

COMMONWEALTH OF AUSTRALIA

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A GENERAL ACCOUNT OF THE INTERTIDAL ECOLOGY OF SOUTH
AUSTRALIAN COASTS

By H. B. S. WOMERSLEY and S. J. EDMONDS

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Summary

An account is given of the environmental features, the intertidal ecology, and the biogeographical relationships of the coast of the State of South Australia.

The central and western coasts of South Australia are similar ecologically in comparable areas. In the supralittoral *Melaraphe unifasciata* (Gray) is dominant (except where conditions are very calm) and at high levels on very exposed coasts

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Calothrix fasciculata C. Agardh is found. The littoral zone where the coast is most exposed consists of barnacles—*Chamaesipho* in the upper littoral, *Catophragmus* in the mid littoral, and *Balanus* in the lower littoral—but where the coast is more sheltered it consists of molluscs in the upper and mid littoral and algae (*Corallina*, *Gelidium*, or *Hormosira*) in the lower littoral. In the upper sublittoral fucoid algae or in calm regions marine angiosperms are dominant. The south-east coast, however, differs in some respects from the central and west coasts. The number of barnacles found in the littoral zone is much reduced and the giant brown algae, *Durvillea potatorum* Areschoug and *Macrocystis angustifolia* Bory, are dominant in the upper sublittoral. This is associated with slightly lower sea temperatures.

Sheltered coasts are more prominent in South Australia than in the eastern States of Australia. These include the shores of Spencer and St. Vincent Gulfs, the northern shores of Kangaroo I., and a number of scattered bays.

The similarities between the coasts of South Australia and Victoria (Bennett and Pope 1953) are greater than the differences. Consequently the proposal of Bennett and Pope to recognize the Victorian and Tasmanian coasts as the Maugean Biogeographical Province and the South Australian and the south-west Western Australian coasts as the Flindersian Province appears to be unjustified. It is suggested that the Maugean is best regarded as a subprovince with the Flindersian. The latter includes most of the coast of southern Australia.

Considerable differences are noticeable between the organisms which inhabit the rocky coast of South Australia and the south coast of Western Australia. The available evidence indicates that a transition from the Flindersian to the tropical Danpieriian Province occurs along the south and west coasts of Western Australia. The terms "Indo-Australian Province" and "Baudinian Province" have been proposed by previous authors to describe this transitional region.

The Flindersian Province appears to be intermediate between cold-temperate and warm-temperate regions, becoming distinctly cool-temperate in Tasmania. It is relatively distinct from the warm-temperate Peronian Province of the coast of New South Wales.

I. INTRODUCTION

Ecological surveys of the coast of South Australia over the past 10 years have reached a stage where a general account of the marine intertidal ecology can be given. The first zoological survey of the coast near Adelaide was that of Johnston and Mawson (1946). Early work by the present authors (Womersley 1947, 1948; Edmonds 1948) was concentrated on Kangaroo Island, because this showed almost the full range of environmental conditions found along the South Australian coast. Since then the rest of the coastline (some parts of which are rather inaccessible) has been studied in somewhat less detail. Two field trips (both during January and February) have been made along Eyre Peninsula as far west as Fowler's Bay, one being extended to Eucla. The coast in the south-east of the State, extending into Victoria, is better known from visits at different times of the year. Most field work in South Australia must be done during the summer months, since the sea-level in winter is significantly higher than in summer, and in winter the lowest tides occur during the night.

Studies in recent years by Dakin, Bennett, and Pope (1948) in New South Wales, Bennett and Pope (1953) in Victoria, and Endean, Kenny, and Stephenson (1956) in Queensland have given the general picture of the intertidal zonation in these States. Certain localities in Tasmania have been described by Guiler (1951, 1952a, 1952b, 1954) and Cribb (1954). The Western Australian coast is known only from

unpublished M.Sc. theses of G. G. Smith (algal emphasis) and Mrs. L. Marsh (animal emphasis), and observations and collections made by Miss E. Wollaston, of the Botany Department, University of Adelaide, on a field trip from Rottnest Island to Esperance in February 1957.

This paper aims at giving a general account of the South Australian coastline, linking with Bennett and Pope's account of Victoria and with what is known of the Western Australian coast. The biogeographical provinces of southern Australia are also discussed.

The accounts of Dakin, Bennett, and Pope (1948) in New South Wales, Bennett and Pope (1953) in Victoria and Edean, Kenny, and Stephenson (1956) in Queensland, deal intentionally only with rocky coasts. Such coasts probably comprise most of the eastern Australian shores (apart from sand beaches). In South Australia the gulf region, with sheltered waters, and sandy or muddy intertidal areas and rocky outcrops in the northern parts, is of considerable importance. Together with calm bays and inlets (such as American River inlet on Kangaroo I. (Womersley 1956)) these areas form a distinctive part of the coastal ecology, and considerable attention has been given them. Long stretches of sandy beach and smaller sandy bays are common in South Australia.

