Phil. Trans. Roy. Soc. B **255**, 459–516 (1969)
Printed in Great Britain

The biomorphology of Solomon Islands shores with a discussion of zoning patterns and ecological terminology

By J. E. Morton and D. A. Challis
Department of Zoology, University of Auckland, New Zealand

[Plates 71 to 74]

CONTENTS

Introduction

The descriptive ecology of the Solomon Islands shores will be dealt with in a series of Reports from the marine party of the 1965 B.S.I.P. Expedition of the Royal Society, now in preparation. This paper is a preliminary attempt to sketch out a biological classification of the shores of those Islands, and to set up some form of descriptive methodology in the light of the special character of the shores observed, in relation to existing zoning systems. It must be followed by extended Reports on the adaptive ecology and the distribution of life forms in particular habitats.

We may begin here with a study of the patterns of occupation of living space on Solomon Islands shores. The close of the earliest era of descriptive coral shore ecology, and the beginning of a new phase, was marked by the Great Barrier Reef Expedition of 1928–9, when two important lines of new work were inaugurated, neither of them even as yet completed. Side by side with the classic contributions of Yonge and his co-workers on coral physiology (Yonge 1930, 1940) we have the earliest of the series of papers by Stephenson and his school (Stephenson, Tandy & Spender 1931) dealing with the ecological analysis of coral, and later more fully, of temperate rocky shores. The most comprehensive account of a tropical shore-line yet written is probably to be found in the description of the Low Isles, Great Barrier Reef. That paper may fittingly be called 'pre-Stephensonian' in the sense that its material was never thoroughly incorporated into the terminology of the later scheme of Universal Zonation on Hard Shores.* Advanced by Stephenson (1943) and Stephenson & Stephenson (1949) this is a system that—particularly on temperate shores—

* The forthcoming book projected by the late Professor Stephenson and being completed by Mrs Anne Stephenson will be eagerly looked forward to for such a further synthesis.

has won the adherence of a whole generation of shore ecologists as one of the greatest creative generalizations of descriptive marine ecology. With some adjustment of nomenclature, for which we believe a good case is made by Lewis (1961), and indeed much earlier by Womersley & Edmonds (1952), the essential concepts of the Stephenson system hold good. Their framework has not only explanatory value but great heuristic power. It makes possible detailed comparisons, and reveals widespread homologies between life forms and biotic zones of many different sorts of shores. Those who have used it on sea coasts over a world span will realize most fully the naturalness and necessity of such a system. Far from it being true, as a biological colleague provocatively said in discussion, that 'such a tripartite system can obviously be fitted to any shore that simply presents three (or more) tiers of organisms', the zones recognized are far from forced or arbitrary. Their reality arises from a basic correspondence in ecological and physiological requirements of the diversity of plants and animals that may compose them in different parts of the world. Indeed such a characterization of the zones in terms of physiological ecology, rather than by tidal levels or organisms, will be a refinement in depth towards which we shall later be looking in this paper.

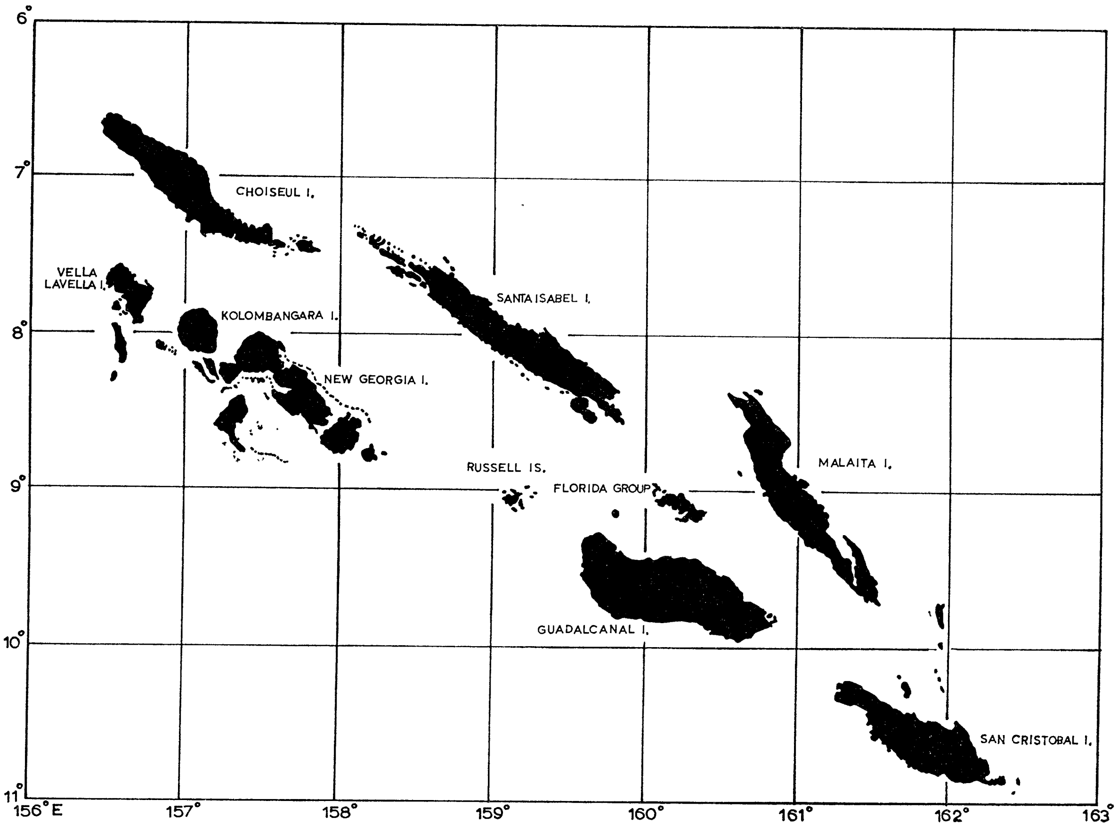


FIGURE 139. The British Solomon Islands Protectorate.

Coral reefs and other tropical shores have a complexity of structure probably rivalled on this planet only by the many-layered tropical rain forests. To some biologists this diversity and complexity is an abiding delight; to others accustomed to the more austere conditions where 'problems' for experimental analysis stand out more clearly, a broad-based concern with what is here called—if a new term be allowable—'biomorphology' is, like much that Expeditions do, apt to seem unsophisticated. With the limited stay and the frequent mobility necessarily enjoined on the Expedition of 1965, and the poverty of existing literature we believed that such a descriptive approach had a logical priority in time.

The analysis of community patterns should not mean that by pursuit of over-elaboration for its own sake we are losing sight of the essentials: the very complexity of ecological structure carries in itself the real challenge. It is here that precision of description is needed to reveal dynamic and causal relationships, most of all by those who are to embark meaningfully upon studies in physiological and experimental ecology.

The Solomon Islands shores are as yet undescribed in the literature of marine ecology and after the 1964 reconnaissance of the Group by the senior author with Professor E. J. H. Corner, there appeared—at the outset of our 5 months' intensive study—to be the following questions still to be asked: first, in what respects may the Stephensonian Scheme require modifying or amplifying to express the greater complexity and variety of structure of tropical shores? Secondly, with the complex intermixing of hard and soft terrains so characteristic of the tropics, can the scheme be extended to integrate descriptions of shores of every type into the system originally envisaged for rocky shores alone? And thirdly, if this can be achieved what will be the distinctive characters of the broad divisions, extending, as they will, from mud flats through reef coral to weather shores, without any broad continuity of species, or even life forms, crossing the whole spectrum?

The tripartite zonation pattern

The zonation pattern of the Universal Scheme can be reduced to a relative simplicity where it stands out most starkly on a well-chosen temperate or subtropical rocky shore. The situations chosen for the two illustrations in figure 140 are from shore-lines under heavy to moderate wave exposure, well-sloped and devoid of loose rock cover or of pockets of sand and silt. The biotic subdivisions are physiognomically characterized as successive bands of animals and plants that stand out in obvious sequences of colours and life forms. The dominant organisms usually encrust or grow upon the exposed surface; they may be variously stalked or sessile, though some—notably the gastropod molluscs—are freely mobile. The Littoral Fringe is the most sparsely inhabited, generally by blue-green algae, certain lichens—especially black *Lichina* and *Verrucaria*, while the most typical molluscs are *Melarhaphe* and related littorinids. The Eulittoral Zone is marked off from this fringe by the upper limit, in quantity, of balanoid barnacles. These most generally dominate in the Upper Eulittoral of temperate shores. In cold temperate northern shores they are followed lower down by species of fucoid algae (often in several subzones) in the middle eulittoral with a lower eulittoral formation in which tufted red algae predominate. On the warm temperate shore, illustrated in figure 140 for the North Island of New Zealand, the middle eulittoral carries most often a band of sessile animals, shelled molluscs such as mussels, oysters, vermetids, or tube-worms of the Serpulidae or Sabellariidae. In the Sublittoral Fringe laminarian brown algae or—in the southern hemisphere—low level fucoids predominate. Beyond the low water level of extreme spring tides, this Fringe gives way to a Sublittoral Zone, never even at low spring tides emersed. Some writers hold that it

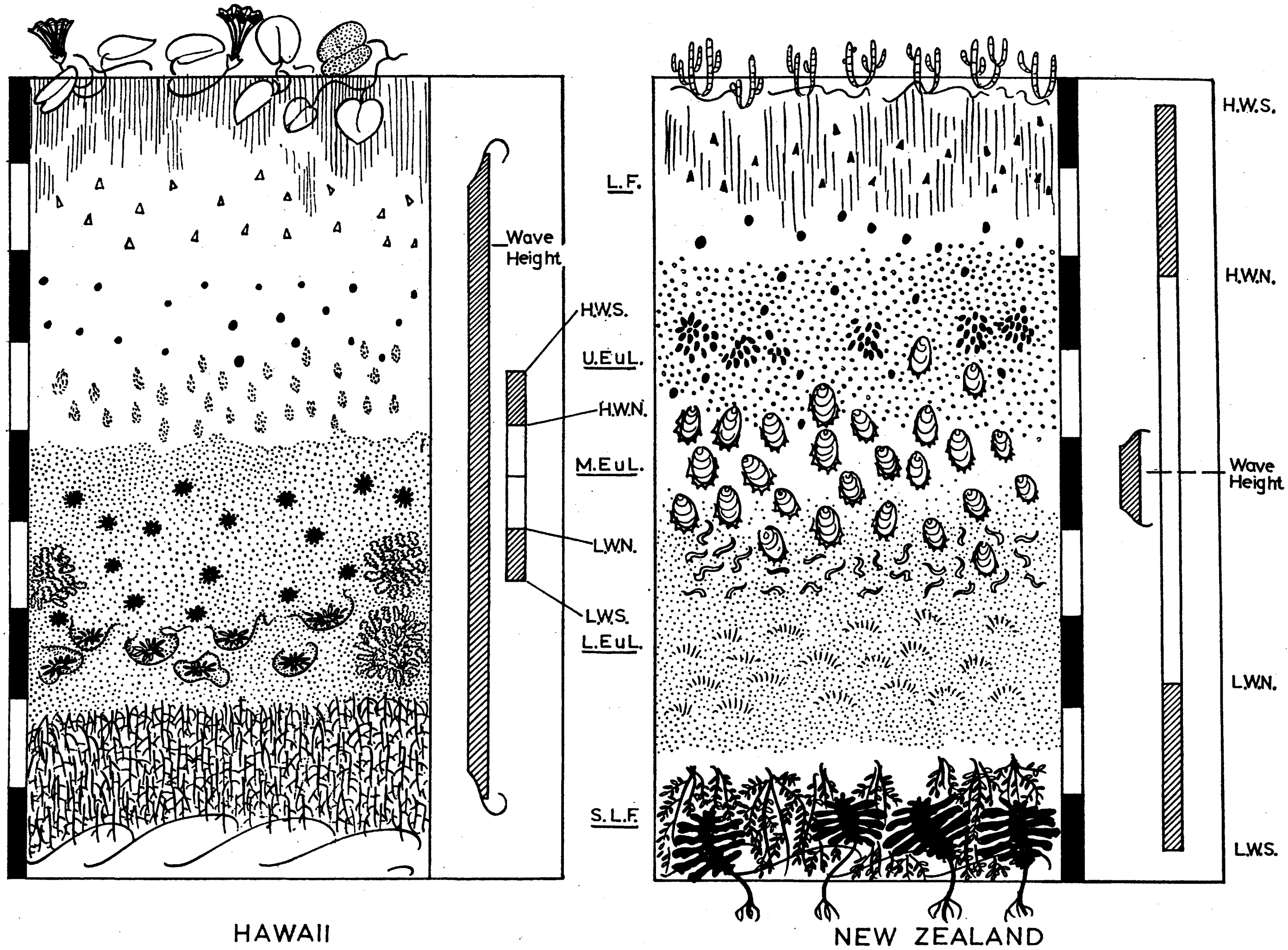


FIGURE 140. Arrangement of the zonation on rocky shores, in the scheme proposed by Stephenson (1943) and employed in this paper. Examples are chosen from Hawaii, showing a shore under high wave exposure, with a short tidal range; and from Auckland, New Zealand, for a shore of moderate shelter with a long tidal range. In the first example the principal controlling factors appear to be wave splash and surge, in the second the régime is a predominantly tidal one. The columns to the right of each panel show wave height from wave crest to trough at the time of mean tide; and the vertical limits of high and low spring and neap tides. Vertical pole marked in feet. For detailed examination of the zones and their organisms, refer to table 28.

depends merely upon the locality and biotic composition whether or not a sublittoral fringe can be justifiably distinguished from the marginal and occasionally exposed, part of the Zone proper. As the highest extreme of the shore, beyond the normal reach of splash, but affected by spray, lies the Maritime Zone, where yellow or grey lichens predominate on temperate shores, or—with the development of small pockets of humus—the lowest and most halophile of the terrestrial angiosperms appear.

The Stephensons (1949) stressed that the definition of zones by tidal limits was in itself meaningless, and that differences in 'exposure'* led to highly variable vertical limits. By

* By the term 'exposure' we mean throughout this paper the effects of waves, surge, splash and spray, most accentuated on weather coastlines away from the shelter of inlets and harbours. For the diurnal uncovering and covering by the tide, sometimes confused with 'exposure' we use the terms 'emersion' and 'immersion'.

contrast with the single New Zealand shoreline pattern selected, figure 140 shows a zonation on igneous rocks of a shore on an Island of the Hawaian Group. Here the pattern of zonal composition and vertical limits is predominantly controlled by wave action rather than by tides. With a comparable vertical height of the zoned shore, the intertidal range is far narrower than on the shore in figure 140, right. By contrast, the height from wave trough to wave crest at the middle state of the tide is very much greater, and the influence of this factor predominates. (For details of organisms, see table 28.)

TABLE 28. COMPARISON OF THE STRUCTURE OF THE INTERTIDAL ZONATION PATTERN OF AN EXPOSED AND A SHELTERED ROCKY SHORE

Hawaii: *Poipu*, *Kauai Is*. Exposed shore, with zonation under predominant control of surge and splash (J. E. Morton, unpublished information).		*New Zealand*: Takapuna near Auckland, N.Z. Moderately sheltered shore, with zonation under predominant tidal control (see Morton & Miller 1968).
Ipomaea pes-caprae	maritime zone	*Salicornia australis*. *Samolus repens*
Ellobiid snail: *Melampus castaneus*		Ellobiid snail: *Ophicardelus costellaris*
Littorina picta	littoral fringe	Littorine: *Melarhaphe oliveri*
no barnacles. *Nerita pica*. *Smaragdinella viridis* in pools: *Cellana sandvicensis*, *Siphonaria normalis*	upper eulittoral zone	barnacle: *Chamaesipho columna*. *Nerita melanotragus*. *Modiolus neozelanicus*, *Cellana ornata*. *Melagraphia aethiops*. pools: *Siphonaria zelandica*
Nerita pica, *Morula granulata*, *Ectocarpus breviarticulatus*	middle eulittoral zone	*Crassostrea glomerata*, *Pomatoceros caeruleus*, *Lepsiella scobina* with pink '*Lithophyllum*' or basal *Corallina officinalis*
pink '*Lithophyllum*' paint, *Sargassum polyphyllum*, *Acanthophora* and *Caulerpa*. *Cellana sandvicensis*, *Drupa* sp. eroding echinoids: *Echinometra mathaei*, *Podophrya atrata*, *Heterocentrotus mammillatus*	lower eulittoral zone	turfing *Corallina officinalis*, *Hormosira banksii*. sponge: *Hymeniacidon perleve*
Pterocladia capillacea and a diversity of other Rhodophyceae, including *Gymnogongrus proliferus* and *Chnoospora pacifica*	sublittoral fringe (= upper sublittoral zone of some authors)	*Ecklonia radiata*, *Carpophyllum maschalocarpum*, *Cystophora retroflexa*, *Sargassum sinclairii*

Notwithstanding this early recognition of the exposure factor, most of the classical descriptions of zoned shores have dealt with locations under moderate exposure, neither land-locked nor—in general—maximally exposed; in such places the limits setting off the two Fringes from the Eulittoral Zone fall at approximately 'average high water mark' and 'average low water mark', mid-way between the respective spring and neap levels. Yonge (1949) in his valuable introductory study, uses these limits explicitly. One of the merits of Lewis's recent book, was to re-emphasize—so far as this might be needed—the wide freedom of the zonal boundaries from particular tidal levels. Zones are entities biologically defined, appearing and maintained in response to a complex of factors—still measurable as a whole only by the effects on plant and animal species.

An important theme of Lewis's book (1964) which others have sought to propound from southern shores (see Morton & Miller 1968) was that of the wide range of zoning patterns based upon the spectrum from extreme shelter to maximal exposure. Such sequences can be strikingly illustrated in one neighbourhood with local exposure differences, as in Pembrokeshire where Ballantine (1961 *b*) has proposed a five-point biological scale of exposure/shelter. With the geographical effects of latitude, a third dimension of variation is to be added to these of vertical height and degree of exposure. This has been critically studied by Ballantine (unpublished) in a survey from northern Norway to Spain and in a later investigation of New Zealand shores through thirteen degrees of latitude.

Broadly speaking it would be fair to say that shore zonation has generally been studied upon moderately sloped, structurally uniform intact surfaces, or at least upon stretches not excessively interrupted by such topographic accidents as pools, ledges, overhangs, movable rock cover, or patches of fine sediments where animals burrow. Zones have been taken to mean visibly discernible arrays of plants and animals. To say this is not to overlook the attention sometimes given to less prominent habitats, as notably by Lewis (1964) and, for a particular type of habitat, in the papers on rock crevices by Glynne Williams & Hobart (1953), Morton (1954) and Kensler (1967). Such complications of the surface picture have generally been regarded as interruptions rather than as of the essence, or as playing any salient part in the total pattern of habitats.

