COMMONWEALTH OF AUSTRALIA

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INTERTIDAL ECOLOGY OF SOUTH AUSTRALIAN COASTS

Good examples of such areas are Point Sinclair and Cape Carnot on the restrictions of Eyre Peninsula, and Cape Du Couedie and the south side of Point Ellen; Vivonne Bay, on Kangaroo I.

Supralittoral zone

On smooth rock faces with extreme wave action and considerable spray, two subzones occur; under less extreme conditions the upper subzone may not be present.

Upper supralittoral.—The blue-green alga Calothrix fasciculata C. Agardh forms an extensive black covering on the rock, from a few feet above the highest barnacles upwards for 6 or 10 ft vertically. This zone is particularly well developed at Point Sinclair (Plate 1; Plate 2, Fig. 1), less so on the south side of Point Ellen, Vivonne Bay, but is often absent if conditions are less extreme or the substratum is more dissected.

The upper edge of the Calothrix association fades out, but the lower edge is irregular and sharply defined. Clear areas of rock with similar sharply defined edges occur within the association (Plate 1, Fig. 2). In each of these a small crevice or slight depression retaining moisture is found, inhabited by a cluster of Melaraphe unifasciata (Gray). The sharp and irregular edge of these "Melaraphe patches" and the similar lower edge of the association are probably due to feeding of the Melaraphe (during or after high tide, or at night). It is possible that the Melaraphe is unable to obtain a foothold on the slippery Calothrix mat.

Lower supralittoral.—This zone, lying between the Calothrix association and the barnacles of the upper littoral, is normally characterized by Melaraphe unifasciata (Plate 2, Fig. 1). During low tides in summer, however, Melaraphe migrates downwards, and may be more common among the Chamaesipho barnacles of the upper littoral. When this happens mostly bare rock is left in the upper part of the lower supralittoral.

At higher levels, *Melaraphe* seeks shelter in cracks or crevices or around pools, where it occurs in very dense clusters. The banded *Melaraphe praetermissa* (May) may also occur in sheltered places.

A thin black film on the rock in less extreme places is often due to the lichen Verrucaria.* Where rocks or boulders occur, the isopod Ligia australiensis (Dana) is usually found, and in pools or crevices the orange-yellow crab Leptograpsus variegatus (Fabricius) may occur.

Littoral zone

The littoral zone, especially under extreme wave action with strong surge up the rock face, is dominated throughout its height by barnacles (Plate 2, Fig. 2). Only in the lower littoral do algae become codominant. In less extreme conditions, or where there is broken rock, algae dominate the lower littoral and gastropods and mussels the mid littoral. On smooth rock faces there is little overlapping of the zones, but more on irregular or broken rocks.

Upper littoral.—On the roughest slopes this is characterized by a well-defined band of the honeycomb barnacle, Chamaesipho columna (Spengler) (Plate 3, Fig. 1).

^{*}Probably V. microsporoides Nyl, according to the late Mr. P. Bibby.

With less extreme wave action, Chthamalus antennatus Darwin is often present slightly above or mixed with the Chamaesipho. At an upper littoral level, but in heavy shade under rocks, Tetraclita purpurascens (Wood) occurs.

Under hot, dry conditions, *Melaraphe* is often found amongst the upper littoral barnacles. In such cases it is more satisfactory to consider the upper limit of barnacles rather than the lower limit of *Melaraphe* as marking the littoral—supralittoral boundary.

Mid littoral.—On steep, exposed slopes, the surf barnacle Catophragmus polymerus Darwin dominates the mid littoral; few other organisms are present (Plate 2, Fig 2). On gentler slopes (e.g. some areas of Point Sinclair), the mussel Brachyodontes rostratus (Dunker) occurs in the lower Catophragmus zone (or just below), very much as it does along the Victorian coast (Plate 4, Fig. 2) (Bennett and Pope 1953, p. 116). Scattered among the barnacles and mussels, isolated gastropods such as Patelloida latistrigata (Angas), Siphonaria diemenensis Quoy & Gaimard, and Neothais textiliosa (Lamarck) occur. Blue-green algae, mainly Rivularia firma Womersley, Isactis plana (Harvey) Thuret, and sometimes Hydrocoleum comoides (Harvey) Gomont, occur in the lower part of the mid littoral, occasionally extending well up into it. Polysiphonia sp. and Nemalion helminthoides (Velley) Batters may also be found.

On somewhat less rough coasts the gastropods listed above, together with Notoacmea septiformis (Angas), Patelloida alticostata (Angas), and Cellana tramoserica (Sowerby), may become codominant through the mid littoral, and the serpulid worm Galeolaria caespitosa Lamarck becomes prominent in the lowest part of the mid littoral. Galeolaria usually occurs as scattered tubes on the rock, and only rarely in local shelter around pools have masses up to 1 cm thick been seen.

Along this type of coastline then, as conditions of roughness become less extreme, the surf barnacle decreases in importance while gastropods and *Galeolaria* become more prominent. The blue-green algae *Rivularia firma* and *Isactis plana* are usually present, but vary greatly in abundance.