The rough conditions on exposed coasts and tidal irregularities prevent accurate correlation of zones of organisms with tidal levels. Studies on Kangaroo I. gave an adequate conception of where the zones lay in relation to tidal levels, and the zones and ecology in other areas were studied mainly by reference to indicator organisms disclosed in earlier work. Transects were used in early studies where necessary. Basic to broad ecological studies is the realization that the intertidal organisms are reacting to their whole environment, of which tidal exposure is only one factor. Indicator organisms, once their position and prominence are established, form the best basis on which accounts of zonation on brief coastal visits can be given.

The flora plays a considerably more prominent part in this account than in those of the eastern Australian workers. The reasons for this are, firstly, that the algae and marine angiosperms are probably more important in southern Australia than on eastern Australian coasts; and, secondly, that one of the present authors is an algologist. The only other account of Australian algal ecology is that of Cribb (1954), who describes Port Arthur, Tas. The general picture of Australian intertidal ecology that has emerged in recent years is more adequate on the faunistic side than on the floristic.

Many more animals were collected during field trips than those mentioned in this paper. Attention has been given chiefly to those which were important ecologically. Thanks to the help of a number of specialists most animals except those belonging to the Porifera and the Bryozoa have been identified. Efforts have been made to obtain specific nomenclature uniform with that of other Australian workers in shore ecology. It is well known that some animals (particularly the molluscs) show considerable variation within a species. This has made rather difficult in a few cases the task of naming closely related or possibly identical species collected from localities 500-1500 miles apart.