The habitat space of coral shores

Coral shores have fundamental differences from hard substrata of sedimentary or igneous origin. First, whether the substratum be dead or—in its surface layers—still living, they are formed of calcium carbonate secreted by living organisms. Womersley & Bailey (1969) would be reluctant to talk of 'coral reefs' alone, preferring the term 'biotic reef', in view of the large calcareous red algal component on the reef fringe of exposed shores. The hard shores of temperate coasts, where their slope is not low enough to arrest wave attack and initiate progradation with deposit of sediments, are being characteristically cut back by the eroding action of waves. A receding cliff-line is often typically fronted by a cut-and-built platform. On a coral shore the physical forces of erosion are augmented by heavy biological erosion of boring and tunnelling organisms; but these tendencies are balanced, and in a dynamic equilibrium with the processes of living growth and maintenance of the substratum.

Secondly, the intertidal coral shore is no longer in essence a sloping surface at all. Interrupted and richly variegated with pools, loose cover or stacks of emergent coral rock or micro-atolls, a coral shore is basically a horizontal platform of wide extent. On Solomon Islands coral coasts, as distinct from atolls (Wells 1957; Guppy 1886) the forces of land uplift have been predominant and the chief shore forms are fringing reefs. Thus a basement of raised coral rock may have become welded to an igneous hind-structure, or coral rock may—with a series of inland raised terraces—constitute by itself the whole coastal landmass. In some places the upper-eulittoral and the zones lying above it will thus be carried on non-calcareous rocks of igneous origin. In only one locality, Taraoniara in the Florida group, was there a rocky shore of sedimentary origin, though a feature of some sandy shores is the appearance of areas of consolidated 'beachrock' formed *in situ* (see Stoddart & Cann 1965). But most frequently, as on North Guadalcanal, the islands of the Florida group, San Cristobal, the Russell Group, Gizo and New Georgia, uplifted coral rock forms a landward terrace, and carries a maritime zone and littoral fringe as well as the upper and middle divisions of the eulittoral.

It is below and to the seaward of the middle eulittoral that the reef produces its broad-living extension, often many hundreds of metres wide. This represents a prolonged lower eulittoral and sublittoral fringe. Not only is it—as on any shore—by far the richest part of the intertidal zone; but the wide horizontal fringe at this level gives a far greater physiognomic prominence to the lower shore, shelving and uncovered only at lower than neap tides, than its fringe-like marginal status in any temperate region can ever allow.

A coral shore has new complexities in other characteristics too. First, its biospace is hugely and variously extended in depth. The variety and available area of its firm substrata is profusely multiplied, not only on the branches of living coral but upon the concealed surfaces of dead coral.

TABLE 29. STRATIFICATION INTO ZONULES ON DEAD COLUMNAR CORAL OR UNDER TABLES AND MICRO-ATOLLS

(See figure 141)

	zonule	conspicuous occupants
1	exposed zone of bleached calcareous algae upon dead coral surface	*Lithophyllum Neogoniolithon* cement. *Dendropoma maximum*, other vermetids, *Tridacna crocea*
2	living coral polypes	*Coralliobia violacea* (on Poritidae)
3	dead or bleached calcareous algae, with living small green and red species	*Neogoniolithon* and other algae; festooned with *Halimeda opuntia* or other species; *Valonia*; *Hypnea*
4	zone of reduced-light algae	*Peyssonnelia rubra* and other encrusting species
5	deeper zone of dead encrusting coralline algae	ophiuroids and crinoids (*Comanthus*) (here and above)
6	the 'hypobion' of light-avoiding animals, without algae	compound ascidians (*Aplidiium* and *Didemnum candidum*—*Ectoprocta*, sheet-like and clathrate (*Retroporidae*). Hydrozoa. Tubeworms, esp. *Salmacina*. Sessile forms (*Homotrema* and *Miniacina*). Sheltering species: Crustacea, incl. xanthid and carpilid crabs, *Liomera* and the grapsid *Percnon planissimum*, axiid shrimps in *Lyngbya*. Gastropods: trochids, turbinids, *Haliotis*, *Scutus*, a wealth of cowries (*Cypraea lynx*, *ursellus*, *asellus*, *erroneus*, *isabella*; *Staphylaea nucleus*; *Monetaria moneta*; *Cypraea arabica*. Ophiuroids: *Diadema setosa*, *D. savignyi*

In reefs built of loose, or only slightly compacted coral growth forms, dark, cavernose spaces may reach downwards for more than a metre. Predominantly dead branches of the corals—stag's horn *Acropora* species, *Porites* cf. *compressa*, and *Goniopora* spp.—may form wide expanses of brittle terrain, alive only at the tips and with the interspace-system precariously roofed over by calcareous and other algae, together with *Halimeda* and a wealth of subordinate species. With increasing depth and reduction of light, successive vertical zones of organisms are clearly demarcated, as shown in an extended sequence in figure 141.

The appearance and composition of these zones is characteristic for a given depth; and the same or comparable sequences may be concentrically produced under low tidal boulders, micro-atolls, or coral tables, with the more lighted zones increasingly peripheral in position. For such communities, comparable in number of situations and arranged in different patterns and proportions according to the shape and extent of the habitat space, we propose the term '*hypobion*'. This may be used comprehensively for all concealed communities dependent upon shaded living space, in or under the substratum. The 'hypobion'

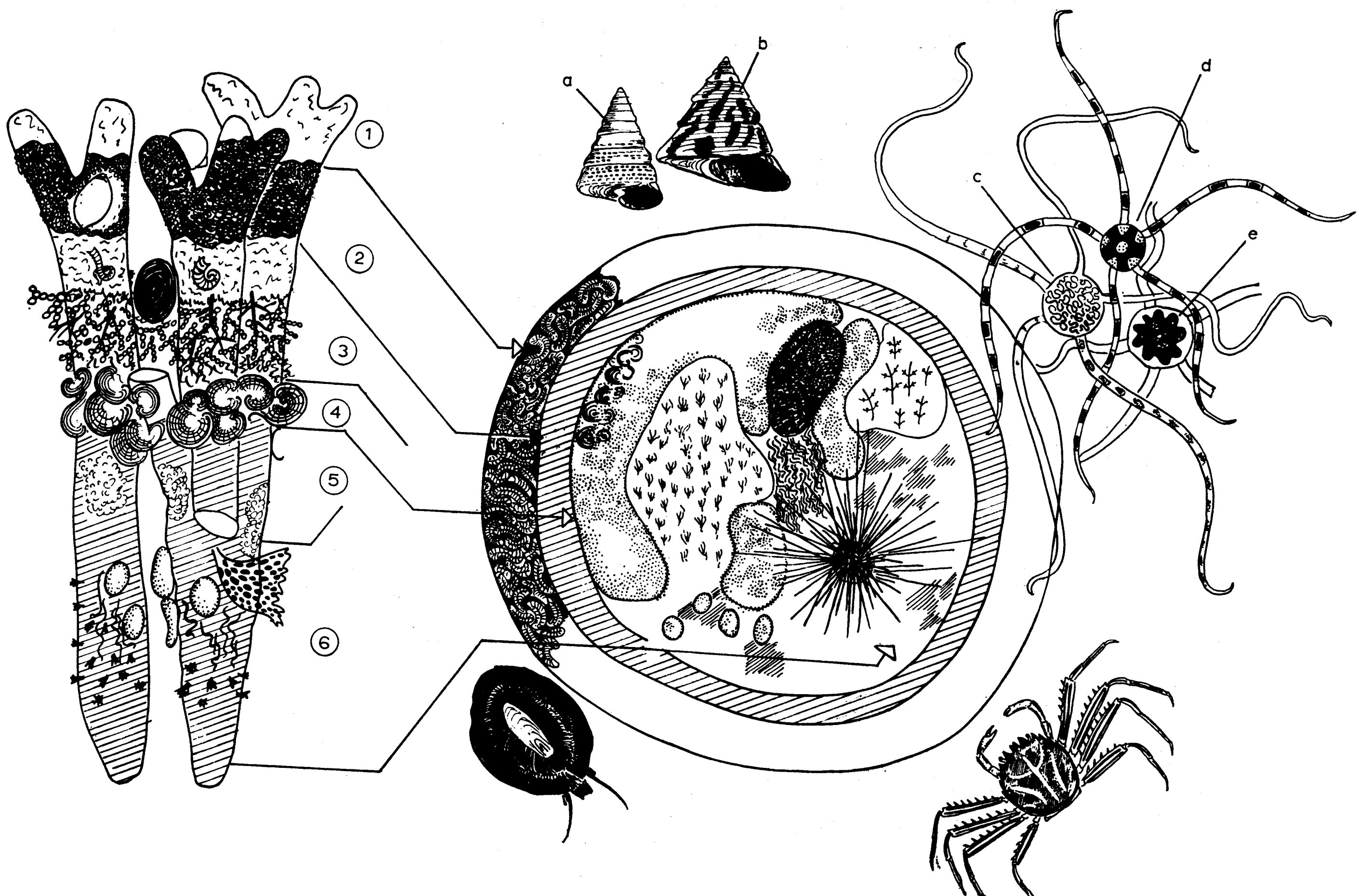


FIGURE 141. The arrangement of the zonules of the 'hypobion' (left) in the shaded reaches of dead columns of *Goniopora* and (right) underneath a micro-atoll of *Symphyllia*. The zonules are analysed in detail in table 29. They comprise: (1) bleached calcareous algae or green algae upon dead tips of coral, or surface of micro-atoll; (2) extent of living coral, with (on *Goniopora*) the snail *Coralliobia violacea*; (3) dead or bleached calcareous algae with encrusting vermetids and further down living algae such as *Halimeda*, *Valonia*, *Hypnea*, etc.; (4) strongly shaded *Peyssonnelia rubra*; (5) deeper zone of dead *Lithophyllum* or cementing coralline algae, not always separately developed; (6) unlighted expanse of sheltering and encrusting sessile animals. Some characteristic sheltering animals from (5) under *Symphyllia* micro-atolls and *Acropora* tables are represented in the figure. They include the top-shells *Trochus tectus* (*a*) and *T. niloticus* (*b*), the fissurellid *Scutus sinensis*, the fast-running grapsid crab *Percnon planissimum* and the ophiuroids *Ophiarthrum pictum* (*c*), *Ophiolepis superba* (*d*) and *Ophiarthrum elegans* (*e*).

is indeed one of the most all pervasive of intertidal formations. It occurs not only in the rich sublittoral fringe, or beneath coral tables and micro-atolls, but is regularly to be recognized under loose rocky cover, or in open crevices at any level of the shore. It has a distinct and characteristic composition not only in the sublittoral fringe, but also in the lower, middle and upper parts of the Eulittoral Zone.

A subordinate zonation of boulders and other loose cover, extending from the exposed surfaces round the sides to the dark reaches beneath, is thus controlled not by the complex of tides and wave action, but primarily by light. A single boulder may replicate in miniature many of the same zones shown upon the surface across a whole intertidal transect (see discussion in Morton & Miller 1968).

Communities of other sorts are associated with coral branches exposed to the light, and for these too a special nomenclature is needed. It is hoped that these new terms, introduced with due diffidence, will justify themselves by their attempt at precision and extension of description rather than as merely a new manifestation of the language habits of marine ecologists.

The distal parts of dead coral branches, while poorer in animal life than living coral, and the loosely compacted rubble of broken coral, support a rich algal flora, predominantly of calcareous and other rhodophyte species but including many inconspicuous though collectively important green and red algae. These characteristic algae and their ecology will be reported upon separately in a detailed account by Womersley.

Animals frequenting living coral vary greatly in looseness or intimacy of association. Many species are freely mobile and resort to coral for shelter only when quiescent or during tidal emersion. These include numerous small fishes and the smaller and lighter-bodied crab species, such as xanthids, porcellanids and galatheids, and the wealth of alpheid prawns and stomatopod species. The crabs of the genera *Trapezia* and *Tetralia* are good examples of forms peculiarly adapted to corals of one genus (*Pocillopora* and *Acropora* respectively (see Knudsen 1967). Many species, however, feed specifically upon the coral tissues, characteristically the parrot-fishes or wrasses among the larger mobile forms, and the colourful *Phyllidia* species among the nudibranchs (see Miller 1969). The carnivorous grazers among the molluscs include the highly important family Coralliophilidae, derived from Thaisidae and with highly specific affinities for particular species and genera of coral. All these snails have lost the radula and jaws, developing instead a suctorial mode of ingestion with a strongly muscular pharynx. Their further evolutionary offshoots include the genus *Leptoconchus*, the species of which acquire a permanently embedded position, and the deeply penetrating *Magilus*, with a shell like a vermetid. A counterpart with the Coralliophilidae is shown by the retreat from the surface of the gall-forming crabs; *Hapalocarcinus marsupialis*, well described by Potts (1915), is characteristic of the terminal branch-forks of *Pocillopora* species.

The more solid substratum of massive coral rock, dead goniastreid and meandrine faviids, is in the lower and middle eulittoral scarred and furrowed by the urchins *Echinometra* and *Heterocentrotus*; and the depressions so formed harbour a rich profusion of gastropods and crustaceans.

Living algae with their variety of shape and texture also support distinctive animal populations of their own. *Sargassum* and *Turbinaria* yield their peculiar crabs and amphipods and many other sheltering animals, generally with ingenious and elegant camouflage. *Halimeda* species will support different populations again, and the smoother and ribbon-like foliage of the sea-grass species, *Thalassia* and *Cymodocea*, have their own, rather specialized biota. Green algae, especially the *Caulerpa* spp., are widely known as the obligate resort of sacoglossan opisthobranchs highly specifically adapted to feed suctorially upon their cell contents (see Miller (1969) for Solomon Islands species).

We may recognize first, by the collective term '*parabion*', those animals living in the lighted reaches of the interstices of living coral, or upon other physiognomic animals or algae that provide biospace. They often remain so intimately in contract with the host species, that—even in the absence of trophic dependence—their body shape as well as their habits become adapted in a high degree to the living substratum. Species on the other hand actually attached or growing upon surfaces recently dead, including the encrusting and festooning red and green algae, may be distinguished by the separate term '*epibion*'.

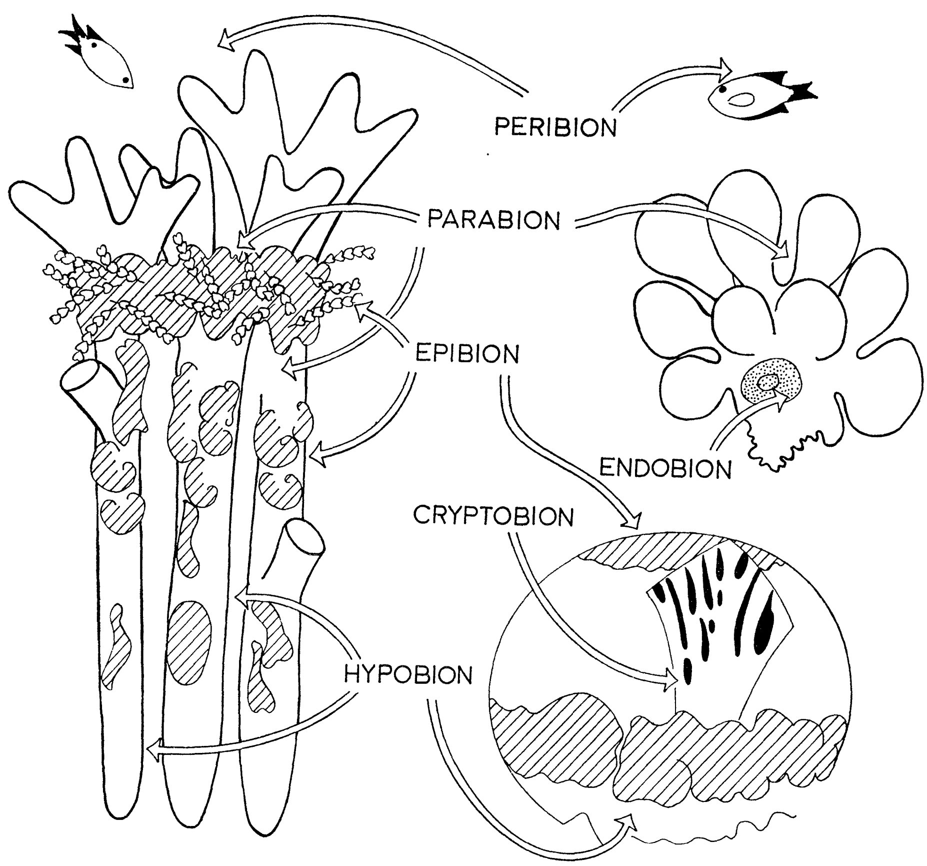


FIGURE 142. Schematic diagram to show the spatial distribution of the biota, with the nomenclature proposed for it, on coral shores.

Far more loosely associated with the coral or other substrate-providing organism, though still depending to some extent ecologically upon their host species, are those mobile forms such as fish and Crustacea, freely swimming in the neighbourhood of the coral but alighting upon it for temporary shelter or for grazing upon coral tissues or attached algae.

Examples of the wide range of fish with their varying dependence upon corals comprise the small-sized Apogonidae or cardinal fishes; the bold and beautifully marked Chaetodontidae, foraging with narrow snouts for food among corals; the coral-hiding Pomacentridae or damsel fishes (this family includes the well-known *Amphiprion* and *Premnas*, nestling among the tentacles of *Stoichactis* anemones: see Verwey (1930)), the Acanthuridae or surgeon fishes feeding on algae amongst coral, the Scorpaenidae (with the highly venomous (*Pterois sphex*) predators hiding among coral.

The Labridae (wrasses) and the Scaridae (parrot-fishes) are frequent grazers upon coral tissues. In close association with coral reefs are the distinctively shaped Balistidae, or trigger fishes, Ostracionidae (box fishes), Tetraodontidae (puffers) and Diodontidae or porcupine fishes. The ecology of tropical fishes has been well surveyed by Marshall (1965), and the most detailed study of Pacific reef fish ecology has been given by Hiatt & Strasburg (1960).

It is proposed to call those animals, including reef fishes, regularly living in the close neighbourhood of coral, but generally without major structural adaptations to coral as a special substrate form, the '*peribion*'.

