intertidal ecology. It has been suggested by the Stephensons that the upper limit of the Midlittoral, therefore the lower limit of the Supralittoral fringe, is the top of the barnacle belt. Further, following the Stephensons, the Supralittoral fringe is characterised by the presence of littorinid molluscs of one or more species, by *Ligias,* and by black encrusting Myxophyceae and lichens. Lewis (1955) points out that the upper limit of the midlittoral will vary locally, depending on the species, or in England—the genus, of barnacle found in that particular locality. However, he goes on to point out that, although the British Isles are of considerable local complexity, he does not advocate any alteration from the top of the barnacles as the demarcation line of the top of the Midlittoral. Prof. and Mrs. Stephenson, in a footnote to Lewis' paper point out that the barnacles, despite their drawbacks, are the best indicators available. They go further and point out that there is not expected to be a common level around a country, and, therefore the world, at which the barnacle belt cuts out. The work of Burrows *et al,* (1954) on Fair Isle shows that no constant level for any one zone can possibly exist.

At Montemar, near Valparaiso, there is a *Littorina* belt which lies within the top portion of the barnacle belt, that is to say, the *Littorina* belt forms a strip within the barnacle belt. By nature of the arguments expressed above, this means that the *Littorina* belt is part of the Midlittoral. Above this, there is a region of bare rock which is devoid of any apparent Myxophyceae and lichens. In certain other localities where there are cliffs, as on the coast adjacent to Montemar, there is a belt of lichens developed at very considerable heights, about 20 metres, above the water level but separated from the Midlittoral by a broad belt of bare rocks. This belt of lichens is usually very close to, if not continuous with, the terrestrial plants. Thus, in the Valparaiso area the Supralittoral fringe, as an ecological unit and neglecting small atypical patches, is either devoid of animal or plant life or else such life as exists is close to or almost a part of the terrestrial realm. The lichen belt must in many cases be considered as a part of the terrestrial rather than as intertidal in affinities.

How does it come about that there is neither a littorinid belt nor a lichen belt in the Supralittoral fringe or supralittoral zone? Part of the answer may be seen on Guano Island, where seabirds rest or breed in large, often fantastic, numbers. On a small island off the mouth of the Rio Aconcagua at Concon, to the north of Montemar, the barnacle belt has bare rock above it which is covered a short distance above the barnacles by guano deposits. The guano supports little plant life. This may in part be due to over-richness in nitrogen or to mechanical trampling by the birds. The effect of either of these factors will certainly be carried on to the bare rock below so that the lichens which might be expected to occur do not develop. Admittedly, the Guano Island is a very specialised habitat, but it is possible that smearing of the rocks with guano, always present on the Chilean coast, acts as an inhibitor to growth of lichens. It is noticeable on the desert coast in the north of Chile that there are no lichens whatsoever but the rocks are all liberally smeared with guano.

It was pointed out in an earlier paper (Guiler, 1959) that a lichen belt did not develop on the rocks at Montemar on account of their low height above sea level, i.e., all these rocks are in a bare supralittoral fringe.

The Midlittoral

This zone is easily recognised by the barnacle belt at its upper limit and by either algal turf or mussels at the lower limit. It should be noted that an entirely false impression of the zonation can be gained from an examination of the shore during the spring or early summer than when seasonal growths of algae of the genera *Scytosiphon, Iridaea* and *Porphyra* cover considerable areas of the shore, both in the horizontal and vertical planes. Indeed, *Porphyra* extends into the Supralittoral fringe in early summer at Montemar.

All of the Midlittoral can be considered as a Balanoid zone, since it is populated over most of its vertical range by barnacles of one species or another. In all places the dominant species on the upper part of the zone are barnacles and there is usually a very numerous barnacle population on the mussels found in the lower part of the zone. However, in places where there is an algal turf, few barnacles are found. The important point is that all of this belt is exposed at low water.

The Infralittoral Fringe

Throughout all of the Chilean coast the Infralittoral fringe is nearly always dominated and can be recognised by the presence of one or both of the two large algae *Durvillea* and *Lessonia.* A notable exception to this is at Antofagasta, where these algae are replaced by the ascidian, *Pyura.* This feature will be discussed later in this paper. The upper limit of the fringe is, of course, very variable in the level at which it occurs. Wave action is the principle factor controlling the height at which the zone occurs on the shores (Guiler, 1959).

There is no reason for abandoning the Midlittoral and Infralittoral fringe as regions on the shore since both are easily recognisable as such and this terminology is obviously suited to the conditions. However, due to the special conditions of rainfall operating on the Chilean coast, the Supralittoral fringe, as defined, was found to occur in separate patches, the usual condition being that the littorines occur on the top of the barnacle belt. It must be borne in mind that all my shore examinations were carried out in the summer so that an examination carried out in the winter may find different conditions brought about by a seasonal migration of the littorines. At present, the only conclusion which may be drawn is that the Supralittoral fringe is often absent in the summer on parts of the Chilean coast.

The different tidal levels are designated following Chapman's (1938) nomenclature and the terms zone and belt follow their definitions in Guiler (1953).

(3) THE PHYSICAL ENVIRONMENT

(*a*) *Currents.*

The coast of Chile, although of great length and extending, at it does, well into the tropics, is nevertheless washed by cool waters. Cold surface waters extend closer to the Equator on the west coast of South America than on any other southern continental mass. The coastal current system is first distinguished in about 38° S. and it moves slowly northward along the coasts of Chile and Peru to 4° S. where is sets W.N.W. and flows past the Galapagos Islands, ultimately becoming lost in the south equatorial drift. The current is primarily confined to the coastal belt of Chile and Peru where it diverges from the shore, but it extends for almost 10° of longitude into the Pacific just south of the equator.

A result of the divergence from the shore is an upwelling of phosphate-rich cold water (see below).

The current system has two sources of water. In the southern portion the water of the coastal current is sub-Antarctic in origin and flows north as a result of the west wind drift hitting the South American land mass. This cold oceanic water, as it moves north, is reinforced by upwellings of Antarctic water and becomes the Peru Coastal Current. According to Gunther, the southernmost limit of these upwellings changes in position, varying with the season, but, when the *William Scoresby* was on the coast, the upwellings were strong at Copiapo and extended to Cape Carranza (Lat. 35° 40′ S.). Gunther states that the extreme southern limit can be placed at 40-41° S. and he found that the current flowed faster inshore (10-12 miles per day) than 100 miles offshore (3½ miles per day). There is some evidence of a seasonal variation in the rate of flow in the charts published by the Meteorological Office (1938), but Barlow (1938) found the rate of flow constant throughout the year, though with a maximum in August.

It happens from time to time that the trade winds, normally southerly along the west coast of South America, fail due to the southerly movement of a low pressure belt normally situated to the north of the equator. The trades are replaced by a north wind bringing with it a flow of hot equatorial water of low salinity along the coasts of Peru and Chile. This hot water, known as El Nino, kills fish and plankton in immeasurable quantities and must cause a tremendous mortality among intertidal organisms. El Nino is most strong in Peru, where it usually occurs in the period January to March. The northerly winds bring rain to the normally dry coast, e.g., in 1925 the amount of rain that fell was ten times the total that fell over the preceding 10 years (Murphy, 1936). It is interesting to note that this total would only be 70 mm. The Nino traditionally occurs strongly every seven years and even more strongly on a thirty-four year cycle (Murphy, loc. cit.), though Sverdrup, Johnson and Fleming (1942) do not find any periodicity. The Nino, when it does occur, is a narrow current only two or three miles in width. It is usually recognised that the Nino effect reaches as far as Arica (18° 20′ S.) in northern Chile, though I have been told by Chileans that the Nino may extend as far south as Talcahuano. Insufficient sea temperature records are available as yet to check this view but there may be some confusion between the Nino effects and certain large scale natural mortalities, such as have occurred amongst the squids in southern Chile. However, Murphy (1926) records an abnormal temperature of 17.7° C. in Lat. 34° 42′ S. in March, 1925, which is ascribed to an abnormally strong Nino. The description of the effects of a Nino given by Murphy in this paper is very full and gives an excellent picture of the catastrophic conditions which prevail during Nino years. Mears (1954) suggests that catastrophes occur due to local warming in the absence of upwellings.

There is another hot current which runs off the Peruvian coast from April to July and it is usually accompanied by a change in colour of the surface water. This effect, known as aguaje, apparently is confined to Peru and has no effect on Chilean intertidal life.

(*b*) *Winds.*

The winds immediately offshore on the Chilean coast fall into two major regions. There is a southern region, south of 38° S., which is characterised by westerly winds of the "Roaring Forties". This region shifts north and south during the period of Austral winter and summer respectively. To the north of this there is the major part of the Chilean coast as far north as 18° S. on the Peruvian frontier, which is dominated by the southerly winds. These are sea surface winds and usually do not extend above 5,000 or 6,000 feet and so are dominated by the Andean Cordillera. This influence extends almost to the Peruvian coast where the winds become the South-East Trades and blow away from the coast (see Mossman, 1909; and Gunther, 1936).

Gunther (loc. cit.) notes that the winds actually blowing on the Chilean and Peruvian coasts and the land immediately behind the coast are very weak and consequently least certain in direction while the strength of the winds increases with the distance offshore.

The south-westerly sea breeze plays a very considerable part in the influence of wave action on the Chilean coast. It has been noted at Montemar that a sea breeze usually appears in summer at some time in the late morning or early afternoon and blows, at times appreciably severe, for most of the afternoon. The sea is whipped up into short sharp waves which are superimposed upon the normal south-westerly oceanic swell prevalent on the coast, and render collecting virtually impossible during most of the day. On one occasion at Montemar I estimated that a sea breeze reached a Beaufort Scale velocity of Force 5. Bowman (1916) describes the sea breeze as entering deeply into human affairs since it can inhibit or even stop loading of ships at the open roadstead ports of northern Chile and Peru, e.g., Arica, Callao, &c. The breeze loses strength during the afternoon and usually has died out by 1700 hours. The sea breeze is purely a coastal phenomenon and does not extend far out to sea.

Winter gales from the N.W. are often very severe and could have a very appreciable local affect on the intertidal flora and fauna. These gales caused havoc in the fleets of sailing ships on the coast during the boom years of the nitrate trade.

(c) *Upwellings.*

Upwellings of cold phosphate-rich water take place at various places on the Chilean coast, largely as a result of the wind diverging from the shore. It is usual to use the normal surface temperature of the latitude compared to the observed temperature of the sea as the indicator of upwelling and its amount. Gunther compares the inshore surface temperatures with the temperature at 150 metres and also with the mean surface temperatures at the 100° W. meridian. He found evidence of upwelling at Cape Carranza (Lat. 35° 40′ S.), Pichidangui (Lat. 32° 12′ S.), Caldera (Lat. 27° 10′ S.), Antofagasta (Lat. 23° 29′ S.), Arica (Lat. 18° 28′ S.), and the Peruvian ports of San Juan (Lat 15° 25′ S.), Callao (Lat. 12° 15′ S.), and Guanape Is., Lobos Is., Punta Agujo, Cabo Blanco and Santa Elena, all on the Peruvian coast.

The actual location of the upwelling is variable according to the wind strength and distant winds apparently are as important as local breezes (Gunther, 1936). The upwelling is a shallow phenomenon, the water coming from a depth less than 380 metres.

The upwelling, combined with the current system, has, as we shall see later, a profound effect on the intertidal life of Chile and Peru. The water off these coasts is cold, phosphate-rich and reasonably uniform. Murphy (1936) notes that plankton samples taken along two-thirds of the Peruvian coast are identical in their species composition.

(d) *Salinity.*

The North Chilean coast is characterised by no large rivers which would have any effect upon the salinity of the sea over any appreciable distance from the mouth of the river. The greatest changes in salinity occur in the north of the coast when the Nino is flowing and at places where upwellings sporadically take place. Gunther (loc. cit.) shows the salinity in the coast as in Fig. 1.

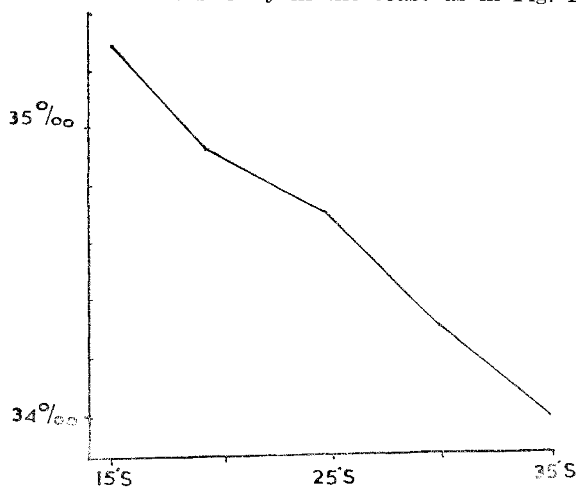

FIG. 1. Salinity gradient off the Chilean Coast (based on Gunther, 1936).

(e) *Sea Temperatures* (TABLE 1)

The Mean Monthly Sea Temperatures (in °C.) recorded at Antofagasta and Arica.
(From U.S. Coast and Geodetic Survey (1952).

Period	Jan.	Feb.	Mar.	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
						Antofagasta.							
1946-51	20.7	20.1	18.8	17.3	16.2	15.5	14.9	15.0	15.7	16.5	17.9	19.3	17.3
Maximum	25.0	22.8	21.2	19.4	17.8	17.8	17.2	17.8	17.8	18.9	20.0	27.2	
Minimum	17.8	17.8	16.7	15.6	15.0	13.9	13.3	13.3	13.9	15.0	16.1	17.2	
						Arica.							
1951	19.2	18.7	18.2	17.6	18.0	17.8	17.8	17.6	17.2	18.0	18.1	18.05	

TABLE 1A

Mean Monthly Sea Temperatures in Degrees Centigrade at Five Chilean Ports (from U.S. Coast and Geodetic Survey, 1952).

