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THE MARINE ALGAE OF KANGAROO ISLAND

IV. THE ALGAL ECOLOGY OF AMERICAN RIVER INLET

By H. B. S. WOMERSLEY

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Summary

An account is given of the marine ecology of American River inlet on the north coast of Kangaroo Island, S.A. The plant and animal associations are described, with emphasis on the marine algae, and an attempt is made to relate levels of zones to tidal means.

I. Introduction

American River is a tidal inlet extending from the north coast of Kangaroo Island, S.A., to within half a mile of the south coast. The term "river" is a misnomer as the amount of fresh water entering the lagoons is negligible.

From a narrow neck about a quarter of a mile wide at the mouth, the inlet widens into several extensive lagoons, measuring some 5 miles in a north-south direction and 4 miles from west to east (Plate 1, Fig. 1). From the opening a narrow channel (2-3 fm deep) extends past Muston jetty and into Pelican Lagoon, where several small islands occur (see Fig. 1). The channel is bordered by sandy or muddy tidal flats which are covered by less than 2 ft of water at low tide, with the shoreward parts usually exposed. The drop-off over the flats is very gentle, sometimes less than 1 ft on a flat 600 ft wide. Parts of Pelican Lagoon are from 2 to 5 fm deep (shown by denser dotting in Fig. 1).

In paper I of this series (Womersley 1947) a brief preliminary account of American River inlet was given. The basic terminology used in describing the zonation of organisms on the coasts of Kangaroo Island was outlined, and this has been further discussed and slightly modified in a separate paper (Womersley and Edmonds 1952). The terminology adopted is similar to that found satisfactory by many marine ecologists, and differs from that of Stephenson and Stephenson (1949) in retaining the older use of littoral and mid littoral, and thus avoiding illogical nomenclature for the zones. "Sublittoral fringe" is used in the original sense of Stephenson and Stephenson, and as this is then a term of restricted (though useful) application, the more widely applicable term "upper sublittoral" is used for the zone from mean low tide level downwards when the dominant(s) extend well below lowest tide level. Bennett and Pope (1953) have used for Victorian coasts virtually the same scheme as supported by Womersley and Edmonds, though relating their scheme to that of Stephenson and Stephenson. Gislén (1930), Feldmann (1951), and Sundene (1953) use essentially the same scheme as that adopted here. The new terminology of Stephenson and Stephenson is supported in large measure by Chapman and Trevarthen (1953) and Guiler (1953), who, however, give no adequate reasons for changing the older and reasonably well-established nomenclature of zones.

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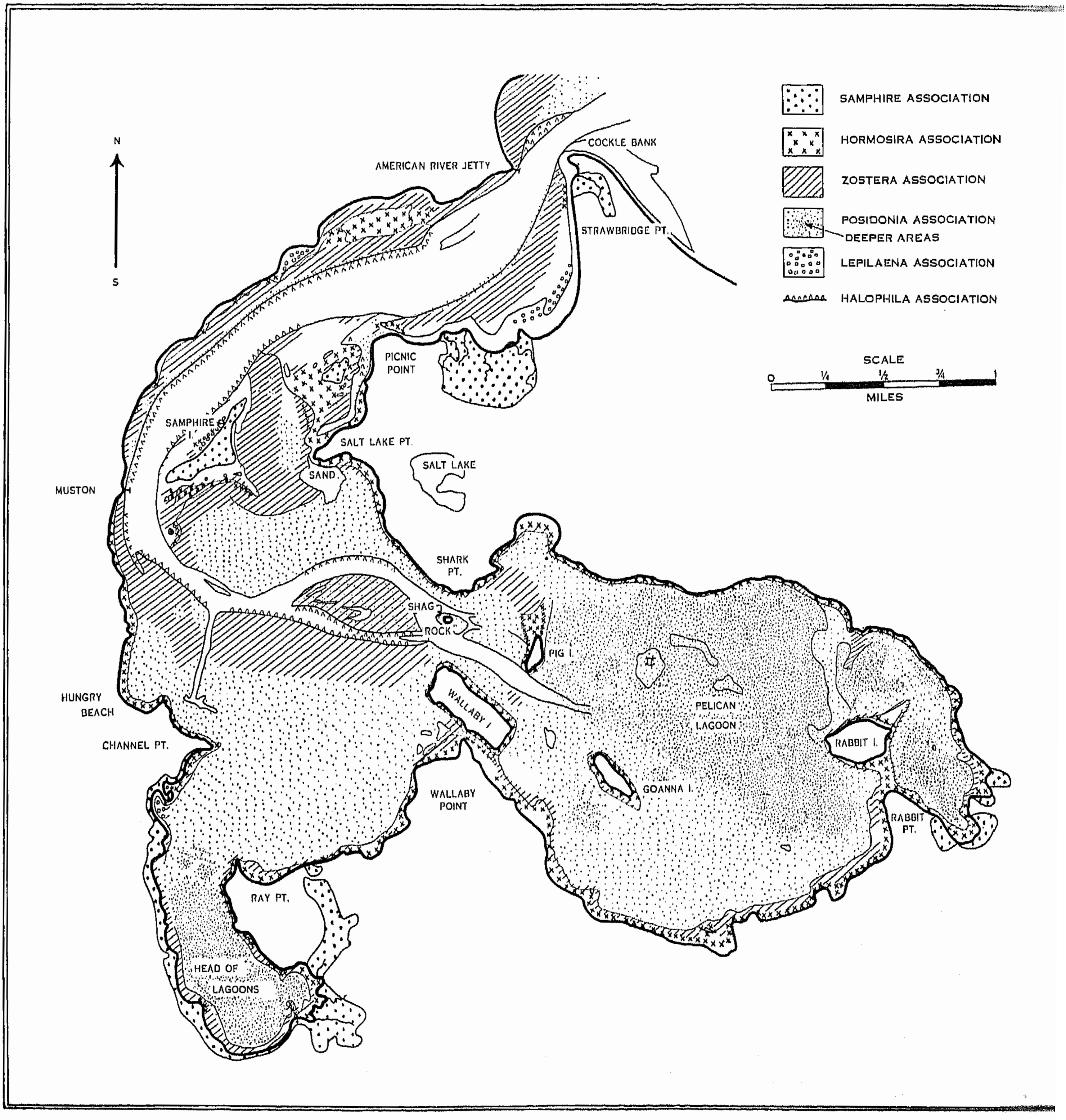

Fig. 1.—Map of American River inlet. In delimiting the *Posidonia* association, denser dotting is used for the deeper areas (as shown in an aerial ph graph), and lighter dotting for shallow areas where the leaves are at or near to the surface at low tide.