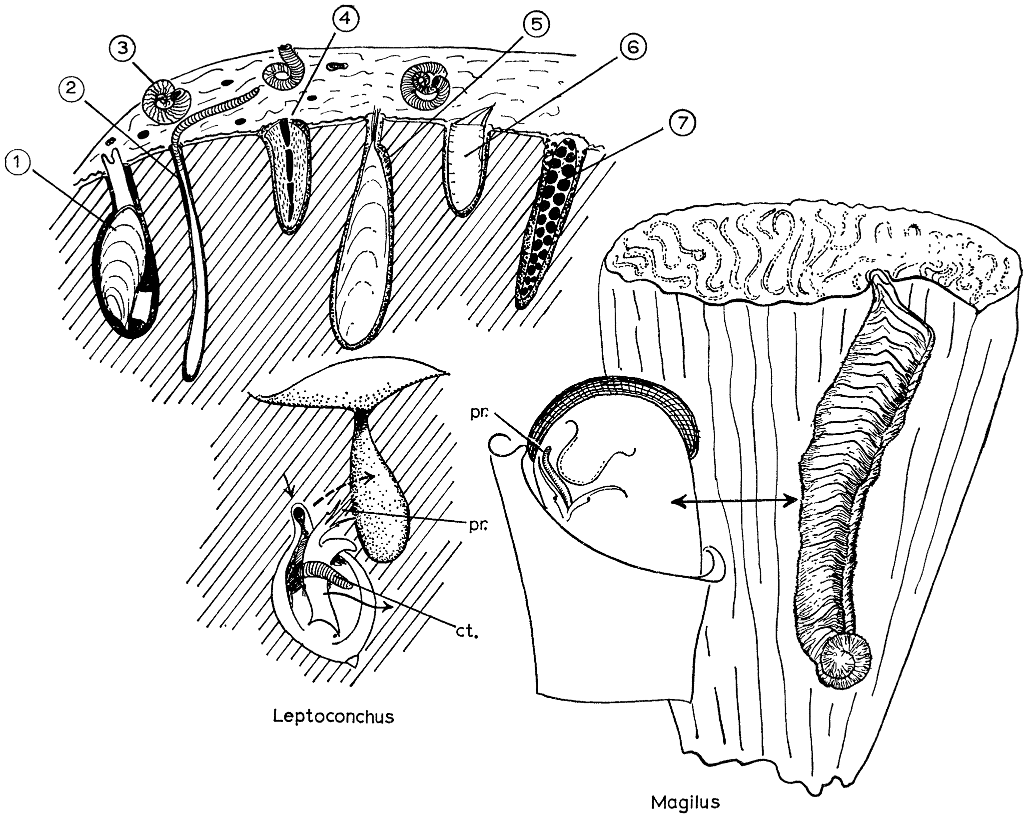


FIGURE 143. Some boring and embedding animals of the 'cryptobion' of massive coral. (Left upper): in a substratum of algal-encrusted dead coral rock, showing—(1) *Rocellaria cuneiformis*; (2) a rock-boring sipunculid worm; (3) a vermetid *Dendrostomum* sp.; (4) the chiton *Cryptoplax japonica*; (5) *Lithophaga* sp.; (6) the tunnelling barnacle *Lithotrya*; (7) a polynoid worm. (Below left): detail of the burrow and animal of *Leptoconchus* and (right) of *Magilus*. *ct.*, ctenidium; *pr.*, proboscis.

Not only is a coral shore a habitat with lavish interspaces and loose shelter. It is also a penetrable substrate with a burrowing fauna at least as rich as that of shores of open texture composed of sand or mud. Many organisms bore into living coral, especially in the massive growth forms of *Porites*, fast-growing and relatively less dense in texture than most, and thus more easily penetrable. The best examples are probably the increasingly specialized series of embedded Coralliophilidae, mentioned already, beginning with the scar-forming *Coralliobia* and *Quoyula* and leading, in corals of the Faviidae, to the completely enclosed *Leptoconchus* and the deeply embedded vermiform shells of *Magilus*. Communities thus enclosed within living or dead coral and revealed only by cracking the substratum open may be referred to under the separate term '*cryptobion*'. Such a fauna has an especially lavish development in dead coral. The animals may be divided into pioneering species that actually bore or excavate galleries, and secondary species that nestle or take refuge in the burrows abandoned by the pioneers. The boring species include first a number of bivalves such as the specialized mussel, *Lithophaga*, byssus-fixed within the burrow and boring by acid secretion (Yonge 1955), and the mechanically boring *Rocellaria*. (It was only on the few examples of sedimentary reefs that true piddocks, *Jouannetia globulosa* (Pholadidae), were found, tunnelling deeply into soft sandstone.) The specialized burrowing cirripede, *Lithotrya*, is also very abundant in coral rock. An active eroding role must be assigned also to the urchins *Echinometra* and *Heterocentrotus*, permanently and deeply confined to scars. Several species of the vermetid genus *Dendropoma*, while attached at the surface deeply erode the coral rock or surface algal crust, and the species of Arcidae and larger embedding clams, especially *Tridacna crocea*, must be accounted important eroders of the rock.

Collectively more numerous in individuals than all other species of the coral rock 'cryptobion' are the sipunculoid worms, *Aspidosiphon*, *Phasocolosoma* and *Dendrostomum*, which fit closely within long deep galleries, striking obliquely downwards and pitting and riddling all coral rock below the upper eulittoral. The introverts of these worms are extruded with a rolling motion of a glove-finger over the moist rock surface, even while the tide is out, and the close examination of the rock surface will disclose huge numbers of these roving proboscides exploring the surface for food. Hardly less numerous than the sipunculoids are the polychaete worms boring or nestling in coral rock. These include a host of species, described and discussed in detail by Gibbs (1969); they are predominantly but not exclusively nereids and euniciids, and become richer in species at the expense of the sipunculoids with approach to the lower eulittoral. An attractive feature of *Porites* and faviid mounds is the embedded serpulid worm *Spirobranchus giganteus*, with brightly coloured tentacle crowns.

In the galleries or burrows abandoned by the pioneers, other species of molluscs, crustaceans and worms appear. Especially characteristic here are the flexible slug-like chiton, *Cryptoplax japonica*; several polychaete worms, either commensals or tenants on their own account, and small brachyuran and anomouran crabs, alpheid prawns and stomatopods, particularly *Odontosquilla*.

In each of the habitats recognized above, the fauna is enriched by the presence of multifarious parasitic, inquiline and commensal species, almost all with detailed and host-specific camouflage devices. In the Solomons, as on every tropical shore of which we have knowledge, these forms occupy a seemingly unending diversity of niches and host-relationships that closer inspection continues to multiply. They have been well reviewed in general articles by Dales (1957) for commensals and Hopkins (1957) for parasites. An account of the special relationships of commensal species on Solomon Islands hard and soft shores will be given in a paper by Gibbs (1969) in this Discussion.

The biological diversity of a tropical hard shore is not exhausted yet. A further dimension of complexity is offered by the teeming populations of photosynthetic symbionts (zooxanthellae and zoochlorellae) and small penetrant multicellular algae, including chlorophyte and other rhodophyte species. Yonge (1968) has given a review of the ecological status of some of those species. Wainwright (unpublished) has made an important contribution to the experimental cultivation of zooxanthellae. As is being increasingly realized, these inconspicuous plants support a significant photosynthetic primary industry, being sufficient, as shown by Sargent & Austin (1954), to maintain a complex economy with its dependent ecosystem where the externally derived phytoplanktonic food supply has been demonstrated to be insufficient.

To do justice to the first task of describing and evaluating a coral reef, each of these facets should be taken systematically into account. To represent and describe the physiognomic zoning pattern of a relatively smooth, visible surface is no longer enough. The appropriate picture must deal with the manifold and ingenious exploitations of space by the concealed life forms, the overwhelming majority of which—under the conditions of high insolation and evaporation, and strong illumination in the tropics—have retreated from the surface. In coral reefs of atoll structure all homology with the zoning pattern of temperate shores may indeed seem to have disappeared. As will be shown, the topography and structure of Solomon Islands shores have certain features that make possible a much more direct link comparison of the biotic patterns with those of temperate zoned shores.

No doubt, by comparison with the familiar picture of a temperate shore, a general reduction will be noticed in the visible importance of eulittoral algae. But the algae are an important element in the moats and on the rubble expanses and—in particular—in the sublittoral fringe. They present in the tropics a change of predominant life-form, rather than a reduction in total biomass. The calcareous red algae are the first and most conspicuous. Womersley & Bailey (1969) identify as *Neogoniolithon myriocarpon* the common cementing species of the moat rubble, found also to a lesser extent on the reef crest where *Porolithon onkodes* becomes the characteristic and basic organism. *Lithophyllum moluccense* is a strikingly branched species common in intermediate conditions between high exposure and extreme shelter.

Turf-forming red algae (*Amphiroa foliacea* on the reef crest, and *Cheilosporum* and *Jania* species) are a prominent feature within surge gulleys and on the flat-topped wave-swept divides between them. In the same surf-swept places, a golden brown colour is given by expanses of short, stiff-leaved *Sargassum cristaefolium* and *Turbinaria ornata*, less commonly *T. murrayana* and *T. conoides*. The profusion of sublittoral fringe algae includes numerous Chlorophyceae: *Chaetomorpha antennina*, *Dictyosphaeria cavernosa* and the species of *Caulerpa*, both wave-washed and in pools: *C. cupressoides* var. *mamillosa*, *C. peltata*, *C. racemosa*, to name a few.

The flexibly jointed and calcified green algae *Halimeda* are the foremost element under more sheltered conditions, festooning dead coral branches, tables or mounds, or attached to the soft gravel or mud substrate of moats.

To survey a coral reef by confining examination to the zonation upon the visible surface would be in itself as insufficient as mapping an equatorial rain forest by aerial survey, or by the quadrat methods appropriate for grassland. Yet the recognition of the patterns of physiognomic zonation is at all events a beginning, and a necessary preliminary to any accurate description. It is the surface zonation pattern, too, with the status and relationships of its organisms, that will best serve as a linking theme between temperate and tropical shores, and point up the widespread homologies these shores may have in common.

Reef forms and coastal topography of the Solomon Islands

Stoddart has clearly shown (1969*a*) how striking are the differences in physiognomy and topography of the Solomon Islands reefs from those of other coral coasts. In some sense, they make the transition from the straightforward zoning patterns on the hard non-coral rock of temperate shores easier to understand. Unlike the atolls which were the geographical areas from which Darwin (1842) arrived at his classical and comprehensive theory of coral reef formation, the Solomon Islands reefs are formed on coastlines of emergence. The coasts, for example, of North Guadalcanal are formed of raised coral-rock terraces of uncertain post-Pliocene age. In successively uplifted benches they form a land-mass several hundred feet in elevation, to which living coral is applied at the present sea level. On the north coast of New Georgia, we find a series of raised barrier reefs forming the island chain by which the Marovo Lagoon is curtained from the outer sea. A less complete chain of islands survives from a second raised barrier within the lagoon. These islands are composed of coral rock, and their slope-off to seaward is today relatively bare of zoned coral. The intertidal reef is very narrow, lying below a deeply notched supratidal bench; and at low tidal level there is no more than a short portico of living reef coral. Only in the gaps between the island links of the barrier chain is there a more extensive formation of reefs in shallow waters.

An alternative to a land mass of uplifted coral rock is presented by those islands of igneous (andesitic or ultrabasic) rocks. To these a living coral reef may be welded at such a level on the shore that the coral bench begins in the lower eulittoral, and the rest of the zonation is on a hard igneous surface, extending through middle and upper eulittoral, to the littoral fringe and so to landward.

Very different reefs are to be found on the low-lying sand cays as exemplified by some of the islands of the Marau Sound, East Guadalcanal (see Stoddart 1969*c*). Here with a cluster of central trees and a shoreline fringe of *Scaevola* and *Ipomaea*, the whole island mass may reach only a metre or two above mean sea level. The upper half of the shore may lack any hard substratum, formed of a steep intensely white sand beach. In many such localities there may appear a high-tidal platform of low-pitched rather level beachrock, formed *in situ* (see Stoddart & Cann 1965) on which a rather impoverished upper shore zonation may be displayed.

The widest of spreading reefs will be found attached to islands or sand-cays within the shelter of spits or the lee side of larger islands. In the Marovo Lagoon and the small archipelago of the Russell Group, the broad reefs lie to the leeward side and—on the islands with a south-facing weather coast—contrast with the narrow surf-pounded and moated reefs on these exposed shores.

The simplest example of a zoned intertidal shore, though one unusually abbreviated for a coral coast, has been shown in figure 145, selected from the seaward face of Matiu Island, forming part of the outer bastion of the Marovo Lagoon, as described by Stoddart (1969*b*).

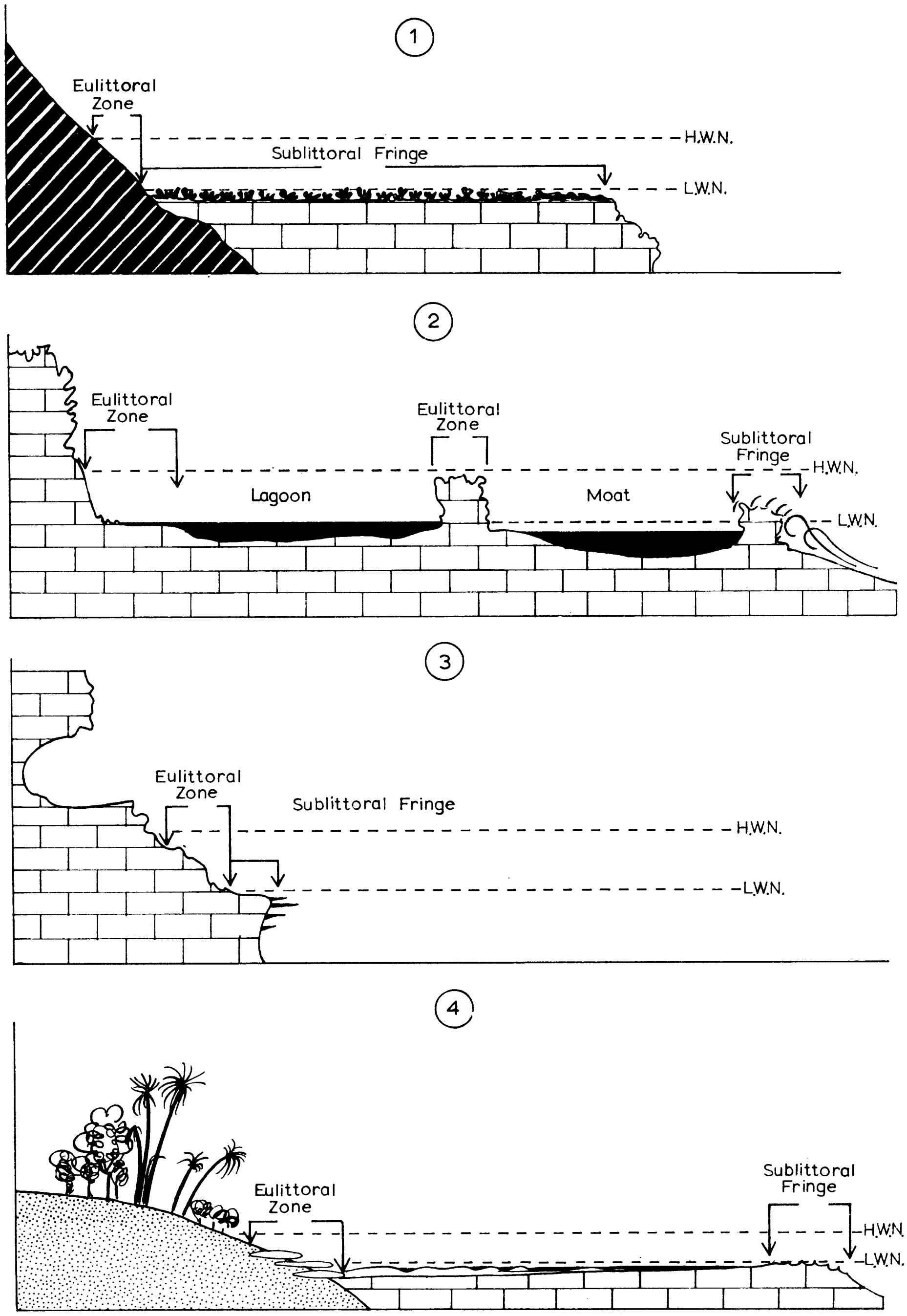


FIGURE 144. Some characteristic shore forms in the Solomon Islands: (1) a fringing reef built on a coral platform reaching the level of low water neap, and built out from a landmass of igneous rock; (2) a fringing reef with two moats and a rain-etched and pitted supratidal area, carved from a coastal terrace of raised coral rock; (3) a narrow fringing reef, with a steep 'cliff' falling off to seaward and a pronounced supratidal niche, cut in limestone rock of an old, uplifted barrier reef; (4) a small island or sand cay, with a fringing reef or lagoon flat developed upon a platform of coral rock or rubble. 'Beachrock' derived from calcareous sand (see Stoddart & Cann (1965)) may occur in scattered outcrops at beach level.

On a north-facing open coast, this shore does not come under the highly exposed régime of the southern weather coasts; but it is confronted by open water and is clearly a shore of greater than average exposure. The sequence of the zones is very straightforward. Their chief character is perhaps the depauperate state of the algae (other than encrusting calcareous rhodophytes); *Sargassum cristaefolium*, a constant feature of open weather coasts, was almost lacking at Matiu Island, and *Turbinaria* was excessively scarce. The zonation is based upon a relatively few, well-distinguishable animals and calcareous algae. Table 30 compares the zoning characteristics and relative vertical heights of the zones upon the exposed and sheltered sides of this narrow islet.

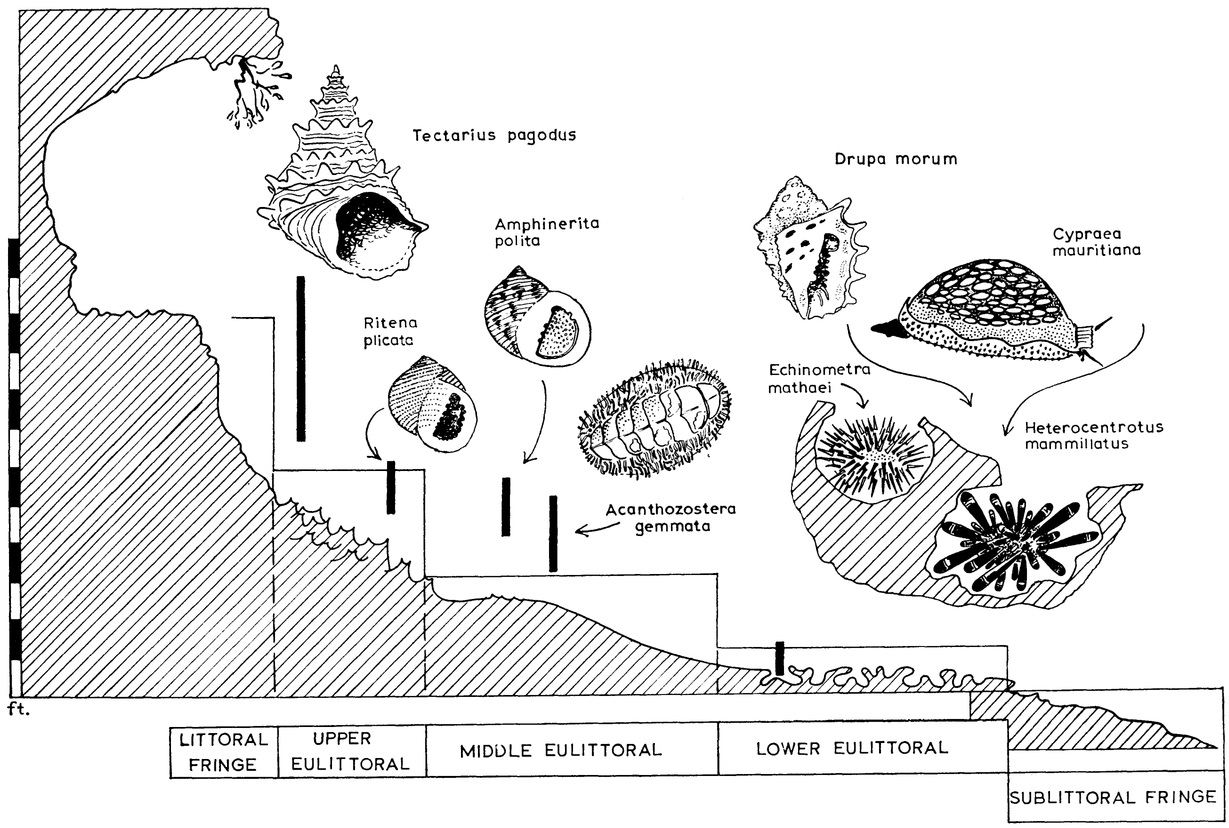


FIGURE 145. Matiu Island, New Georgia. The pattern of intertidal zonation on a narrow fringing reef on the north-exposed outer coast of one of the barrier islands. Some molluscs and echinoderms characteristic of the various zones are shown, with their approximate vertical ranges. For the fuller details of zonation, see table 30, and Womersley & Bailey (1969).