On granitic and gneissic rock, in moderately rough places with considerable surge (e.g. Point Sinclair in parts, Point Drummond, and Point Westall), a community of the brown alga *Splachnidium rugosum* (L.) Greville occurs superimposed among the *Catophragmus* (Plate 3, Fig. 2; Plate 4, Fig. 1). The alga may occur as scattered plants, but more often as a fairly dense cover over several square yards, similar to its occurrence on Victorian coasts (Bennett and Pope 1953).

Lower littoral.—In the roughest places this is essentially a Balanus-coralline alga association, the presence of the barnacles being indicative of extreme wave action (Plate 5, Fig. 2).

At Point Sinclair, and in areas at Cape Du Couedic and Vivonne Bay (south side of Ellen Point), Balanus nigrescens Lamarck is well developed, extending a foot or so above the coralline mat as a fairly pure Balanus community (Plate 5, Fig. 1). The coralline algae, mainly Corallina officinalis L. or C. cuvieri Lamarck, grow as a dense mat up to 3 cm high, covering the barnacles to some extent. In a few localities, such as the roughest parts on Ellen Point, a crustose lithothamnion up to 1 cm thick

replaces Corallina. Small patches of thin encrusting lithothamnia are not uncommon in this zone.

In somewhat less rough places, Balanus disappears and the lower littoral is dominated by the coralline algae. The lower littoral zone provides the severest conditions of wave action of the intertidal region, and any organism growing there is well adapted to the habitat. Apart from the chitons Poneroplax albida (Blainville) and P. costata (Blainville), few macroscopic animals occur. Algal species are short and stunted, and include Laurencia heteroclada Harvey, Wrangelia plumosa Harvey, Dasyopsis clavigera Womersley, Nemastoma feredayae Harvey, Centroceras clavulatum (Agardh) Montagne, and Gigartina sp.

Sublittoral fringe zone

The roughness of the sea and the steep rock faces on this type of coast usually prevent thorough studies of the sublittoral fringe zone or deeper regions. The dominant organism, however, is the brown alga *Cystophora intermedia J.* Agardh, which forms a distinct zone from about mean low water down for 4 or 5 ft (Plate 6, Fig. 1). The whole zone is exposed during the suck-back of waves at a very low tide.

Under the Cystophora fronds (up to 2 ft long) a coralline mat occurs (mainly Corallina cuvieri), forming an almost complete cover on the rock. Corynophloca cystophorae J. Agardh is usually epiphytic on the Cystophora. In roughest areas other large algae are few, but with slight shelter browns such as Scytothalia dorycarpa (Turner) Greville and Ecklonia radiata (Turner) J. Agardh appear. Many species of smaller algae may occur, including Caulerpa brownii Endlicher and sometimes patches of Xiphophora chondrophylla (R. Brown) Montagne. Any bare areas of rock are likely to be covered with thin encrusting lithothammia.

Animals are not conspicuous in this zone, though the mutton-fish *Haliotis* (*H. roci* Gray, *H. emmae* Reeve, *H. laevigata* Donovan, or *H. improbula* Iredale) and the stalked ascidian *Pyura pachydermatina* (Herdman) var. *gibbosa* Herdman occur. The starfish *Coscinasterias calamaria* (Gray) and *Patiriella calcar* Lamarck, are often found where there is some protection. Crustaceans are always common among the algal mat.

Cystophora intermedia is an indicator species of rough to very rough conditions, and disappears if local shelter occurs. Here other species of Cystophora, C. spartioides (Turner) J. Agardh, C. subfarcinata (Mertens) J. Agardh, C. paniculata (Turner) J. Agardh, and C. siliquosa J. Agardh dominate the upper sublittoral, extending down well below lowest tide level. This is tending to the sheltered rocky coast type, which is described later.

Pools

Pools at various levels of the intertidal region contain such a variety of microhabitats and flora and fauna that the main types only are listed briefly. In general, pools at any one level contain organisms which occur at a lower level on sloping rock, except at high littoral and supralittoral levels, where distinctive pool species occur. Some coasts, such as on the south side of Ellen Point, Vivonne Bay, are remarkably rich in rock pools of many types; others such as Point Sinclair have few pools. Pools at a supralittoral level are subject to great ranges in temperature and salinity. Many have no obvious inhabitants except Melaraphe around the edge. Others may have a covering of blue-green algae (Hydrocoleum and other genera) or green algae such as Enteromorpha and Chaetomorpha aerea (Dillwyn) Kützing.

Pools at a littoral level, or large pools higher up, often show dense growth of encrusting lithothamnia (especially at Ellen Point); Hormosira banksii (Turner) Decaisne may fringe shallow pools, while a variety of small red algae (Centroceras spp., Ceramium spp., Laurencia spp., Polysiphonia spp.) occur. Shaded pools may contain algae normally only found in deep water. Molluscs and Galeolaria, typical inhabitants of the mid littoral, are common in shallow littoral pools.