Chapman and Trevarthen (1953) also believe there is no advantage in correlating zonation on different types of substratum under one terminology.

At American River inlet two types of substratum occur: sandy mud in the lower tidal levels and (sometimes) rock at the upper levels. Here it is obviously necessary to use one scheme for both types of substratum. It is interesting also that Dahl (1952) has found that sandy beaches can be subdivided (based on the organisms present) into three horizontal belts to which he applies the names of Stephenson and Stephenson (the older nomenclature applies just as well).

In December 1949 the South Australian Harbours Board established an automatic tide gauge at American River jetty. The continuous tidal records from this have made possible an attempt to correlate the zones of algae and animals with tidal fluctuations, and to define critical tidal levels.

The entire coast of the inlet has been examined during the survey, at all seasons of the year. From these detailed observations broader generalizations have been drawn, and it is clear that while the basic zones of organisms are quite stable, minor species of the sublittoral fringe and lower littoral may vary in their presence and distribution in different seasons. Sufficient boat traverses have been made across the deeper parts of the lagoons to show the dominant organisms.

The names of the islands in Pelican Lagoon are those used locally, but the more prominent points around the lagoon have been given names for convenience as there seem to be no locally used names.

This paper also deals briefly with those animals which form a conspicuous and important part of the zonation. The animal life of the inlet is rich, and a detailed zoological survey would be of great interest. Taxonomic references for the algal species are given by Womersley (1950).

II. The Environment

(a) *The Substratum*

The tidal flats are composed mainly of black mud, 4-10 in. deep, often with a layer of sand on top. Near the shore the mud or sand layer is shallower, sometimes with exposed rock. The mid and upper parts of the littoral zones consist of either sandy beach, samphires, or the base of low rocky cliffs of calcareous sand rock (see Plate 1, Fig. 2; Plate 2, Figs. 1 and 2).

Where rock is exposed marine algae occur directly attached to it, but wherever there is a layer of mud the algae grow on either molluscs or pebbles in the mud (e.g. *Hormosira* on *Brachyodontes*) or on the marine angiosperms which cover most of the tidal flats.

The channel supports plant growth mainly on the upper sides, as the bottom consists of loose shells and the current (up to 2½ knots) prevents a stable substratum. Occasional patches of rock near Muston and American River jetty allow the development of some brown algae, mainly *Sargassum biforme* Sonder.

(b) *The Tides*

The continuous tidal curves obtained at American River jetty were graphed in weekly periods for 12 months from January 1, 1950, and from them mean sea-level and means of the higher and lower daily tides were calculated (see Table 1). Several 24-hr surveys carried out at American River jetty, at Muston, and in Pelican Lagoon simultaneously show that the tides are of the same form throughout the inlet and of very nearly the same amplitude (see Womersley 1947, p. 232 and Fig. 2). Differences in amplitude at American River jetty and Pelican Lagoon are usually less than 2 in. in a rise of 3½-4 ft and this difference may sometimes be due to wind effect.

The tidal range at American River jetty is usually 3·9-4·3 ft (extremes of 3·4 and 4·8 ft) for spring tides and 3·0-3·6 ft (extremes of 2·0 and 3·75 ft) for neap (dodge) tides, but the range is extremely variable.

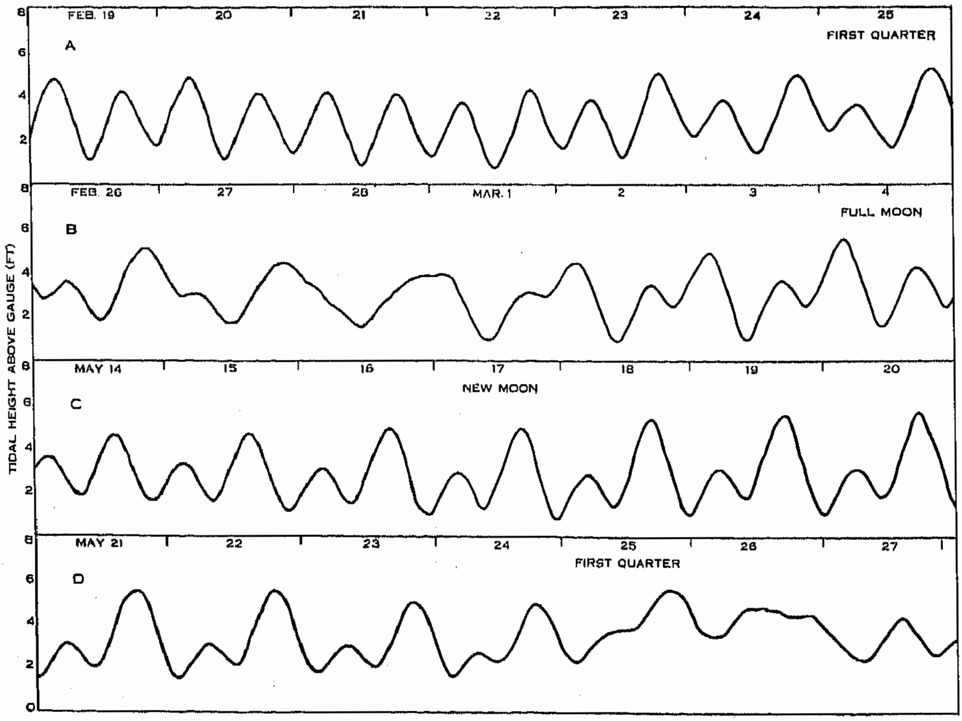

Fig. 2.—Representative tidal curves from American River inlet, 1950. *A*, typical spring tides with almost equal amplitude (semi-daily type). *B*, neap tides with one tide per day over 2-3 days. *C*, spring tides with marked diurnal inequality (mixed type). *D*, dodge (neap) tides showing "dodging effect" on May 26.

The tides at Muston are ½-1 hr behind, and in Pelican Lagoon up to 2 hr behind, the tides at American River jetty.

An examination of the tidal curves for 1950 shows their great irregularity compared with those from many other regions (e.g. compare the curves given by Doty (1946, Fig. 1) for the Pacific Coast of the United States of America). Tides in many localities in South Australia are noted for their irregularity, both at one locality and between different localities. Some examples of the American River inlet tides are given in Figure 2. Curves *A* and *C* are of spring tides, curves *B* and *D* of neap (dodge) tides.