A good account of the zonation pattern of this area will be presented by Womersley & Bailey (1969). The curtailment and apparent simplicity of the zoning does not mean that the wealth of the cryptobion, and other special habitats, is reduced. A description of the boring and embedding annelid sipunculid worms of this shore will later be given by Gibbs, and Morton will separately analyse the molluscs and their ecology.

To turn to a wider reef fringe, extending seawards from an igneous land mass, an interpretation on the basis of the Universal Zonation Scheme is given in figure 147. Within the shelter of the reef crest, where the white line of the surf breaks over the more vivid colours of the living coral, there is found a wide expanse of sheltered water, turbid and of pale green colour strongly contrasting in aerial view with the deeper blue of the sea beyond. This enclosed area may constitute a permanent shallow lagoon; or an expanse of dead, or partly growing coral subjected to a brief emersion at low spring tides. In the most sheltered situations, such protected reefs may reach up to a mile in width and consist in varying proportions of coral finger rubble, or stretches of comminuted coral sand, cream-white in colour to silty grey, with the sea grass *Halimeda* developed to varying extents. In areas where there is greater water movement, as in channels through which the tide ebbs and flows, for example between the islands of the Marovo Lagoon barrier, or in the reaches of the Sandfly Passage or the Marau Sound, there may be much greater profusion of living corals, branched, corymbose, foliose or massive, generally sited upon a basement of clean or sand-strewn coral rock, or on well consolidated rubble.

TABLE 30. ZONATION OF SEMI-EXPOSED SHORE ON MATIU ISLAND, NEW GEORGIA

zone	algae	surface animals	cryptobion
1 littoral fringe	(lichen *Verrucaria*)	*Tectarius pagodus*	—
2 upper littoral zone	—	*Ritena plicata*, *Amphinerita polita*, *Acanthozostera gemmacea*, *acutirostris Isognomon*	—
3 mid eulittoral zone	*Porolithon onkodes*	*Acmea saccharina*, *Cellana rota*, siphonariids. *Tetraclita squamosa* algal pools, with carpeting zoanthids, *Turbinaria* and *Caulerpa serrulata*. *Phyllochaetopterus* tubes	chiefly sipunculids
4 lower eulittoral zone	*Porolithon onkodes* and rhodophyte turf. *Dictyosphaeria*	numerous drupids, thaids, trochids, turbinids, *Haliotis varia*	greatly enriched with polychaetes and embedding molluscs; urchins *Echinometra mathaei* and *Heterocentrotus mammillatus*
5 sublittoral fringe	*Lithophyllum molluccense* *Porolithon onkodes*	*Acropora*—small heads and encrusting sheets; *Porites* nodules, *Stylophora mordax*, *Pocillipora elegans*, small *Goniastrea* heads	as in 4

As an alternative to the sheltered fringing reefs developed in protected bays and along channels, or to the narrow reefs of leeward open coasts, there are the reefs of the exposed, south-facing weather coasts, as on the Russell Islands Group (especially Banika Island), Gizo, part of South Guadalcanal, and Wickham Island, New Georgia. These consist of raised benches over which, from the outermost edge, the surf pounds unremittingly. They were by far the most spectacular coasts encountered, for the study of classical shore zonation, relatively uninterrupted by loose cover, or by fragile living coral forms. The reefs are constructed of massive coral rock, dead and uplifted, carved into several terraces and moats. Even at the living seaward face of the reef, coral is second in abundance to encrusting algae, for it is here that the calcareous reef-building Rhodophyceae come into their own. With pastel hues of pink, mauve and purple and with frequent splashes of more vivid colour, their branched, reticulose or sheet-like growth forms almost entirely replace coral as the living substrate.

The fringing reef benches of the weather coasts are predominantly flat beyond the upper eulittoral to the landward. Recent changes in sea level may however be responsible for stepped terraces, and one or more clean-cut moats may be carved out, enclosing bodies

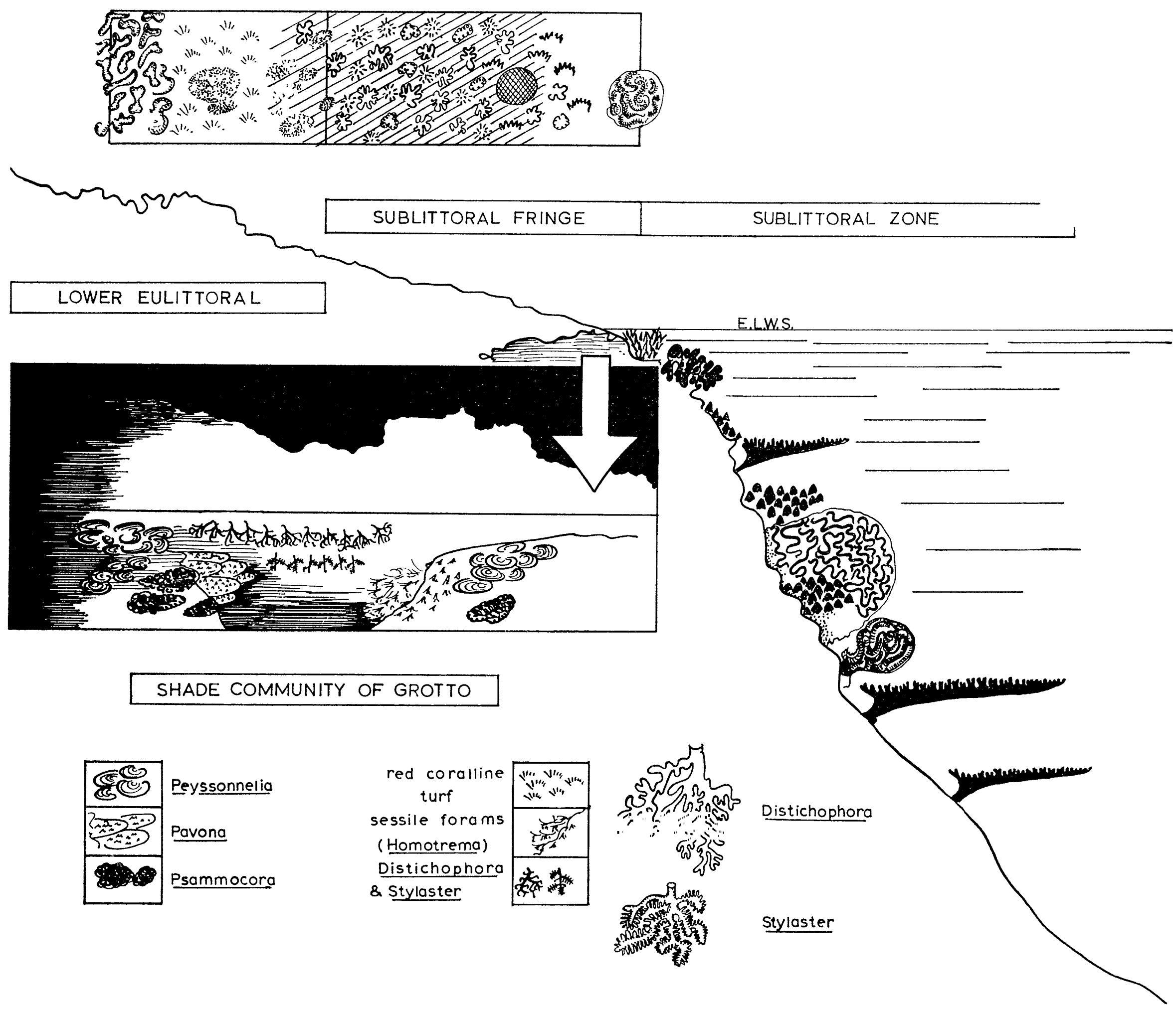


FIGURE 146. Matiu Island, New Georgia. The composition of the sublittoral fringe and sublittoral zone, together with distribution of coral and other organisms in a shaded surge-swept gully at sublittoral fringe level.

of water with varying extents of isolation from the open sea during low tides (see figure 148 for moats on Banika Island). Such stretches of shallow water may form seaward moats constantly replenished by surf splash; here there will be a rich development of coral heads, convex mounds or low crusts of faviids (*Favia*, *Favites*, *Goniastrea*, *Leptoria*), *Porites* cf. *lobata* heads and nodules, and small tables of *Acropora* fingers. Alternatively, farther back from the surge-line and cut off from wave replenishment between tides, the moats are wide and shallow, with temperatures rising at mid-day low tides to above 35 °C; sometimes merely a few inches of standing water lies over a solid coral rock platform, or covers an expanse

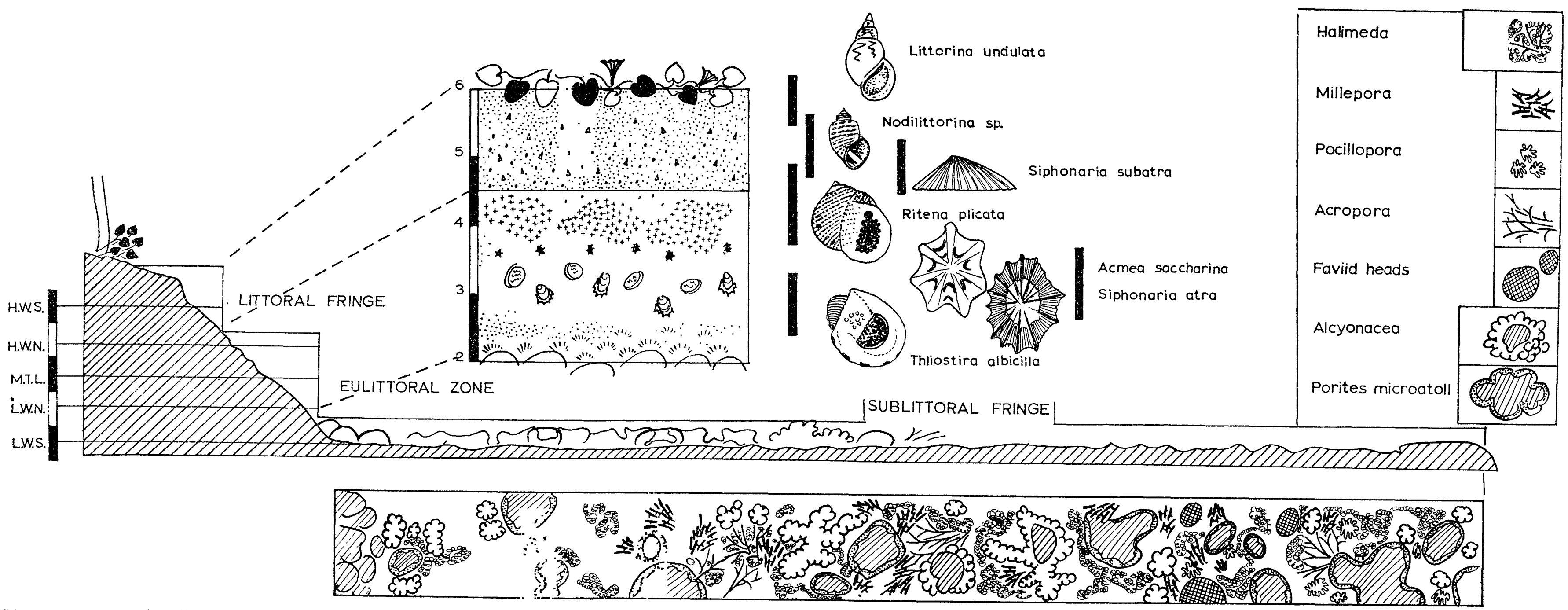


FIGURE 147. An interpretation of the zonation of a shelving reef in moderate shelter, with a steeper backshore of andesitic bed-rock, carrying the littoral fringe and the eulittoral zone. An analysis is given of the zoning pattern of the sloped area, with the ranges of the characteristic common gastropods. The littoral fringe is a littorinid zone (*Littorina* and *Nodilittorina*). The upper mid-littoral zone carries a scatter of a small operculate barnacle (*Chthamalus* sp.). The middle mid-littoral has sessile and cemented bivalves, species of *Chama* and *Crassostrea*. The broad extent of living Scleractinia and other coelenterates is treated as a greatly extended sublittoral fringe.

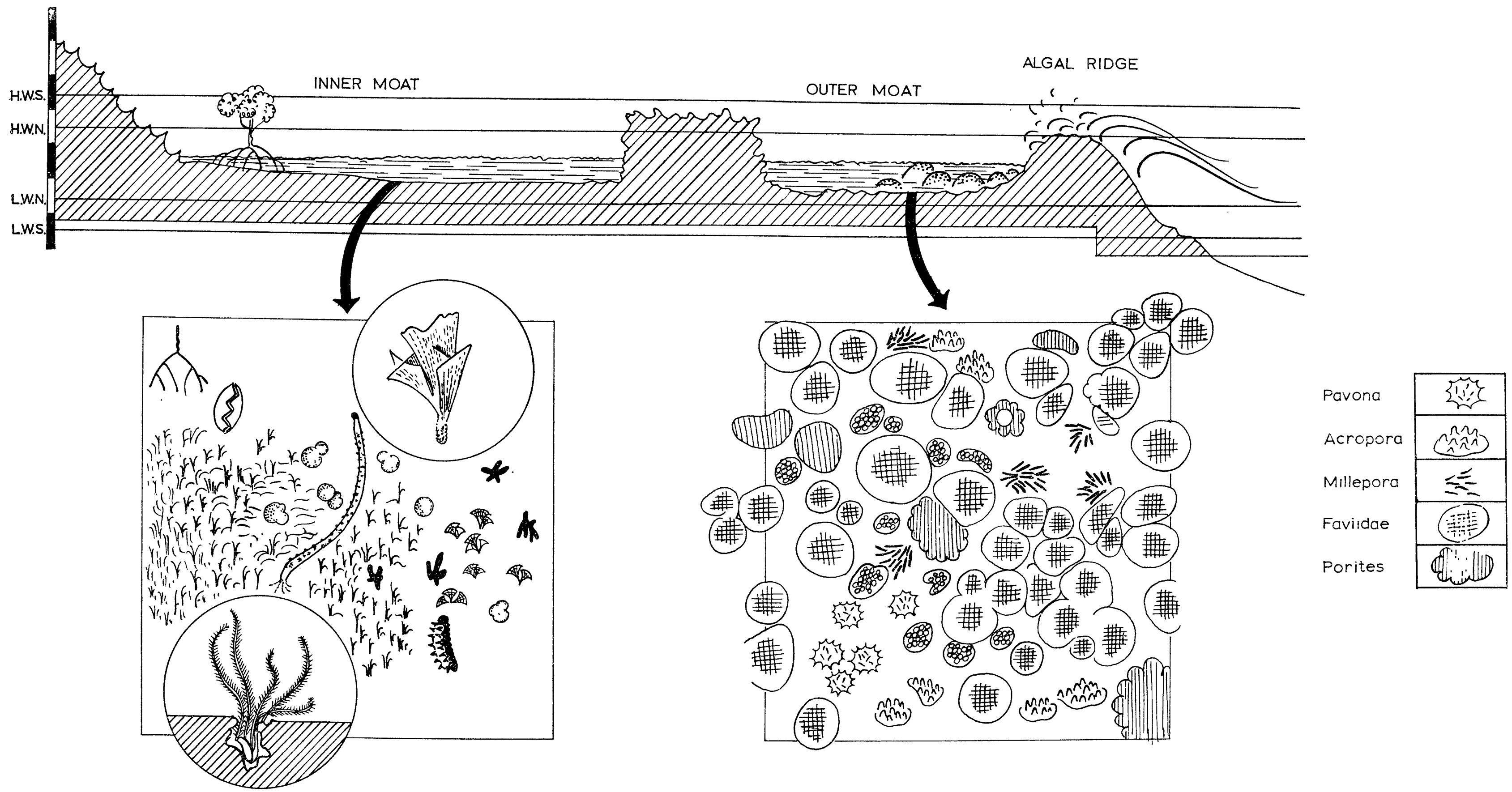


FIGURE 148. Banika Island: Russell group. A two-moated reef bench under strong wave exposure, showing the species composition of the moat floors, represented diagrammatically, from actual 2 m square quadrats. Inner moat: *Thalassia hemprichii*, *Avrainvillea erecta*, (inset) *Padina commersonii*; sapling of *Rhizophora stylosa*; corals: *Montipora ramosa*, *Porites lutea*. *Tridacna crocea*, holothurians: *Stichopus* sp., *Opheodesoma grisea*, *Ophiocomina scolopendrina* (inset). Outer moat: convex coral heads, chiefly Faviidae (*Favia*, *Goniastrea* and *Leptoria*) and *Porites* with smaller clumps of *Millepora platyphyllia*, an encrusting *Pavona* and small tables of *Acropora* fingers.

of strewn rubble, or silty sand with sea grass. The flora of such moats includes notably *Padina* and *Avrainvillea*, with small *Rhizophora* striplings in some places. The shells of vermetid gastropods (*Dendropoma* spp.) may be attached to the bottoms of the pools. On the silty surface may live a wide variety of holothurians (Holothuriidae and Stichopodidae). With sea grass the large and peculiar synaptid *Opheodesoma grisea* may be frequently found.

Pools

Whatever the physiography and temperature régime of these moats and trenches they are all interruptions of the regularly emersed surface of the kind broadly to be described as 'pools'. On a temperate shore it is chiefly the pools of smaller extent that introduce the main discontinuities into a straightforward intertidal zonation pattern. Though the animals and plants of pools are never emersed with exposure to the atmosphere between tides, yet pools offer a physico-chemical régime very different from that of freely circulating open water. During the intervals of tidal withdrawal, they must form an environment with hazards as 'difficult' as those of the emersed rock surfaces. The water temperature régime fluctuates greatly and reaches high upper extremes, maximally so in those bodies of water that are of small volume or shallow and of wide area. Oxygen and carbonic acid content and hydrogen ion concentration fluctuate widely with the metabolic activities of the plants. With the suspension or settlement of fine sediment, illumination may be critically lowered, and the flora impoverished.