Port	Latitude	January	February	March	April	May	June	July	August	September	October	November	December	Years of Records	Temp. Range
Arica	18° 20′	19.2	18.7	18.2	17.6	18.0	17.8	17.8	17.6	17,2	18.0	18.1	18.05	1	2.0
Antofagasta	23° 40′	20.7	20.1	18.8	17.3	16.2	15.5	14.9	15.0	15.7	16.5	17.9	19.3	6	5.8
Caldera	27° 10′	18.2	17.3	17.0	16.2	15.9	14.5	14.9	14.5	15.0	15.6	16.5	16.2	1	3.7
Valparaiso	33° 15′	15.8	15.5	14.7	14.1	13.3	12.6	12.6	12.4	12.7	13.1	13.6	15.0	8	3.4
Talcahuano	36° 40′	12.8	12.9	12.6	12.0	12.3	11.8	11.0	10.9	11.5	12.1	12.6	13.1	8	2.2

Figure 2 shows the isotherms for the Chilean and southern Peruvian coasts following Gunther (1936).

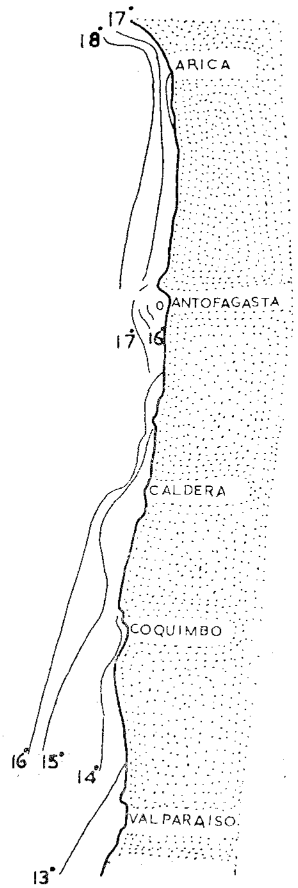

FIG. 2. Isotherms for the Chilean coast for May-June, 1931 (after Gunther, 1936).

Table 1 shows the mean monthly surface temperatures at some Chilean ports as measured by the U.S. Coast and Geodetic Survey. Some discussion of this table is desirable since there are some deviations in temperature conditions to be observed. Firstly, it is to be noted that September is the month of coldest water at Arica. Admittedly, this is based solely on one year's records but this is at least some information. The warmest sea temperature for the year throughout the coast is January, except at Talcahuano where, surprisingly, December is the month of highest sea temperatures. This feature may be variable from year to year since the breakdown of the averages for Montemar (see Guiler, 1959) shows a maximum in either February or January of subsequent years.

The most interesting information to come from these figures is the very large annual range of sea temperature at Antofagasta (5.8° C.). The sea at Antofagasta is warmer in the summer than at Arica, over five degrees of latitude nearer the Equator, and the winter minimum monthly mean temperature is only slightly above that of Caldera, four degrees further to the south. It is unfortunate that there are no temperature records made at ports nearer to Antofagasta than Arica or Caldera since much light would be thrown on the distribution of the isotherms in relation to seasonal changes.

The figures for Antofagasta as given in Table 1, particularly those relating to summer conditions, do not correspond with the isotherms as given by either Gunther or Sverdrup, Johnson and Fleming (1942). The correspondence between the winter isotherms of Gunther and the figures in Table 1 is fairly close at the ports of Talcahuano, Valparaiso, Caldera and Arica, and even at Antofagasta there is a fair degree of correspondence. Antofagasta is one of the ports off which there is a major site of upwelling (see above) which explains the low winter temperatures.

Gunther notes (p. 191) that a southerly current runs close to the coast, seldom more than two or three miles in width, especially in places where water movement, especially upwelling, is conspicuous. He goes on to postulate two wedges of warm, highly saline water lying off central and southern Peru respectively. It is not possible that this wedge of warm water, moving south with the trade wind system in summer, reaches as far as Antofagasta. Dr. H. N. Carruthers suggested (personal communication) that the warm waters at Antofagasta are due to local meteorological effects, probably brought about by an offshore wind causing an upwelling inshore of warmer water.

Leipper (1955) showed that the fluctuation in coastal temperatures in shallow water are caused not only by internal waves but also by the periodic migration of patches of cold water over an irregular bottom due to variations in the velocity of the tidal current. These conclusions, based upon observations made at La Jolla, California, would be particularly applicable to the Chilean coast, where meteorological effects are known to have a profound effect upon the behaviour of the Peru Coastal Current. The variations caused by these factors would be strengthened by the cold upwellings giving rise to sources of cold water at varying distances off shore.

It was noted earlier (Guiler, 1959) that the mean monthly sea temperatures at Antofagasta are closer to the absolute minimum temperatures than to the absolute maximum temperatures. This shows the steady cool influence of the Peru Coastal Current. The greatest temperature observed at Antofagasta was 27.2° C. in December, which is 7.9° C. above the monthly maximum temperature.

It is clear that the temperatures in the sea off the Chilean coast require much greater continuous study than has been carried out in the past and the isotherms as shown at present may only represent a temporary stage in an alternating pattern. Figure 3 shows summer coastal isotherms as calculated from the U.S. Coast and Geodetic Survey results and this picture differs very sharply from those of Gunther showing Antofagasta to have warmer water than the surrounding areas.

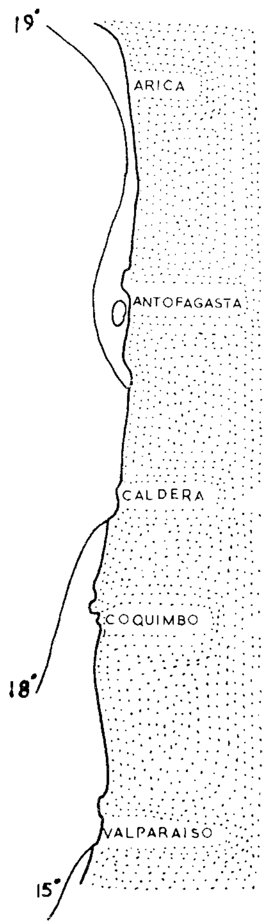

FIG. 3. Suggested summer isotherms for the Chilean Coast.

The sea temperature gradient for the Chilean coast is shown on Figure 4. In this figure, which is based on the January and August mean temperatures, the higher summer temperature at Antofagasta is especially to be noted. The figure emphasises slightly that Antofagasta has apparently a slightly lower winter temperature than might be expected. The sea temperature at Arica is 0.1° C. lower in September and the Talcahuano summer temperature is 0.1° C. higher in February than those shown on the figure.

Gunther notes that the wind causes appreciable changes in the surface temperatures, his Table III shows the distance the isotherms are encountered offshore under differing wind conditions. The least wind force gives the greatest rise in sea temperature and easterly winds give a cooling tendency in the sea, since this causes increased upwelling.

Gunther found that the sea temperature changes seasonally at a rate of .23° C. per week. At Antofagasta, using the figures in Table 1, the rate of temperature change from January to July is .24° C. per week, which corresponds closely with the figure derived by Gunther, while for the 12 months the rate of change is .21° C. per week. The most rapid change takes place during March, April, November and December, when the change is 0.35° C. per week. During July and August the rate of change is only 0.01° C. per week.

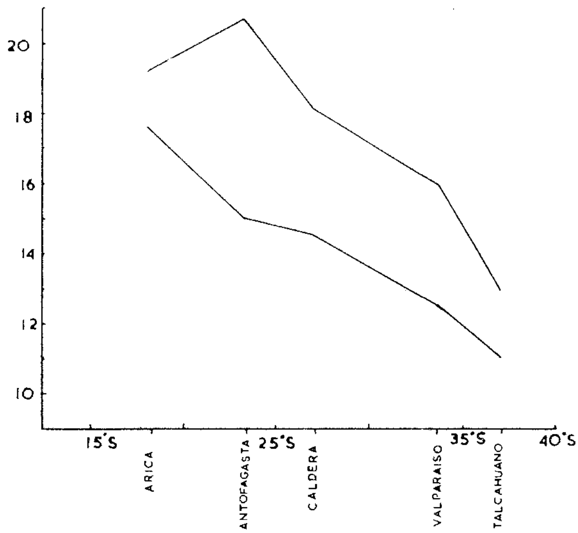

FIG. 4. Summer and winter sea temperature gradients for the Chilean Coast.

(*f*) *Air Temperatures* (Table 2)

The summer (January) and winter (July) temperature gradients on the Chilean coast are shown in Figure 5, which was constructed from the data supplied by the Oficina Meteorologica de Chile. Neither of the gradients are smooth, both showing irregularity in the curve at Antofagasta, Coquimbo, Valparaiso and Concepcion.

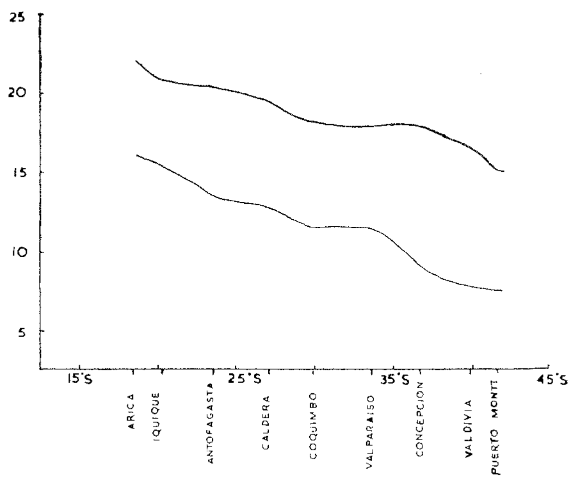

FIG. 5. Summer and winter air temperature gradients for the Chilean Coast.

The summer temperature at Concepcion is warmer than on adjoining parts of the coast, while the winter temperatures are cooler, but at Valparaiso both the summer and winter temperatures are higher than might be expected, being similar in many respects to those prevailing at Coquimbo, four degrees to the north.

The irregularity at Antofagasta is due to a lowering of the winter temperature to a figure somewhat below expectation.

The most important factor which emerges from figure 5 is the small difference in the temperatures at Arica and Valparaiso. In the summer this difference is only 4° C. and in the winter 5° C., this occurring in a distance of 15° of latitude.

Schott (1935) calculated the difference between the temperature of the air and that of the sea, subtracting the air temperature from that of the sea. The resultant figures, the "negative Anomalie" or "positive Anomalie" can be graphed using "Isanomalen" or lines of equal departure.

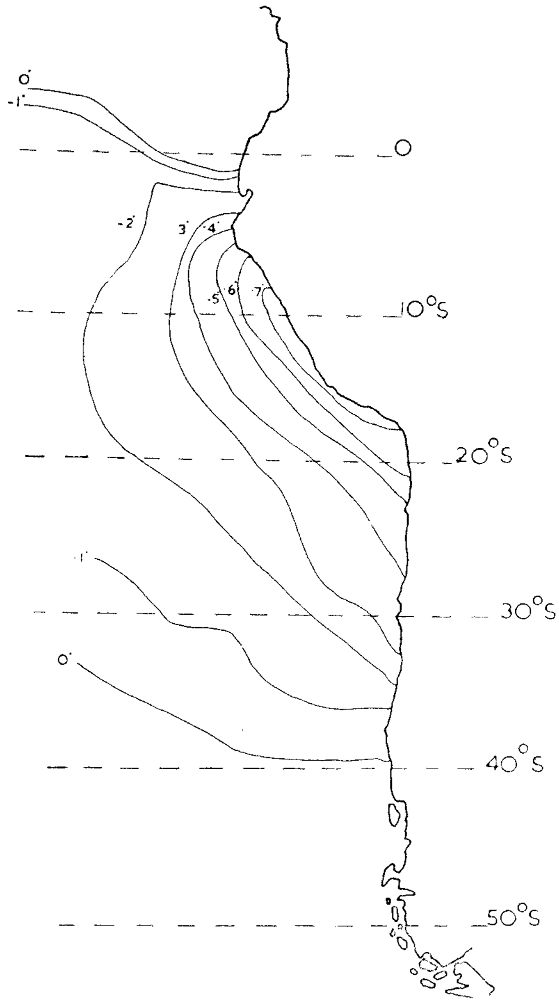

Fig. 6. Summer isanomalous lines for the Chilean Coast.

The isanomalous lines for the Chilean coast are shown in Figures 6 and 7. The line of zero departure, i.e., where the air and sea temperatures are the same, starts on the Chilean coast about Lat. 39° S., near Tolten, and runs more or less due west out to sea. To the south of Tolten there is a positive "Anomalie" of 1° C. as far as the Taitao Peninsula (46° S.) followed by a region extending to Cape Horn (54° S.) where the sea is 2° C. warmer than the air.

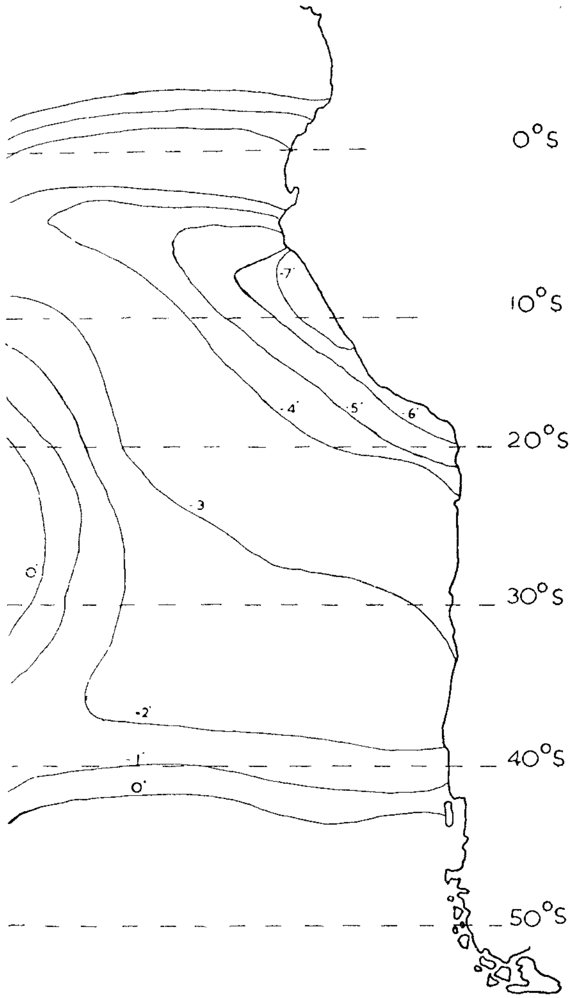

Fig. 7. Winter isanomalous lines for the Chilean Coast.