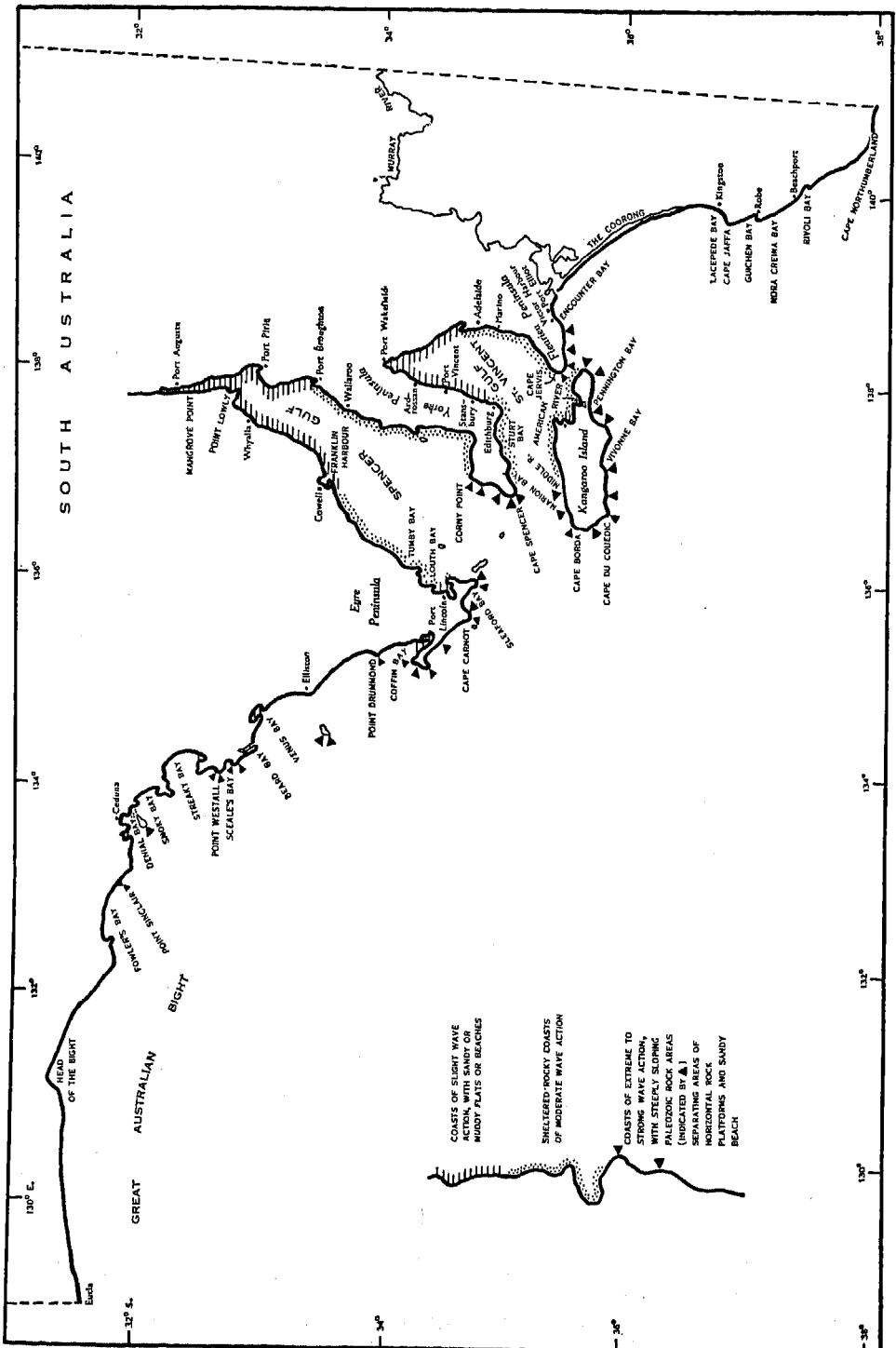


Fig. 1.—Map of South Australia, showing the broad classification of the coastline based on the intertidal ecology, and also most of the localities which were studied during the survey.

II. ENVIRONMENTAL FEATURES

(a) Coastal Geology and Topography

Much of the South Australian coastline is of Recent or Pleistocene age and consists of beach sands and dunes which in many areas have become consolidated to form calcareous sand-rock cliffs and reefs. This coastline is usually "supported" by capes or headlands of more resistant Palaeozoic rocks such as quartzites and schists or of igneous rocks such as granites.

The coastal features are shown in the accompanying map (Fig. 1, after the Geological Map of South Australia of 1953).

The south-eastern region, from Encounter Bay to the Victorian border, consists of a continuous sandy beach from Port Elliot to Robe, then alternating areas of Pleistocene sand-rock cliffs and reefs and loose sandy beaches. In the extreme south-east the cliffs and reefs are of Recent to Upper Oligocene age.

Fleurieu Peninsula, from Encounter Bay to Cape Jervis, comprises steep cliffs of Palaeozoic rock. Lower cliffs or stony beaches occur in calmer areas of Gulf St. Vincent from Cape Jervis to Marino.

On Kangaroo I. the south and west coasts consist of capes and headlands of Palaeozoic rocks, between which are extensive areas of sand-rock cliffs and sand beaches. The north coast is formed of Palaeozoic rocks, with high cliffs in the west and low land in the east. Sandy and muddy tidal flats are found in American River inlet and other parts of Nepean Bay.

The gulf region, including St. Vincent and Spencer Gulfs, is of Palaeozoic rock in the more exposed southern parts, which are similar to the south coast of Kangaroo I. The upper half or more of the gulfs is of Recent age and sandy-muddy beaches and tidal flats have developed under calmer conditions.

The south-west of Yorke Peninsula, and the south and whole west coast of Eyre Peninsula, extending almost to the head of the Great Australian Bight, are formed of Recent or Pleistocene calcareous sand-rock cliffs or sand beaches, supported by granitic points. From the head of the Bight westwards to the Western Australian border the coast is of Pliocene age; for 50 or more miles east of the head of the Bight it is sandy beach, backed by high sand dunes. West of the head of the Bight the Nullabor Plain reaches the sea, with calcareous cliffs up to 400 ft high dropping sheer to wave-cut platforms.

The coastal topography thus falls into four classes:

- (1) Steeply sloping Palaeozoic rocks, often granite, schists, or quartzites, dropping fairly steeply into deep water on rough coasts, less steeply under calmer conditions.
- (2) Calcareous sand-rock cliffs of Recent or Pleistocene age, which form wave-cut platforms at low tide level.
- (3) Sandy beaches between calcareous platforms or areas of older rock.
- (4) Sandy or muddy tidal flats, developed in bays or inlets or in the upper part of both Gulfs.

(b) Degree of Wave Action

Coastal waters in South Australia vary from very rough with constant breakers on exposed coasts to a "dead calm" in fully protected areas.

Coastline fully exposed to the south or west is subject to the prevailing winds from the same direction, and a heavy surge or lines of breakers up to 6 ft high or more are typical. Only on fairly calm days with an offshore wind are conditions greatly moderated, and such days occur only a few times during summer. The accompanying map shows that most of the South Australian coastline falls into this category, except the gulf region, the north coast of Kangaroo I., and small bays along otherwise exposed coast.

Within the gulf region, and along the north coast of Kangaroo I., a grading in degree of wave action occurs from exposed coast to strongly sheltered or land-locked areas. Thus conditions become calmer proceeding north in both gulfs, while the west coast in each gulf is calmer than the east, since winds are predominantly from the west. The calmest part of the north coast of Kangaroo I. is the almost land-locked area of American River inlet. Here wave action is almost negligible on the tidal flats except when strong winds blow across the lagoons. Other bays similar to American River inlet are Proper Bay (Port Lincoln), Franklin Harbour, parts of Coffin Bay, Venus Bay, Beard's Bay, and parts of Streaky Bay and Denial Bay.