At spring periods the tides are semidiurnal, but the two daily tides may be almost equal in amplitude ("semi-daily")* (Fig. 2*A*) or markedly unequal ("mixed") (Fig. 2*C*), or intermediate between these two types. The highest tides usually occur between 0 and 3 days after new or full moon, but may occur at other times. The three highest tides recorded during 1950 occurred at full moon, 1 day after, and 2 days before full moon. 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 the neap period the "dodge" effect occurs, but is shown in different ways. In most cases only one tide per 24 hr occurs over 2-4 days at the neap period (Fig. 2*B*), but occasionally two tides of lesser amplitude occur; on other occasions a more typical "dodging" tide occurs, with the water level remaining almost stationary for 6-10 hr (Fig. 2*D*). When the single tide occurs, the low level is usually lower than tides before and after, whilst the high may be nearly as high as some spring tides. The neap period occurs at varying times, from a day before the first and third quarters of the moon to 4 or 5 days after.

Little is known of the cause of the dodge effect, which is largely confined to the gulf region in South Australia. The hypothesis of Chapman (1924) is that during the neap period the sun and the moon, together with other tide-producing forces, exert almost equal but opposite effects, one nullifying the other. It has been suggested that the abnormally large effect of the sun is due to the synchronizing of the natural period of swing of the basin of water between Australia and Antarctica with the period of the tide-producing forces.

A partial cause of the tidal irregularities is wind. Strong westerly winds across Investigator Strait (26 miles wide) raise the sea-level generally in the gulf region, as the water is not forced out through Backstairs Passage (10 miles wide) to the same extent. This results in higher tides at American River inlet. A south wind tends to have the opposite effect.

Even when the tide is ebbing or flowing relatively strongly, it may be very irregular over short periods owing to seiche effects, sometimes dropping or rising as much as 4 to 6 in. from the general trend of the tide.

Owing to these irregularities, it was found to be meaningless to average such levels as high and low water of spring and neap tides. Means of the following levels could, however, be calculated and are given below (Table 1):

Mean of the higher of the two daily high waters (M.H.H.W.),
Mean of the high waters (M.H.W.),
Mean of the lower of the two daily high waters (M.L.H.W.),
Mean sea-level (M.S.L.),
Mean of the higher of the two daily low waters (M.H.L.W.),
Mean low water (M.L.W.),
Mean of the lower of the two daily low waters (M.L.L.W.).

* See Marmor 1951.

These levels are similar to those used by Doty (1946), though not so comprehensive. At the neap periods, when only one high and one low tide occurred, L.H.W. and H.L.W. were omitted. Records for January, February, and April are incomplete, as about 1 week's readings were not taken in each month. Curves from the corresponding period about 29 days later were interpolated in each case.

TABLE 1

TIDAL DATA, AMERICAN RIVER JETTY, 1950

All tidal figures (ft) are based on, or corrected to, the Harbours Board tide gauge at American River jetty. Highest high water in 1950, 7·1 ft. Lowest low water in 1950, −0·1 ft

Month	M.H.H.W.	M.H.W.	M.L.H.W.	M.S.L.	M.H.L.W.	M.L.W.	M.L.L.W.
January	4·79	4·09	3·27	2·90	2·21	1·66	1·25
February	4·35	3·89	3·40	2·64	1·77	1·28	0·80
March	4·35	3·85	3·32	2·64	1·77	1·34	0·99
April	4·59	3·95	3·28	2·82	1·79	1·52	1·27
May	5·13	4·21	3·13	3·13	2·00	1·81	1·66
June	5·33	4·32	3·21	3·29	2·47	2·03	1·73
July	5·16	4·38	3·41	3·16	2·36	1·94	1·61
August	4·94	4·47	3·83	3·11	2·16	1·78	1·40
September	4·95	4·47	3·86	3·18	2·20	1·81	1·48
October	4·89	4·20	3·45	3·07	2·07	1·81	1·57
November	4·89	4·12	3·18	3·07	2·07	1·85	1·66
December	4·81	3·85	2·99	2·82	2·14	1·60	1·28
Mean, 1950	4·85	4·15	3·35	2·99	2·08	1·71	1·41

Table 1 gives various means calculated for each month during 1950. All show the same yearly trend, being higher during the winter months and lowest during summer months. Mean sea-level, for instance, was lowest during February and March 1950 (2·64 ft), and highest in June (3·29 ft), the difference being 0·65 ft. The means for January (higher than December and February) are possibly higher than normal, perhaps due to northerly winds during the month. Very low tides during January are frequent, and from experience the mean sea-level would be expected to be as low as that of February.

General features of the tides at American River inlet are as follows:

(i) The higher of the two daily high tides occurs in the early hours of the morning (often 2-7 a.m.) during the summer months (November to February) but changes over to the afternoon (12 noon-5 p.m.) during the winter (April to September). March and late September-October are the "change over" months.

(ii) The lower of the two daily high tides is virtually the opposite of the highest: between 3 and 6 p.m. from October to February, and between 3 and 7 a.m. from April to August.

(iii) The lower of the two daily low tides occurs in the middle of the day (10 a.m.-2 p.m.) from late November to April, and in the middle of the night (8 p.m.-4 a.m.) from June to October, with April-May and October-November as "change over" months.

(iv) The higher of the two daily low tides is opposite to the lower, occurring in the middle of the night from November to April and in the middle of the day from May to September.

(c) *Exposure to Air*

The percentages of the total time during which different heights are covered by water are given in Table 2 for each month of 1950. The values vary considerably from month to month, and even more for weekly periods within each month. This is a direct result of the tidal irregularities. The heights for which exposure to air has been calculated correspond to the main changes between zones and to tidal levels given in Table 1 which lie within a zone. Table 2 will be referred to later when dealing with critical levels.

The degree of exposure to the air at any particular level is greater during summer months than during the winter. This, together with the much higher summer temperatures, means that the severest environmental conditions will occur when a hot day in summer coincides with a very low tide. Such critical summer day conditions are possibly of greater importance than any tidal means in determining the levels at which any particular alga can grow.

(d) *Wind*

The prevailing winds are from south to west, with some northerly winds in summer. The effect of westerly winds in causing generally higher tides has been referred to above. Within the inlet mild breezes have little effect except to cause waves in the channel. However, on one area of the north coast of Pelican Lagoon the water is 4 ft deep or more at the base of vertical cliffs, and even a light southerly wind (having passed over 2 or 3 miles of water) causes continuous lapping of waves on the base of the cliffs. This results in some 200 yd of coast which is more allied to other areas of the north coast of Kangaroo Island than to the rest of American River inlet. At Salt Lake Point also, wave action is more pronounced, and some organisms characteristic of the "sheltered rocky coast subformation" (see Womersley 1947) occur here.