The species composition of the pool fauna and flora is markedly different from that of either exposed surfaces or unimpounded waters at comparable levels. The most important biological characteristic of pools is to produce a translation into a higher zone of some of the organisms typical of the regularly emersed general surface in the zone next below. Thus the lower moat in figure 148, situated in the lower eulittoral zone, will contain similar corals to those occurring on the briefly emersed stretches of the sublittoral fringe. The wider moat of the upper eulittoral contains not corals, but vermetid gastropods, bivalves (chamids and arcids) and ophiuroids (especially crevice-lodged *Ophiocomina scolopendrina*) typical on emersed stretches of the middle eulittoral, which is the zone next below. At the level of the sublittoral fringe (as illustrated for Matiu Island in figure 146) there may be rich grotto-like pools in the form of shaded channels briefly cut off from the open sea. Here there will appear numerous representatives of a rich faunule, normally typical of the lowered light intensities of the permanently immersed sublittoral zone. As well as fragile *Acropora* species and encrusting *Psammocora* and *Pavona*, the hydrocorals, pink *Stylaster* and apricot to mauve *Distichophora*, are here well developed. Prominent algae include the brittle, dark red *Peyssonnelia*. The sessile animals constitute a 'hypobion' which in these dimly lighted conditions has become deployed on the open surface; it includes as well as sponges, serpulid tubeworms and polyzoa, several species of sessile foraminiferans, *Homotrema rubrum* and *Miniacina miniacea*, like splashes of red sealing wax, and a pale or colourless species sometimes as fragile as spun glass (see table 31).

The distribution of coral growth forms and genera has been represented for a fringing reef and its seaward slope, on a leeward coast and without a significant development of algal ridge. A broadly generalized pattern of zones may be recognized on the following lines.

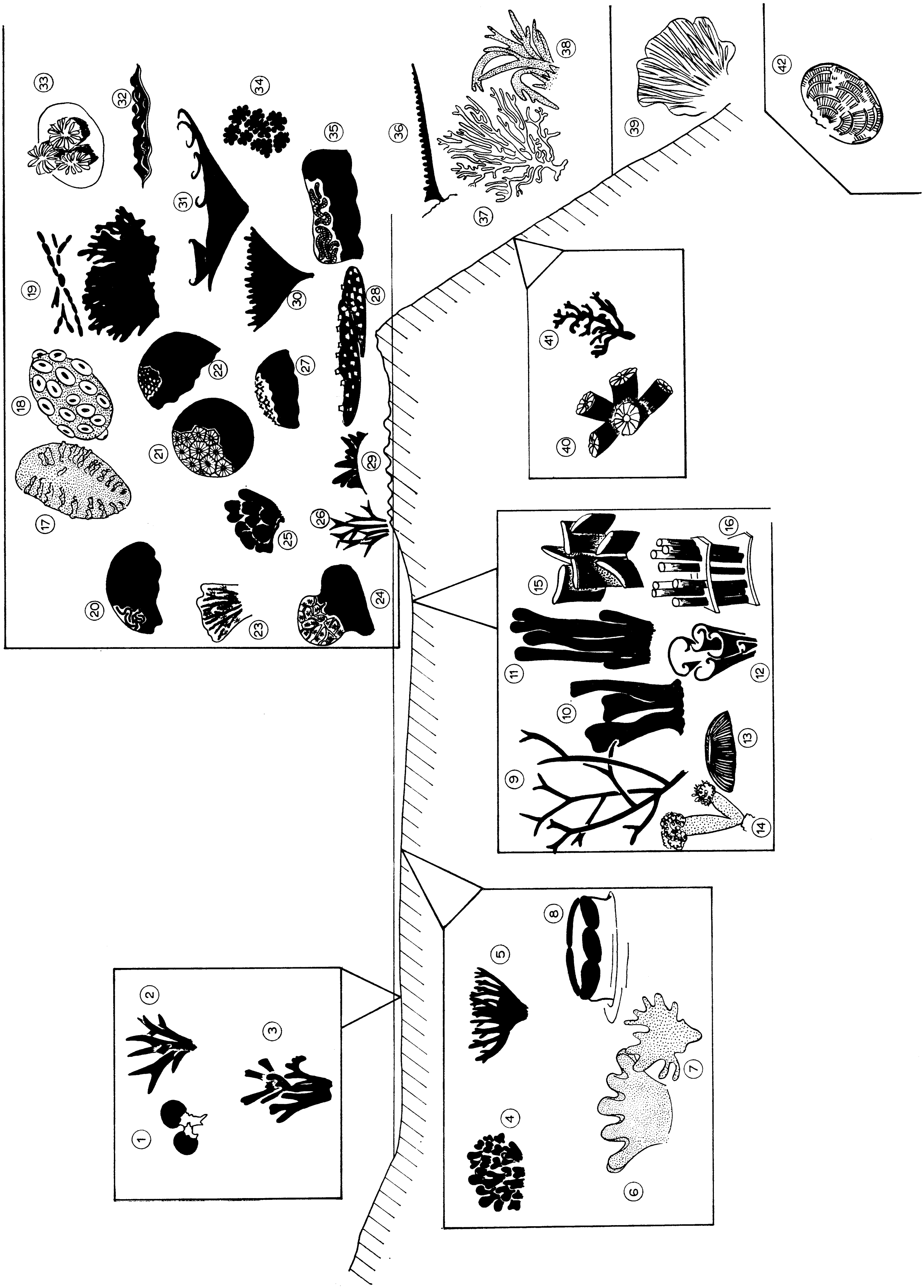


FIGURE 149. For legend see facing page.

TABLE 31. TRANSLATION EFFECT IN INTERTIDAL POOLS

zone	emersed rock surface	pools
upper eulittoral		
mid littoral	vermetids; *Chama*; *Ophiocomina*; *Porites lutea*; finger *Montipora*	
sublittoral fringe	*Porites* and faviid mounds. *Stylophora*; *Pocillopora*	corymbose *Acropora* (shaded grotto pools)
sublittoral zone	*Peyssonnelia*, sponges, serpulid tubeworms (*Salmacina*) sessile Foraminifera, Hydroids, stylasterine corals; *Psammocora*, *Pavona*	

(i) A landward zone where the water depth at low tide is no more than a few inches over silty sand or rubble. This is the equivalent of the landward shoaling *Porites lutea* zone branches of *Acropora palifera*, *A. hispida* and the ragged branching *A. brueggemanni*. Free-standing columns of the poritid *Goniopora* are often welded into a continuous cover, and in calmer water are the free-standing scrolls of *Montipora foliosa*. Between the stands of massive structural coral appear smaller forms that are a feature of zone (iii) as well; branched *Pocillopora elegans* and *damicornis*, heavy flanges of *P. eydouxi*; club-tipped *Stylophora mordax*, and more delicate *Seriatipora hystrix*. On the sand or rubble floor lie loose specimens of *Fungia*. Smaller corymbose species of *Acropora* reach up to a foot in head diameter.

(iii) The region of surf-break, in leeward conditions too calm to develop an algal ridge. Coral growth forms are strongly built and depressed against the surface to offer little resistance to wave attack. The *Acropora* species are very numerous: broadly shelving brackets (*A. reticulata*) tables and shallow funnels, clusters of thumbs of mauve *Acropora hebes*. A low encrusting species of *Acropora* covers wide areas of rock, as may encrusting *Montipora* c.f. *erythraea*. Shelving or small-bracket species include a second *Montipora* and the yellow *Turbinaria*.

Low-domed heads of the faviid corals are very frequent, as of *Goniastrea pectinata*, *G. retiformis*, *Platygyra lamellina*, and *P. phrygia*. So too are smaller heads of *Favia* and *Favites*, and massive micro-atolls of *Porites* c.f. *lobata* and *Symphyllia*. *Pocillopora eydouxi*, *P. elegans* and *Stylophora mordax* are firmly attached to the surface in surge-swept localities. *Lobophytum expansum* forms a flat or corrugated sheet.

(iv) A similar zone, in leeward shores, extends around the reef crest, below low water mark, and gives its character to the immediately subtidal area, with a predominant emphasis of large *Acropora* brackets, especially *A. corymbosa* and *A. reticulata*. Micro-atolls of faviids, *Symphyllia*, and *Porites* form a firmly stablized cliff-edge before the drop to deep water, and the soft corals *Sinularia* are a common feature.

(v) A special coral fauna is found in the shelter of ledges and recesses in the sublittoral fringe and on the sloping faces of the sublittoral fringe from low water downwards. It includes the hydrocorals *Distichophora* and *Stylaster*, and other ahermatypic forms *Tubastrea*, *Culicia* and *Caryophyllia*.

(vi) Below the level where corals were effectively sampled in representative quantity, a number of SCUBA dive collections brought up specimens of *Echinophyllia* species and, at lowest depths reached at *ca.* 90 ft. of the agariciid corals, *Leptoseris* and *Pavona*. These marked the existence of the zones comparable with the wide-ranging *Echinophyllia* Zone, from about wave base to about 50 ft. and a *Leptoseris* Zone below that depth to the limit of living coral occupation (see Wells 1957).

The sloping offshore face of a lagoon reef has a character very different from that just described. Such habitats are not commonly found on the Solomon Islands shores; but one at Paruru Bay, in the Marau Sound, east Guadalcanal forming the leeward back-slope of the spit cutting off a lagoon from the sea, is illustrated in figure 150. The spit forms a sandy, or rubble strewn shore, just awash at low water neap tide. Its slope is built chiefly of the fused vertical branches and fingers of *Porites* c.f. *columnaris*, forming a solid mass, with the living corallites of the fingers greenish brown. At 15 ft. and below, the reef slope is fringed with large flanges and brackets of *Montipora foliosa*. Very common here is a delicate 'bottle-brush' *Acropora* species, found only in such habitats. There are also clusters of the brittle, foliose agariciid *Pavona cactus*. The ground near the bottom is littered with dead coral boulders on which grow *Seriatipora hystrix*, *Pocillopora damicornis*, and the branches of a problematic cord-like ramose *Psammocora* species.

The plastic growth forms of *Acropora* are profusely variable with degree of shelter, wave impact and current flow. They include corymbose heads (*convexa*, *hyacinthus*), flat topped shelves and brackets (*A. reticulata*), slender branched antlers (*cervicornis*, *echinata*), heavy clubs and flanges (*A. hispida*). At the one extreme are found the fragile brush-branches with long tubular calices (such as *A. rayneri*) typical of leeward and lagoon slopes; at the other extreme heavy surf may break over fingerless expanses of *A.* c.f. *monticulosa*, *pyramidalis*, forming a spreading crust over the rock surface.

The problem of 'dead reefs'

Those experienced in coral ecology by common consent remark that the Solomon Islands reefs lack the luxuriance of those in many other parts of the Pacific, in particular the rich Great Barrier Reef and the widespread atoll and small island formations. Much of the intertidal coral is dead. Frequently in sheltered localities, where a wide sublittoral fringe had at no distant time been occupied by luxuriant coral growth, the prevailing colours were those of grey or dull khaki brown; at some of these places, as during mid-day low spring tides, there was the slight pervasive odour, soon to become familiar and even nostalgic, of dead or moribund coral tissues. Two examples of dead reefs near Honiara are shown in figure 151. A further sketch from Tetel Island, in the Sandfly Passage of the Florida Group, shows the typical aspect of a largely dead sublittoral fringe.

Such an expanse as that illustrated for Honiara or Mamara might be designated as 'sublittoral fringe' if its coral were living. At present live coral and calcareous red algae are confined, apart from pools, to the seaward zone next below the dead reef, which wears a pink aspect in contrast to the prevailing grey. With its present status the dead reef raises a nomenclatural problem, but would seem best to deserve the term 'lower eulittoral'. So far as tidal criteria can be helpful, this part of the reef was regularly laid bare at higher than average low tides (June to October 1965) when the seaward zone of living coral remained covered.

From the intact condition of the dead and naturally brittle corals, chiefly small *Acropora* heads and tables, and *Montipora foliosa*, these are unlikely to be of great age; and while it is difficult with the restricted period of observation to assess local growth rates, Yonge (personal conversation) considers possible the formation of a coral cover such as that described over one or a only a few seasons.

The first need is for a knowledge of tidal patterns and cycles. Few predictions or continuous past records of tides for any part of the Protectorate were available for use. In the course of the Expedition, several fortnightly tidal cycles were continuously recorded. The record in figure 152 shows that so far as our widespread observations could assess, these seemed to be general during June to November for the Protectorate as a whole. The tide is diurnal, with vestigial peaks of a second high tide. The major tide of the 24 hours tends to move from one peak to the other. The spring range recorded was 3·5 ft. and the neap range 1·5 ft. During the 5 months of the Expedition the time of low tide remained fairly constantly close to mid-day; for the other half of the year, the consensus of local information, as confirmed by changes noted by us from the beginning of October, was that low water would move to around midnight. Irregular shifting of low tide had already begun during the final month of the Expedition's stay.

Obviously the next programme of investigations must begin with a full year's cycle of tidal records, in the first instance at Honiara where an automatic tidal recorder would be

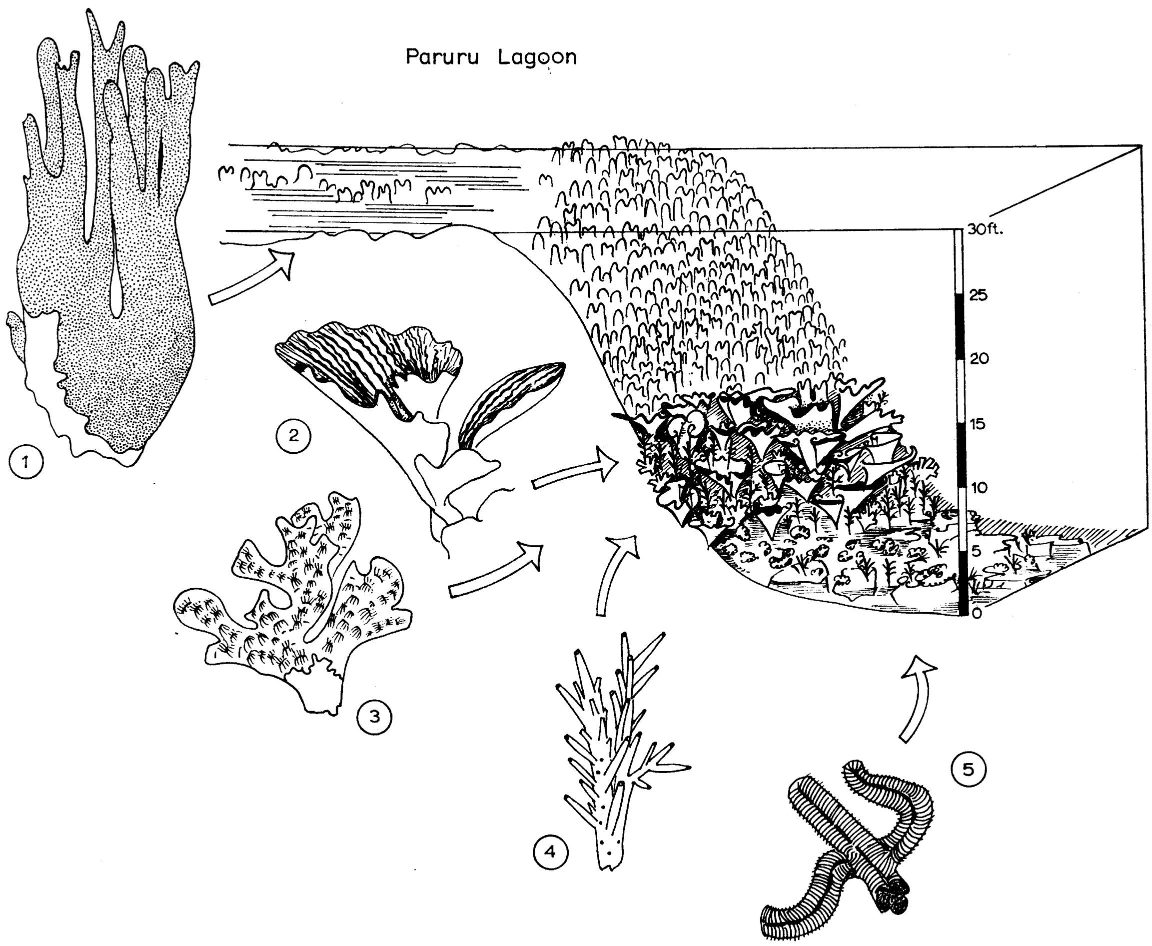


FIGURE 150. Schematic view of sheltered slope of a lagoon reef at Paruru Bay, Marau Sd., east Guadalcanal. Some corals typical of the various levels are illustrated. 1, *Porites* c.f. *columnaris*; 2, *Montipora foliosa*; 3, *Pavona cactus*; 4, a bottle-brush *Acropora*; 5, a cord-like ?psammacorid.

easy to install and maintain. Tidal observations should be correlated with fluctuations in the seasonal or longer period growth of corals on the Mamara and Honiara 'dead reefs'.