Large pools, subject to water inflow even at low tide, provide good growth conditions for many brown algae—especially Cystophora spp., Ecklonia radiata, Myriodesma latifolia Harvey, Scytothalia dorycarpa, Pachydictyon paniculatum J. Agardh, and smaller red algae.

(2) Horizontal Intertidal Rock Platforms.—Under conditions of strong wave action the coast between the headlands and capes of Palaeozoic rock consists of either horizontal calcareous rock platforms or sandy beaches (Plate 1, Fig. 1). Such rock platforms occur from Sorrento or further east in Victoria along South Australian rough coasts and into Western Australia, where similar platforms are found east of Esperance and on the southern part of the west coast. The western part of the south coast of Western Australia is mainly granitic, with only occasional calcareous platforms.

These rock platforms are characteristic in form and structure. Formed by wave action or possibly by solution (Fairbridge 1950) from calcareous consolidated sand dunes of Recent or Pleistocene age, they present a horizontal surface, with more or less numerous pools or depressions of varying sizes. The surface lies at about mean low water neaps and drops off vertically into deep water. The edge is frequently undercut or dissected. At the rear of the reef, the cliffs are more or less vertical, from 20 to 100 ft high, usually with a wave-cut notch near the base. The rock consists of coarse sand grains cemented together with a calcareous matrix, weathering to a rough surface which is especially pitted and jagged above high tide level. Wave action at the edge of the reef is severe, but as waves pass across the reef conditions moderate. Degree of wave splash at the rear varies with distance from the reef edge and with the height of the tide. These rock platforms have been described in some detail at Pennington Bay on Kangaroo I. (Edmonds 1948; Womersley 1948) and the main features only are summarized here. Variation in the ecology of these reefs in the central and western parts of the South Australian coast is relatively minor, although the very rich algal flora permits considerable chance variation in minor species. Similar reefs form most of the coastline in the south-east of South Australia, but as certain ecological, floristic, and faunistic differences are apparent, their description is left till later in this account.

In general, vertical rock at the rear of the reef (mid and upper littoral and supralittoral) is dominated by animals, while the reef surface and edge is dominated by algae.

Zonation on cliffs at the rear of reefs Supralittoral zone

This zone begins some distance (4–8 ft) up the vertical cliffs and extends up for 3 – 30 ft depending on wave splash. The dominant organism is Melaraphe unifasciata, which occurs as scattered individuals, together with M. praetermissa and Ligia australiensis. The blue-green algae Symploca hydnoides Kützing and Calothrix fasciculata (mainly around the Great Australian Bight) are found as scattered patches where there is shade. The lichens Lichina confinis (F. Muell.) Agardh (more prominent in local shelter) and occasionally Verrucaria may occur, while the crabs Leptograpsus variegatus and sometimes Ozius truncatus (Milne Edwards) forage for food.

Littoral zone

Upper littoral.—Where wave splash is heavy, the upper littoral is dominated by the barnacles Chthamalus untennatus and Chamaesipho columna.

At the rear of large reefs, where wave splash is consequently less, barnacles are fewer, while the molluse community of the mid littoral extends upwards and is codominant with the barnacles. If wave splash is relatively slight, few barnacles occur and the molluses dominate both mid and upper littoral zones, which can then scarcely be separated as distinct zones.

Both Melaraphe and Lichina often extend down into the upper littoral zone.

Mid littoral.—This is typically a molluse-Galeolaria-blue-green algal zone, ranging from 2 to 6 ft in vertical height (Plate 7, Fig. 1).

At the roughest places *Catophragmus polymerus* does occur, but usually as scattered individuals and never like the dense masses on capes of Palaeozoic rock. With the greater wave splash where it occurs, *Catophragmus* is often at the same height as upper littoral organisms under less wave splash, and above the main molluse zone.

Molluses occur through the mid littoral, the commonest being Austrocochlea odontis (Wood), A. rudis Gray, A. torri Cotton & Godfrey, A. adelaidae (Philippi), Cominella lineolata (Lamarck), Cellana tramoserica, Siphonaria diemenensis, Patelloida latistrigata, P. alticostata, Notoacmea septiformis, Chizacmea conoidea Quoy & Gaimard, Subninella undulata (Solander), and Neothais textiliosa. Where fallen rocks and more shelter occur, Melanerita melanotragus (Smith) and Bembicium melanostoma (Gmelin) are common, while Siphonaria baconi Reeve inhabits flat and rather level rock.

The serpulid worm Galeolaria caespitosa is found throughout the mid littoral, but is best developed in the lower part of the zone. Blue-green algae, mainly Rivularia firma and Isactis plana, are similarly best developed relatively low in the zone, though Symploca hydnoides (Plate 7, Fig. 1) and Hydrocoleum glutinosum (Agardh) Gomont occur higher where there is partial shade. Thin encrusting lithothamnia may also be common in the lower mid littoral, and thin mats of Gelidium pusillum (Stackhouse) Le Jolis and Bostrychia simpliciuscula Harvey or B. mixta Hooker & Harvey may be found in heavy shade.