Strong winds (especially in late winter) will cause wave action along the edge of the channel sufficient to remove many epiphytic algae from their angiosperm hosts.

(e) *Wave Action*

Wave action is completely dependent on wind; on the whole it is slight, often almost absent. This is one of the main causes of the distinctiveness of the American River inlet. Several minor exceptions have been mentioned in Section II(*d*).

(f) *Water Turbidity*

The water carries a certain amount of fine suspended mud, especially in and near the channel when strong tides are running. The bottom of the channel (2-3 fm deep) can only be seen when there is no tidal current. The turbidity doubtless

TABLE 2

EXPOSURE OF ZONES TO AIR: PERCENTAGES OF TOTAL PERIOD DURING WHICH EACH LEVEL WAS COVERED

Month / Level:	Upper *Bostrychia*	M.H.H.W.	M.H.W.	M.L.H.W.	M.S.L.	Upper *Hormosira*	M.H.L.W.	M.L.W.	M.L.L.W.
Height (ft):*	5·3	4·85	4·15	3·35	3·0	2·55	2·1	1·70	1·40
January	3	6	14	32	43	58	75	85	92
February	0	2	9	28	38	51	66	78	85
March	0	2	10	25	35	50	66	77	86
April	2	5	13	28	40	57	71	82	91
May	4	9	21	38	48	62	81	91	96
June	8	13	23	40	53	70	86	93	98
July	6	11	22	40	50	68	80	88	93
August	3	9	21	40	52	65	79	87	93
September	3	7	20	42	52	69	81	90	96
October	2	6	18	35	49	65	79	91	95
November	4	8	17	33	46	64	80	91	96
December	2	6	14	28	36	52	75	85	91
Mean, 1950	3	7	17	34	45	61	77	87	93

* Based on American River tide gauge.

has some effect on the organisms, and is possibly a partial cause of the yellow, grey, or brownish colour of most of the Rhodophyceae, in contrast to the brighter red colour of deeper- and cleaner-water forms. Many algae have a fine coat of mud or silt over their thalli.

(*g*) *Temperature*

(i) *Air Temperatures.*—Those given for Kingscote (Womersley 1947, p. 234), probably apply fairly well at American River inlet, though cool southerly breezes would have greater effect in the inlet. The Kingscote temperatures show a range (monthly averages) from 8·7-14·2° C in July to 15·6-22·7° C in February. Probably more important than mean temperatures, however, are occasional very high temperatures (up to 100° F) in summer, which may cause extreme conditions during low tides on the tidal flats.

(ii) *Sea Temperatures.*—These range from about 10° C on the tidal flats and channel on cold winter days to 23° C in the channel and over 30° C on shallow flats on hot summer days. The annual, and also the daily range in summer, is great, and doubtless prevents some algal species from occurring in the inlet. The annual range in temperature is three to five times as great as on the south coast of Kangaroo Island.

(*h*) *Shade*

Most of the intertidal zones are exposed to full sunlight except the upper littoral (occasionally also the mid littoral) which may occur at the base of low cliffs. The upper littoral is often completely shaded, or has many shaded hollows and crevices which allow the development of the algae *Bostrychia simpliciuscula* Harvey and *Gelidium pusillum* (Stackhouse) Le Jolis. In the shade under large samphires (*Arthrocnemum arbuscula* (R. Brown) Moq.) at about high tide level, mats of *Chaetomorpha capillaris* (Kützing) Borgesen as well as *Bostrychia* and *Gelidium* occur.

(*i*) *Salinity*

The following ranges in salinity were obtained during a 24-hr survey on January 20-21, 1946: American River jetty, 35·9-36·1‰; Muston jetty, 35·9-36·3‰; Pelican Lagoon 37·0-37·2‰. The higher salinity in Pelican Lagoon is due to increased evaporation in summer from the relatively shallow and isolated lagoons.

The amount of fresh water entering the inlet is negligible except after heavy rain, when a few creeks may flow, and even then they exert only a minor local effect. On rare occasions very heavy rain during low tides may lower the chlorinity on the tidal flats. During January 1946, over 5 in. of rain fell in 4 days, and at one stage the salinity on the tidal flats was 30·2-31·8‰. For several days afterwards there was a noticeable stench of decay, apparently from algae killed by this low salinity.

(*j*) *Oxygen*

Oxygen saturation of the water varies considerably during the day and night. Values of 130 per cent. saturation during the day in summer are common, dropping to 50-60 per cent. at night. Broken water tends to keep this latter value higher.

In shallow water over dense algal growth, saturation values as high as 200 per cent. occur.

The oxygen in the water is controlled, firstly, by the plants and animals present, and secondly, by wave action and broken water, which tend to keep the saturation nearer 100 per cent. Oxygen saturation is rarely, if ever, likely to be a controlling factor in algal growth or distribution in this type of habitat.

(*k*) *Phosphate*

Samples taken in January 1946 showed varying phosphate values, mostly between 2 and 16 parts per 1000 million of phosphate phosphorus. One sample from Pelican Lagoon contained 63 parts per 1000 million, but this was probably a local effect due to bird colonies.

(*l*) *Nitrate*

In six samples taken at the same time as the phosphate samples no nitrate could be detected. Low nitrate is usual in South Australian waters. Both low phosphate and low nitrate are due largely to the absence of any large rivers in the region, but at American River inlet may also be due to a high phytoplankton population.

On Shag Rock in Pelican Lagoon, *Gayella polyrhiza* Rosenvinge occurs plentifully on rocks where shags roost. As in many localities in other countries, *Gayella* (and *Prasiola*) occurs where there is nitrogenous excrement from birds.

III. Zonation in Relation to Tidal Levels

Zonation of algae and animals is relatively constant throughout the inlet, especially at or below the mid-littoral level where tidal flats always occur. However, two types of coast are found within the inlet, resulting in differences at the upper littoral and supralittoral levels:

(1) Rocky cliffs (6-30 ft high) descending to the mid littoral, with shaded hollows at their base (Fig. 3, section *B*; Plate 2, Fig. 2). Cliffs occur around most of the islands in Pelican Lagoon, on much of the north side of Pelican Lagoon, and as outcrops elsewhere in the inlet.