All of the rest of the Chilean coast to the north of Tolten, that is the part with which this survey is concerned, lies in a region of negative departure, the sea being cooler than the air. The maximum departure is reached in Southern Peru and Arica where it reaches 7° C. off Callao in Peru. The departure reaches 8° C. in August, which is by far the largest departure in the oceans of the Southern Hemisphere. On the eastern coast of South America at the same latitude as Arica there is a positive departure of 1° C. (Schott, 1926).

(*g*) *Rainfall* (Table 2)

The Mean Monthly Rainfall (in mm) at four Northern Chilean ports from data supplied by The Oficina Meteorologica de Chile.

Station	Period of Records	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Coquimbo	1911-49	0.1	1.6	0.2	2.2	20.4	36.1	22.8	16.9	4.6	3.2	0.9	0.8	109.6
Antofagasta	1911-49	....	....	....	0.3	0.1	0.7	2.4	1.2	1.0	0.8	0.2	....	7.7
Iquique	1911-49	0.1	....	....	....	....	0.2	0.7	0.7	0.3	0.1	....	....	2.1
Arica	1911-49	0.3	....	....	....	....	0.1	0.1	0.1	....	....	....	0.1	0.7

Murphy (1936) notes that there is a great, often startling biotic change associated with a negative departure and he cites the Galapagos Islands as an example of this. Chiloë Island, a region regarded as being the boundary between the cold temperate and warm temperate faunas of western South America, lies close to the line of zero departure.

It can be deduced from the above that the intertidal region is kept cool by the effects of a cool breeze blowing off a sea which is considerably colder than the air temperature.

It should be noted that monthly sea and air temperature charts are given by the Air Ministry (1950). These charts have been consulted in this section of the present paper but have not been reproduced since the scale on which the maps are drawn is too small to show the isotherms in sufficient detail for my purposes.

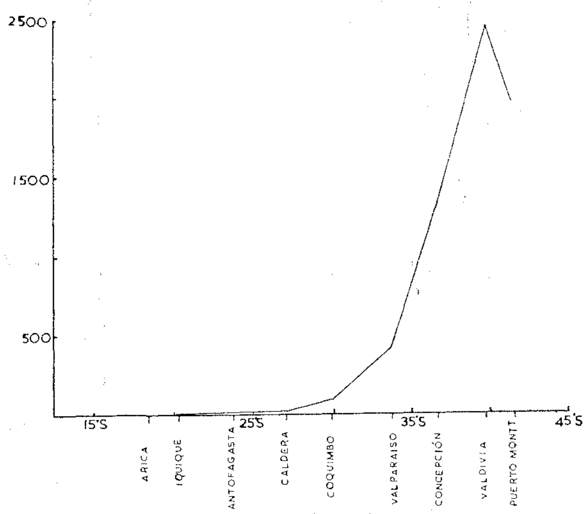

FIG. 8. Rainfall gradient on the Chilean Coast.

The rainfall on the Chilean coast is seasonal, most of the annual precipitation taking place during the months of May-August. However, in the parts of Chile lying to the north of Coquimbo the rainfall is extremely sporadic and, although there is a mean monthly rainfall quoted in weather reports, this figure is of little significance since rain may not fall for fifteen years or more and then a relative deluge may occur. Coquimbo is sufficiently far south to show evidence of the Mediterranean type of climate which is experienced by much of the central coastline of Chile, 90% of the precipitation taking place between May and August inclusive. Antofagasta, Iquique and Arica are very much desert ports as regards the amount of rain which they experience.

However, the rainfall figures shown in Table 2, while giving an impression of the rain encountered, do not give a true picture of the monthly rainfall at Antofagasta, Iquique and Arica since there may be no rain at these ports for many years until a sudden deluge occurs. Murphy (1926) gives a vivid description of the catastrophic effect of such a deluge upon parts of the Peruvian coast where similar conditions prevail. Rainfall over the northern Chilean and southern Peruvian coasts is therefore practically unknown and its absence can be important to intertidal organisms.

Under conditions of heavy wave exposure such as exist along the west coast of South America there is always some spray being blown inland. This spray falls on and above the intertidal region where it leaves a salty residue. Thus, hypersalinity is a feature of the Supralittoral to Midlittoral zones of this coast. Relief from this condition is obtained at high tides or during storms. A toleration of high salinities and a resistance to dessication are the prime requisites of life for intertidal organisms living at high tidal levels on a coast experiencing extremely low rainfall. To this may be added a resistance to the products of decay since there may occur little washing away of dead organisms.

The presence of spray in itself will act as a factor modifying the effect of dessication and it has been shown that mists and fogs help intertidal organisms to exist at levels above the height at which they are usually found (Burrows *et al*, 1954). Fogs and mists are frequent on the Chilean desert coast and must be considered as important elements in reducing the dessication factor.

The rainfall gradient on the Chilean coast is shown on Figure 8, which was constructed from the data given by the Oficina Meteorologica de Chile. The rainfall increases very sharply from Coquimbo (Lat 30° S.), reaching a maximum at Valdivia (39° 50′ S.).

The relative humidity curve for the Chilean coast is shown in Figure 9, based upon data supplied by the Oficina Meteorologica de Chile.

(*h*) *Relative Humidity* (Table 3)

The Mean Monthly Relative Humidity at four Chilean ports from data supplied by the Oficina Meteor ologica de Chile.

Station	Period of Records	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
		%	%	%	%	%	%	%	%	%	%	%	%	%
Coquimbo	1911-46	77	78	80	81	82	80	81	80	80	79	77	77	80
Antofagasta	1919-40	73	74	75	75	75	74	76	76	75	74	71	72	74
Iquique	1911-45	79	79	83	80	81	80	79	79	79	79	78	78	80
Arica	1911-46	72	71	73	75	76	76	78	78	78	76	74	72	75

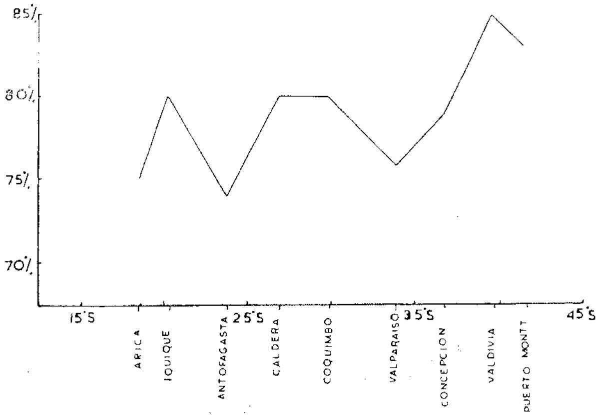

FIG. 9. Relative humidity on the Chilean Coast.

It is most noticeable that the southern areas of Valdivia and Puerto Montt, where the temperature is lowest, have the highest relative humidity. However, the converse does not hold true though Arica and Antofagasta do have low relative humidities whereas Iquique has a much higher figure.
Comparison of Figures 4, 5, 8, and 9 shows that, in general the climate, going from south to north becomes progressively warmer, very much drier, with slightly warmer seas and slightly less relative humidity. However, Antofagasta forms an important exception to the general rule in that Gunther found the sea colder in winter than might be expected. The temperatures taken by the U.S. Coast and Geodetic Survey do not fully reflect this feature but do show that the summer temperatures are greater than might be expected. The records at Antofagasta have been taken for six years while those at Caldera and Arica, to the south and north respectively, have only been taken for one year.

It should be noted that when considered in relation to the latitude, the seas are colder than in any other part of the ocean masses.

(*i*) *Fogs and Mists*

Mention has been made earlier of the mists and fogs which are persistently found on this coast. These mists, reaching fog dimensions at times, arise adiabatically out at sea in the area of the Peru Current and are blown inland by the wind. Bowman (1916) wrote that the mist or clouds hung at between 2,000 and 4,000 feet on the coast, rising during the day and settling almost to sea level at night. These mists are not always present on the coast, though reference to the Air Ministry charts (1950) shows that mists are very persistent, except during the months of January and June. Their effect on the shore is to cut down insolation and, combined with the on-shore breeze blowing off seas up to 7° C. cooler than the air temperature, make the temperature lower than otherwise might occur.

During the afternoon the coastal belt is cooled down by a sea breeze which may reach Force 5 or more at times. The sea breeze causes short, sharp seas and is of considerable importance in wetting the intertidal region. It is not possible to determine in any satisfactory fashion the actual wetting power of the waves but at times on the exposed places the spray reaches the highest point of animal or plant colonisation. This is an important factor since the wetting may occur at the period of low water and maximum insolation.

(*j*) *Tides*

The amplitude of the tides plays an important role in controlling the distribution of the belt forming organisms. Brattstrom and Dahl (1951) give details of the amplitude of the tides at various ports on the Chilean coast.

The average amplitude was calculated for those ports for which annual tide tables are prepared annually by the Chilean Navy (1954) and is the average of all the tides during the year, but tide tables are not prepared by the Navy for all Chilean ports. The amplitude of the tides decreases towards the north of Chile, with a probable narrowing of the vertical width of the intertidal zones, which would result in a relative increase in the importance of the spray factor.

TABLE 4

Tidal Amplitudes at various Chilean ports, partly after Brattström and Dahl (1951).

	Lat. °S.	Spring Tidal Amplitude in metres.	Average Amplitude in metres.
Arica	18° 20′	1.40	....
Iquique	20° 15′	1.50	....
Tocopilla	22° 06′	1.20	....
Antofagasta	23° 40′	1.60	0.78
Coquimbo	29° 55′	1.50	....
Valparaiso	33° 15′	1.82	0.92
San Antonio	33° 35′	1.25	....
Talcahuano	36° 40′	1.80	....
Lota	73°	1.90	....

It has been shown that the highest tides in the summer occur during the midday-midnight period (Guiler, 1959) and this, combined with the cool air from the sea and mists, together with a not inconsiderable spray, must cause a considerable reduction in the effect of insolation on intertidal forms. Similarly, it was found that the tidal behaviour in the winter tended to protect intertidal organisms from the full effect of cold nights, since the " higher high " tides occur during the midnight-midday period.

Figures 10 to 21 show monthly exposure curves at Antofagasta.

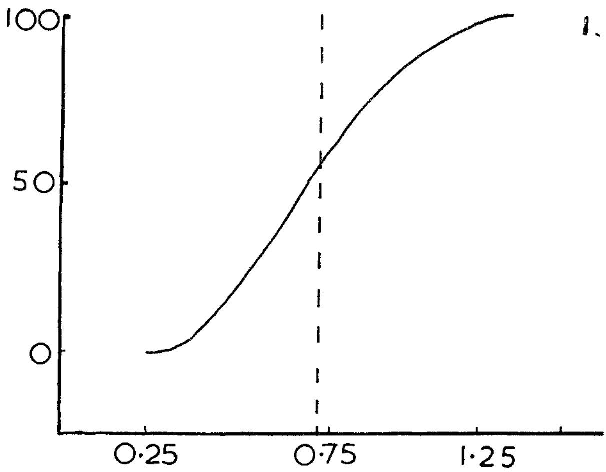

Fig. 10.

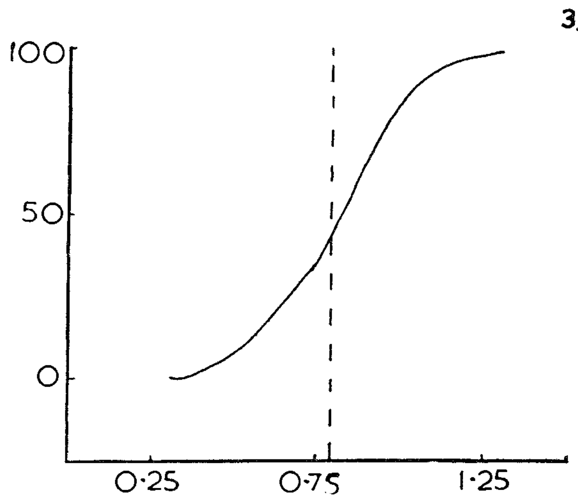

Fig. 12.

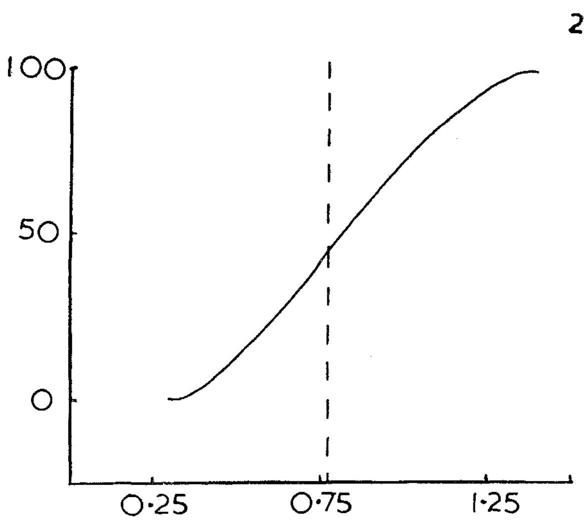

Fig. 11.

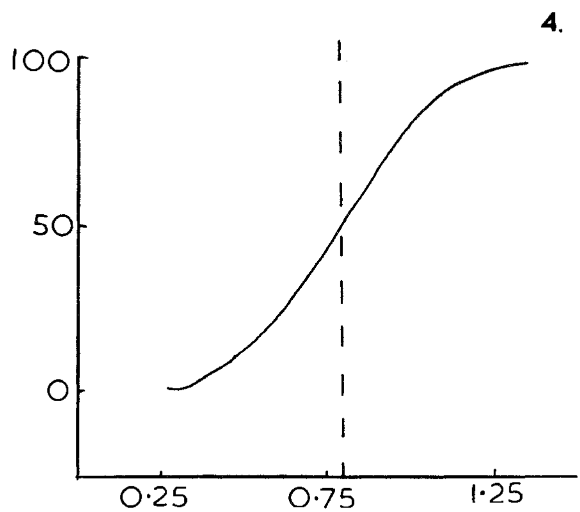

Fig. 13.