Well-developed communities of the black mussel *Brachyodontes rostratus* occur at a mid littoral level at the rear of some reefs but not on others, e.g. on a reef at the end of Pennington Bay, Kangaroo I., at Sleaford Bay (Plate 6, Fig. 2), and outside Venus Bay on Eyre Peninsula.

Around pools at a mid littoral level, and in moister places, the red anemone Actinia tenebrosa Farquhar and the green Oulactis muscosa (Drayton) and Cnidopus verater (Drayton) may be common. Along the coast of Eyre Peninsula Oulactis mcmurrichi (Lager) and Isanemonia australis Carlgren occur.

The commonest rock-borers are the sipunculid *Phascolosoma tasmaniense* (Fischer) and an isopod, *Sphaeroma* sp.

Organisms of the reef surface

Lower littoral.—This zone includes the base of the cliffs and any higher areas on the reef surface which are exposed at a very low tide—even though occasional waves (perhaps every 5 or 10 min) will wash over the reef. In vertical height this is a narrow zone of 6–15 in., in contrast to the broader mid littoral.

The dominant organism is the brown alga Hormosira banksii (forma sieberi (Bory) Harvey), which often forms a pure and dense association over many square yards of higher areas of reefs (Plate 7, Fig. 2). Notheia anomala Bailey & Harvey is usually parasitic on the bead-like thallus.

Other prominent algae at the rear of reefs are *Ulva lactuca* L. and *Enteromorpha clathrata* (Roth) J. Agardh, which extend from the lower littoral down into pools, and the brown tufts of *Ectocarpus confervoides* (Roth) Le Jolis (in winter) and *Bachelotia fulvescens* (Schousboe) Bornet (in summer). Each may form a pure community in suitable habitats, especially where waves wash up sloping rock. *Lophosiphonia scopulorum* (Harvey) Womersley is also common, and on the west coast of Eyre Peninsula to at least the head of the Great Australian Bight, *Cladophoropsis herpestica* (Montagne) Howe, basal parts of *Struvea plumosa* Sonder, and *Codium capitulatum* Silva & Womersley are common. These green algae grow under shaded conditions.

Reef communities normally under water.—Near the outer edge of the reefs, communities in which coralline algae are codominant are often developed on slightly higher areas. Such areas are subject to heavy wave action, and are only exposed for a short time between waves at an extremely low tide. The most prominent algae are Corallina cuvieri on the rock and Jania fastigiata Harvey, growing on Cystophora subfarcinata; C. paniculata is also common, and numerous smaller algae, more characteristic of the sublittoral fringe, may enter this Cystophora—coralline community (Womersley 1948, p. 157). Balanus nigrescens is found as scattered individuals where conditions are very rough.

The most prominent organisms of the reef surface, lying in pools or depressions where they are normally never uncovered, are the fucoid algae Cystophora subfarcinata, C. siliquosa, C. uvifera (C. Agardh) J. Agardh, Cystophyllum muricatum (Turner) J. Agardh, and Sargassum decipiens (R. Brown) J. Agardh. These form a "mixed Cystophora complex" (Womersley 1948). Normally most species occur together, though Cystophora uvifera and Cystophyllum muricatum are more characteristic of

inner calmer parts, where they may form fairly pure communities. Cystophyllum is tolerant to partial burial by sand.

The number of species in this complex, which covers a large proportion of the surface of most reefs, is comparatively small. This is probably due to the destructive effects of the moving fronds of the fucoids on germlings of other algae and to the less suitable conditions on hot summer days.

When hot summer days and offshore winds coincide with periods of low tide, both *Hormosira* and the *Cystophora* species may suffer considerable damage. Shallow pools of water on the reefs become sufficiently warm to leach fucoxanthin from the thalli, colouring the water brown. The ends of the fronds lying on the surface are killed and blackened, and whole reefs may be affected in this way.

Several other communities of algae occur on the inner reef surface, two of the commonest being Jania fastigiata and Liagora harveyana Zeh (often coloured bluegreen by epiphytic Calothrix confervicola (Roth) Agardh). Ulva lactuca, Cladophora valonioides Sonder, Cladosiphon filum (Harvey) Kylin, Colponenia sinuosa (Roth) Derbes & Solier, Gracilaria furcellata Harvey, Champia obsoleta Harvey, and Wrangelia plumosa are also common. On reefs on the west coast of Eyre Peninsula and towards the head of the Great Australian Bight, encrusting lithothamnia, and often the mutton-fish Haliotis, are common (Plate 8, Fig. 1); these reefs are probably always wave-washed.

Blue-green algae sometimes colour large areas of the reefs in shallow water, especially where water streams over ledges at low tide. The chief species are Rivularia firma on rock, and Calothrix confervicola and Lyngbya spp. as epiphytes on larger algae.