(2) Areas where the tidal flats shelve gently through the littoral, with samphires or shelly beaches in the upper littoral and supralittoral (Fig. 3, section *A*; Plate 1, Fig. 2). Most of the coast from American River jetty to Muston and on to the head of the lagoons is of this type, while smaller areas occur in Pelican Lagoon. The larger areas of samphires are shown in Figure 1, but a fringe of samphires occurs around most of the coast where there are no rocky cliffs.

(*a*) *The Typical Zonation*

The typical zonation where cliffs occur is shown in Figure 4 (see also Fig. 3, section *B*).

(i) *The Supralittoral.*—The supralittoral is generally almost bare of macroscopic organisms. Occasional *Bembicium melanostoma* Philippi may extend into it, and

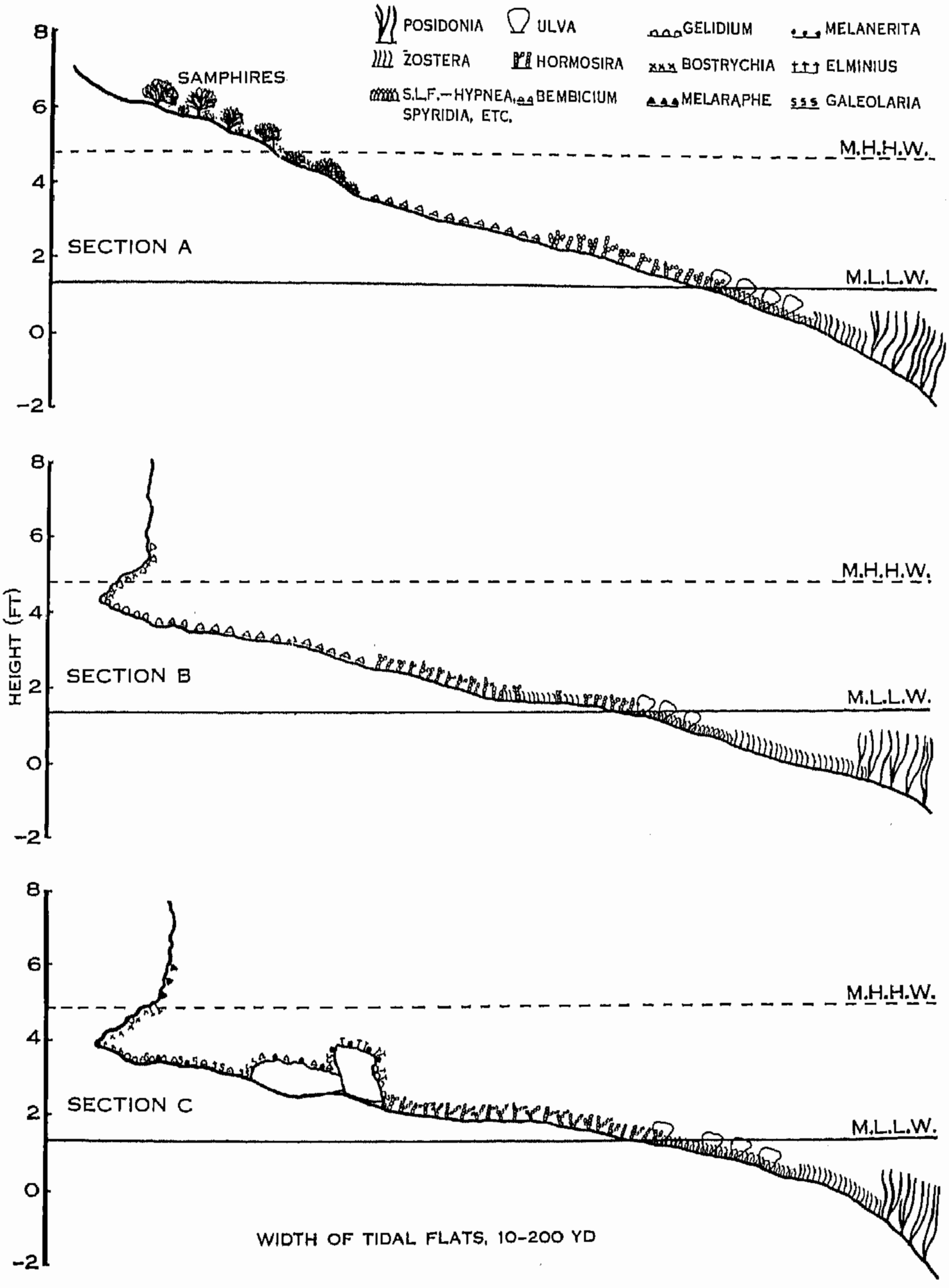

Fig. 3.—Zonation diagrams for representative coasts in American River inlet. Section *A*, sandy beach with samphires at rear of tidal flats. Section *B*, low cliffs at rear of tidal flats. Section *C*, an area on the north coast of Pelican Lagoon subject to greater wave action, resulting in *Melaraphe*, *Elminius*, and *Galeolaria* occurring at higher levels.

the lichen *Verrucaria microsporoides* Nyl. occurs in the lower part as tiny black spots which in some places give a dark appearance to the rock. In restricted areas of greater wave action, *Melaraphe unifasciata* Gray may occur in small numbers.

(ii) *The Littoral.*—For convenience the littoral may be divided into three zones.