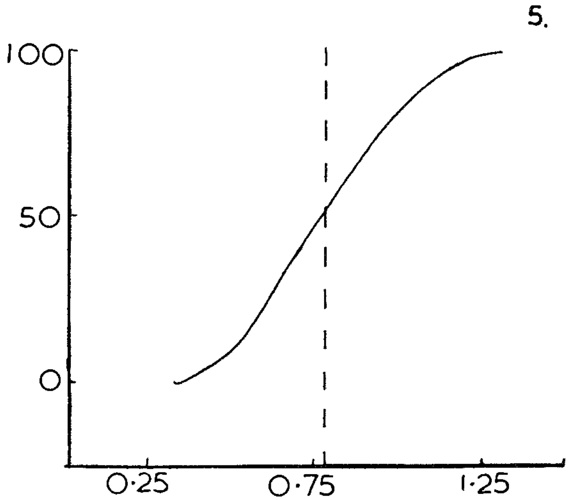

FIG. 14.

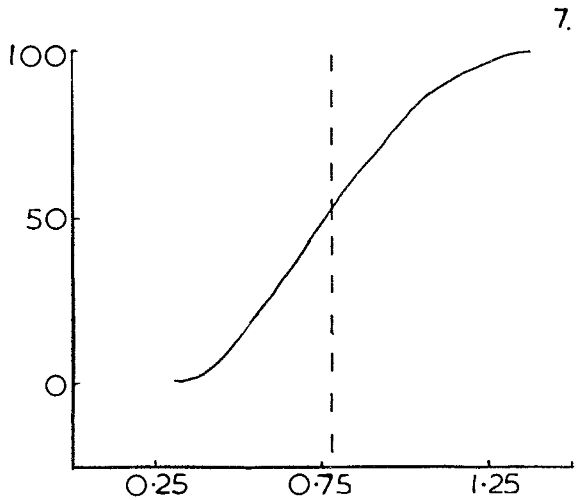

FIG. 16.

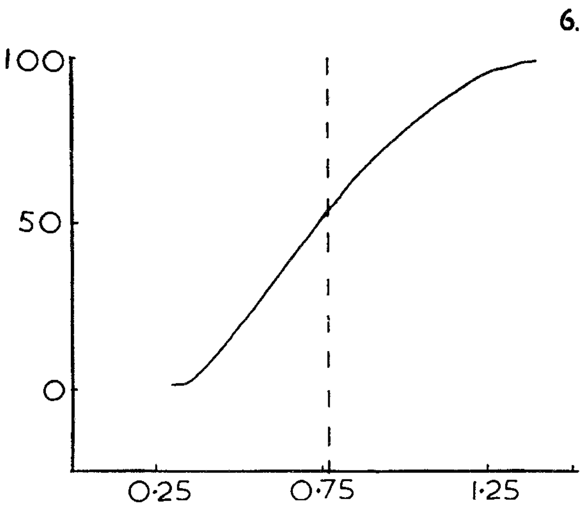

FIG. 15.

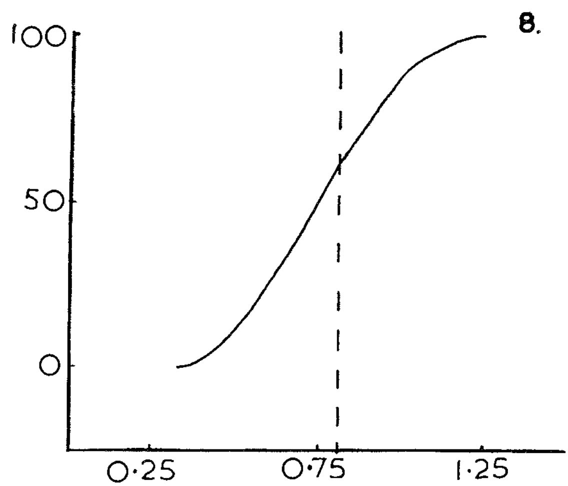

FIG. 17.

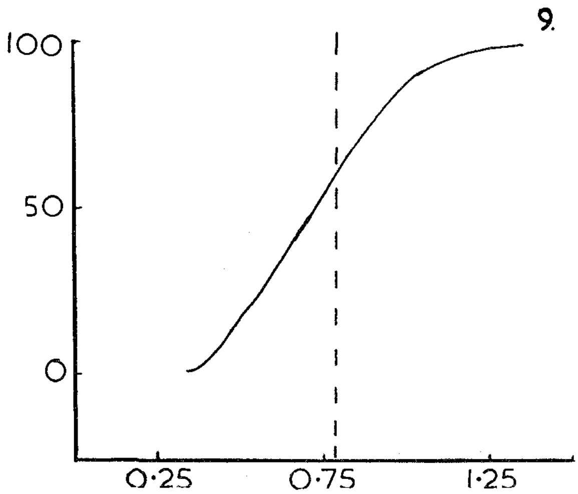

FIG. 18.

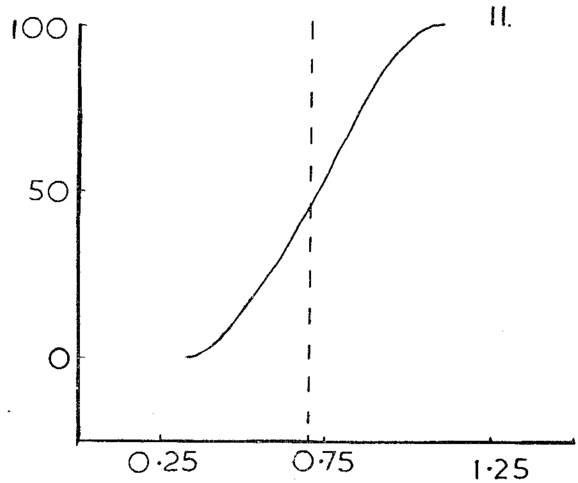

FIG. 20.

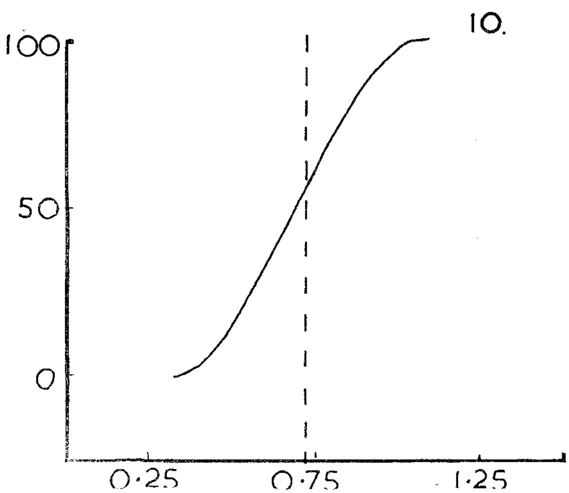

FIG. 19.

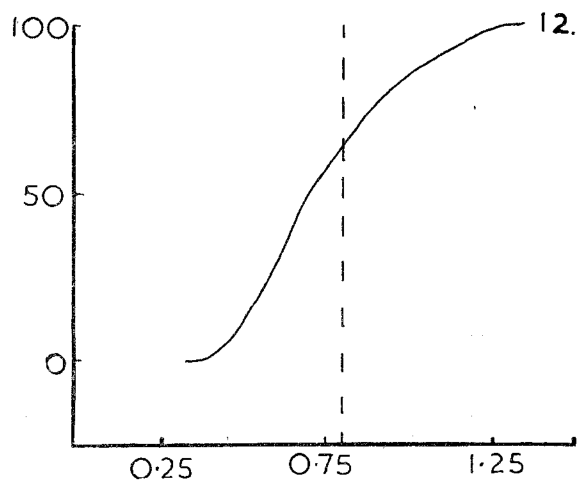

FIG. 21.

Monthly tidal exposure curves for Antofagasta were calculated using the same methods as those described for Montemar (Figs. 10-21). Examination of these figures shows that the exposure at any one level on the shore increases gradually from January to August when it decreases again. This means that intertidal organisms are exposed for longer periods of the day to the extremes of summer heat and winter cold.

(*k*) *Wave Action*

The prevailing wind on the central and northern coasts is the trade, here southerly, with strong sea breezes in the afternoon in the summer. The prevailing swell is S.-S.W. in direction. Most of the coastline with which this paper is concerned is exposed to the full effect of the wind and swell with the result that the wave action is among the most continuous in the world. I discussed the effect of the waves in the first paper of this series and it is not necessary to repeat those earlier remarks. It is necessary to re-emphasise that wave action and associated spray are the dominant factors controlling the width of the intertidal bands on exposed coasts such as this.

There are no bays to the north of Chiloë Island which can be described as sheltered. On the central and northern parts of the Chilean coast sheltered conditions can be said to be non-existent. There are a few semi-sheltered positions, e.g., in the Talcahuano, Concepcion and Tocopilla areas but these are comparatively exposed when compared to other sheltered localities in the world.

The wave action is very much more powerful and persistent than encountered on British coasts, though some of the very exposed parts of the west of Ireland and the Western Isles of Scotland may measure up to Chilean standards of intensity. The severity of the wave action on the east coast of Australia. especially in New South Wales and on the west coast of Tasmania, would be similar in strength to that encountered in Chile. I have no experience of New Zealand wave action nor of South African.

To sum up the physical features of the Chilean coast we find that the coast is bathed by cold to cool waters, refreshed by cold upwellings caused by the cool trade winds blowing along the line of the coast. The air temperatures are cool, especially in the north, due to the winds being cooled over the sea; mists are prevalent, again especially in the north and the general climatic factors and tidal behaviour combine in such a fashion as to protect the intertidal organisms from the full effect of the sun. The rainfall is seasonal over most of the coast but on the desert coast it is sufficiently infrequent in occurrence for its absence to be a major ecological factor to intertidal organisms. The wave action is intense and is considered to be the major factor, over-ruling the tides, in determining the width of the intertidal zones.

Although there is little range in the climatic factors and the sea temperatures are fairly steady throughout the year, the coastal forms certainly as far South as Arica, if not much further, are liable to suffer virtual extinction from the hot Nino current and heavy rains which occur periodically.

(4) THE ZONAL PATTERN

The zonation was examined at each place visited and will be described below separately for each port.

(*a*) *Coquimbo*

Coquimbo was visited on 20th February, 1955.

The area on which the zonation was examined is Punto Tortuga, to the north of the harbour area of Coquimbo. The particular area examined lies on the north-east side of the port and is not exposed to the full effects of the south-westerly swell. The substratum is a coarse sandstone.

The zonation is—

Bare rock.
Chthamalus cirratus Darwin.
Chthamalus cirratus + *Littorina peruviana* D'Orb.
Chthamalus cirratus + *Endarachne binghamiae* J. Ag.
Chthamalus cirratus + *Balanus flosculus* Darwin.
Balanus psittacus Darwin + *Corallina chilensis* Decaisne
Lessonia nigrescens Bory + *Lithothamnia* + *Acanthopleura echinata* (Barnes).

As at Montemar, the most notable feature of the shore is the absence of any belt above that dominated by barnacles. The *Littorina* belt, so usual in many parts of the world above the barnacles, forms a discontinuous sub-belt within the upper part of the barnacle belt.

The barnacle belt is very well developed, both as regards the vertical height of the band and numbers of individuals inhabiting it. It is noteworthy that cirripedes form the principal zone-forming group on the shore at this place.

Chthamalus cirratus is dominant over most of the shore but in the lower part of the barnacle belt it is joined by *Balanus flosculus* and these two species together form a very dense covering to the rocks.

Chthamalus cirratus favours places where there is wave action with some spray. This species is not found in large numbers in places where it is exposed to strong sunlight. *Balanus flosculus* prefers similar situations but, being found at a lower tide level, its distribution is less influenced by the direction of the sunlight.

In the lower part of the *Chthamalus* belt there is a strip formed by the alga *Endarachne binghamiae* J. Ag. The weed forms a sub-belt just below the middle of the *Chthamalus* belt, but this strip is very thin, rarely being more than 5 cm. in vertical height. The weed favours places where there is some wave action and spray.

The large and prominent *Balanus psittacus* is very obvious at the top of the Infralittoral fringe. It occurs only in places where there is wave action. *Balanus psittacus* particularly favours the edges of rocks which are beside deep water and which always have waves breaking on them. In this type of situation *Balanus psittacus* extends down the seaward face of the rock into the Infralittoral. Also found in the Infralittoral fringe with these barnacles are *Balanus laevis laevis* and *Balanus flosculus*, though these species do not necessarily live in places with continuous broken water.

The nereid worm *Pseudonereis gallapagensis* Kinberg is common on the shore living amongst scattered clusters of the mussel *Brachidontes purpuratus* Lam. and also in dead shells of *Chthamalus*. The edible mussel *Mytilus chorus* Molina is common, forming clusters in slightly sheltered positions, e.g., just inside the entrances to gulleys. Another species of mussel, *Brachidontes granulatus* Hanley, is not nearly as common but it is found in similar situations. In some restricted areas, where the wave exposure factor is suitable, both or either of these species may form sheets over gently-sloping surfaces.

Limpets and siphonarians are common in the *Chthamalus* belt. *Siphonaria (Pachysiphonaria) laeviuscula* Sowerby and *S. (Pachysiphonaria) lessoni* (Blainville) are both common as are the limpets *Acmaea viridula* (Lam.) and *A. araucana* D'Orbigny. Of these species *S. lessoni* is the most common. The mussels *Brachidontes purpuratus* and *Mytilus chorus* are both found in ponds on the shore, but in the case of *M. chorus*, the individuals so found are small in size. The prawn *Rhynchocinetes typus* H.M.Edw., is frequently found in these ponds as are *Siphonaria lessoni* and the chitons, *Chiton cumingsi* Frembly and *C. latus* Sav. *Siphonaria lessoni* is usually found living on rocks but is frequently found on the bottom of ponds. Below the stones found in either ponds or lying loose on the floors of gulleys and clefts are the Porcellanid crabs *Petrolisthes tuberculatus* (Guerin) and *Petrolisthes angulosus* (Guerin). Of these two species *Petrolisthes tuberculatus* is the less common. *Paraxanthus barbiger* (Poepping) and *Pilumnoides perlatus* (Poepping) are both found in the same semicryptic habitat but *Pilumnoides perlatus* is also found among the "roots" of the holdfast of *Lessonia nigrescens* Bory. *Tegula atra* (Lesson) and *Turbo niger* (Wood) were found at the upper limit of the Infralittoral fringe in regions of submaximal exposure.