A number of animals are associated with the algae which dominate the reef surface. The commonest are the molluses Austrocochea adelaidae, Subninella undulata, Phasianotrochus bellulus Dunker, Zemitrella lincolnensis Reeve, Dardanula melanochroma Tate, Floraconus anemone (Lamarek), Cantharidus pulcherrimus Wood, and Phasianella ventricosa Swainson, and the crustaceans Naxia tumida (Dana), Halicarcinus ovatus (Stimpson), and Euidotea peronii (Milne Edwards). Among the holdfasts of the algae are the polychaetes Platynereis dumerilii (Audouin & Milne Edwards) s. sp. antipoda Hartman, Nereis cockburnensis Augener, Micronereis halei Hartman, and the ophiuroid Amphipholis squamata (Delle Chiaje). The starfish Patiriella calcar occurs on well-washed surfaces.

Sublittoral fringe zone

This includes the edge of the reef, extending down the vertical side for the 2-3 ft uncovered during the suck-back of waves at very low tide.

The dominant alga is Cystophora intermedia, with a dense and rich undergrowth of numerous algae. The larger species include Sargassum bracteolosum J. Agardh, Scytothalia dorycarpa, Ecklonia radiata, Cystophora spartioides, C. paniculata, stunted C. subfarcinata, and sometimes Myriodesma latifolia. Corynophloea cystophorae and sometimes Dasya urceolata Harvey are epiphytes on Cystophora intermedia. Among the smaller species Xiphophora chondrophylla (central and eastern parts of South Australian coastline), Dictyosphaeria sericea Harvey, Codium pomoides J. Agardh,

Choetomorpha darwinii (Hooker) Kützing on Ballia scoparia Harvey, Perithalia inermis (R. Brown) J. Agardh (to 18 in. high), Dasyopsis clavigera, Laurencia heteroclada, Chrondria sp., and encrusting lithothamnia may be mentioned; but up to 60 species may be found in a very few square yards of this zone. Womersley (1948, p. 159) gives a comprehensive list for this zone at Pennington Bay, Kangaroo I.

The algae of the sublittoral fringe are so dense that animals are usually hidden under them. Haliotis roei, Subninella torquata (Gmelin), Neothais textiliosa, and Pyura pachydermatina var. gibbosa are the commonest. Crustaceans are prolific amongst the algae, and polychaetes amongst holdfasts of larger species.

(3) Sandy Beaches (on the Open Coast).—Long sandy stretches and smaller sandy bays are common along the open coast of South Australia. The coastline which separates the Coorong from the sea in the south-east of the State is a stretch of sand about 120 miles long. The action of the sea on these exposed beaches is usually strong. If the sand is coarse and loose, conditions are inimical to animal life. Where the sand is finer and the beaches firmer more life is found. Macroscopic algae are absent. The localities studied were a part of the Coorong near Goolwa, Vivonne Bay (Kangaroo I.), Sleaford Bay (Eyre Peninsula), and the sandy beach at the head of the Bight. South Australian sandy beaches show similarities, especially in the supralittoral and littoral zones, with those described by Dahl (1953).

Supralittoral zone

The supralittoral is much reduced from that of the rocky coast. It is usually marked by cast-up seaweed and debris. The dominant animal is the amphipod *Talorchestia quadrimana*, which is found amongst the cast-up plant material. If a piece of seaweed containing the animals is shaken they fall onto the sand and quickly bury themselves.

Littoral zone

The upper level of the littoral, especially if the beach is scoured with waves, is usually bare and shows little trace of animal life. A small isopod, Actaecia pallidu (Nicholas & Barnes), and a small springtail, Pseudanurida billitonensis (Schött), are sometimes collected on the moist sand. If dead animals are cast up, the isopod Cirolana woodjonesi (Hale) may gather about them. If the beach is smooth and firmer the small wedge bivalve Amphidesma cuneata (Lamarck) may be found near the surface at about the mid and low tide level. At Goolwa the cockle Plebidonax deltoides (Lamarck) has been collected in the lower littoral and the upper sublittoral on calm days.

$Upper\ sublittoral\ zone$

Very few animals have been found here. Other than the *Plebidonax* the only animal collected is the erab *Ovipales bipustulatus* (Milne Edwards), which is sometimes buried in the sand just below low tide level.

(ii) Sheltered Coasts of Moderate Wave Action.—Almost half of the coastline of South Australia is sheltered from strong wave action. Most of the north coast of Kangaroo I. and the gulf coasts, apart from those at the southern end facing south

or west, are subject to waves only 1-3 ft high, with comparatively little force. Frequent calmer periods occur when wave action is slight. The upper parts of the gulfs, consisting mainly of sandy or muddy beach, are discussed later in this paper.

Much of the sheltered rocky coast consists of cliffs of varying height with rocks and boulders, sometimes sloping rock platforms, at the base. The rock is usually of Palaeozoic age, frequently with sandy substratum in 3–12 ft or more of water. Sandy beaches are of common occurrence.

The rock and boulder substratum affords a home for many animals not found along exposed coasts. With calm conditions, the zonation is not so spread out as under strong wave action, and some zones may be limited in vertical extent. Tidal range, however, is greater than on exposed coasts. Water temperatures also show a greater range, being higher in summer and lower in winter, than on exposed coasts.