Present hypotheses upon coral death can be no more than speculative, though some tentative suppositions can be fairly and perhaps usefully offered. The effect of a widespread pathogen could perhaps be discounted in favour of a tidal explanation, in view of the position of the dead coral at an anomalously high level. Coral death could conceivably be brought about from tidal causes, if:

(*a*) Changes could be demonstrated between the lowest levels reached by spring tides at different times of the year. Variation in the mean sea level at Kukum, near Honiara,

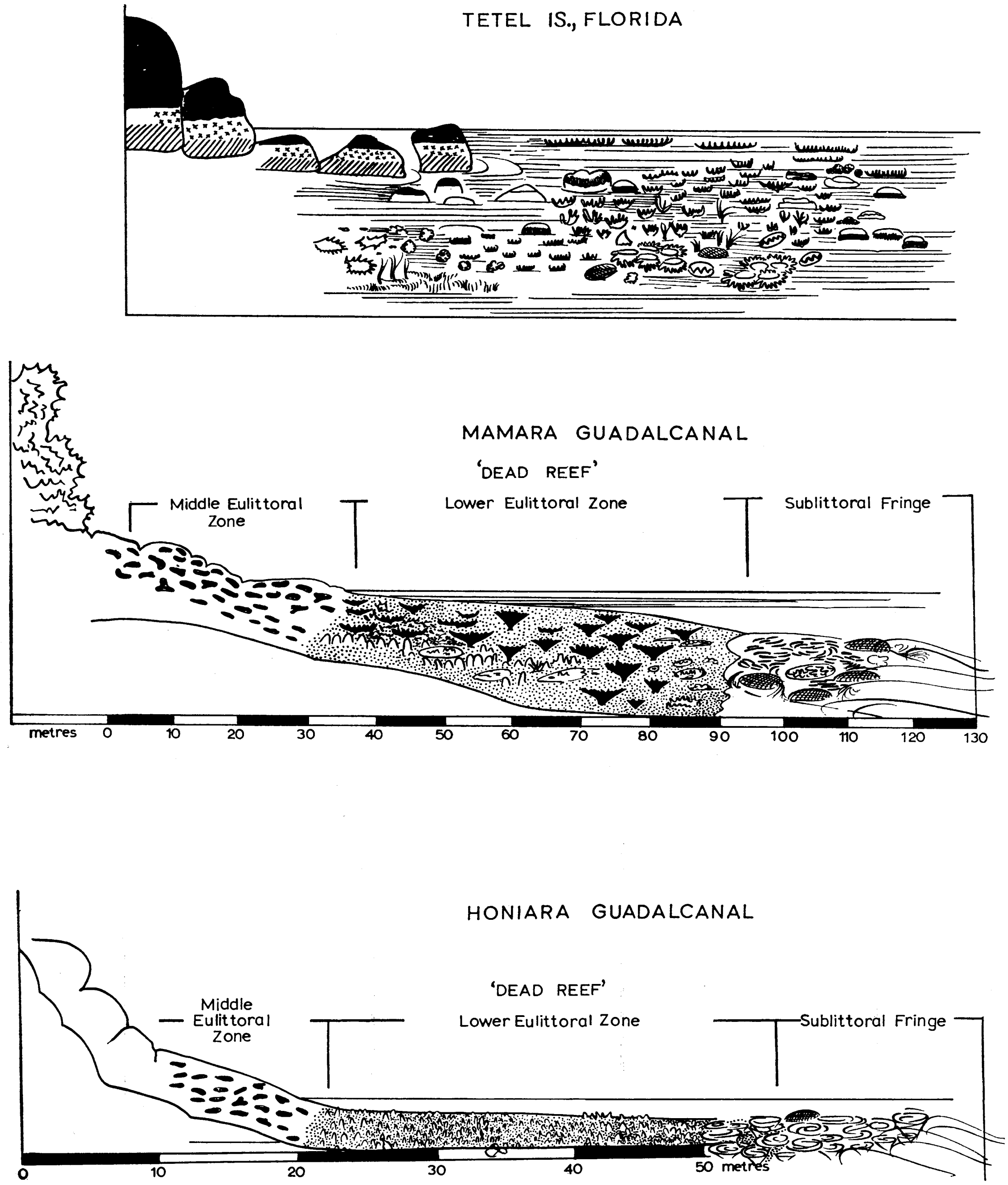


FIGURE 151. The formation of 'dead coral reefs'. (Upper): an expanse of intertidal reef flat, with coral heads of *Acropora*, microatolls of *Porites*, seagrass and soft corals *Sarcophyton* exposed at low spring tide. The shore above the lower midlittoral is of andesitic boulders. (Middle): the intertidal reef flat at Mamara, near Honiara, north Guadalcanal. The middle eulittoral zone is an expanse of urchin-scoured coral rock. The 'dead' lower eulittoral zone is of dull grey-brown hue, having a basal stratum of *Acropora* and *Montipora* finger rubble with a lightly attached superficial cover of recently dead *Acropora* tables. Cementing coralline algae usually dead and bleached include *Neogoniolithon* and *Lithophyllum moluccense*. The sublittoral fringe is freely wave-washed at low water. The principal living corals are convex heads of *Goniastrea pectinata*, *G. retiformis* and meandrine faviids (*Leptoria* spp.). Upright flanges of *Millepora platyphyllia* are abundant. A pink surface hue is given by the cementing calcareous algae, especially living *Lithophyllum moluccense*. Green *Chlorodesmis comosa* is also conspicuous. (Lower): a 'dead reef' under greater shelter than the previous example, at Honiara waterfront, north Guadalcanal. The lower midlittoral zone shows evidence of contamination by sediment, freshwater run-off and debris from the land. Its dead expanse is a cemented rubble of fingered *Acropora* and *Montipora* species. A pure zone of cornets of *Montipora foliosa* comes partly into this dead region at the seaward edge. The pink sublittoral fringe is predominantly of living *Montipora foliosa*, *Goniastrea* heads and encrusting coralline algae.

shows a range as between July and January of 0·6 ft., and Captain Taylor, of the Marine Department, B.S.I.P., Honiara, advises that this is a general phenomenon throughout the Group (table 32).

Table 32. Seasonal variation in mean sea level at Kukum, Guadalcanal,* with approximate times of diurnal low tides

	1 Jan.	1 Feb.	1 Mar.	1 Apr.	1 May	1 June	1 July	1 Aug.	1 Sept.	1 Oct.	1 Nov.	1 Dec.
M.S.L. (ft.)	+0·2	+0·2	+0·1	0·0	0·1	−0·3	−0·4	−0·3	−0·1	+0·1	+0·2	+0·2
low water (1965)	—	—	—	—	—	mid-day	mid-day	mid-day	mid-day	early afternoon	early afternoon	—

* Data from *Admiralty Tide Tables*, vol. III (1963), p. 470.

(*b*) The lowest levels of low tide, with maximal extent of emersion, fell during the half years with middle day low tides. The accompanying table shows this to be the case during the 5 months of the Expedition. The combined effects of high illumination and air temperatures during periods of more than usual emersion of the sublittoral fringe might have enhanced lethal effects on organisms. This might be in some part an annual phenomenon, perhaps mitigated or accentuated in particular years by other climatic effects.

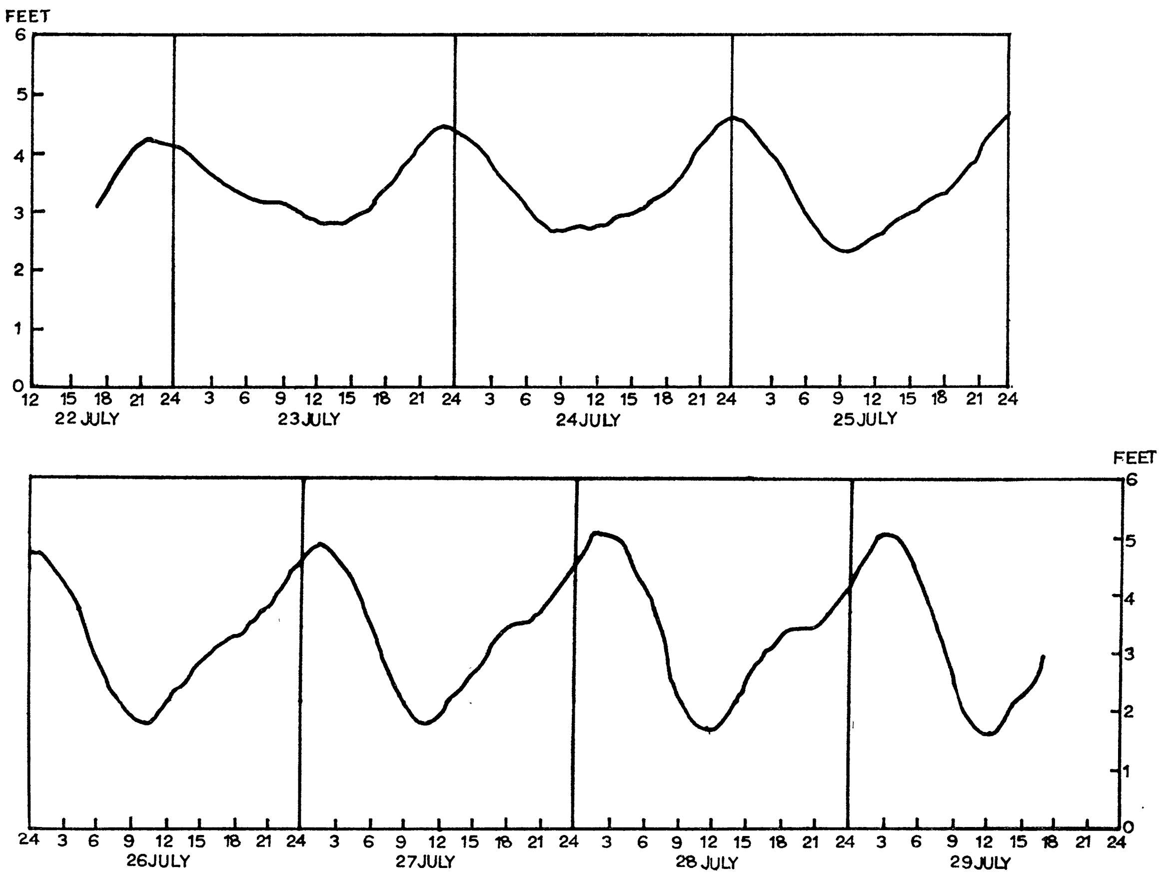


Figure 152. Tidal curve for Tetel Is., Florida Group, from 22 to 29 July 1965.

In addition, it has been postulated that the effect of heavy rainfall on emersed coral might contribute to the death of reefs. In most parts of the Protectorate this would seem unlikely to be a phenomenon acting cyclically, since high rainfall is experienced daily or at very short intervals though Honiara, on the north coast of Guadalcanal, has a lower rainfall than is general. On terraced shores with a sloping terrain, and near river mouths, estuaries and harbours, the effects of concentrated run-off of fresh water from the land, could be far more injurious to corals than on low-pitched sand-cays or atolls.

To conclude, the most profitable single operation with which to follow up the Expedition's work will be an investigation into fluctuation of tidal levels and patterns over one or more full years, and a correlation of this data with the short-term events on the reefs. Such a programme properly directed could be well within the range of a secondary school or local naturalists in the Protectorate.

'Hard' and 'soft' shores

The distinction between 'hard' and 'soft' shores is a working demarcation that has tended in the past to run sharply through descriptive shore ecology; so much indeed that studies of shores of soft sediments and of those where rocky substrata are predominant have tended to remain in the hands of different workers, using different methods and dealing with lists of species having little or no overlap. Though an obviously arbitrary division, this is one that has not on temperate shores been found easy to bridge; though some authors—notably Dahl (1953) with a sketch based upon burrowing Crustacea—have suggested the use of a tripartite system for sandy shores.

On tropical shores, though the extremes of the series 'hard' to 'soft' appear remote and utterly unlike, these shore types intergrade so closely towards the centre that a line of demarcation is virtually unable to be drawn. The reasons for this lie in part in the special nature and properties of the 'hard' coral substratum, as well as in the high tendency to the disposition or entrapping of fine sediments in local patches.

First, any reef flat is obviously a complex mosaic of hard and soft substrata. A lagoon with sand-strewn bottom has characteristic corals such as loose-lying *Montipora* and small nodules of *Porites* as well as unattached *Fungia*. In a continuous coral stretch sandy patches with burrowing fauna regularly intervene amidst hard substrata. Flats of silty sand are frequently dominated by a vegetation type such as the calcified green alga *Halimeda* and or occasionally by *Caulerpa racemosa* that would more usually appear under coral rubble or rock. Some green algae such as certain *Halimeda* species (*cylindracea*, *macroloba*, *simulans*) and sometimes *Avrainvillea erecta* are indeed associated typically or exclusively with silty flats. Methodologically it would be frustrating to reserve these types of habitat for separate description in the way tacitly followed for temperate shore ecology.

Secondly, a coral shore of whatever nature can no longer be described sufficiently as a hard substrate characterized by particular patterns of surface zonation. It is, as we have seen already, subdivided and 'microspaced' in a way true for no igneous or sedimentary shore; and it is frequently particulate and even mobile. There is, moreover, no natural break in size or kind of loose particles, in a long series from loose micro-atolls, blocks or nodules of coral, through coral fingers and rubble, coarse coral gravel to clean white coral foraminiferan sand, or finely comminuted powdery sand from coral and calcareous algal remains.

Thirdly, like all particulate substrata, coral is freely penetrable by animals. Its fauna retreats in large part from the surface, has special adaptations for a burrowing or penetrating habit, and has frequently to be sought by digging or prising it out. There is between sandy and muddy shores, and coral substrates of less solid texture such as massive *Porites* a surprisingly large series of interconnecting life forms. Bivalves, for example, burrow into coral rock as well as sand, albeit as rather specialized life forms such as *Lithophaga*, gastrochaenids and pholads. Rock-burrowing sipunculoids such as *Aspidosiphon* and *Dendrostomum* have parallels among the *Sipunculus* species of sandy shores. The Eunicidae and other polychaete families with coral-boring representatives are on temperate shores much more typical inhabitats of soft substrates. The Terebellidae, Cirratulidae and Sabellidae are worm families conspicuously developed on both kinds of substrate. Abandoned borings and galleries in coral rock lodge crustaceans such as alpheids, axiids, porcellanids, galatheids, stomatopods and certain Brachyura, which all have slow counterparts in soft sediments. Furthermore, blennioid fishes and echinoderms (particularly holothurians and echinoids) are life forms equally common in coral rock and in finely divided soft sediments.

There will remain to be considered an important category of soft shores consisting not of organic remains such as coral products, foraminiferan or shell sand, but of some of the numerous sorts of non-calcareous sediments: coarse river-borne gravel, siliceous sand sometimes dark with grains of magnetite or various ferromagnesian minerals, and clays and muds of terrigenous origin. In the Solomon Islands non-calcareous beaches are frequently developed as steep-sloped fringes on open coasts where there are no reefs. They must consist of black iron sand or light coloured siliceous sand; while under maximal surf exposure as on parts of the south coast of Guadalcanal, the beaches may form high-banked, concave ramps of coarse gravel, inhospitable to any life at all.

At the other extreme extensive soft shores will be laid down in estuaries and in enclosed or landlocked channels, where coral growth is impeded by freshwater run-off from the land, as illumination is cut down by the heavy content of silt and clay. Such muddy shores, of level profile, will support predominantly a vegetation of phanerogams, both mangroves and marine monocotyledons. They frequently, to the seaward edge, retain an accompaniment of coral, sometimes in conditions of surprisingly high turbidity; in particular, nodulose *Porites* and certain *Montipora* species have a distribution extending a good way into silt-laden waters.

The zones and their characteristics

If we are to recognize, from the tripartite division of both reefs and sedimented shores, a comparable Eulittoral Zone with Littoral and Sublittoral Fringes, extending through from exposed weather coasts to estuaries, we shall clearly be unable to characterize these belts by reference to any single species or life form throughout. We must ask the question whether the zones have any natural correspondence between sand beaches and reefs, other than as convenient threefold subdivisions. Cross-reference between zoning levels on reefs and beaches or flats has not been found difficult, as—for example—where a coconut log falls across a beach and develops a displaced hard shore zonation, where a zoning pattern essentially of the upper half of the hard shore appears on mangrove trunks; or where patches of permeable sediment or sea grass are present as mosaic-work in a coral reef or rubble-bed.

If a common frame of reference is to be found, linking such zones into a unified system, it must emerge from the physiological status of the organisms under the varying actions of the sea and the atmosphere, and the demands made on them in particular niches and environments. The ecology of zonation must become regularly augmented by the methods of physiological ecologists and ethologists.

As on every shore, the Eulittoral Zone may be defined first, whether in 'hard' or 'soft' terrain, as a *zone of regular alternation*. Its entire fauna and flora lying between the extremes of neap tides (or comparably wetted daily by surge and splash under the exposure-elevation effect) experiences a daily intermittence between submersion and emersion. The algae, when represented, have physiological adaptations to reduce evaporative water loss, and to respire and photosynthesize in both atmospheric and aqueous conditions (see, for an excellent example, the study by Bergquist (1957) of the temperate eulittoral fucoid *Hormosira*, as compared with the sublittoral fringe kelp *Ecklonia*). Likewise with most of the animals, periods of emersion do not preclude full activity. Many crabs and gastropods are regularly able to move about and feed while the tide is out, and with night conditions mitigating evaporation and illumination, may reach a peak of activity seldom observed by day-time collectors. Limpets, chitons and siphonariids tend to develop a homing behaviour, returning to their scars or resting sites with the ebb of the tide.

With those species obtaining their food by filtering, the activity of feeding must clearly be adjusted to ecological intermittence. The activity cycles of a middle beach bivalve, such as a *Donax*, the filtering rhythms of an acorn barnacle, or of a sand-burrowing mole-crab, *Hippa*, or the irrigation pattern of the lugworm, *Arenicola* (Wells 1957), all express the essence of life and adaptation in the eulittoral zone. Such forms as mussels and barnacles, filter-feeding on bare rock surfaces, abandon feeding and close their shells for a large part of the tide. Yet barnacles in the upper eulittoral have developed adaptations for prolonging their filtering time at high levels, by using the cirri as passive strainers intercepting particles from sheets of splash and wave run-off. The small eulittoral bivalve *Lasaea rubra* maintains a full activity under splash conditions (Morton, Boney & Corner 1957). The lugworm *Arenicola* is perhaps typical of many eulittoral burrowers in reducing its irrigating action to do little more than periodically to test warmed up or oxygen-poor standing water until full re-immersion.

With sessile and surface-exposed eulittoral species, avoidance of desiccation and quantitative and qualitative hazards of illumination must be an important achievement at these shore levels. This may be achieved by the development of a hard shell or other protective integument, as with barnacles, bivalves, tube-worms and ascidians, or by the physiological adaptations evident with many algae. It is characteristic of tropical shores that balanoid barnacles are poorly developed and are seldom zone-forming under the high desiccation hazards of the middle and upper eulittoral. The characteristic species, when found at all, is a massive *Tetraclita*, with a tiny, much restricted aperture and an immense body volume in relation to exposed surface.

The eulittoral zone of 'hard' shores shows almost always a tendency to subdivision into three subzones with their characteristic organisms. Some species, however, are distributed throughout the eulittoral zone and may show marked physiological gradation between their upper and lower limits (for examples, the alga *Hormosira* (Bergquist 1957); the bivalve *Lasaea rubra* (Morton *et al.* 1957); the limpet *Patella vulgata* (Ballantine 1961 *a*) and the chiton *Sypharochiton pelliserpentis* (Johns 1960).

The sublittoral zone, lying beyond the intertidal area, need concern us less in this survey. It is a region never at any stage of the tides emersed, and its several subdivisions support different populations according to the quantity and quality of light penetration, differences of temperature and turbidity and relation to wave base (for coral shores, see Wells 1957).

The sublittoral fringe which, under average conditions of shelter, extends from a little below low water neap to the extreme of low water spring (with appropriate change of level by exposure/elevation effect), is thus marked off from the zone by its experience of brief emersion at times of lower than average tides. The fringe was always separately recognized (as 'infralittoral fringe') by the Stephensons, and by other authors, such as Lewis (1961), and Womersley recognized it to exist in particular situations where the biota is locally sufficiently distinct from that of the upper part of the sublittoral zone. The fringe is a *region of occasional tolerance* of brief emersion to the atmosphere. It is here only, apart from pools, that zoning corals can exist within intertidal limits. The number and diversity of animals and plants is greatly increased as compared with the eulittoral zone. But none of these shows a true alternation between regular phases of emersion and submersion. The hard rock surfaces of the sublittoral fringe and the organisms they carry are never fully dry; they may remain in contact with wave break or be kept damp by the recumbent thalli of algae. The leading adaptive achievement must be generally the ability to tolerate occasional emersion to the air with consequent differences in the quality of illumination. Where moving air currents with high evaporating power coincide with a mid-day low spring tide, injury to organisms can occur over a very short time. The time of day of incidence of low spring tides, or (in a diurnal tide régime) whether the lowest tides fall by day or night, can thus have great influence in determining the kind and variety of organisms able to appear in this briefly emersed strip.

The littoral fringe is, on the other hand, a *region of aerial adaptation*. It is, in an average exposure régime, immersed only by higher than average tides, sometimes with several days between; or—with the exposure/elevation effect, its wetting by splash is of similarly reduced duration. There are no filtering animals, but the wave-carried organic debris and micro-organisms may be lodged in surface irregularities to serve as food for surface grazing molluscs. Blue green algae and black lichens (e.g. *Verrucaria*) are characteristic of this fringe in temperate latitudes, and are also found—though much less commonly—in the Solomon Islands. The rock surface is for much of its extent bare and highly insolated. The animals are highly resistant to desiccation, the molluscs having close-fitting shells or tightly sealing opercula. The principal gastropod groups, the Littorinidae, Neritidae and some of the Patellacea, use the moist gill surfaces as a facultative lung; by their reproductive processes they remain however tied to the shore. Some species such as those of *Nerita* and *Onchidium* are resistant to prolonged immersion. The characteristic crabs are the fast-running grapsoids, behaviourally specialized to avoid desiccation and variously adapted to respire from spray-damp air.