The Infralittoral fringe, in which it was impossibel to collect satisfactorily due to the high tide at the time of my stay in Coquimbo, is characterised by *Lithothamnia* and two other species, depending on the amount of wave exposure experienced. Near the port of Coquimbo, where the wave action is reduced, *Lessonia* becomes rarer and ultimately absent. It is not replaced by any other species but the belt is thus left dominated by the *Lithothamnia* and *Acanthopleura echinata*. It must not be assumed that the lessening of wave action has suited the growth of *Lithothamnia*. It is more true to say that the reduction of the wave action has eliminated *Lessonia* leaving the other species.

There is no similar reduction in the number of *Acanthopleura echinata*, this species being found sparsely distributed throughout the whole area. Although sparsely distributed this chiton is very conspicuous by its size.

Other species found in the Lessonia belt are the urchin *Tetrapygus niger* (Molina) and the thaid *Thais chocolata* (Duclos) which are very common in clefts and deep ponds. The latter species is not as common as at Montemar nor is it as large. Another species which is smaller than the Montemar specimens is the "loco" *Concholepas concholepas* (Bruguiere). The large *Balanus psitticus* is also found in the *Lessonia* belt.

(*b*) *Antofagasta*

Antofagasta wis visited on 22nd February and 2nd March, 1955.

The zonation was examined at Playa Blanca opposite the Artillery Barracks beyond the southern end of the town on the road to the Automobile Club.

The zonation:—

Bare rock.
Chthamalus cirratus.
Chthamalus cirratus + *Littorina peruviana.*
Chthamalus cirratus + *Enteromorpha* sp.
Chthamalus cirratus + *Colpomenia sinuosa* (Roth) Derby & Sol.
Pyura chilensis Molina + *Corallina chilensis* Decaisne.
Pyura chilensis.
Lithothamnion sp.

The shore topography in this area has considerable bearing on the type of zonation. The rocks are all of a shale which gently dips away from the sea forming a wide erosion platform which is swept by the usually heavy surf. During the period of both visits to Antofagasta the shore was covered with white foam which acts as a very efficient protection from the sun. The foam filled the clefts and gulleys in the rocks and covered all the shore from the top of the barnacle belt down, except in places where the waves were actually breaking across the rock.

It has been noted above that the less rainfall means that a high toleration of the products of animal and plant decay must be possessed by organisms living at high levels on the shore. During both visits to Antofagasta the dominant feature of the shore was the excessively strong smell of decay. When I first encountered the smell I assumed that is was sewage but it later became apparent that the stench arose from thousands of decaying ascidians which were lying at or above high-water mark.

The ascidians covered several miles of beach (Plate 1) and their stench carried up to a quarter of a mile inland. Undoubtedly the cause of death of the ascidians was the strong summer sun. All the ponds had one or more decaying ascidians in them and a scum, as well as the foam mentioned earlier, covered these ponds which the wave action did not disturb.

The barnacle belt which is formed by *Chthamalus cirratus* has a considerable vertical range. On the upper part of the shore the barnacle belt is characterised by a strip of the littorine, *L. peruviana*. The lower part of this belt has a number of siphonarians, *S. lessoni*, living in it but nowhere do these gastropods form a belt. The Siphonarians within this belt are often found in sun-sheltered places such as clefts or shaded sides of rocks, though they may also occur frequently in considerable numbers on rocks which, although exposed to the sun, also are wave-washed. The interaction of spray and sun towards gastropods was noted at Montemar (Guiler, 1959) where the distribution of the *Littorinas* was partly controlled by these two factors.

It is interesting on this shore to see that algae play such a large part in the zonation. Immediately below the *Littorina peruviana* belt a species of *Enteromorpha* becomes very common and forms a sub-belt within the barnacle belt. In turn the *Enteromorpha* yields place to *Colpomenia sinuosa* var. *lacunosa* Taylor.

Siphonaria lessoni is common in the barnacle belt together with *Acmaea viridula*. There are no large limpets of the genera *Patella, Cellana* and *Nacella*.

The barnacle belt is replaced by the Pyura-Corallina belt. *Pyura chilensis* forms a dense covering to the rocks (Plate 1) and *Corallina chilensis* Decaisne utilises the ascidian as a sub-stratum. This belt is not very wide and is followed by a belt dominated by *Pyura,* though it usually has *Ulva lactuca* L. living on it. *Ulva* is generally found on the upper surface of the ascidians, i.e., around the oral and atrial siphons. The ascidians are very densely packed together, forming a continuous carpet on the rocks. On the death of an ascidian the test remains intact for some time and decay of the internal organs continues within the test causing a white sticky substance to ooze out of the apertures. This is probably the material from which the foam on the shore is formed.

Some words are necessary about the *Pyura* belt, especially since the presence of such a belt is a feature not experienced in the northern hemisphere. This ascidian possesses a very tough, almost cartilaginous test, the integument of which is strengthened by included sand grains. The individuals are closely united into a coalesced mass which offers a very strong resistance to wave action, and the space between the ascidians and the rock offers a sheltered habitat for more delicate organisms.

The *Pyura* belt, where it is together with *Corallina* and/or *Ulva,* forms a habitat for numerous individuals of smaller species. The porcellanid *Petrolisthes angulosus* (Guerin) is very numerous in clefts between the tests of the ascidians as well as living between their " roots " and the rock. This crab is also very common under stones in gulleys and ponds. The crab, *Acanthocyclus gayii* H.M.Edw. & Lucas, is found in the same type of habitat in the ascidian beds and along with *Petrolisthes angulosus* is also found under small beds of the mussel, *Brachidontes purpuratus*.

The very large barnacle *Balanus psittacus* occurs at the lowest part of the *Pyura* belt, especially in places where the platform ends. These barnacles are not conspicuous since they may be confused with *Pyura*, especially as they are about the same size and both *Balanus psittacus* and *Pyura* are frequently covered with algae. These algae mainly fall into two species, an *Ectocarpus* sp. and *Halopteris hordacia* (Harv.) Sauv.

The " loco " *Concholepas concholepas,* is fairly common in the Infralittoral fringe as are the chitons *Enoplochiton niger* and *Acanthopleura echinata* and the large fissurellid *F. costata* Lesson. *Fissurella limbata* Sowerby is found not only in the Infralittoral fringe but also on the rock under the *Pyura* beds.

The algal flora of gulleys consists of *Halopteris hordacea, Glossophora kunthii* (C. Ag.) J. Ag., *Ulva lactuca, Coralina chilensis, Colpomenia sinuosa Ectocarpus* spp., *Chaetomorpha linum* (Muller) Kutz., and *Padina triastromatica* Ler.

Below stones in the clefts and gulleys there is a numerous fauna, in addition to the crabs mentioned above. *Pseudonereis gallapagensis* Kinberg, *Lumbrinereis tetraura* and *Cirriformia* sp. all live in the shale below the stones. The under surface of the stones are frequently covered by *Spirorbis* sp. and a small, strongly radiate barnacle *Balanus flosculus*.

Examination of shell beds revealed numerous *Balanus laevis laevis* Darwin but no living specimens could be found. The same source provided numerous carapaces of the crab *Cancer polyodon* Poepping but as in the case of *Balanus laevis laevis,* no living individuals could be found.

The lowest belt on the shore which represents the extreme lowest part of the Infralittoral fringe is occupied by *Lithothamnion* spp., and the large chitons *Acanthopleura echinata* and *Enoplochiton niger*.

(c) *Iquique*

Iquique was visited on 25th February, 1955. The examination of the shore was carried out first at Primeros Rocas, about four kilometres south of the town and then at Playa Blanca, several kilometres to the south of the town and then at Playa Blanca, several kilometres further to the south near Punta Gruesa. Playa Blanca is the more important of these two localities.

Zonation at Playa Blanca:—

Littorina peruviana.
Chthamalus cirratus.
Chthamalus cirratus + *Balanus laevis laevis.*
Colpomenia sinuosa + *Brachidontes purpuratus.*
Colpomenia sinuosa + *Mytilus chorus.*
Corallina chilensis Decaisne + *Tegula atra.*
Lithothamnion sp. + *Lessonia nigrescens.*

At Playa Blanca the zonation is difficult to determine because the soft shale beds forming the substratum dip towards the sea leaving a series of shallow gulleys running more or less parallel to the shoreline. The shore reefs are protected from full wave action by reefs just offshore. These gullies are continuously inundated by waves coming up to them, i.e., in a direction at right angles to the general direction of the coast so that the wave exposure pattern is very complex. The zonation can be, and often is, completely altered by the degree of wave exposure to which the coast is subjected and with this complex wave exposure pattern it is difficult to decide on a zonation which is characteristic of normal wave exposure, especially since there are reefs just offshore which cannot be inspected.

The most surprising feature is the formation of a *Littorina* zone which is clearly defined and distinct from the barnacle belt. This condition is widespread at Playa Blanca but at Primeros Rocas the *Littorina* belt is incorporated in the barnacle belt in what is to be considered the normal condition for the Chilean coast.

The barnacle belt is divided into two parts, an upper being composed of *Chthamalus cirratus* and a lower of *Chthamalus cirratus* and *Balanus laevis laevis.* At Primeros Rocas the barnacle belt is wide but the barnacles are not numerous and there are a large number of *Siphonaria lessoni* living in the belt, as well as a considerable quantity of *Ulva lactuca* L. There are two species of Patelloids which are sufficiently numerous to give character to the belt and could almost be described as a *Patelloid* belt. The limpets are *Acmaea viridula, Collisella arausana* (D'Orb.). The whole area of Primeros Rocas is very exposed to heavy wave action and this factor gives a considerable amount of spray which is responsible for the development of Patelloids to almost a belt-forming species. *Chiton cumingsi* and *Chiton latus* are found in clefts in the barnacle belt. The larger clefts in the barnacle belt frequently sheltered individuals of the species *Heliaster helianthus* (Lam.) (Asteroidea).

It is with some hesitation that I have granted *Colpomenia* the status of a belt-forming organism. The alga is very numerous, forming typical bladder-like clusters over a large area of the shore. Much of the substratum utilised by *Colpomenia* is formed by mussel beds and these animals are the most numerous on the shore. It is *Colpomenia* that lends character to the shore and for that reason this species is raised to the status of a belt-forming organism. However, it is more than likely that *Colpomenia* is subject to seasonal variation and at times of the year other than summer the species may be almost absent. At Primeros Rocas there is very little *Colpomenia* present, the dominant organism on that part of the shore being *Mytilus* sp. with *Brachidontes purpuratus* in the upper part of the mussel belt. The mussels have *Balanus flosculus* living on their shells as well as a small *Acmaea* sp.

The *Corallina* belt consists not only of *Corallina* but also of four other species of algae, namely *Halopteris hordacea, plocamium pasificum* Kylin, *GlossopPhora kunthii* and *Rhodymenia* (=Dendrymenia) *corallina* (Berg) Taylor.

The lower part of the shore is dominated by algae, namely the small *Corallina chilensis* followed at lower levels by *Lessonia nigrescens* with *Lithothamnia* forming a continuous covering to the rocks. There are three obvious species of *Lithothamnia,* a purple-red coloured species, a deep red and a pink, the latter being the most common. The species of these *Lithothamnia* occur mixed altogether at different levels though the purple-red species prefers situations with some degree of sun shelter. The *Lithothamnia* belt is also occupied by *Lessonia nigrescens* and *Acanthopleura echinata, Enoplochiton niger, Concholepas concholepas, Fissurella costata, F. limbata, Thais chocolata* (in clefts), *Turbo niger* and *Tegula atra.* The roots of *Lessonia* holdfasts offer a sheltered habitat to the crabs *Pachycheles grossimanus* and *Petrolisthes patagonicus* (Cunningham). One specimen of the "patelliform" Isopod, *Ahphoroidea typa* H. M. Edw., was collected on the stipe of *Lessonia* and the roots were the subject of attacks by the Acmaeid *Scurria scurra.* One small octopus, *Polypus fontanieanus* D'Orb., was captured amongst the *Lessonia* holdfasts.

(*d*) *Arica*

This port was visited between 26th and 28th February, 1955.

The area examined was on the rocks to the south of the Balneario to the south of Arica.

The zonation: On the rocks beyond the shipyard at the southern end of the Balneario:—

Chthamalus cirratus.
Chthamalus cirratus + *Littorina peruviana.*
Chthamalus cirratus + *Balanus flosculus.*
Chthamalus cirratus + *Balanus flosculus* + *B. laevis laevis.*
Barnacles + *Brachidontes purpuratus.*
Lessonia nigrescens.
Lithothamnia.

The top of the *Chthamalus* belt varies in different places. There are three such varieties. The most common is that given above where the barnacles are the only organisms living high on the shore. In sun-sheltered situations which have some spray there is the expected reversal of *Littorina* and *Chthamalus* with the barnacles occurring lower than the littorinids. In some places the *Chthamalus* and *Littorina* belts occur together as a mixed belt at the top of the shore. The places where this happens presumably are intermediate in sun and wave exposure to the exposures experienced by the areas showing the first two types of zonation. It is apparent that the mixed zones at the top of the shore occur in places where there may or may not be sun exposure.

The barnacle belt changes in constitution further down the shore. *Chthamalus cirratus* is still found but it is mixed with *Balanus flosculus* and a few *Balanus laevis laevis,* the latter species being specially numerous on mussel shells only in very shaded places. In the lowest parts of the barnacle belt there are more *B. l. laevis* with proportionately fewer *C. cirratus* and a large number of *B. flosculus.* In this region it is difficult to decide the dominant species of barnacle, since dominance changes from place to place and it can only be referred to as a barnacle band. *B. flosculus* is very common on *Brachidontes* and *Mytilus* and *B. l. laevis* is also found on these species as well as on Concholepas. It is interesting to note that Darwin (1854) recorded *B. flosculus* as occurring together with *Chthamalus scabrosus* Darwin, especially upon *B. psittacus.* I did not collect any *C. scabrosus* in Chile in 1955.

Siphonaria lessoni and *Acmaea viridula* are both very numerous in the barnacle belt together with *Chiton cumingsi, C. latus* and *Fissurella concinna* Philippi.

The lower part of the barnacle belt consists of *B. flosculus, B. l. laevis,* and *Chthamalus cirratus,* together with *Brachidontes purpuratus.* The mussel appears at first fairly high up the belt as a cleft dwelling species but at the lower tidal levels it is present in large numbers forming a dense covering to the rocks. The mussels themselves serve as a substratum for the barnacles, *Ulva lactuca, Enteromorpha* sp., *Acmaea* sp., *Siphonaria lessoni, Chiton cumingsi* and *C. latus.*

The top of the Infralittoral fringe, characterised by *Lessonia nigrescens,* occurs very abruptly at the lower end of the *Brachidontes* belt. The red alga

Gigartina lessonii (Berg) J. Ag. is found on the mussels in the lower parts of the mussel beds and this alga also extends into the Infralittoral fringe.