High air temperatures and low humidity become important on these coasts, particularly in summer when hot days and lack of spray must be limiting factors in the height of intertidal zones. In extreme cases (e.g. at Mangrove Point in Spencer Gulf), although the tide rise is about 10 ft, few organisms occur more than 2 or 3 ft above low tide level; on hot summer days intertidal rock exposed for a few hours may be too hot to touch.

Supralittoral zone

Melaraphe unifasciata is normally dominant, though with a restricted vertical range; in extreme conditions on rocky outcrops in the upper part of Spencer Gulf it may be virtually absent. In most places it is found in nooks and erevices, rarely on the bare face of the rock. M. praetermissa and Ligia australiensis may also occur, but the erab Leptograpsus variegatus is rare. Its niche on the protected coast is taken over (at a lower level) by Ozius truncatus, an inhabitant of the littoral zone.

Orange and grey lichens become conspicuous on sheltered coasts, but mostly at a high supralittoral level; so high in fact that they are rarely wet by spray, and can scarcely be considered as "intertidal" organisms.

The black lichen *Lichina confinis* is commonly found in the supralittoral or upper littoral.

Littoral zone

Upper littoral.—The dominant organism is Chamaesipho columna, with which may be associated Chthamalus antennatus and sometimes Lepsiella vinosa (Lamarck). The lichens Lichina confinis and Verrucaria may occur.

Under extreme conditions of summer heat and great tidal range in the upper gulfs, the upper littoral may be very sparsely populated. Where barnacles do occur their upper limit is well below high tide level.

Mid littoral.—This is a mollusc-Galeolaria—blue-green algal zone, with the molluses and serpulid tubes more pleutiful than on other coasts in South Australia. Rocks, boulders, and shaded and sheltered habitats provide favourable conditions for three gastropods in particular: Melanerita melanotragus, Bembicium melanostoma, and Austrocochlea concamerata. Other common molluses are Austrocochlea torri, Siphonaria diemenensis, S. baconi, Patelloida alticostata, P. latistrigata, Cominella lineolata, Cellana tramoserica, Notoacmea septiformis, Subninella undulata, and

Neothais textiliosa. Many of these gastropods extend upwards or downwards from the normal mid littoral region.

Sometimes the mussel *Modiolus pulex* Lamarck forms a community on horizontal platforms very much as *Brachyodontes rostratus* does on the open coast.

Occasionally, as at Wittelbee Point (south of Ceduna) Chamaesipho extends down through the mid littoral, where it is codominant with the molluses.

Galeolaria caespitosa is best developed along the sheltered coast, as a white band 3–9 in. in vertical height and up to $\frac{1}{2}$ in. thick (Plate 9, Fig. 1). Scattered tubes occur on the rock above this main band, which occupies the lowest part of the mid littoral, giving way abruptly to mat-like algae of the lower littoral. In some cases, especially on the sheltered side of boulders or around pools, two distinct subzones occur—the lower of dense Galeolaria, the upper of gastropods (Plate 9, Fig. 1).

The best development of Galeolaria in South Australia is on jetty piles where it forms encrusting masses up to an inch or more thick, much as it does in New South Wales (Dakin, Bennett, and Pope 1948). A number of other animals shelter in the thick masses of tubes—Modiolus pulex, Desis crosslandi Pocock, Perinereis amblyodonta (Schmarda), Kellia australis Lamarck, Ibla quadrivalis Cuvier, and Leptoplana sp.

Blue-green algae, principally Rivularia australis Harvey, R. firma, R. atra Roth, Isactis plana, and Brachytrichia quoyi (Agardh) Bornet & Flahault are rather variable in occurrence. Brown crusts of Ralfsia sp. are common in the lower part of the mid littoral. Enteromorpha spp. may be plentiful, especially in depressions and in pools.

Lower littoral.—In contrast with the higher intertidal levels, the lower littoral is dominated by algae. With moderate wave action, a Corallina mat is dominant, but mostly on this type of coast the algal mat varies from mixed Corallina and Gelidium pusillum to pure Gelidium. These algae form a mat or turf up to 1 in. thick, completely covering the rock, and some 6-15 in. in vertical height. Gelidium pusillum tends to occur higher than the Corallina, particularly if shaded, and may be pure in the upper part of the lower littoral though mixed with Corallina below. On rock platforms (as at the Port Willunga-Aldinga reef) two lower littoral associations are prominent; Gelidium pusillum in a dense yellow-brown mat, and at a slightly lower level, where slight pools are left at low tide, Hormosira banksii.

Brown crusts of Ralfsia are also common in the lower littoral, while Colpomenia sinuosa is common on rock or on other algae. Ulva lactuca and Cladostephus verticillatus (Lightfoot) Agardh may extend up into the lower littoral.

Large animals are few, owing to the density of the algal covering, but the chitons *Poneroplax albida* and *P. costata* occur in small numbers. Crustaceans and polychaetes are common in the algal mat, as they are at lower levels.