The maritime zone, in the sense recognized by Lewis (1961), is the 'supralittoral zone' of the Stephensons. It may be designated as that portion of the shore lying above the littoral fringe and thus always out of effective tidal reach, though still frequently moistened by spray and subject to the effects of salt. For plants and animals this is a terrestrial economy, with however numerous adaptations to existence close to the fringe of the sea. Most of the seed plants are halophytes with structural resistance to 'physiological drought' and to incidence of often intense illumination. On the rock surfaces, yellow and, farther up, grey lichens may be common, though much more so in temperate regions than in the Solomon Islands. This is the first level of the shore where permanent humus accumulates, though lichens grown on bare rock surfaces and many seed plants take anchorage in shifting sand. The rock surface, where bare, is highly insolated. Animal life is sparse and swiftly mobile, including land Brachyura and Anomura, insects and lizards. In the maritime zone of estuarine shores, the characteristic plants are mangroves; in vertical height these may span several of the zones: *Rhizophora*, with foliage permanently aerial, carries upon its trunk a representation of middle and upper eulittoral zones, while its lower foliage, with littorinids corresponds to a littoral fringe. As in the littoral fringe, atmospheric air is normally respired. In situations protected from desiccation, the primitive pulmonate family Ellobiidae is especially characteristic and widespread.

The zonational effects of elevation

The vertical limits and total extent of a zoned shore vary widely according to the exposure régime. Under increased influence of waves, splash and spray, with the greater exposure of the weather coasts, the zonal limits move upwards and their total span increases: such an elevation effect has been well established for temperate shores (see Stephenson 1953; Lewis 1961; and numerous other workers). Even in the same geographical area, local differences in shelter (see p. 435, of Womersley & Bailey (1969) for Matiu Island) make any equation of zones with specific tidal levels impossible.

In the temperate regions, increased impact and eroding power of the waves frequently result in greater steepness of the shore profile, and on such surfaces, the heights and vertical ranges of the successive zones become further increased as we proceed through barnacles to littorines and finally to lichens. There are also major changes in the species composition of the zones according to the exposure régime (see p. 464). But the most characteristic effect of exposure is to raise the levels, until the vertical extent of the normally 'intertidal strip' may be many times greater than the nominal tidal range, and the pattern is under the control not of the tides, but of waves (see figure 140).

On coral shores the elevation/exposure effect is still to be found, notably, as at Matiu Island where the shore is unusually narrow. But there are many circumstances tending to lessen it, and to replace it by other exposure/shelter effects equally striking. A coral reef grows and alters its proportions primarily in a horizontal direction. Within the intertidal area, coral is confined to a narrow vertical range, and is almost restricted to a horizontal direction of spread. Under whatever conditions of surge and wave attack, living coral will not be raised significantly above the level where it remains permanently covered between tides by shallow standing water, or at least by repetitive surge. At Wickham Is., S. New Georgia, the latter condition was still obtained where the surf-swept coral bench at the seaward front was raised a metre and a half in height (see figure 153). This was the extreme of such exposure/elevation effects found. On the most exposed shores where calcareous red algae replace corals as the dominant life form, these appear to have the same submersion requirements as the corals themselves.

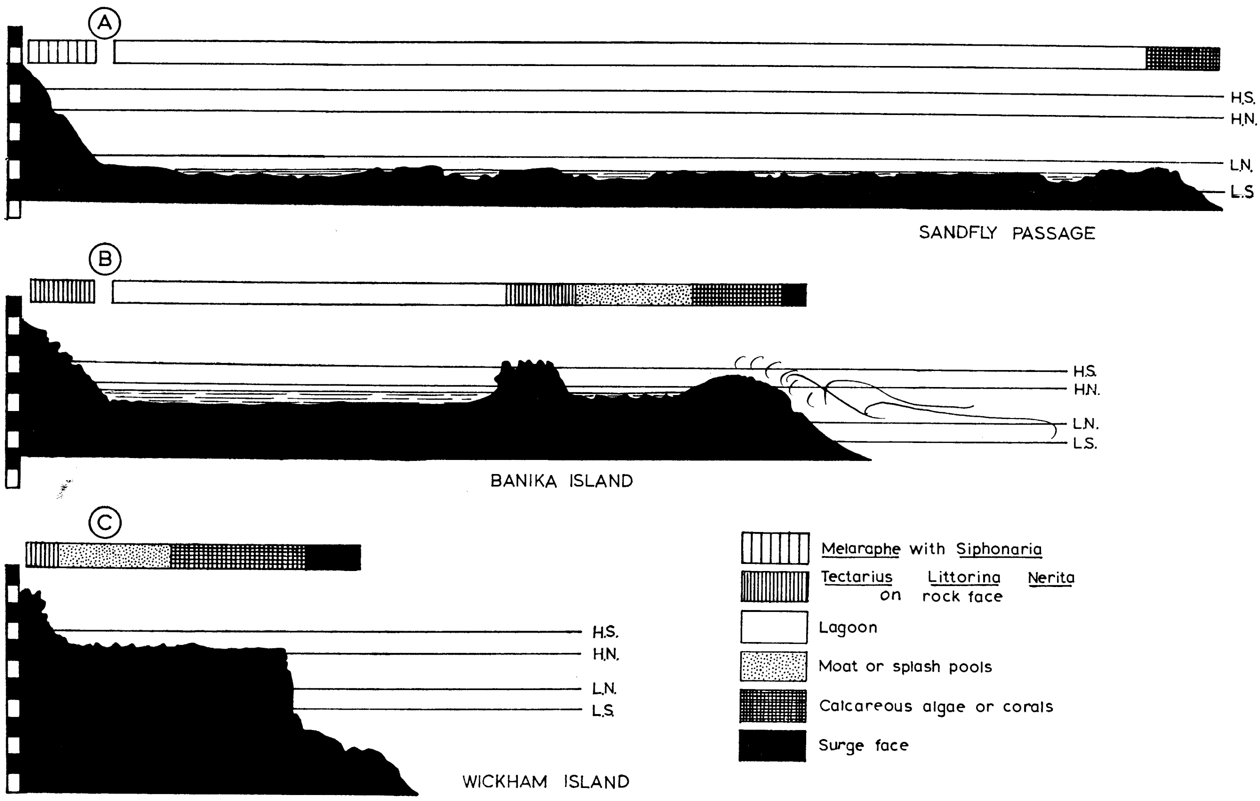


FIGURE 153. The effect of increasing wave exposure (and its associated complex of factors) on the profile and species composition of fringing coral reefs. The upper section is from a reef platform in Sandfly Passage, Florida Group, under moderate shelter; the middle section from a two-moated coral bench forming a reef under strong exposure at Banika Island, Russell Group; the third from a wave bench under maximal surf assault at Wickham Island, New Georgia. (The vertical scale is in feet, and the tidal levels for Wickham Island are an approximate estimate.)

The tendency for the 'upper shore', by which we may understand the upper eulittoral, littoral fringe and maritime zones together, to be pushed to extended limits under increased exposure is likewise far less pronounced on coral shores than in temperate regions. Small islands are frequently set low or flat, consisting of coarse sand or rubble with no massive backshore on which an elevated zonation could be established. Moreover, with the great horizontal extension of the shore platform, with spreading reef-flats and benches of up to 100 m wide, the higher zones, lying far back from the surf edge, are—even on the weather coasts—protected from the full effect of wave action, and the upper shore shows no dramatic adjustment of zonal heights. Indeed, even on very exposed shores, an inner moat will usually develop a sheltered flora, as of *Padina* sometimes *Avrainvillea*, sea-grasses and even striplings of *Rhizophora*. The contrast then between 'exposed' and 'sheltered' zonation is to be sought not between geographically different parts of the coast, but between the landward and seaward portions of the same transect. The profile sections in figure 153 show the pattern of changes in shore structure and occupation of the surface, with the transition from weather coasts to extended reef flats in relative shelter. Figure 160 presents a schematic view of coastal forms over the whole sequence from maximal exposure to the extreme shelter of mangrove-fringed estuaries.

The fauna and flora: coral and rock

A. *The littoral fringe and the maritime zone*

In the littoral fringe, with its régime of aerial adaptation, and moistened by splash at every high tide, the dominant animals are snails of the Littorinidae. *Littorina* and *Nodilittorina* species are common throughout, often accompanied by the clink shells (Modulidae). *Littorina* (*Melarhaphe*) *scabra* is found on *Rhizophora* leaves. On weather coasts, the variety and importance of littorinids (especially *L. undulata*) increases. Highest on the shore are *Tectarius* species, including the heavy and nodulose, 2 in. tall *T. pagodus*, and several *Echininus* species. Common in the lower part of the fringe is the pale apricot *Littorina coccinea*. The neritid snails also reach the littoral fringe in quantity, notably *Ritena plicata* and *Amphinerita polita*. The region is also remarkable for fast-running crabs, such as the semi-terrestrial grapsids, e.g. *Grapsus grapsus*, and the hermits, particularly the very common *Coenobita rugosa*. The lichens include black *Verrucaria*, generally very sparse, and in shaded damp places grow small red algae, *Bostrychia tenella* and sometimes the green *Rhizoclonium*.

In the maritime zone humus accumulates in small pockets and allows the establishment of the pioneer seed plants, very different in structure from the submerged intertidal angiosperms, and showing extensive halophytic adaptations and also leaf modifications such as heavy polished cuticle, or dense tomentum, under the incidence of strong light. The scrambling *Ipomaea pes-caprae* is a common plant of the maritime zone, throughout the tropical Indo-Pacific. The bushy *Scaevola sericea* is often found immediately above it, where the rock is fringed with white sand beaches. The profusion of lichens—yellow, grey and pale greenish—so familiar on the maritime zones of temperate shores was never found in the Solomon Islands.

B. *Eulittoral zone*

(i) *Upper eulittoral*

Acorn barnacles are almost universal in this zone on temperate shores, but in the tropics—with the high level of insolation—cirripedes are sparse or generally altogether lacking. In more shaded situations, there may be a scatter of a *Chthamalus* species here, but the large conical *Tetraclita squamosa* occurs farther down. In general, however, the upper eulittoral is a zone of bare rock where particles of splash and wave-lodged plant remains or diatoms are available as food. Sparse blue-green algae grow in depressions and moister places. The characteristic molluscs of the upper eulittoral are grazing herbivores: the biggest contingent is that of the Neritidae including commonly *Ritena plicata* and *Amphinerita polita*. Some littorinids are found here, though they are chiefly characteristic of the littoral fringe. The limpet species are collectively an important group: they include *Acmea saccharina*, *Cellana rota* and the *Siphonaria* species *subatra* and *sirius*. The only common chiton of the open surface, the large *Acanthozostera gemmata* is characteristic of more exposed coasts. There is no cryptobion penetrating the coral rock surface: submersion time is evidently too short and the heating up of the rock too extreme. Where shallow pools are formed, the water becomes tepid and often turbid with suspended matter: common inhabitants are sedentary vermetid gastropods and often the crevice-lodging ophiuroid, *Ophiocomina scolopendrina*.

(ii) *Mid-eulittoral*

In this zone a discernible algal cover is sometimes present, though it generally constitutes only the thinnest of film of *Neogoniolithon*, sometimes mauve, more often dead and bleached white. The large barnacle *Tetraclita squamosa* appears singly or in clusters. The mid-eulittoral zone is also, as on temperate coasts, a zone of attached bivalves. Small byssus-tied *Isognomon* appear at the highest level, with tiny individuals reaching the upper eulittoral. Farther down appear cemented chamids and oysters and spondylids, as also aviculids. Most of these bivalves are commoner on shaded wharf-piles than on sun-warmed rock faces. Sessile vermetid gastropods, *Dendropoma* and *Petaloconchus* species, are frequently important here; while the mobile nerites and limpets reach plentifully down to this zone. The rock surface becomes deeply scarred by urchin-boring, which we found even more prominent in the next zone below.

Common carnivorous gastropods are *Virroconus ebraeus*, *Pusiostoma mendicaria*, *Drupa granulata* and *Strigatella paupercula*.

The rock-boring *cryptobion* contains an immense variety of species at mid-eulittoral level; this is the richest biotic facet of this part of the shore. The boring sipunculoids, especially *Aspidosiphon*, are far in majority, with bivalves, *Lithotrya* and nereid and euncicid worms, the last to become more prevalent at the next level down. Pools when formed in this zone are intermittently reached by splash and spray; they are frequently floored by wide carpets of zoanthids, sometimes with the brown alga *Padina*, or small nodules of *Porites*. The massed parchment tubes of the polychaete worm *Phyllochaetopterus* may be locally abundant.

(iii) *Lower eulittoral*

As on warm temperate shores, this zone is rhodophyte-dominated and its prevailing colours are reddish brown, pink or mauve. The algae consist of calcareous encrusting forms (*Neogoniolithon*, *Porolithon*), interspersed with a mixed turf of inconspicuous red algae. Where splash pools develop, there is upward migration of living corals and particularly of the very common, branched calcareous red alga, *Lithophyllum moluccense*. As in the zone above, by far the richest fauna is the *cryptobion*, with its representation of boring species, especially the variety of euniciid worms, greatly enriched. The most typical members of the *parabion* are the abrading and scar-forming echinoids, the slate-pencil *Heterocentrotus* *mamillatus* and the more common *Echinometra mathaei*. Within the depressions so formed, the wealth of gastropod molluscs is very great. Grazing or browsing herbivores include members of the Haliotidae, Trochidae, and Turbinidae (esp. *Turbo petholatus*) and the Cypraeidae, most frequently *Cypraea mauritiana*. The carnivores include Thaisidae and Mitridae, many of them inserting proboscides into the burrows of cryptobiontic prey, such as sipunculoids. *Drupa* species comprise *albolabris*, *rubuscaesius*, *morum* and *grossularia*. In addition, there are *Thais clavigera*, *Thais persica* and *Latirolagena smaragdula*.

C. *Sublittoral fringe*

Although on many shores this fringe appears to form merely an upper band of sublittoral zone distinguished by brief periods of spring tidal emersion, it well deserves its distinct recognition on Solomon Islands shores. It is here, apart from splash pools or moats at higher level, that the first representation of living corals appears in quantity. The species and life forms differ in composition and dominance according to degree of exposure. Generally common are small clusters of *Acropora* fingers and a low sheet-like *Acropora* forming a grey to mauve surface crust; *Pocillopora elegans*; *Stylophora mordax*; strong flanges of *Millepora*; small nodules and mounds of *Porites*, and convex heads of the faviids *Favia*, *Favites*, *Goniastrea*, *Platygyra* and *Leptoria*.

There is also a profusion of algae near low-water mark. The coralline red algae include clumps of *Lithophyllum moluccense*, and a heavy, brittle turf of *Amphiora anastomans*. Encrusting *Porolithon onkodes* is dominant under heavy wave exposure. Rhodophyceae forming a turf of finer texture include branching *Jania* and *Cheilosporum* species. Green algae much in evidence are *Dictyosphaeria cavernosa*, *Caulerpa* (sometimes *Caulerpa cupressoides*), *Chaetomorpha antennina* and tresses of the deep green *Chlorodesmis comosa*. On the rougher and more exposed south-facing shores, *Sargassum cristaefolium* and *Turbinaria* spp. become characteristic of surf-swept tops; but *Sargassum* was not found, and *Turbinaria* seldom seen on north-facing coasts. The algae have a specialized *parabion*, notably of crabs, other crustacea, and gastropods, the *Caulerpa* spp. being rich in sap-sucking Sacoglossa.

D. *Sublittoral zone*

Marked by permanent submersion at whatever state of the tide, the seaward slope below extreme low water springs remains the least satisfactorily known part of the coral shore. Though it was not studied intensively during this survey of littoral communities, Wainwright will later present brief notes on its characteristics obtained by SCUBA diving on exposed weather coasts. This part of the shore has been variously divided into subzones, evidently controlled by changes with depth in the amount and quality of light penetration. Water movement in relation to current—set, and level of wave-base are also important factors. From low water mark of spring tides downward, there is a full and free development of coral and alcyonarians. One of the best descriptions of exposed reef face zonation is that of Wells (1957). An upper zone of about 50 ft. is referred to as 'mare incognitum', a region mainly above wave base and often barren except for crusts and nodules of calcareous red algae. Beyond this zone, that is below wave normal base in moderately illuminated waters, is an 'echinophyllid zone', characterized by *Echinophyllia* and *Mycedium* as common life forms. Abundant here too are the hydrocorals *Stylaster* and *Distichophora* (especially where there is local shade and confined spaces), as well as delicately branched forms of *Acropora* and *Montipora*. Gorgonians are often lavish and varied here, with their own characteristic attached faunule. They may reach into a third zone, which goes down as far as the lowest depth where a few hermatypic corals are able to survive. With an extreme limit of 500 ft., this may be called a '*Leptoseris* zone', with delicately branched and vasiform coral growth forms. The cup corals *Culicia*, *Balanophyllia* and *Tubastrea* are also important, as illumination falls, both below wave base and in locally shaded recesses.

Beaches and flats

The zonation of life on the soft shores of the Solomon Islands can be assimilated—in the scheme adopted in this paper—to the universal system of classification first employed for hard intertidal substrata. A separate description however is first needed, dealing with the topography and visible character of soft shores, as deriving from the nature and origin of their sediments and the degree of wave attack. Two broad classes of soft shores of mobile sediments may thus be recognized: first, those shores built chiefly of sand, on open coasts, or in bays and channels where wave actions is still an important contributor to their formation; secondly, shores of estuaries and land-locked channels, or back-shores receiving maximal shelter from reefs, where wave action is slight or absent, and there is a predominance of silt and clay; mangrove fringes are here generally developed.

Shores under wave action

These consist very generally of a steep-sloped beach cut away at or a little above the level of low water neap by a pronounced 'beach step'. Beyond the step, the shore continues in a prolonged formation, better described as a 'flat' than a beach: it is almost level and very wide in comparison with the steep, narrow 'beach'. The sediments are moreover permanently waterlogged, being only briefly emergent to the atmosphere at lower than average tides.

The beach step forms a rather constant or general threshold at the level of wave break, in situations of diurnal tides of small amplitude. It is a formation with a major ecological influence on Solomon Islands shores. Not only has it a special character in respect of its own sediments and fauna; but it demarcates above and below two regions very different in topography and biology. Above the step at wave-break point, the sloping shore is regularly uncovered at low water of each day, and it is here that the eulittoral zone, as well as littoral fringe and maritime zone are to be found represented. The prolonged low-tidal flat corresponds—by the criteria adopted here—to a sublittoral fringe.