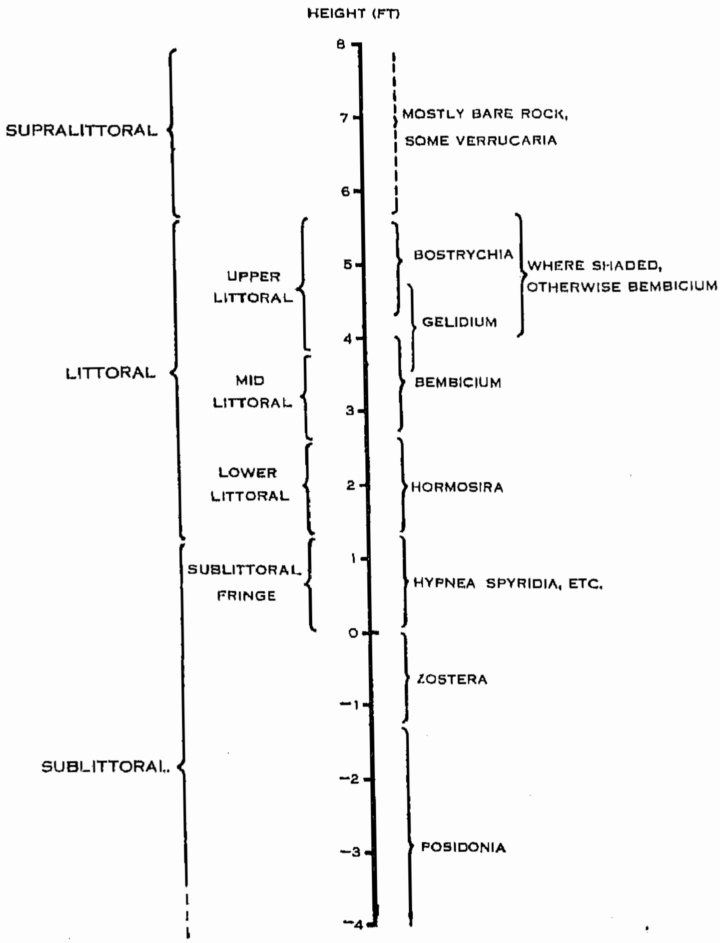

Fig. 4.—Scheme of the typical zonation in American River inlet, showing relation of organisms to tide levels.

(1) *Upper Littoral.*—On rock not in shade, the upper limit of the littoral can probably best be placed at or just above M.H.H.W. (about the 5·0 ft level). The chief organism here is the mollusc *Bembicium melanostoma*, which extends upwards from the mid littoral. In some places *Verrucaria* darkens the rock.

In shaded places, *Bostrychia simpliciuscula* occurs from 5·4 to 4·5 ft, and *Gelidium pusillum* from 5·0 to 3·4 ft. The levels of these algae are as much dependent on shade as on tidal exposure, and are therefore rather variable. *Gelidium* tends to occur in less shaded places than *Bostrychia*, sometimes where direct sunlight falls on it for short periods.

(2) *Mid Littoral.*—This zone is dominated by *Bembicium melanostoma* (Plate 4, Fig. 1), which is one of the few organisms able to withstand the exposure to air and to direct sunlight of the zone. The lower limit lies at the 2·5-2·6 ft level; above about 3·5 ft on unshaded rock *Bembicium* becomes less common, but individuals can be found well above this level. The bivalve *Modiolus areolatus* Gould may form patches in the mid littoral and become co-dominant with *Bembicium*. Small communities of *Enteromorpha clathrata* (Roth) J. Agardh may also occur here.

(3) *Lower Littoral.*—This zone is dominated by *Hormosira banksii* (Turner) Decaisne throughout most of the inlet. Its limits are from 2·5-2·6 to 1·3-1·4 ft; the lower limit corresponds closely to M.L.L.W.

(iii) *The Sublittoral.*—The littoral-sublittoral boundary lies at the junction of the *Hormosira* zone and a zone of red algae dominated by *Hypnea musciformis* (Wulfen) Lamouroux and *Spyridia biannulata* J. Agardh. The upper limit is at 1·2-1·4 ft (M.L.L.W.). This zone extends down for only a short distance, rarely more than the 0·0 ft level, though isolated plants may occur lower. This *Hypnea-Spyridia* zone may be referred to as the sublittoral fringe in view of its restricted vertical range.

Zostera muelleri occurs from about 0·5 to —3 ft or lower, though in some areas it occurs as high as 2·0 ft. Growth is best where it is never exposed.

Posidonia australis forms dense "meadows" from —0·5 ft downwards, especially in deeper water in Pelican Lagoon.

(*b*) *Zonation where Cliffs Do not Occur*

This is essentially similar to the zonation described above, except that samphires (*Salicornia australis*, *Arthrocnemum arbuscula*) occur in the upper littoral (3·5 ft upwards) and supralittoral (Fig. 3, section *A*; Plate 1, Fig. 2; Plate 2, Fig. 1). The roots and lower stems of these plants are flooded at high tides, and low plants may be completely covered. In the shade of the samphires, *Bostrychia simpliciuscula* and *Chaetomorpha capillaris* occur, with *Gelidium pusillum* on the lower stems.

(*c*) *Variations on the Typical Zonation*

On Shag Rock in Pelican Lagoon, *Gayella polyrhiza* grows as mats on the rock in the supralittoral where shag excrement is plentiful. Only occasional spray reaches this zone.

At Salt Lake Point, wave action becomes moderate as the prevailing south-west wind blows across 2 miles of water. Owing to the wave action the zones are slightly elevated, and several species occur here which are more characteristic of the sheltered rocky coast subformation (see Fig. 3, section *C*). Zones below the mid littoral are typical, but in the mid littoral serpulid worm tubes (*Galeolaria caespitosa* Savigny) occur at the base of the cliffs and on rocks, while in the upper littoral the barnacle *Elminius modestus* Darwin is common on rock faces exposed to the waves (i.e. facing the south-west). Scattered *Melanerita melanotragus* Smith also occur. Nevertheless, *Bembicium* is dominant in the mid littoral generally. In the supra-littoral a few *Melaraphe unifasciata* occur. The lichen *Verrucaria* is also more prominent in the upper littoral and lower supralittoral.

An area of the central north coast of Pelican Lagoon, some 300-400 yd long, consists of cliffs dropping vertically to below low tide level, with no intertidal flat. Here wave action is greater than elsewhere in the inlet, owing to deeper water at the base of the cliffs and also to stronger wind action across Pelican Lagoon. As a result of the stronger wave action, the zonation here is more like that outside American River inlet. The organisms mentioned in the previous paragraph occur here, and in addition the sublittoral fringe is dominated by the brown alga *Cystophora polycystidea* Areschoug. This alga is not found elsewhere in the inlet, but is characteristic of the north coast of Kangaroo Island. *Hormosira* occurs as a very compressed zone (with dense tufts of *Jania* sp. amongst it) on a small rocky ledge in the lower littoral. *Peyssonnelia gunniana* J. Agardh and a lithothamnion growing on *Brachyodontes erosus* Lamarck are other unusual components of the sublittoral fringe.

This area of coast is really a fragment of the sheltered rocky coast subformation within American River inlet, and demonstrates the fundamental importance of wave action in determining the algal formations.

(*d*) *Critical Levels*

Doty (1946), Beveridge and Chapman (1950), and others have found that certain tidal levels ("critical levels") correspond to the breaks between zones on the shore. An attempt has been made to relate the zones at American River inlet to tidal levels, but owing to the relatively small tidal rise and great irregularity in the tides, the attempt has met with only limited success.