The grading of wave action along coasts with otherwise similar environmental features (e.g. north coast of Kangaroo I.) provides an interesting series of ecological changes showing clearly the important effect of degree of roughness. Unfortunately objective measurement of wave action is seemingly impossible. As well as average conditions, extreme conditions over short periods are of great importance. The personal factor is always considerable in any estimate of wave conditions, and particularly on brief field surveys much latitude must be allowed for variation from conditions observed. It is frequently better to use indicator organisms to compare the degree of wave action in different areas. The height of zones and of rock pools can also be useful. The presence of rock pools with marine species some 100 ft above sea-level at Cape Bridgewater, near Portland in Victoria, indicates the extreme roughness of this locality. Here the cliffs descend vertically into very deep water. No area in South Australia has been seen which is comparable to Cape Bridgewater in these respects.

(c) Tides

Tides along the South Australian coast are of relatively small amplitude and may show considerable variation from place to place.

On exposed coasts the spring range is about $2\frac{1}{2}$ -4 ft, increasing to 4-5 ft on the north coast of Kangaroo I., to about 6 ft in the lower gulfs, 9-11 ft at the head of Gulf St. Vincent, and 12 ft at Port Augusta at the head of Spencer Gulf. The height of the tide may be greatly modified by winds. On exposed coasts, a strong offshore wind keeps the sea-level down and invariably gives the best collecting conditions. Within the gulfs the contour of the coast, and local winds, are important. At Port Augusta south-west winds send up the highest tides, while at Port Adelaide north-west winds have the greatest effect.

The tides at American River inlet during 1950 have been analysed by Womersley (1956). Many features apply generally to other parts of South Australia where conditions are not rough. The tides are considerably more irregular than in many parts of the world. At spring periods the tides are semidiurnal, but the two daily tides may vary from almost equal to markedly unequal amplitude. The highest tides usually occur between 0 and 3 days after new or full moon but may occur at other times. The lowest tides of the spring period rarely occur at the same time as the highest tides, but are most irregular. In fact, the lowest tides more often occur at the "dodge" periods.

At neap periods, the "dodge" effect occurs in many parts of South Australia, especially in the gulf region (Chapman 1924). In most cases only one tide per 24 hr occurs over 2-4 days at the neap period, but two tides of lesser amplitude may occur. Particularly in parts of the gulfs a more typical dodging tide may occur, during which the water level is almost stationary (subject to wind) for up to 24 hr. When the single tide occurs, the low level is usually lower than tides before and after, while the high may be nearly as high as some spring tides. The neap period varies from a day before the first and third quarters of the moon to 4 or 5 days after.

Mean sea-level, and other tidal means, are highest during the winter and lowest during the summer months, the difference being as much as 6-8 in. January-February is the period of the lowest sea-level and thus the lowest tides.

In general, the lower of the two daily low tides occurs during the middle of the day in summer (October-April) and in the middle of the night from June to September. The higher of the two daily low tides occurs in the early hours of the morning during summer, and in the afternoon during the winter. The lower of the high tides is the opposite of this.

Thus both the lower sea-level in summer and the time of the lowest tide make the summer months, especially January-February, most suitable for intertidal studies, and often prohibit work during the winter. The calmer conditions and more frequent offshore winds during summer also help field work.

(d) *Currents*

Most publications (e.g. "Australia Pilot", Vol. 1 (1937)) refer to a slow drift from west to east. Halligan (1921) describes how the cold Southern Ocean current bifurcates south-west of Cape Leeuwin, one part flowing northwards along the west coast of Western Australia and the other flowing eastwards along the south coast as far as Bass Strait. A warm current from the Indian Ocean also passes around Cape Leeuwin and flows eastwards across the Great Australian Bight as a surface current, above the cold Southern Ocean current. These currents mix in the vicinity of Tasmania, accounting for the cooler water in Bass Strait. Little is known, however, of currents near the coast in the region of the Great Australian Bight. The best recent information is the series of charts published by the Royal Netherlands Meteorological Institute (1949). These give little data for the continental shelf waters of the Great Australian Bight, and indicate the very variable nature of the currents off the shelf. There is clearly no sustained current along the shore of southern Australia, although the general tendency is probably for a slow drift from west to east, subject to variable