The *Lessonia* belt is very well developed and also found in this belt, being very common, is *Gigartina lessonii.* During the period of examination of the rocks it was not possible to examine this belt satisfactorily on account of a heavy ground swell. The crabs *Petrolisthes angulosus* (Guérin), *Pachycheles grossimanus* (Guérin), and *Gaudichaudia gaudichaudii* (H.M. Edw.) live in the " roots " of the holdfast of *Lessonia.* Also found in the same habitat are *Concholepas concholepas, Acanthopleura echinata, Enoplochiton niger, Fissurella costata, Tegula atra* and *Thais chocolata,* together with an Asteroid *Stichaster striatus* Muller and Troschel.

In the shale below stones in gulleys and ponds there is a numerous annelidan fauna consisting of ten species. These are *Lepidasthenia virens* (Blanchard), *Halosydna fuscomarmorata* (Grube) (Polynoidae), *Eulalia personata* (Gruvier) (Phyllodocidae), *Nereis grubei* Kinberg (Nereidae), *Lumbrinereis* sp. (Lumbrineridae), *Pherusa* sp. (Flabelligeridae), *Dasybranchus* sp., and another capitellid (Capitellidae), *Phragmatopoma moerchi* Kinberg (Sabellaridae) and *Thelepus* sp. (Terebellidae).

The *Lessonia* belt is replaced by a *Lithothamnia* dominated region. Most of this latter belt is submerged at low tide but the prevailing heavy swell is such that a considerable part of the top of the *Lithothamnia* is exposed intermittently.

Discussion

Throughout this paper I have not raised *Brachidontes* to the status of a belt-forming species. I am reluctant to do this since it has been found that mussels are a rather unstable indicator, being liable to fluctuations in numbers due to storms and long term variations in population numbers. For this reason, I prefer to think of mussels, of either of the two genera *Brachidontes* or *Mytilus,* as forming part of the lower barnacle belt. This is in contradiction to my earlier papers wherein I refer to a belt dominated by *Mytilus* or other mussels.

The large chitons *Enoplochiton niger* and *Acanthopleura echinata* are found at all of the localities visited in the Infralittoral fringe on the rock unoccupied by the holdfasts of *Lessonia.* However, while these chitons are large and obvious, there are certain other species which are of small size but of no less ecological significance. The most numerous chiton is *Chiton cumingsi,* found at high tidal levels and in clefts and ponds at all four localities. *Chaetopleura peruviana* (Lam.) is an equally widespread species being found not only in clefts but also under stones. Leloup (1956) records it from clefts, under stones, from low to high tide level, from rocks embedded in sand, from rock cavities and in association with *Brachidontes purpuratus. Chiton granosus* Frembly was recorded from Coquimbo and Iquique by the Lund University Expedition (Leloup, 1956) and I found it high on the shore in clefts at both these places as well as at Antofagasta but not at Arica. Brand (1945) apparently did not find the species in Arica. *Chiton latus* Sowerby was found at Coquimbo living at the level of *Endarachne* and at Iquique living on stones at the level of the top of the *Lessonia* belt. I did not find this species at Arica, though Brand (1945) recorded it from there, but without any habitat notes.

It has been found that in other parts of the world the zonation pattern is controlled in the widest sense by the geographic range of the belt-forming species. In the more restricted local areas one of the prime causes of changes of zonation is the amount of wave action to which any particular part of the coast is exposed. On a much incised coast line care has to be taken that the area examined is typical of the coast as a whole and is not just a small local patch exposed to a certain amount of wave action. On the Chilean coast, north of Chiloë Island, this factor plays a relatively important part. Most of the coast between Valparaiso and Arica is exposed so that the zonal pattern is easy to identify and the pattern in any restricted area was found to be typical of a considerable length of coastline.

One of the most surprising features of the central and northern Chilean coasts is the uniformity of the zonation. Table 4 summarises the zonation encountered at the five places where an examination of the shore was carried out.

The above table shows firstly that there is very little change in the belt-forming species on the shores of Chile throughout 15 degrees of latitude. There may be some slight changes in the actual species composition but, with the one important exception at Antofagasta, the zonation falls into the one type, namely, barnacle, barnacle and littorinid, barnacle, algae and mussels, algae. The exception at Antofagasta is most interesting. It has been shown in the section above that there is some evidence for assuming that the sea temperatures at Antofagasta are higher than at other adjoining places both to the north and to the south. If we are to accept that the species inhabiting the Infralittoral fringe reflect the nature of the waters washing them, then the presence of *Pyura* as an intertidal indicator at Antofagasta can be interpreted as a biological indication of warm water conditions. *Pyura* in other parts of the world. e.g., Australia, forms extensive and ecologically very similar belts in warm temperate seas. *Pyura chilensis* is by no means confined to the Antofagasta area, but is found on the Infralittoral fringe amongst the holdfasts of algae from Peru to 42° S. approximately (Van Name, 1954). However, throughout the rest of the range of the species there are no large beds formed in the same fashion as at Antofagasta.

It could well be that at Antofagasta there exists some set of local conditions which does not favour the growth of the Infralittoral fringe algae. It may even be that some catastrophe befell these algae and they were replaced in the shore by the ascidians which became so numerous that the algae are unable to compete in their accustomed habitat. If the latter had taken place, one might expect to encounter scattered patches of *Pyura* throughout the whole Chilean coast, in places where gales had temporarily removed the algae. However, this is not the case.

The absence of the littorinid belt from the Supralittoral fringe is a feature of the Chilean coast which has already been noted earlier (Guiler, 1959). There may be some competition between the littorinids and the barnacles and field evidence suggests that there exists a very delicate balance between the rate of drying and the amount of wetting experienced which may confer some advantage upon the barnacles. However, it is by no means general to find the Supralittoral fringe devoid of littorines, e.g., at Iquique there exists a well developed *Littorina* belt and these conditions are duplicated at several places on the coast at Montemar where local conditions give rise to restricted areas showed that there was not heavy spray beating upon the rocks. In areas where the spray was heavy and more or less continuous it was noted that the littorines formed a sub-belt within the barnacle belt.

The most common of the intertidal belt-forming barnacles is *Chthamalus cirratus,* this species being recorded as that which forms the upper Midlittoral belt at all places visited. It is particularly interesting to note that Darwin (1854) recorded *Ch. cirratus* as frequently occurring with *Ch. scabrosus* Darwin. My collections failed to yield any of the latter species at any of the stations visited, nor were any collected as dead material washed ashore. The absence of *Ch. scabrosus* can only be a matter of speculation.

Ch. cirratus is a widespread species in South America, ranging from Peru to the Falkland Islands. Over all this range it is an important belt-forming species.

The lower parts of the *Ch. cirratus* belt become mixed with other species of barnacle, namely *Balanus l. laevis* and *B. flosculus.* Darwin records both the species from the lower parts of the shore but Pilsbury (1910) only records *B. l. nitidus* from Peru. However, there is little doubt that *B. flosculus* occurs in Peru, Darwin recording its range from Peru to Tierra del Fuego. *B. flosculus* is a highly characteristic species, having a purplish shell.

While discussing barnacles it is desirable to mention the large *B. psittacus.* This is the largest of the operculate species, often reaching more than nine inches in length. Darwin did not record this species as being of intertidal occurrence but I found it to be numerous in the Infralittoral fringe at all parts visited. However, the only place where *B. psittacus* formed a belt was at Coquimbo, but it is certainly of considerable ecological importance on the other part of the coast on the rock living among the holdfasts of the large algae. The presence of a belt formed by this species in the lower Midlittoral was attributed to special conditions which resulted in an elimination of the algae. Perhaps Darwin did not find any of this species intertidally because it happens to be edible and thus liable to predation. He found it living on the mollusc *Concholepas* and he gave its range as from Arica to Chiloë Island. Pilsbury (1910) extended the range of *B. psittacus* to Callao and the Chincha Islands in Peru.

B. psittacus is often associated with other species of barnacles which make use of its shell as a substratum. These species are *B. laevis, B. flosculus, B. trigonus* Darwin and *Verruca laevigata* Sowerby. The latter two species were not found by me but were recorded by Darwin.

The lower parts of the Midlittoral are occupied by various species which form belts at different parts of the coast. Mussels reach considerable importance at various places and are usually utilized as a substratum by barnacles, e.g., *B. flosculus* and *B. laevis.* There is little uniformity in the belts found on the coast and the species forming them will be discussed later.

TABLE 4.

Zonation at Five Places on the Central and Northern Chilean Coast

	Montemar Lat. 33° 12′ S.	Coquimbo Lat. 29° 55′ S.	Antofagasta Lat. 23° 40′ S.	Iquique Lat. 20° 15′ S.	Arica Lat. 18° 20′ S.
Supralittoral fringe	Vacant	Vacant	Vacant	*Littorina peruviana*	Vacant
Midlittoral	*Chthamalus cirratus*	*Ch. cirratus*	*Ch. cirratus*	*Ch. cirratus*	*Ch. cirratus*
	C. cirratus + Littorina peruviana	....	....	....	....
		Ch. cirratus + Endarachne binghamiae	*Ch. + Enteromorpha* sp.	*Ch. cirratus + Balanus l. laevis*	*Ch. cirratus + Balanus flosculus*
		Ch. cirratus + Balanus flosculus	*Ch. Colpomenia*	*Colpomenia + Brachidontes purpuratus*	*Ch. cirratus + B. flosculus + B. l. laevis*
				Colpomenria + Mytilus chorus	*Barnacles + Brachidontes purpuratus*
			Pyura chilensis + Corallina chilensis	*Corallina chilensis + Tegula atra*	
		B. psittacus + Acanthopleura echinata	*Pyura chilensis*		
Infralittoral fringe	*Lessonia nigrescens* Bory	*L. nigrescens*	*Pyura chilensis* (Molina)	*L. nigrescens* with *Lithothamnion* spp.	*L. nigrescens*

The Infralittoral fringe is generally dominated by algae, with the important exception of the *Pyura* at Antofagasta. *Lessonia nigrescens* is the dominant alga of this belt. In northern Chile this species is the only large alga of the fringe but in central Chile, at Valparaiso, the large southern kelp *Durvillea antarctica* appears in small numbers, gradually increasing to replace *Lessonia* in southern Chile. These species are extremely easy to distinguish, *Lessonia* being short—about four feet in length, dark-chocolate in colour, with a many-branched holdfast, so typical of the Laminariales, while *Durvillea* is long, six feet or more in length, olive-brown or even yellow in colour, with a single sucker forming the holdfast.

(5) NOTES ON SOME INTERTIDAL SPECIES

Only those species which are common and of considerable ecological importance are described here.

(a) The Littorinids

There are three species of *Littorina* which occur in Chile. These are *L. araucana* D'Orbigny, *L. umbilicata* Orb. and *L. peruviana* (Lam.). The most common species, *L. peruviana*, is to be distinguished by a series of angled white marks on the shell. A synonym of this species is *L. zebra*.

The range of both these species has been recorded by various authors. Dall (1910) records *araucana* as occurring from Nicaragua to Valdivia and *umbilicata* ranging from Ecuador to Chile. Neither Gigoux (1934), Brand (1945), nor Bahamonde (1950) record the latter species from the north of Chile.

It is interesting to note that both *L. araucana* and *L. peruviana* are tropical in their ranges and in Chile, especially in the south, they are approaching the end of their geographical range. This may have some part to play in the absence of a well-developed littorinid belt over much of the Supralittoral fringe. At Iquique Playa Blanca there is a *Littorina* belt, formed by *L. peruviana*, but at Arica, to the north, and at all other places to the south of Iquique the *Littorina* belt is a strip contained within the barnacle belt. It has been noted in the case of some other species that animals approaching the end of their geographical range seek less rigorous environment. Unfortunately, there is no information on the shores of Peru, Ecuador or Colombia to enable conclusions to be draw regarding the habitat of the species on the shores of these countries, but it should be remembered that it is possible that their vertical range in Chile is not the characteristic habit of this species.

(b) The Chitons

The most obvious of the Chilean chitons are *Enoplochiton niger* (Barnes) and *Acanthopleura echinata* (Barnes), both species being widespread in distribution on the coast. *A. echinata* is easily distinguished by the presence of spines on the girdle, large size, and complex sculpturing. Although of large size, this species is not the most common on shore but is one of the most obvious. It is found in the lower Midlittoral and in the Infralittoral fringe, living on rocks or in clefts. Leloup (1956) records it from coarse sand. The individuals can tolerate the heaviest wave action and prefer the presence of some surf, being absent from sheltered places. *Acanthopleura* is found from the Galapagos Islands to San Vincente (37° S.). Plate (1898) records a specimen 20 cm. long x 10 cm. wide.

Enoplochiton niger can be differentiated from *Acanthochiton* by the presence of scales on the girdle. It occupies much the same type of habitat on exposed coasts as *Acanthochiton echinata* but it is not as widespread a species, being absent or scarce on parts of the coast not receiving the heaviest of wave action. This species ranges from Peru to Valparaiso and I collected specimens from Arica, Iquique, Antofagasta, Coquimbo and Montemar.

The smaller chitons are very numerous on the Chilean coast and the most common of these is *Chiton cumingsi* Frembly. Leloup (1956) records this species from Chiloë Island to Iquique but Dall (1910) found it in Peru and I collected specimens at Arica, as did Brand (1945). Dall noted that the chiton occurs in rock pools and on rocks so that it is apparent that this species occupies the same habitat in Peru as in Chile. Bartsch and Rehder (1939) give the range of the species as Callao to Chiloë.

Chiton cumingsi lives attached to rocks in the Midlittoral both on open faces and in clefts. It also frequents ponds and clefts in the bottom of ponds as well as occupying a semi-cryptic to cryptic position below rocks and boulders.

In the upper Midlittoral *C. cumingsi* is partially replaced by *C. granosus* Frembly. This species ranges from Callao to Magellan (Dall, 1910). Leloup records this chiton from the Infralittoral to the highest part of the tidal region, living under stones and in cracks in the rocks.