Table 1 gives the means of tidal levels which were calculated. If these are compared with the breaks between zones (Fig. 4), it is evident that two levels can probably be termed critical; these are M.L.L.W., which is very close to the *Hormosira*-sublittoral fringe break, and M.L.H.W., which corresponds to the lower limit of *Gelidium*. The other tidal levels in Table 1 come within zones and do not appear to be critical.

In the upper littoral, the determining factor is shade rather than tidal fluctuations, so that close correlation of *Bostrychia* and *Gelidium* limits with tides would not be expected.

There remains, however, one clear-cut level that cannot at present be related to tidal levels, i.e. the upper limit of *Hormosira*, which falls about half-way between M.H.L.W. and M.S.L.

The degree of exposure to air is probably an important determining feature of the zonation, and is directly dependent on tidal fluctuations. Table 2 gives monthly percentage times during which certain levels are covered, and the following are the limits for the main intertidal zones:

The upper littoral (*Bostrychia* and *Gelidium*) is covered between 3 and 25 per cent of the time (monthly extremes, 0-8 and 16-32 per cent.)

The mid littoral (*Bembicium*) is covered between 25 and 61 per cent. of the time (monthly extremes, 16-32 and 50-70 per cent.).

The lower littoral (*Hormosira*) is covered between 61 and 93 per cent. of the time (monthly extremes, 50-70 and 85-98 per cent.).

The sublittoral fringe (*Hypnea-Spyridia*) is covered for more than 93 per cent. of the time (monthly extremes, 85-98 per cent.).

The monthly variation (and to an even larger extent the daily variation) in exposure to air of the different zones is very considerable. It seems impossible to consider any particular organism as sharply limited by a certain degree of exposure, partly no doubt because of the importance of the other factors, such as shade and, in *Hormosira*, the presence of reservoirs of water in each vesicle.

IV. The Plant and Animal Associations

The more extensive plant associations of the tidal flats are shown in Figure 1, which was drawn from aerial photographs. Owing to the scale, it is not possible to show associations higher (i.e. nearer the shore) than the *Hormosira* association, as they form comparatively narrow bands. For the same reason the sublittoral fringe association of *Hypnea-Spyridia* is not shown, but it occurs between *Hormosira* and *Zostera*, often mixing with the latter.

The tidal flats are very largely covered with plant growth, but there are a few sandy areas which do not provide a suitable substratum for many algae or any of the angiosperms. These sandy areas are left unshaded in Figure 1, but they may bear communities of *Ectocarpus confervoides* (Roth) Le Jolis and *Polysiphonia patersonis* Sonder, both growing on cockle-shells buried in the sand.

Most of the tidal flats are covered by marine angiosperms. These are the only plants which can colonize sandy or muddy areas, but they provide a substratum on which many small algae can grow.

The main plant and animal associations will be described as they occur from the supralittoral downwards. Species for which the seasonal distribution is not given almost certainly occur throughout the year. Variations from the typical zonation have been described previously, so only the main associations will be described here.

(a) *The Supralittoral*

(i) Gayella polyrhiza *Association.*—*G. polyrhiza* occurs only on Shag Rock, where there is excrement from a shag (cormorant) colony. It forms thin green mats over the rock and is best developed during winter. Previously (Womersley 1947, p. 239) it was reported as *Prasiola*, and like this closely related genus it is dependent on an increased supply of nitrogen. *Gayella* on Shag Rock is rarely wet by spray and is as much a terrestrial as a marine alga.

(b) *The Littoral*

(i) Bostrychia simpliciuscula *Association.*—*Bostrychia* occurs only in well-shaded places of the upper littoral, usually as scattered patches but frequently lining the floor and sides of small caverns (6-8 ft long) in the base of the cliffs. It forms soft, dark brown mats, ½-1 cm thick (Plate 3, Fig. 1). *Bostrychia mixta* Hooker & Harvey sometimes occurs mixed with *B. simpliciuscula.* The latter also occurs in the shade of the samphires, growing on mud or at the base of the plants.

(ii) Gelidium pusillum *Association.*—*Gelidium* occurs mainly below *Bostrychia*, but they often grow in the same area, though never intimately mixed. In growth habit they are very similar, the *Gelidium* being firmer and coarser than *Bostrychia* (Plate 3, Fig. 2). *Gelidium* grows in less-shaded places than *Bostrychia*, and may even receive direct sunlight for a short time each day.

Both the *Gelidium* and *Bostrychia* associations are relatively pure. Few other algae occur in the upper littoral zone, though *Cladophora repens* (J. Agardh) Harvey and *Chaetomorpha capillaris* are occasionally found. The mollusc *Bembicium melanostoma* occurs on otherwise bare rock between patches of *Gelidium* and *Bostrychia*, but mainly where exposed to sunlight.

During the winter months (July-November) *Porphyra umbilicalis* (Linnaeus) J. Agardh occurs in the lower *Gelidium* zone in Pelican Lagoon, on the more exposed rock. It is very variable in occurrence and seems to be absent in some years. The plants are not well developed, being only 6-12 cm high.

(iii) *The Samphire Association.*—Three species of Chenopodiaceae occur in the upper littoral and extend into the supralittoral, viz. *Salicornia australis*, *Arthrocnemum arbuscula*, and *Kochia oppositifolia* F. Muell. These are commonly called "samphires", and may occupy relatively large areas (see Fig. 1; Plate 1, Fig. 2; Plate 2, Fig. 1). *Salicornia australis* is the smallest (6-8 in. high) and occurs lowest. Some plants are completely submerged at high tide. *Arthrocnemum arbuscula* grows to a low bush 3 ft high, while *Kochia oppositifolia* grows to 5 ft in height and occurs highest on the shore. The roots and stems only of the latter two species are covered by high tides.

In the shade of the samphires *Bostrychia simpliciuscula*, *Gelidium pusillum*, and *Chaetomorpha capillaris* occur. *Bostrychia* and *Chaetomorpha* form loose, soft mats on the mud, while *Gelidium* grows mainly on the stems of the samphires. *Microcoleus chthonoplastes* (Mert.) Thuret (together with *Calothrix scopulorum* (Weber & Mohr) Agardh (?)) also forms mats on the mud.

(iv) Bembicium melanostoma* *Association.*—This mollusc dominates the mid littoral and extends up through the upper littoral, occurring on rock or mud (Plate 4, Fig. 1), throughout the inlet. On upper littoral rock not in shade, tiny black spots of the lichen *Verrucaria microsporoides* occur with *Bembicium*.