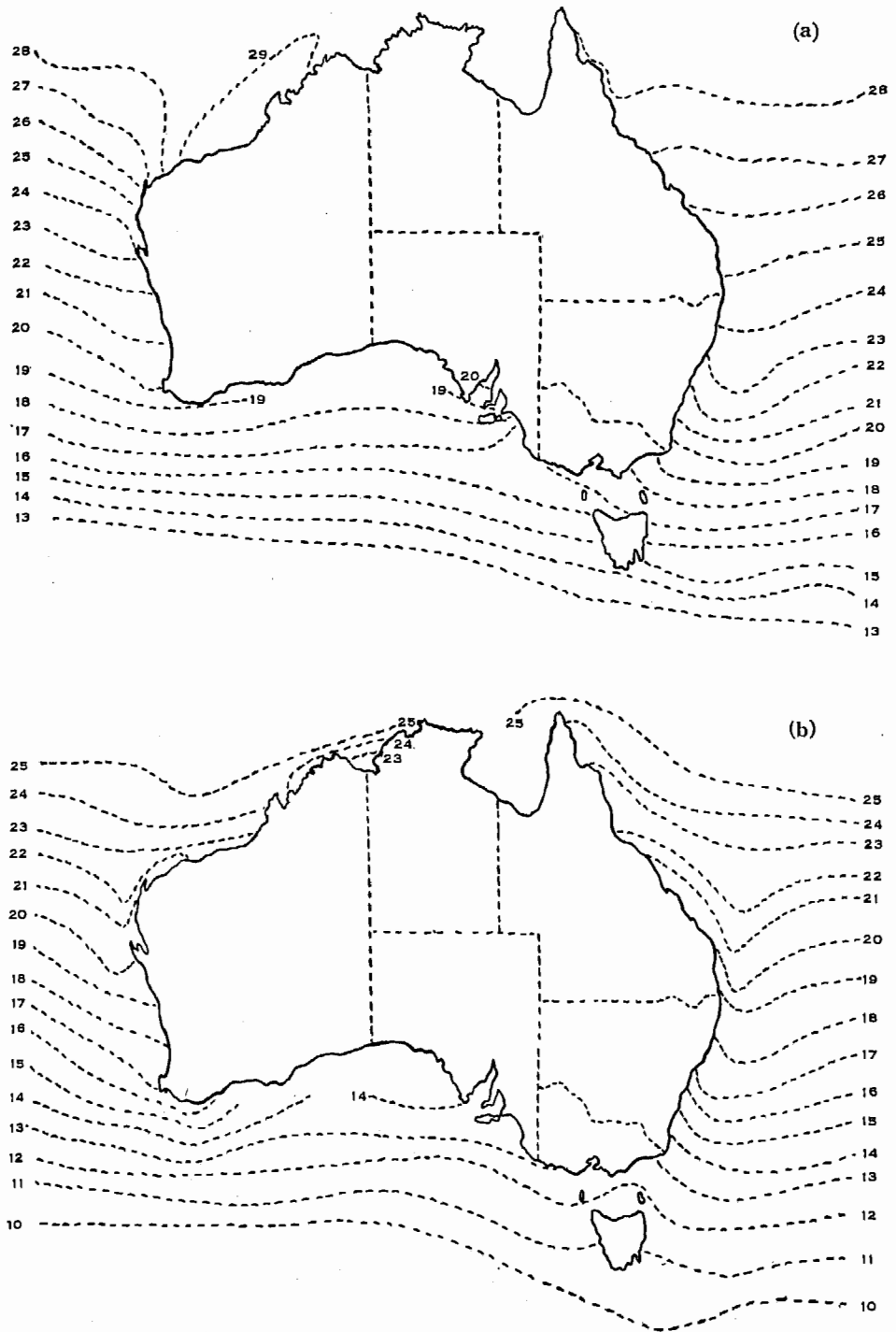


Fig. 2.—Mean sea temperatures around Australia during (a) February, and (b) August.

local counter-currents. From April to November there is a slight easterly current around south-west Western Australia, but not for the rest of the year. The 18th Annual Report of the Council for Scientific and Industrial Research (1944), which refers to results of drift-bottle experiments in Western Australian waters, indicates a flow southward around Cape Leeuwin and eastwards along the south coast in winter, and a reversal of this flow in summer.

(e) *Winds*

Winds blow mainly from directions between west and south, but are greatly influenced on the coast by local sea breezes. Northerly winds in summer are of the greatest importance. On a hot day (up to 100°F shade temperature) with an offshore wind (usually northerly) the sea-level is depressed, and should the wind be strong enough or coincide with a low tide, organisms at a low littoral level may be exposed for several hours and suffer considerable harm. Extensive areas of *Hormosira* and fucoids on reefs have been seen blackened and often killed under these conditions. While such conditions usually occur on only a few days in summer, they may be of importance in limiting the intertidal growth of many species.