The third common widespread small chiton of the Chilean coast is *C. latus* Sow. Dall (1910) only recorded this species from a restricted part of the Chilean coast, namely from Valparaiso to Coquimbo, but Leloup (1956) gives the range of this chiton as from Callao to Magellan. It is found at all tidal levels. I collected it from all places visited and both Brand (1945) and Bahamonde (1950) record it from northern Chile.

Tonicia elegans (Frembly), which I collected only from below rocks embedded in sandy shale at Montemar, is a widespread species. Gigoux (1934) recorded it from the Atacama region, and Dall (1910) stated its range to be from Callao to Chiloë. Leloup followed Dall in his statement of the range of the species. Leloup recognised four forms of this chiton, *f. chilensis* Frembly from Coquimbo, Valparaiso, Talcahuano, Puerto Montt, San Vicente and Lota, *f. chiloensis* from Chiloë and S. Chile, *f. gravi* from Tocopilla, Ancud and Canal Chacao and *f. lineolata* from Valparaiso, Talcahuano, Coquimbo and Iquique.

Chaetopleura peruviana (Lam.) is a widespread species occurring along the whole of the Chilean coast. Leloup (1956) records it as being found from Iquique to the Magellan Straits. Gigoux (1934) records the species from the Atacama and Bahamonde (1950) found this chiton on the Tarapaca coast, at Cuya, Los Gringos and Caleta Vitor. I collected the species at Montemar in clefts at about mean sea level and in a similar habitat at Coquimbo. I did not find this species at Antofagasta, Iquique or Arica.

Leloup cites three chitons having a Magellanic distribution, eight from Chile and Magellan, nine from Chile and Peru, seven from Peru to Magellan, and two from Chile to Mexico. The centre of distribution of the chitons is thus more concentrated in central Chile than in the north or south, although some of the species are of very widespread distribution, reaching the Antarctic, e.g., *Tonicia elegans*, and the Argentine, e.g., *Chiton latus*.

(c) *The Fissurellids*

The family Fissurellidae reaches a considerable degree of development in Chile, Riveros (1950) describing no fewer than 37 species. One of the most evident of the fissurellids is the large *F. crassa* Lam. This species reaches 85 mm. in length and has a somewhat depressed shell. Its geographic range is from Callao to Corral. The larger *F. nigra* Lesson is less common than *crassa* but more widespread in range, reaching from Callao to Magellan Straits.

Several other fissurellids are found intertidally in Chile, notably *F. exquisita* Reeve, *F. concinna* Philippi and *F. limbata* Sowerby. However, all of these species are found in clefts or other semicryptic or cryptic places.

The fissurellids are most common and show the largest number of species in southern Chile. Riveros (1950) records 13 species which are exclusively Magellanic in distribution. These species have a very wide range from Magellan to Peru, four species range from Valparaiso to the north, but only two species range from Valparaiso to Magellan. Two species range from Magellan to Chiloë Island and two range from Chiloë to Valparaiso, while four species are of widespread occurrence from Valparaiso to Peru. Of the remaining seven species, five are local in occurrence and some doubt exists as to whether two species occur in Chile. The distribution of the species superficially shows that the Valparaiso area is of geographical importance since no fewer than 10 species appear to end their ranges at that port. However, there has always been much greater emphasis of collecting in the Valparaiso area than in other parts of Chile and undue emphasis must not be placed upon these records. It is apparent that there is a general diminishing of the number of Fissurellids in northern Chile, from the 20 species in the Magellan region to seven at Arica.

(d) *Other Species*

One prominent member of the Infralittoral fringe fauna is *Concholepas concholepas* Bruguiere. This large mollusc is found from Peru to S. Chile. As this species approaches the northern end of its range it is smaller than in southern Chile and at one time the Peruvian specimens were described as a different species *C. peruviana* Lam. *Concholepas* appears to fill a *Haliotis*-like niche, being an alga grazer living at or below the Infralittoral fringe.

The limpet *Scurria scurra* (Lesson), although not conspicuous, is of very considerable ecological importance since it lives in amongst the roots and stalks of *Lessonia*. It causes damage to the plants and eventually may be indirectly responsible for the removal of the plant from the substratum.

(6) GENERAL

The north Chilean coast, throughout its great length shows a considerable change in its climate. The northern parts of the coast are characterised by rare rainfall, heat, strong insolation and dry conditions generally, whereas the central coasts have a Mediterranean climate with dry warm summers and wet mild winters. From the north to central Chile the analysis of the physical environment shows that some amelioration of the full possible effects of insolation and dehydration on the desert coast are found in the almost continual spray and frequent mists but this has the disadvantage that hypersalinity becomes an almost permanent feature of the intertidal region. The central Chilean coast, on the other hand, shows a very sharp difference between summer and winter conditions, with seasonal rains playing an important part in altering the exposure and salinity factors. Therefore it might be expected that the species inhabiting the central parts of the Chilean coast could be different from those found in the north, if not on account of the large geographic distance between them, but because of the different climates experienced in this distance. However, this is not the case. Not only are the species to be found on the shore the same but they occupy the same ecological levels on the shore and apparently have the same ecology at Arica as at Valparaiso.

There could be expected that a physiological difference exists between, say, an individual *Chiton latus* from Arica and one from Valparaiso. The northern individual must be physiologically adapted to withstand different climatic conditions from one from the south. It would be very interesting to carry out transplant experiments upon some of the intertidal species.

All northern and central coasts show the same type of zonation, namely barnacle, littorine, barnacle, algal with mussels and, finally, algal zones. Minor variations of this may occur, but the basic pattern is unchanged. The important exception to this is at Antofagasta. At this port the lower part of the shore is occupied by *Pyura chilensis* and not by large Phaeophyceae. In the discussion of the physical environment at the port I concluded that local meteorological factors produce somewhat warmer conditions at Antofagasta than at places on either side of this region. This, apparently, has no effect upon the intertidal fauna with the exception of *Pyura*, which becomes dominant. *Pyura* is widespread along all of the coast of Chile, but it is only at Antofagasta that it forms a belt and it is this feature which gives a clue as to the factor controlling the zonation on the Chilean coast.

Obviously, since the zonation is the same both in north and central Chile, air temperature, insolation and other climate factors can be ruled out as controlling influences. The sea temperature must be the factor which controls the distribution of these organisms. Figure 4, showing the sea temperature gradient graphically, illustrates that there is only 3° C. difference in the mean winter temperatures. Such a small gradient as this spread over such a great distance could not be expected to give major change in biogeographical regions.

The warmer maximum temperatures prevailing at Antofagasta are sufficiently greater to encourage the development of *Pyura* which is a species that favours warmer seas than those preferred by the Phaeophyceae.

The direction of the currents probably plays no small part in the apparent inability of tropical elements to penetrate into Chilean waters. Any larval recruitment to shore faunas on the Chilean coast must come from the south, i.e., from cold waters so that warm water species have little chance of spreading south.

The tropical element is entirely lacking on the northern Chilean coast. Although Arica lies well within the tropics there are no coral reefs to be found and mangroves are not a significantly important member of the flora to the south of Tumbes (Lat. 3° 30′ S.) in northern Peru (Peterson, 1949).

It is recognised that there are two main elements in the marine fauna of Chile, namely the cold temperate (Magellanic) and the warm temperature or Peruvian. It is convenient to start with the review of knowledge as interpreted by Ekman (1953) who thought it probable that there are two elements in the Chilean fauna and considered that the northern limit of the cold water province was at the northern end of Chiloë Island. He went on to note that nowhere else in the world is the limit of the tropic-subtropic so near to the Equator, being at Punta Aguja (6° S.).

Madsen (1956), in describing the distribution of the echinoderms of Chile, states that there are only three exclusively warm temperature species in the Chilean echinoderm fauna. There is also a transitional element occurring both to the north and south of Chiloë Island with a cold temperate element which is restricted largely, though not entirely to the south of Chiloë Island.

Haig (1955) and Holthuis (1952) record that numbers of species of Anomurous and Macrurous Decapod Crustacea reach the ends of their geographic ranges in the vicinity of Chiloë Island. In view of these conclusions it seems that the area of change from the Peruvian to the Magellanic Regions is fairly uniform and well defined.

However, there appears to be a considerable region of mixed faunas lying to the north of Chiloë Island. The echinoderms, for example, have a number of species which reach as far as Iquique but also extend well into the Magellanic province.

If we consider the zonal forces as indicative of the biogeographic provinces of Chile, we see that southern Chile with mussels, the large brown fucoid *Durvillea antarctica,* and a barnacle-littorine zonation on the upper part of the shore is characteristic of the generally accepted southern cold temperate type of zonation.

The southern warm temperature region is characterised by the presence of littorines, barnacles, *Lessonia* sp., *Phyllospora* sp. (large Phaeophyceae other than fucoids) with ascidians becoming important, e.g., in the Sydney area (Dakin, Bennett and Pope, 1948). This type of zonation is found over nearly all of the central Chilean coast where *Lessonia nigrescens* is the dominant alga of the Infralittoral fringe, with *Pyura chilensis* of some importance and even in some localities becoming of major zonal significance, e.g., at Antofagasta. Van Name (1954) recorded *Pyura chilensis* as not being a Magellanic species, but one which is intermediate between the warm waters of north Peru and the Magellanic region though reaches latitude 43° S.

There are certain other features shown by the non-zone forming species which lend support to evidence given by the belt-forming species. The very restricted ecological importance of the large limpets in northern seas is a warm temperate feature, since limpets apparently are smaller in size and less numerous in warm seas.

The work of Madsen (1956), Haig (1955), and Holthuis (1952) shows that, although there is a biographical boundary somewhere in the region of Chiloë Island, there is a very great deal of penetration of the Magellanic forms into the Peruvian Region. This is particularly true of the Crustacea and it is further supported by the work of Riveros (1950) on the Fissurellids, this latter author finding 15 Magellanic species out of a total of 37, and five species having a range extending from the Magellan Straits to beyond Chiloë Island and it would appear as if this group, while primarily Magellanic in character, extends its range well into the Peruvian Region. The distribution of fissurellids is shown in Table 4.

The region of Chile to the north of Chiloë Island can be considered as an area having the ecological characteristics of a warm temperate region but with a considerable penetration of cold weather elements. This penetration is assisted by the cold northerly flowing Peru Coastal Current and the presence of this current must be considered as the main element in maintaining the warm temperate fauna as far north as central Peru.

TABLE 4.

Species Distribution of the Fissurellids of Chile based on Riveros (1950)

No. of Species	Range	Province
13	Magellan Area	Magellanic
2	Easter Island	?
2	Magellan-Valparaiso	Magellanic and Peruvian
3	Magellan-Peru	Magellanic and Peruvian
2	Chiloë-Valparaiso	Peruvian
4	Valparaiso-Peru	Peruvian
2	Magellan-Chiloë	Magellanic
4	Valparaiso-N. Chile	Peruvian
3	Valparaiso only	Peruvian
2	Doubtful	
37		

(7) PHYSICAL FACTORS ON THE EAST AND WEST PACIFIC COASTS

Throughout this section the reference to the western Pacific coasts will be understood to refer to the coast of Chile to the north of the 35° of latitude, unless it is specifically stated otherwise. In this section a full review of the factors is not given, this having been done earlier, but a brief summary of these factors is given below.

(a) *Currents and Upwellings*

The currents on the Australian coast and the Chilean coast are opposite in their direction of flow. On the western shore the current, the Peruvian Current, flows north and it has been shown to be cold in nature and is frequently kept cool by reinforcements of cold water from upwellings. The latter are the result of the effect of trade winds blowing on the Andean chain and so being diverted to a direction parallel to the coast. There is a counter current, warmer in temperature than the offshore Peruvian Current, which runs south down the coast. This can be compared with the Australian current system where a warm current pursues a southerly course down the Australian coast.

The sea temperatures differ greatly on the eastern and western sides of the Pacific. The temperature of the sea is a result of the current pattern and, whereas the Australian sea thermocline shows an inverse relation to latitude, the Chilean and Peruvian coasts may even show a decrease in temperature towards the tropics (Fig. 22).

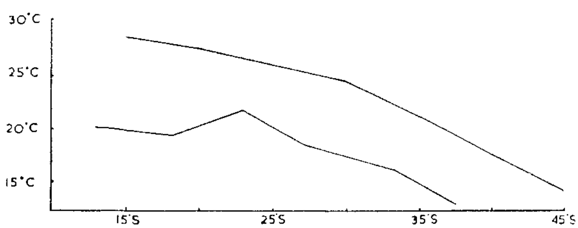

FIG. 22. Comparison of Australian and Chilean sea temperatures.

The Australian coast at comparable latitudes is over 5° C. warmer than the Chilean and southern Peruvian coast. The difference becomes more pronounced in the tropics where there is almost 10° C. between the temperatures at latitude 17° S. This divergence becomes marked to the north of 17° S., but there is no very marked divergence in the temperatures to the south of 33° S.

(b) *Winds*

In both cases the coasts are subject to the trade winds and also the southern part of each coast, i.e., Tasmania and southern Chile, are battered by the westerlies of the " Roaring Forties ". The trade winds of Australian seas are not diverted by any mountain chain comparable to the Cordillera of Chile so that the pursue their normal sontheasterly course, whereas those of Chile are diverted from their normal course to southerlies. Both coasts are subject to sea breezes in summer which may reach considerable strengths, but they are purely local coastal phenomena and do not whip up strong heavy seas, but they can create a short sharp sea which has a considerable effect in producing spray. However, the two coastlines have similar winds, although they on the shore are each the result of different conditions.

There are small variations in the salinities encountered on both the Australian and Chilean coasts but it seems unlikely that these are sufficiently great to cause major changes in the flora and fauna on any part of the coast.

The air temperature gradients of the two coasts show that the Australian air temperatures are warmer than those at comparable latitudes on the Chilean coast. The temperature difference becomes more marked in the tropical rgions of each country, being in the order of 10° C. at 20° S., whereas at 40° S. the difference between the temperatures is about 7° C.

The isanomalous lines on the Chilean and Peruvian coasts show a greater negative departure than those on the Australian coast, but the greatest difference lies, not in the negative departure, but in the fact that most of the Australian coastline shows a positive departure with the exception of the Tasmanian-Victorian region in summer. That is to say, the annual mean sea temperature is greater than the annual mean air temperature in Australia, whereas the opposite holds good on the west coast of South America.