$Upper\ sublittoral\ zone$

The dominant algae of this zone extend from about low water neaps down for several feet (up to 10 or 12) to well below extreme low tide. The term "sublittoral fringe" is therefore not applied to this zone.

Brown algae, up to 3 or 4 ft in length, are dominant (Plate 9, Fig. 2). The laminarian *Ecklonia radiata* is usually present, together with *Cystophora subfarcinata*, *C. polycystidea* Areschoug, *C. spartioides*, *C. retorta* (Mertens) J. Agardh, *Scaberia*

agardhii Greville, Sargassum lacerifolium (Turner) Agardh, and S. decipiens. Cystophyllum muricatum and Cladostephus verticillatus are common in shallow water, and Ectocarpus spp. and blue-green algae (especially Hydrocoleum glutinosum) are common epiphytes. Other common species are Caulerpa brownii, Dictyota spp., Pachydictyon paniculatum, Amphiroa anceps (Lamarck) Decaisne, Corallina cuvierii, Metagoniolithon charoides (Lamouroux) Weber van Bosse, Cheilosporum elegans (Hooker & Harvey) Areschoug, encrusting lithothamnia and other red algae (Hildenbrandtia, Cruoria), Pterocladia capillacea (Gmelin) Bornet & Thuret, and Laurencia majuscula (Harvey) Lucas.

A considerable variety of animal life is found in the upper sublittoral, especially where rocks lying in sand provide suitable habitats for many species not found on the upper side of rocks. The following are common: *Haliotis roci*, *H. emmae*, *H. improbula*, the echinoderms *Patiriella gunnii* (Gray), *P. brevispina* H. L. Clark, *P. exigua* Lamarck, *Coscinasterias colamaria*, *Heliocidaris crythrogramma* (Valenciennes), *Petricia vernicina* (Lamarck), and *Tosia australis* (Gray).

Around the base of rocks, under them or in the sand, occur the anemones Oulactis muscosa, Actinia tenebrosa, Isanemonia australis, Anthothoe albocincta (Stuckey), and Anthopleura aureo-radiata (Stuckey).

Common polychaetes are Idanthyrsus pennatus (Peters), Eunice aphrodite (Palliser), E. australis Quatrefages, Thelepus plagiostoma (Schmarda), Glycera americana Leidy, Thormora versicolor (Ehlers), Nereis cockburnensis, Lepidonotus melanogrammus Haswell; the crustacea Helice haswellianus (Whitelegge), Halicarcinus ovatus, Ozius truncatus, Cyclograpsus audouinii (Milne Edwards), Crangon villosus (Olivier); the echinoderms Nectria multispina H. L. Clark, Uniophora multispina H. L. Clark, Placophiothrix spongicola (Stimpson), Ophionereis schayeri (Müller & Troschel), Heliocidaris erythrogramma, Amblypneustes ovum (Lamarck); and several sponges and ascidians are found.

Where rock gives way to a sandy bottom the marine angiosperms Zostera muelleri Irmisch and (in 2 ft or more of water) Posidonia australis Hooker f. are common. The Posidonia leaves bear numerous epiphytes, particularly Pachydictyon fucellatum (Harvey) J. Agardh, Asperococus bullosus Lamouroux, Colpomenia sinuosa, and Ceramium puberulum Sonder.

(b) Coasts of Slight Wave Action, with Sandy or Muddy Flats or Beaches

This type of habitat includes a number of semi-enclosed or almost land-locked bays on the coast of Eyre Peninsula and the north coast of Kangaroo I., and much of the upper parts of Spencer and St. Vincent Gulfs, particularly the western shores. Wave action is very much reduced compared with coasts previously discussed. Much of the time it is negligible, and only where wind blows across larger areas of deeper water is wave action appreciable. In such cases, fragments of the sheltered rocky coast type of habitat may occur within otherwise calmer areas. In many cases conditions grade from sheltered rocky coasts to calm tidal flats, though at the entrance of many bays the transition covers a relatively short distance.

Typically the shore topography comprises very gently shelving flats above and below low tide level, descending gradually into deeper water or (especially in inlets)

abruptly to a central channel 2 fm or more deep (Plate 10, Fig. 2). The littoral region may rise gently to a sandy beach or low cliffs. Boulders may occur at or above high tide level. This gentle shelving of the intertidal region often results in grading between zones.

The composition of the substratum varies considerably. Apart from rocks or cliffs at high levels, most of the littoral consists of sand, mud, or usually a mixture of the two. Frequently higher levels are sandier than lower ones, and the sublittoral is usually mud. Mud flats are usually calmer than sandy areas. Some of the areas studied were the Cockle Bank in Eastern Cove, Kangaroo I., Coffin Bay, and Outer Harbour, which are chiefly sandy; Proper Bay, Venus Bay, and Streaky Bay on Eyre Peninsula, which are intermixed sand and mud; and American River inlet on Kangaroo I., which is chiefly mud. In the latter and similar localities, the mud is up to 10 in. deep, and often overlain by a thin layer of sand.