(f) *Sea Temperatures*

The charts of the Royal Netherlands Meteorological Institute (1949), reproduced in Figures 2(a) and 2(b), give the best picture of sea temperatures along southern Australia. The sea temperatures from south-west Western Australia to south-east South Australia differ little at any one time of the year.

Few figures are available for the region of the Great Australian Bight, but isolated temperatures taken by the present authors during summer as far west as the head of the Bight were much the same as those known to occur on the south coast of Kangaroo I. The isotherms probably follow the contour of the coast in the central parts of southern Australia.

Temperatures just off exposed coasts are 18–20°C in summer and 14–16°C in winter. In the south-east of South Australia temperatures are lower in summer by 2–3°C, but only 1° or so lower in winter (Figs. 2(a) and 2(b)). This region of lower temperature has been emphasized by Bennett and Pope (1953) in describing Victorian shore ecology, and its significance is discussed later. Bennett and Pope separated the cooler Victorian and Tasmanian coasts from those of New South Wales and South Australia. They did not point out, however, that the uniform temperatures along the rest of southern Australia are matched by those on a relatively small region of the eastern Australian coast, just below and for 100–150 miles north of the Victorian–New South Wales border. Most of the New South Wales coast is subject to distinctly higher temperatures than that of southern Australia.

Sea temperatures within the gulf region are higher in summer and lower in winter than on rougher coasts, and show greater variation. Summer temperatures of up to 25°C or even to 30°C on shallow flats occur in the northern part of the gulfs or in shallow bays and inlets.

On exposed coasts the intertidal organisms when submerged are subject to much the same temperatures as that of offshore water. Air temperatures become important

for intertidal organisms during low tide. Rock pools, and shallow water on calmer shores, are subject to a greater range of temperature.

(g) *Air Temperatures and Relative Humidities*

The information shown in Table 1 was obtained from a publication of the Commonwealth of Australia (Australia, Bureau of Meteorology 1956). Data for January and July have been given as representing conditions in midsummer and midwinter respectively.

The information included in the table shows: (i) that the mean maximum daily temperature during summer and the seasonal variation of daily temperatures are much greater at localities along the coasts of the gulfs than along the open coast; (ii) that the mean minimum daily temperatures during winter along the open coast do not differ

TABLE 1
AIR TEMPERATURES AND RELATIVE HUMIDITIES AT FOUR COASTAL LOCALITIES

Locality	Long. (E.)	Lat. (S.)	Average Daily Maximum Temperature (°F)		Average Daily Minimum Temperature (°F)		Average Relative Humidity (%) at 3 p.m.	
			Jan.	July	Jan.	July	Jan.	July
Fowler's Bay	132° 49'	31° 59'	76.2	62.7	63.0	44.5	65	59
Port Augusta	137° 45'	32° 29'	80.5	62.8	65.3	43.0	33	52
Adelaide	138° 35'	34° 56'	84.8	59.9	61.0	45.4	31	61
Cape Northumberland	140° 40'	38° 5'	69.2	56.2	55.6	44.6	66	74

very much from those along the gulf coasts; (iii) that the seasonal variation of relative humidity is much greater along the gulf coasts than along the open coast. Temperatures are lower and humidity higher at Cape Northumberland in the south-east of South Australia than at the other localities. On exposed coasts the constant spray blown over the intertidal region must keep conditions moist, but again the extreme conditions of hot dry winds combined with low tides in summer are of importance. No measurements of humidity close to organisms in the intertidal region are available. On calm coasts low humidity would be expected during summer months.

(h) *Chlorinity, Phosphate, and Nitrate*

The available information about the chlorinity of sea-water in South Australia has been summarized by Thomas and Edmonds (1956). The chlorinity of surface samples varies from 19.00 to 20.25‰ off the open coasts to as high as 26‰ at Port Augusta. The little evidence available (Howard 1940; Thomas and Edmonds 1956) indicates that the amount of phosphate and nitrate in the sea water is low.

(i) *Dissolved Oxygen*

A number of estimations have shown that the oxygen saturation of sea-water on rough coasts varies from 95 to 110 per cent. The degree of saturation of still

water is more variable. Values of 100–200 per cent. (commonly about 130) saturation were recorded during the day for water covering extensive algal growth, and corresponding values of 50–60 per cent. saturation during the night.

III. TERMINOLOGY AND NOMENCLATURE

The zonation terminology used in this paper has been described and discussed previously (Womersley and Edmonds 1952) and is only outlined briefly here. It closely resembles that used by many other marine ecologists (e.g. Gislén 1930; Feldmann 1951).