The fogs and mists, so prevalent on the Chilean coast, especially the northern parts of it, are lacking on Australian shores which are remarkably free of fog. The origin and effect of the Chilean mists have already been commented upon and no further observations are necessary at this stage, beyond noting that they may bring some moisture to the coast.

The rainfall on the two coasts is notably different. The rainfall in Chile is remarkably Mediterranean in type with maximum falls occurring in the winter and virtually no rain in the summer. North of 30° S. the rainfall becomes very irregular and on the desert coast of northern Chile and southern Peru precipitation may not take place for many years. The Australian rainfall pattern is very different, in general there being more rain in the tropical parts of the coast than in the cool or warm temperate regions.

The mean annual relative humidity figures suggest that the Australian coast is dryer than that of Chile, even including the desert area of northern Chile. The Australian State capitals, all coastal cities, have a mean annual humidity around 68%, whereas in Chile the relative humidity varies from 74% at Antofagasta to 83% at Valdivia (see Fig. 9). The greater moisture in southern Chile is derived from the very heavy annual precipitation and the moist damp climate while that in the north is brought about by the mists and fogs of the Peru Current.

The wave action experienced on the eastern and western sides of the Pacific Ocean is intense. The battering received by the shores of New South Wales, western Tasmania and Chile is among the most intense in the world, while the remainder of the Australian coast receives somewhat less intense wave action.

The Chilean and Peruvian coasts are unique in the world in one feature, namely the Nino effect, the warm tropical water which periodically sweeps down the coast bringing disaster to marine organisms. No other coastline suffers such a phenomenon. The Australian coast has occasional " red sea " blooms which have been noted from time to time. These are very local in effect and also occur on the Chilean coast.

The differences between the two coasts are shown on Table 5. On the west of the Pacific there is a coast bathed by cold water up to 7° C. cooler than the air, with winter precipitation between the latitudes of 30° S. and 40° S. and very little, if any, precipitation at intervals of many years to the north of these latitudes but with some mists or fogs and high relative humidity. The whole coast is subject to intense wave action. The northern portion of the shore is liable to periodic mot tropical fauna and flora. All the physical factor sexcept water invasions which have serious effects on the the last, combine to modify the effect of the warm climate.

On the other hand, the Australian coast is bathed by warm water which gradually cools in the higher latitudes, the precipitation is high and the relative humidity low. The Australian coast can be considered as more normal in its climatic pattern that than of Chile, which is only paralleled by the desert coast of South-West Africa.

(8) THE CHILEAN INTERTIDAL ZONE IN RELATION TO THAT OF AUSTRALIA AND SOUTH AFRICA

The physical conditions of the South African coast are somewhat similar to those prevailing on the South American coasts, namely a warm current flowing southwards along the east coast of the continent with a cold northerly current on the west coast. Further, the South-West African coasts resemble those of Chile in that the similar special oceanographic and climatic conditions produce a cold sea backed by a desert coast with few centres of civilisation. However, the west coast of South Africa is colder than that of northern Chile, the temperature being between 12° C. and 16° C. (Isaac, 1937), whereas that of northern Chile is 16-19° C.

The features of the higher parts of rocky coasts show a uniformity throughout the world, and are dominated by two forms, namely littorines and barnacles. In order to seek significant points of resemblance or contrast between coasts, we must turn to the lower parts of the shore, and for this reason only the Infralittoral fringe and a few of the organisms of the lower Midlittoral are considered here. Before doing this, it is necessary to note the rather special Chilean habitat of the littorines which mainly form a belt in the top of the barnacle band.

The Infralittoral Fringe

It is convenient to start with the cold temperate regions of each continent. The cold temperate region of South Africa is represented by the west coast fauna and the algae of the Infralittoral fringe are *Laminaria pallida, Ecklonia buccinalis* and *Macrocystis pyrifera* (Bright, 1938, Stephenson, Stephenson and Day, 1940). *Pyura stolonifera* and *Lithothamnia* are found amongst the holdfasts of the algae. This type of zonation is somewhat similar to that encountered in northern Tasmania, but there are severai important points of difference. The dominant alga of the Infralittoral fringe in Tasmania is *Sarcophycus potatorum* which differs from *Laminaria pallida* not only in its systematic position but also in the form of the holdfast which in the former genus is a large sucker. Thus, *laminaria* offers a niche for small species which is not found in Tasmania. Both South-West Africa and Tasmania have Lithothamnion and *Corallina* forming important belts in the lower shore, the latter occurring above the large algae in both countries. The Chilean algae of the Infralittoral fringe are similar to those found in Tasmania, namely the large *Durvillea antarctica* with *Lithothamnion* and *Pyura*. Although *Durvillea* is generically separated from *Sarcophycus*, the ecological resemblance is very close.

The genus *Ecklonia* is represented in both Australia and Africa but is of greater ecological importance in South-West Africa. *E. radiata* is found in Tasmania but it is confined to sheltered localities and is not numerous, which is in contrast to the situation in South-West Africa, where *E. buccinalis* is a dominant species over much of the coast. *Ecklonia* is absent from Chile.

TABLE 5

Comparison of the Physical Factors on the Australian and Chilean Coasts

	Chile	Australia
Sea current	Northerly, cold with cold upwelling	Southerly, warm
Winds	South to south-east	South
Sea temperature	No direct relation to latitude	Varies indirectly to latitude
Air temperature	Cool	Warm
Isanomalous departure	Negative up to 7° C.	Positive
Rainfall	Varying from very low and irregular to very high in south	Higher in tropics, regular, moderate
Relative humidity	High	Low
Fogs	Frequent	Rare
Wave action	Intense	Intense
Catastrophes	Frequent, widespread Ninos	Rare, local

Macrocystis, which in South-West Africa is found in more sheltered situations, is found in Tasmania offshore on exposed coasts. I have only found *Macrocystis* occurring intertidally in appreciable quantities at one place in Tasmania, whereas in Chile the species is found quite commonly in an intertidal situation. The sharp difference between the ecology of the species in Tasmania from elsewhere raises doubts as to the specific status of the Tasmanian representatives of the genus.

The Chilean coast in the warm temperate regions is dominated in the Infralittoral fringe by *Lessonia nigrescens*. There are some restricted areas in which *Pyura chilenses* replaces *Lessonia* as the dominant organism of the Infralittoral fringe, e.g., at Antofagasta. A similar state exists in South Africa where *P. stolonifera* replaces *Ecklonia,* e.g., at Port Elizabeth (Stephenson, Stephenson and Bright, 1938), and some parts of the same species of ascidian, e.g., at Sydney. In more northerly parts of South Africa the genus *Ecklonia* is not represented by the very large *E. buccinalis* but by the smaller *E. radiata*. This latter species is very common on the warm temperate Australian eastern coast, where it is the dominant alga of the Infralittoral fringe.

A feature of South African coasts is the presence of a belt containing 38 mixed species of algae in the Infralittoral fringe (see Table IX of Stephenson, 1939). An ecologically similar mixed algal strip is encountered on both Chilean and Australian warm and cold temperate coasts. The species composition of the belt is different in the three continents but the genera *Laurencia, Gelidium, Caulerpa, Iridaea, Dictyota, Centroceros* and *Plocamium* are all represented as well as Corallines of several genera. In many places, the Corallines are dominant in this region.

The Midlittoral

Mussels reach belt-forming importance in the cold temperate regions of all three continents, Chile and Tasmania sharing the same genera, namely *Brachidontes* and *Mytilus*. The former genus is absent from South Africa but *Mytilus* is represented there by three belt-forming species.

The limpets are of small importance in both Chile and Tasmania but are of great importance in South Africa where the genus *Patella* is represented by 11 species (Stephenson, 1936). The genus *Patella* is absent from Chile and Tasmania, being replaced by *Nacella* and *Cellana* respectively. On the other hand, the Siphonariid molluscs are of considerable importance in all three continental masses, the species of this genus being especially numerous on the upper part of the shore. The Fissurellid molluscs, of little ecological importance in Australia and South Africa, are of great significance in Chile, as also are the Turbinids.

It would be possible to contrast further belt-forming species on the coasts of the three continents but little is to be gained by so doing since sufficient has been shown above to illustrate that there exists an *ecological* similarity of the zonation on the coasts of the three geographical areas. However, the Australian coast differs sharply from that of the other two coastlines in that the tropic element, mainly the corals is very well developed. There are no corals in Chile and in South Africa there are only a few zoanthids although these and other tropic elements are represented in Natal.

There exists a closer relationship between the cold water regions on the three continents than is found on warm temperate or tropical shores. This is seen particularly in the algae of the Infralittoral fringe where the same species occurs, e.g., *Macrocystis pyrifera*. An apparent exception to this is *Ecklonia radiata* which does not occur in Chile but is found in South Africa and Eastern Australia, including Tasmania. However, a close relationship exists between the Tasmanian algae and those of Chile, some genera being shared, e.g., *Lessonia, Gelidium, Laurencia, Iridaea* and *Chaetomorpha*. Some species are found on both shores, namely *Adenocystis utricularis* (Bory) Skotsb., *Chaetomorpha aerea* Dilwyn and *Centroceras clavulatum* (C. Ag.) Mont. The same ecological habitat is occupied on each coast by each of the last three species. In these lists I have not included genera common to Chile and Tasmania but which also are elsewhere, e.g., *Corallina, Porphyra,* &c., these genera forming a ubiquitous element. The greatest similarity between Tasmania and Chile is the presence on the coast of the large southern kelps, *Sarcophycus potatorum* and *Durvillea antarctica* respectively. These kelps, although of different genera, are ecologically very similar, occupying the same niche in both countries. There is no anatomically similar South African kelp, though *Laminaria pallida* appears to occupy a similar habitat.

Apart from *Pyura* and the mussel belts mentioned above, there are few close relationships between the belts formed by animals on the Chilean and Australian coasts. Barnacles of the genus *Chthamalus* are found forming extensive belts in both countries. However, the surf barnacle *Catophragmus polymerus* is found in Tasmania but does not occur in Chile. Nor is it found in South Africa and it appears as if this species occupies a position in Australia which is utilised by limpets in the other countries. This supports the view of Ekman that the fauna of the west Pacific region is separable from that of the east. It is true that there are some species which are found in both continents, e.g., *Leptograpsus variegatus* (Fabr.), *Plagusia chabrus* (L.), *Cyclograpsus punctatus* M. Edw., *Halicarcinus planatus* (Fabr.), but the general ecological animal facies is different. At the family level there are a large number of similarities between the two continents but these are of rather doubtful value as a basis for biogeographical conclusions but the absence and relative importance of families is of some importance. The family Fissurellidae is extremely numerous in both species and numbers in Chile as are the Porcellanid crabs. Certain important Australian families, e.g., the Leucosiidae are poorly represented in Chile.

Stephenson (1948, fig. on p. 220) showed that the warm current of the eastern coast of South Africa favoured the spread of the warm water elements further down the coast than on the west where a cold northerly current limited the spread of the warm water element. The maximum penetration of these elements is almost to East London and to

Walvis Bay respectively. Stephenson stated that the fringe of the tropical fauna reaches Natal, say at latitude 30° S. The southern limit of this fauna on the western coast is about Cabo Frio (Lat. 18° S.). Thus the difference in latitude between the southernmost limits of the warm element is 12 degrees of latitude. The cold temperate region on the western coast of South Africa extends through approximately 22 degrees latitude.

The difference in latitude between the southern limits of the tropic regions in Australia and western South America is about 20 degrees, or some 1,400 miles, the tropic region in South America only occupying some six degrees. The warm temperate fauna of Australia extends through 12 degrees of latitude before it is replaced by the cold temperate region, whereas in South America it crosses some 35 degrees of latitude, most of the west coast of the latter continent being in this region. These figures serve to emphasize the profound effect that the strong Peruvian Current has upon the intertidal life.

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PLATE 2.

The zonation at Iquique, 25th February, 1955. *Lessonia nigrescens* is the large alga, the rocks in the foreground are covered with *Lithothamnion*. The upper rocks in the middle distance are barnacle covered.

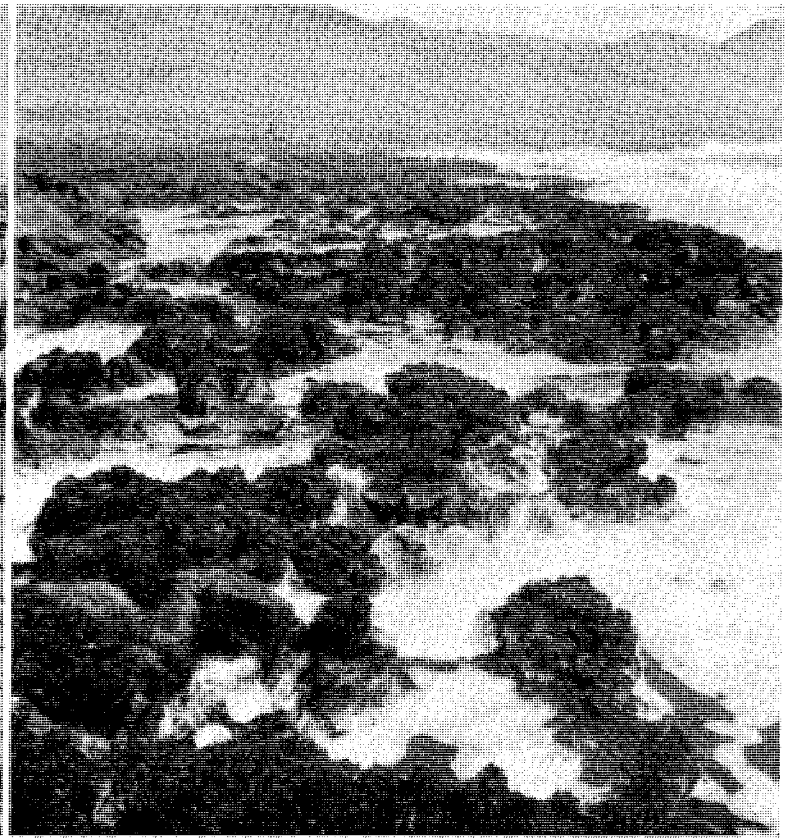

PLATE 1

The *Pyura* belt at Antofagasta, 22nd February, 1955.