The amount of plant life on sandy and muddy shores varies considerably. On sand flats only a few species of small algae occur attached to cockle or other shells in the lower littoral and sublittoral zones. The flora of muddy areas is greater, for here the more stable substratum supports extensive beds of marine angiosperms such as Zostera and Posidonia, and firmly embedded molluses (living or dead) provide a foothold for larger algae. Examples of the latter are Hormosira on Brachyodontes erosus in the lower littoral, and an occasional fuccid alga on molluses in the sublittoral. Extremely few algae can grow directly in the mud or sand.

Most of the animals which are inhabitants of sand and mud flats are able to avoid their enemies and the hazards of desiceation by burrowing. Sand, on account of its tendency to shift, is not a good medium in which to form permanent burrows. Sand flats also tend to dry out more quickly than mud flats owing to the lower water-holding capacity of sand and the generally steeper slope of sandy shores. Consequently, as pointed out by Yonge (1953), animals which live in mud flats do not have to burrow as deeply as those which live on sandy shores.

Distinguishing features of this type of coast, apart from its topography, are the virtual absence of *Melaraphe* and barnacles (except *Elminius modestus* Darwin on jetty piles), the dominance in most localities of the small form of *Bembicium melanostoma* in the mid littoral, the presence of the forma *labillardieri* (Bory) Harvey of *Hormosira banksii*, the virtual absence of large brown algae (Fucales and *Ecklonia*) from the upper sublittoral, and the presence of extensive areas of the marine angiosperms *Zostera* and *Posidonia*.

A detailed account of the ecology (with algal emphasis) of American River inlet is given by Womersley (1956).

Supralittoral zone

The supralittoral may consist of:

- (1) A bare zone of loose or compacted sand of varying degrees of coarseness, or of a mass of broken shells. Few organisms occur here, apart from Talorchestia quadrimana (Haswell) amongst cast-up plant debris.
- (2) Low rocky cliffs, such as in parts of American River inlet, which are generally bare apart from rare occurrences of the green alga Gayella

- polyrhiza Rosenvinge (Womersley 1956, p. 77). If wave splash occurs then Melaraphe unifasciata is present in small numbers, together with Ligia australiensis.
- (3) Low swampy areas with a muddy substratum which extends up through the supralittoral; samphires are prominent, forming a dense cover (see below, under "upper littoral").

Littoral zone

Upper littoral.—Substrata in the upper littoral are similar to those listed above for the supralittoral. Most prominent are the samphires where the substratum is muddy and a few inches or more deep. These include three species of Chenopodiaceae, Salicornia australis Banks & Solander, Arthrocnemum arbuscula (R. Brown) Moquin-Tandou and Kochia oppositifolia F. Muell.; other species may occur. They occur in that order from below upwards, with considerable mixture. Salicornia forms low spreading mats up to 6 or 8 in. high, while the others reach 3–5 ft in height. Under the bushes algal mats of Gelidium pusillum, Bostrychia simpliciuscula, and occasionally Chaetomorpha capillaris (Kützing) Boergesen have been found. Bembicium melanostoma is also common here.

On firm mud or rock, where samphires do not occur, the gastropod Bembicium melanostoma is the dominant organism, though less common than in the mid littoral. Mats of Gelidium pusillum and Bostrychia simpliciuscula (sometimes also B. mixta) occur in shaded parts at the base of cliffs or under rocks.

In the upper gulfs and in parts of Denial Bay, the mangrove Avicennia marina (Forster) Vierhapper var. resinifera (Forster) Bakhuizen van den Brink is common, forming moderately extensive thickets of trees up to 20 ft high. It extends from below high tide level to somewhat above low tide. The mud between the trees is fairly bare, though mats of Enteromorpha occur, and the barnacle Eliminius modestus and serpulid Galeolaria caespitosa occur on the pneumatophores and lower trunks. Brown films on exposed mud are common, due to diatoms and blue-green algae.

Barnacles are only found in the upper littoral where there is local wave wash and rocky outcrops, or on piles and stakes in the water. The chief form is *Eliminius modestus*.

Mid littoral.—The two most important organisms here are the mussel Modiolus inconstans (Dunker) and the gastropod Bembicium melanostoma. Either may be dominant, and often they are codominant. M. inconstans forms extensive beds in some areas (Cockle Bank, Eastern Cove) and affords shelter for a number of other animals including the small bivalve Kellia australis, the polychaete Perinereis amblyodonta, the barnacle Ibla quadrivalis, and the sipunculid Phascolosoma tasmaniense.

Thick masses of Galeolaria caespitosa often occur in the mid littoral, while other common molluses are Siphonaria diemenensis, Melanerita melanotragus, and Cominella lineolata. The crab Helice haswellianus occupies the niche of Ozius truncatus on other coasts.

On sand flats the mid littoral is often a bare zone, though the gastropod Salinator fragilis (Lamarck) may occur.