Within the intertidal and subtidal regions three main zones can be distinguished (Table 2). These are primarily due to tidal fluctuations, modified to a varying extent by other environmental factors such as the degree of wave action and the aspect of the shore. While the limits of these zones correspond (more or less) to tidal limits and means, in many cases it is more convenient to use indicator organisms to distinguish the zones. Correlation between tidal factors and zones of organisms has been studied in South Australia only at American River inlet on Kangaroo I. (Womersley 1956). Unfortunately adequate correlation is very difficult on exposed coasts subject to a small tidal rise.

Indicator organisms are of great importance in delimitating zones in that they (like all organisms) are reacting to their total environment.

The following basic zones are recognized:

(i) *The Supralittoral Zone*.—This extends from the top of the littoral to the upper limit of marine organisms. Here the littorinid *Melaraphe* is dominant on most South Australian coasts and the lichens *Lichina* and *Verrucaria* are often common.

(ii) *The Littoral Zone*.—This is the main intertidal region, which extends from the sublittoral to about high water level or to the upper limit of prevalent wave-wash. This upper limit is difficult to fix satisfactorily on physical factors, and the present authors (like most workers) have used the upper limit of certain small barnacles or other indicator organisms to determine it. The lower limit of *Melaraphe* often corresponds roughly with the upper barnacle limit.

Within the littoral, three subzones can be conveniently distinguished on South Australian coasts:

- (1) *The upper littoral*, dominated by barnacles or various molluscs.
- (2) *The mid littoral*, dominated by barnacles on rough coasts and by molluscs, serpulids, or blue-green algae under less extreme wave action.
- (3) *The lower littoral*, dominated by algae.

(iii) *The Sublittoral Zone*.—This extends from about mean low water neaps downwards (to the limit of algal vegetation). This zone is distinguished in South Australia by brown algae such as *Cystophora*, *Sargassum*, and *Ecklonia*. The uppermost margin of the sublittoral may be exposed for short periods at extreme low tides or during the suck-back of waves.

Upper sublittoral is used for the region where larger brown algae are dominant; it usually extends down for some distance below the lowest low tides.

TABLE 2
SUMMARY OF INTERTIDAL ZONATION ON SOUTH AUSTRALIAN COASTS

Zone	Western and Central Coasts				South-Eastern Coast
	Extreme to Strong Wave Action	Moderate Wave Action	Slight Wave Action	Extreme to Strong Wave Action	
Supralittoral	Steeply Sloping Palaeozoic Rock	Horizontal Rock Platforms	Sand Beaches	Sheltered Coasts	Horizontal Rock Platforms
	<i>Calothrix</i> <i>Melaraphe</i>	<i>Melaraphe</i> <i>Lichina</i> <i>Verrucaria</i>	<i>Talorchestia</i>	<i>Melaraphe</i> <i>Lichina</i>	
Upper littoral	(<i>Chthamalus</i>) <i>Chamaesipho</i>	<i>Chthamalus</i> <i>Chamaesipho</i>	Isopods		Relatively bare when rocky Sampires
	<i>Catophragmus</i> (Molluscs, <i>Galeolaria</i> , <i>Brachyodontes</i> algae)	(<i>Catophragmus</i>) Molluscs, <i>Galeolaria</i> , blue-green algae <i>Brachyodontes</i> <i>rostratus</i>		<i>Chthamalus</i> <i>Chamaesipho</i>	Sampires, mangroves, or <i>Bembicium</i>
Mid littoral					<i>Bembicium</i> , <i>Modiolus</i> <i>inconstans</i> , mangroves, Enteromorpha
					Molluscs, <i>Galeolaria</i> , blue-green algae
Lower littoral					
	<i>Balanus</i> - coralline mat	<i>Hormosira</i> Other algae	Bivalves	<i>Corallina</i> - <i>Gelidium</i> , <i>Hormosira</i>	<i>Hormosira</i> <i>Brachyodontes erosus</i> , <i>Kataysia</i> , <i>Pinna</i>
Sublittoral fringe	<i>Cystophora intermedia</i>	<i>Cystophora intermedia</i>			
	Furoid algae etc.	Furoid algae, <i>Ecklonia</i> , red algae	Bivalves	Other algae	<i>Durvillea</i> <i>Macrocystis</i>
Upper sublittoral					<i>Hypnea</i> , <i>Spyridia</i> , and other algae <i>Zostera</i> <i>Posidonia</i>

Sublittoral fringe conveniently describes a zone often found at the upper margin of the sublittoral, extending down to extreme low water or to the lower limit of the suck-back of waves. This term is used in the original sense of Stephenson (1939), not in the broader sense (equivalent to upper sublittoral) of other workers.