On flat areas of the mid littoral exposed to full sunlight, *Bembicium* is often the only macroscopic organism present, but on some flat rocky areas the bivalve *Modiolus areolatus* may be co-dominant. The *Modiolus* grow in small clumps on the rock, with scattered *Bembicium* between them. Beds of *Brachyodontes erosus* are also found in the mid littoral in a few places, though this bivalve is commoner in the lower littoral.

Algae are not common in the mid littoral, but the following occur:

Enteromorpha clathrata forms isolated patches, especially in slight hollows which remain moister at low tide, or near the base of the cliffs where there is some shade. Occasionally it occurs under the samphires. This alga is very variable in form and frequently stunted, but agrees with type II of Bliding.

* This name includes a complex of forms. The one at American River inlet is sometimes known as *B. nanum*.

Rivularia nitida Agardh occurs as tiny scattered plants on rock on the south side of Pelican Lagoon, but is not common. Several other blue-green algae inhabit the mid littoral in the lagoons; *Isactis plana* (Harvey) Thuret grows on small rocks and old shells; *Palmophyllum crassum* (Nacc.) Rabenhorst (in the gloeocystoid state) forms irregular brownish blobs to 1 cm across, lying very loosely on the mud or rock; and *Lyngbya confervoides* Agardh forms flat mats which become very thin when dry and peel off readily. In a few small areas *Lyngbya* dominates the mid littoral.

(v) Hormosira banksii *Association.*—Throughout most of the inlet *Hormosira banksii* forms a conspicuous zone, varying in width from a few feet to 100 yd (see Fig. 1). On the western coast of the inlet, and between Strawbridge Point and Picnic Point, *Hormosira* is almost absent from long areas, occurring only on small rocky outcrops. The plants grow on rock or on the mollusc *Brachyodontes erosus* Lamarck embedded in the mud, and do not occur where the substratum is mud without *Brachyodontes.*

Hormosira forms a pure and dense association (Plate 4, Fig. 2; Plate 5, Fig. 2). On the lower side it merges with the sublittoral fringe association of *Hypnea-Spyridia*, but only scattered *Hormosira* plants occur in the latter association proper. *Ulva lactuca* Linnaeus (Plate 6, Fig. 1) and *Chaetomorpha billardieri* Kützing (Plate 5, Fig. 1) occur in the lowest part of the *Hormosira* association, and may become co-dominant, while in some places stunted tufts or fragments of *Corallina* are found.

The plants of *Hormosira* at American River inlet are much branched, to 25 cm long, and with individual vesicles up to 3½ cm in diameter. This is the forma *labillardieri*, and is very different in form from forma *sieberi* of rougher localities. Another difference is that *Hormosira* in the inlet is never epiphytized by *Notheia anomala* Bailey & Harvey, as it is on most rough coasts.

Hormosira can withstand the exposure to air, and to high temperatures in summer, because of its large water-containing vesicles. No other alga in the inlet is adapted to withstand lower littoral conditions so well.

Epiphytes on *Hormosira* are few. During winter months *Ectocarpus confervoides* is often densely epiphytic, while at most seasons a small *Lophosiphonia* (?) grows over the vesicles.

The mollusc *Austrocochlea zebra* Menke occurs on *Hormosira*, and a small anemone is found in sand near the base of rocks in the lower and even the mid littoral.

(vi) *Minor Communities of Sandy Areas.*—Two communities, both rather variable in their occurrence, are found on sandy areas of the lower littoral or just below. These are dominated by *Ectocarpus confervoides* (which occurs only in winter) and *Polysiphonia patersonis*. Both species may occur together, or quite separately, in areas around Samphire Island, between Strawbridge Point and Picnic Point, and elsewhere in the inlet. They are usually attached to cockle (*Katelysia scalarina* Lamarck) or other shells in the sand.

(c) *The Sublittoral Fringe*

(i) Hypnea musciformis-Spyridia biannulata *Association.*—This association of the sublittoral fringe occurs for about 1-1½ ft below the *Hormosira* association. It is characterized by a variety of species, with *Hypnea musciformis* and *Spyridia biannulata* usually dominant and *Centroceras clavulatum* (Agardh) Montagne a common constituent.

In a few places this association does not occur. North of the American River jetty *Zostera* extends shorewards to a fairly steeply shelving sand-pebble beach, and only scattered plants of *Hypnea* and *Spyridia* are found amongst the *Zostera*. Similar areas occur between American River jetty and Muston, and between Strawbridge Point and Picnic Point. Throughout the lagoons,* however, the *Hypnea-Spyridia* association is fairly distinct, although in many places this and the *Zostera* association grade over several yards.

The majority of algae in the sublittoral fringe are Rhodophyceae, with a few Chlorophyceae and Phaeophyceae. All the Rhodophyceae are yellow-brown in colour and are covered with a fine film of mud. They grow on cockle and other shells, or on small pebbles, buried in the mud.

The distinctive feature of the sublittoral fringe in the inlet is the dominance of Rhodophyceae and virtual absence of larger brown algae. This was stressed previously (Womersley 1947) and is referred to later in this paper.

Hypnea musciformis and *Spyridia biannulata* may each be dominant in some areas, but more often occur together. *Centroceras clavulatum* is rather variable, and less conspicuous, and has therefore been dropped from the name of the association as given previously (Womersley 1947). Numerous other species occur in the association, but are variable in occurrence and density. Some of them form almost pure localized communities in a few places. Notes on these species are given below. Unless otherwise stated they are restricted to the zone from about the 1·3 ft to the −0·5 ft levels, but some extend deeper while others (e.g. *Ulva*, *Chaetomorpha billardieri*) extend up into the lowest littoral zone. *Ulva lactuca* is often a very common constituent of the sublittoral fringe and extends into the *Hormosira* association (Plate 6, Fig. 1). In winter it may form (with *Enteromorpha clathrata*) a prominent green strip along the shore, often lying partly on the *Zostera* association. The plants reach a length and expanse of 50 cm or more (forma *latissima*). A common epiphyte is *Myrionema strangulans* Greville.

Enteromorpha clathrata is common and widespread throughout the inlet. Bliding's type II often forms a dense belt along the flats (with *Ulva*) where it is just exposed at low tide, while Bliding's type III (*E. plumosa* Kützing) is frequently found as dense masses in the sublittoral fringe.

Local communities of *Acetabularia peniculus* (R. Brown) Solms-Laubach and *Lithothamnion erubescens* Foslie (?) occur in the lagoons. The former grows on old cockle-shells, while the *Lithothamnion* forms unattached nodules (2-8 cm across) or crusts on exposed rock.

* The term "lagoons" includes those parts of the inlet south of Muston.