This terminology has been used in papers on South Australian marine ecology (Womersley 1947, 1948, 1956; Edmonds 1948); and in recent papers on the Victorian coast by Bennett and Pope (1953) (although referred to Stephenson's (1949) scheme) and on Tasmania by Cribb (1954). The account of Womersley and Edmonds (1952) which discussed the terms and nomenclature proposed by Stephenson and Stephenson (1949) has been criticized by Chapman and Trevarthen (1953) and Guiler (1953). However, Chapman (1956, p. 335) in a more recent paper uses zonation terms closely similar to those supported by the present authors.

Within the zones, associations or communities can be recognized. Distinct groupings of one or more species may be termed associations, while less distinct groupings are referred to as communities.

The coast of Kangaroo I. was classed by Womersley (1947) into two formations, following Cotton (1912):

- (1) Rocky coast formation, subdivided into exposed and sheltered subformations.
- (2) Sand and sandy-mud flat formation.

Similar divisions of the coast are used in this paper, since they describe the main coastal types found in South Australia. Whether they be termed "formations" or not is of no great consequence; they can equally well be referred to as "types" of coast or by other noncommittal terms. This concept of "formation", based on both habitat and life form (lithophilous, holdfast-possessing algae on rocky coast and stoloniferous sea-grasses or algae on sandy or muddy flats) is probably closest to the use of "formation" as a major unit in land ecology.

IV. INTERTIDAL ECOLOGY

The following account deals first with the western and central parts of the South Australian coastline, and later with the south-east coast of the State (from Robe eastwards). The latter is similar to the Victorian coast and shows certain differences from areas of South Australia further west. These two coastal regions are separated by some 120 miles of sandy beach. The importance of the differences between the south-east coast and the central and west coasts of South Australia is discussed later in this paper.

A. THE WESTERN AND CENTRAL COASTS

These areas, comprising all the coastline west of Port Elliott, fall into two major types, with convenient subdivisions, dependent on degree of wave action and nature of the substratum. These two factors are, of course, partly interdependent.

The following types of coast are recognized (see Table 2):

- (a) Coasts of moderate to extreme wave action; rocky with sandy beaches interspersed.
- (i) Coasts of strong to extreme wave action.
- (1) Steeply sloping intertidal regions of Palaeozoic rock.
 - (2) Horizontal intertidal rock platforms.
 - (3) Sandy beaches (on the open coast).
- (ii) Sheltered coasts of moderate wave action.
- (b) Coasts of slight wave action, with sandy or muddy flats or beaches.

Since the nature of the substratum and degree of wave action are the two most important factors controlling the occurrence of marine organisms, these divisions are both convenient and natural ones, characterized by distinctive communities or species. There is, of course, grading between these coastal types, particularly within the gulf region. Calm areas are often found on rough coasts where there is local shelter. The sheltered side of large boulders will likewise often show zonation more characteristic of sheltered coasts.

The map (Fig. 1) shows the approximate extent of these coastal types. Small calmer areas on rougher coasts cannot be shown on a map of this scale.

Rocky coast (interspersed with sandy beaches) with strong to extreme wave action comprises all the coastline exposed to prevailing winds from over deep water—the Great Australian Bight, the west coast and southern tip of Eyre Peninsula, the southern ends of Yorke and Fleurieu Peninsulas, the south and west coasts of Kangaroo I., and the south-east coast of the State. Rocky coasts of moderate wave action include the southern parts of Spencer and St. Vincent Gulfs and the north coast of Kangaroo I. Coasts of slight wave action, with sandy or sandy-mud flats, comprise the northern parts of the gulfs (excluding rocky outcrops), and several almost land-locked bays scattered along rougher coasts, such as parts of Denial Bay and Streaky Bay, Beard's Bay, parts of Coffin Bay, Proper Bay in Port Lincoln, and American River inlet on Kangaroo I.

(a) *Coasts of Moderate to Extreme Wave Action;
Rocky with Sandy Beaches Interspersed*

(i) *Extreme to Strong Wave Action.*—These coasts are continually subject to successive lines of breakers and heavy spray. The only relatively calm periods occur occasionally during summer when strong offshore winds blow; then the intertidal region is subject only to low waves.

(1) *Steeply Sloping Intertidal Regions of Palaeozoic Rock.*—Palaeozoic rocks—granite, schists, gneisses, etc.—form the exposed headlands and capes along the South Australian rough coastline, as shown in the accompanying map. Rock in the intertidal region varies from smooth granite, sloping steeply into deep water (e.g. Point Sinclair, Plate 1, Fig. 1), to broken masses of rock presenting a variety of microhabitats. The smooth rock faces are more common and show clearer zonation than the broken areas. Where waves surge up smooth rock for a considerable height, the intertidal zonation may be spread over a vertical height of up to 30 ft (Plate 1, Fig. 1), with well-defined and sharply limited zones.