The slope and general appearance of the beach varies with the particle size and nature of the sediments. The steepest and highest beaches are—as is generally well established—those of greatest mean particle size, and greatest exposure to wave action. At the farthest such extreme, as on the south-east coast of Guadalcanal, near Kopiu, the gravel formation is several metres high, very mobile and disposed in a series of four or five ramps or concave-fronted steps. Such beaches are the most inhospitable to life of any coastal terrain, being

TABLE 33. ZONATION PATTERN OF INTERTIDAL SAND BEACHES IN SOLOMON ISLANDS AS COMPARED WITH TEMPERATE REGIONS

New Zealand*				Solomon Islands
upper beach		Talitrid amphipods: isopods (*Scyphax*)	littoral fringe	*Ocypode*
middle beach		Crustacea: *Cirolana* Bivalves: *Amphidesma* worms: *Armandia* (Travisiidae), Nephthyidae, Glyceridae	eulittoral zone	Crustacea: *Hippa*, *Dotilla*, *Scopimera* bivalves: *Atacdodea*, *Tawera*, *Donax* gastropods: Nassariidae, Naticidae
				wave break step (see Challis 1969 *a*)
lower beach	'neap flat'	*Chione stutchburyi* 'cockle' *Macoma liliana* gastropods: *Cominella*; *Baryspira* (Olividae); *Pervicacia* (Terebridae); *Alcithoe* (Volutidae) crustacea: isopods: *Exosphaeroma*, Amphipods: Haustoriidae and Phoxocephalidae	sublittoral fringe	cockles: Cardiidea: *Vasticardium*, *Fragum* Tellinidae: Gariidae: Codakiidae gastropods: Nassariidae (numerous) Naticidae (*Natica*, *Polinices*, *Sinum*) Olividae Volutidae Terebridae (numerous) crustacea: *Callianassa* portunids: *Scylla*, *Charybdis* oxystomatids: *Calappa*, *Matuta*, *Leucosia* stomapods: *Squilla*, *Lysiosquilla*
	'spring flat'	starfish: *Astropecten* *Balanoglossus australiense* (north) *Arenicola assimilis* (south) synaptids (*Trochodota*): ophiuroids (Amphiura). Worms: polychaetes numerous. *Urechis*. Crustacea: *Callianassa filholi*, *Squilla armata*, *Ovalipes punctatus*. Bivalves: *Dosinia; Angulus* (Tellinidae), *Gari*		starfish (*Archaster*) synaptids and ophiuroids *Balanoglossus* species; *Lingula*

* Scheme of Morton & Miller (1968). See also Dahl (1953).

regularly mobile and with the particles large, almost lacking fine grades, and without inhabitable interstitial spaces.

A much more stable beach, lying above the middle shore step, and composed of white finger rubble and smooth coral pebbles and small blocks, is illustrated in figure 154, from Honiara, in front of the Hotel Mendana. Here the zoning was as follows:

(i) A littoral fringe built of a bank of coral rubble much admixed with humus and leaf mould. The fauna, especially on logs and driftwood was of littorinids (the high-tidal species, *Littorina undulata*), ellobiids (*Melampus coffeus* and another species), and the land hermit crab *Coenobita rugosa*.

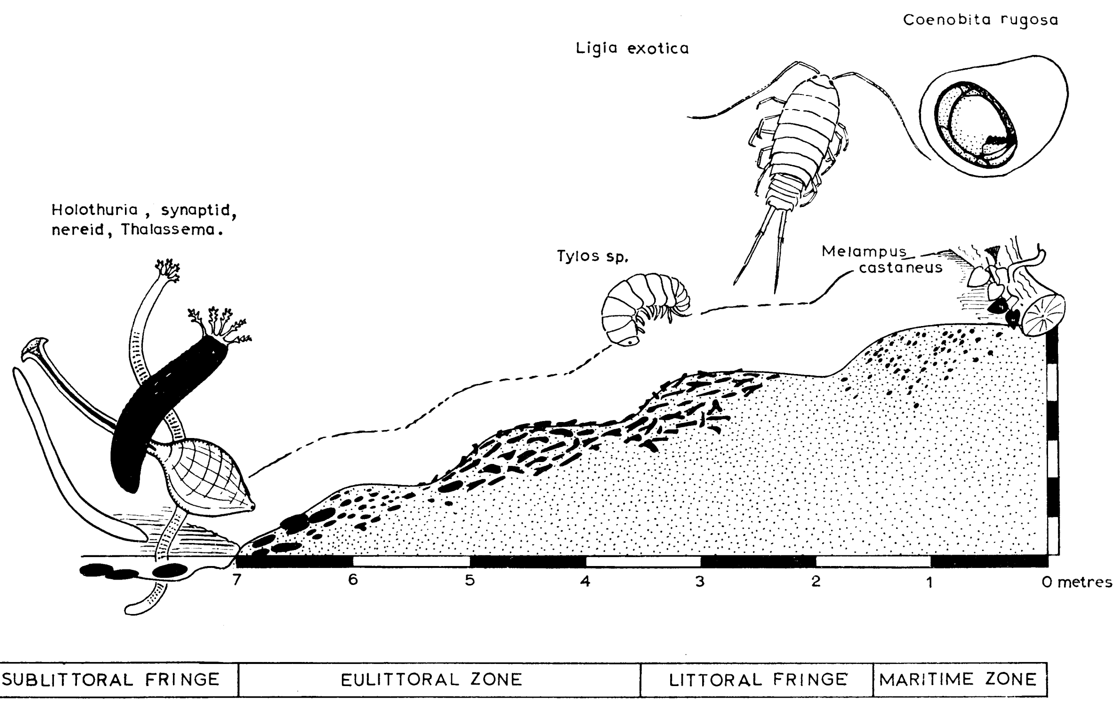


FIGURE 154. Honiara, Guadalcanal. Zonation pattern of a steep-ramped beach of coral finger rubble, showing the principal occupant species.

(ii) An upper eulittoral zone, of white rubble, taking its biological character from the Crustacea. This is a territory of fast-running isopods, *Ligia exotica*, moving about constantly in the rubble interspaces. Slower moving oniscoid isopods, *Tylos granulatus* are less frequent, wedging or bulldozing their way between coarse sand and fine rubble. A special feature is a small, short-legged grapsid, well camouflaged in the opaque white and brown against the rubble background. Talitrid or orchestiid amphipods have none of the abundance they show on temperate shores, either in rubble or finer upper eulittoral sands.

(iii) A mid-eulittoral zone characterized by finer sand lying beneath the rubble layer. This is intermittently reached by a water table, and its chief inhabitants are cirolanid isopods.

(iv) A lower eulittoral zone was composed of small smooth slabs of weathered coral rocks, lying upon permanently waterlogged sediments, with much fine sand and silt. The hypofauna is very characteristic: shiny black, finger-sized *Holothuria*, discharging a water jet on disturbance, a pink sand-immersed synaptid holothurian, a thalassemid echiuran worm, a *Sipunculus*, a glycerid and a nereid polychate worm.

Beaches composed of finer sediments still under wave action are of two principal sorts. With some lack of precision they could be called 'white beaches' and 'grey beaches'. The first are formed by the narrow, intensely white slopes of calcareous sand generally lying to the landward of fringing reefs and encircling small islands and sand cays. They are frequently referred to as beaches of 'coral sand', but their particle composition is in fact rather various, including:

(i) Fragments of comminuted coral rubble, above 1 mm diameter, with a high proportion above 2 mm.

(ii) Coarse to medium shell fragments and particles of weathered rocks, greyish to brown, derived from the land mass, forming an important component in terms of weight.

(iii) Numerous foraminifera, both living (especially at lower levels of the beach) and as recently dead tests.*

(iv) Very fine, powdered coral rubble, forming a silt-like component, not obvious on microscopic examination, but important in sieving analyses.

In certain situations, as in patches and pockets of sand on reef flats, or amidst outcrops of 'beach rock' higher on the shore, fine powdery coral sand may heavily predominate, sometimes intensely white, at other times greyish with much silt admixture.

Grey beaches are very characteristic of the coasts of islands with an igneous land mass, and were particularly studied by the Expedition on the north coast of Guadalcanal, at Tenaru and near Honiara, and at Komimbo Bay and other stretches at West Guadalcanal. They have a high terrigenous content of rather fine grey or black 'iron sand', evidently derived from the decay of andesitic or ultrabasic rocks. Varying amounts of coral fragments or shell sand may mark a transition towards the sands of white beaches.

Beaches of both 'white' and 'grey' types are generally fringed to landward by the scrambling and mauve flowered *Ipomaea pes-caprae*, sometimes backed with sturdy bushes or a thicket of *Scaevola sericea*. Below the maritime zone, with these plants we may recognize two zones, a littoral fringe or 'upper beach' and an eulittoral zone, generally undivided, that may be called the 'middle shore' and is bounded below by the wave-constructed beach step.

Beach formations—unlike hard shores—appear to show little significant elevation effect with increased exposure. The chief effects of variation in amount of shelter are in their horizontal extent and degree of slope. With respect to vertical height, the zones are under the effective control of the movements of the water-table; this in its turn is related to sediment distribution and the nature of the interstitial spaces. Although we shall in this paper define the zones by biological criteria, we shall be able more nearly to relate them to standard tidal levels than would be safe in dealing with hard surfaces.

Thus, the littoral fringe is only occasionally wetted by wave action, lying above the high water mark of average tides. The water-table lies too deep to affect the inhabited surface sand, which often reaches high extremes of temperature. With the reduced action of waves

* Characteristic genera are *Quinqueloculina*, *Bolivina*, *Reusella*, *Discorbis*, *Calcarina*, *Cribroelphidium*, *Amphistegina* and *Cymballoporella* (see Challis 1969*a*).

on the upper shore in sorting and removing fine grades, these tend to be better represented than on the middle shore (see figure 155).

The littoral fringe has in the tropics few of the talitrid Amphipoda one would expect in this strip upon temperate shores. As Dahl (1953) has in a short but valuable paper already

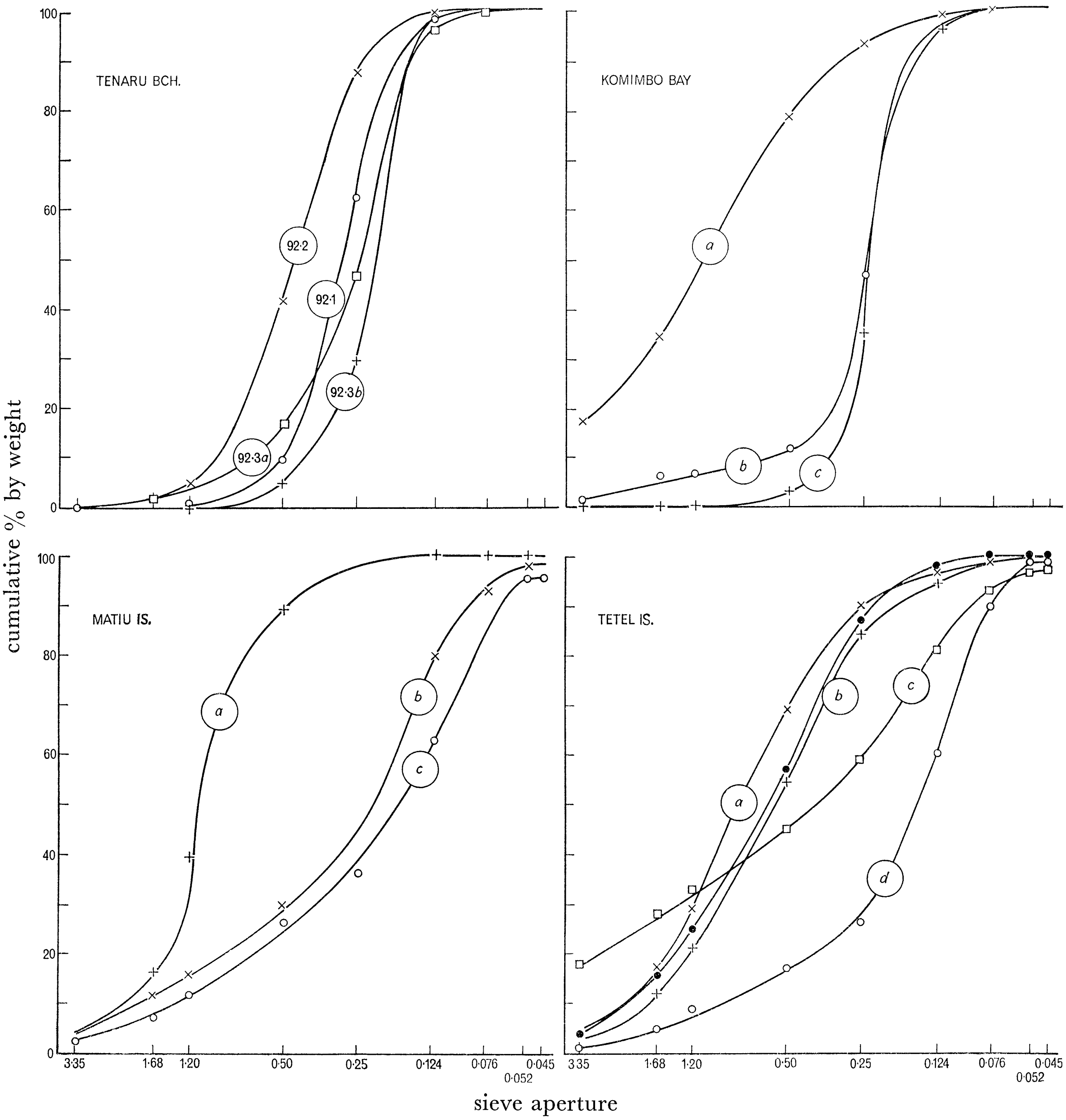


FIGURE 155. Cumulative curves of particle size distribution on soft shores. (Left, upper): Tenaru, north Guadalcanal, grey iron-sand beach. (Right, upper): Komimbo Beach, west Guadalcanal —(*a*) mid-beach, with *Oliva* and *Terebra*; (*b*), (*c*) upper beach with *Ocypode*. (Left, lower): Matiu Island—(*a*) coarse coral/foraminifera sand of supratidal beach; (*b*), (*c*) fine powdery coral sand. (Right, lower): Tetel Is., Florida Group—(*a*) middle beach; (*b*) two curves for lower beach; (*c*) coarse rubble sand; (*d*) silty sand, partly anaerobic.

recognized, these are replaced chiefly by the ghost crabs, in the Solomon Islands *Ocypode cordimanus* and *O. ceratophthalma*. These run nimbly over the whole beach area, normally avoiding the water's edge. Their burrows and excavated spoil, frequently renewed, are a conspicuous feature of the beach. Like every littoral fringe, this part of the beach is a zone

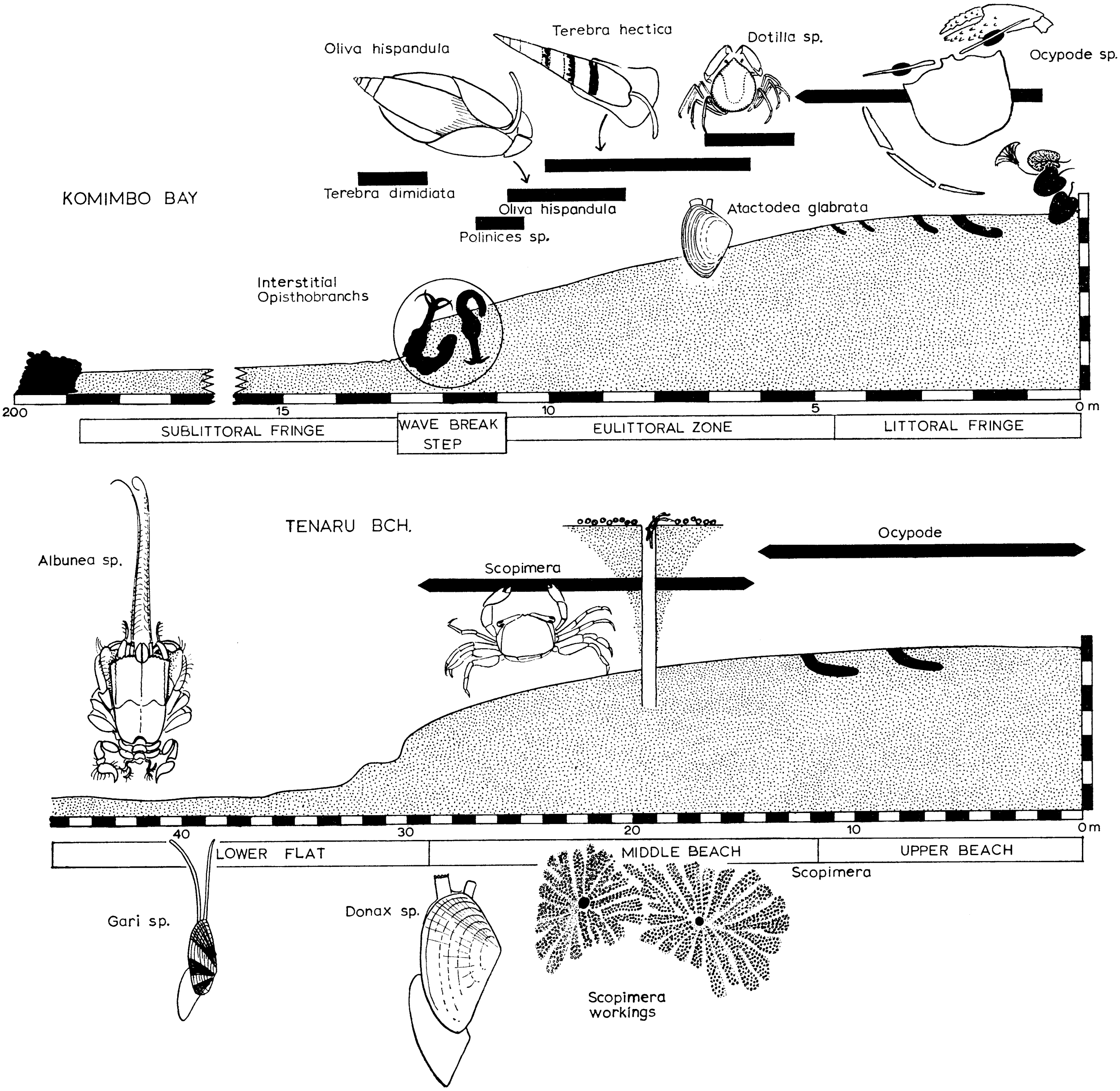


FIGURE 156. North Guadalcanal. Schemata for the zonation patterns of forameniferous shell-sand (upper) and of grey beaches, with considerable content of terrigenous mineral grains (lower). The nomenclature of littoral fringe, eulittoral zone and sublittoral fringe is here presented as equivalent with upper beach, middle beach and lower flat (see comparison in table 33). Note the position of the wave break step referred to by Challis (1969*a*).

of efficient aerial adaptation; a familiar crab under pieces or rock and large beach rubble is the small land hermit *Coenobita rugosa*.

At the next level of the shore, the eulittoral zone forms a rather short slope of firm, well-compacted sediments. The water-table move regularly up and down with the tide and is always near the surface. The sand is moist and well oxygenated throughout, never developing a black anaerobic layer, nor reaching high extremes of temperature. At this level, the fauna becomes enriched, being composed chiefly of molluscs and burrowing crustaceans. In both white sands and black, suspension-feeding bivalves are abundant:

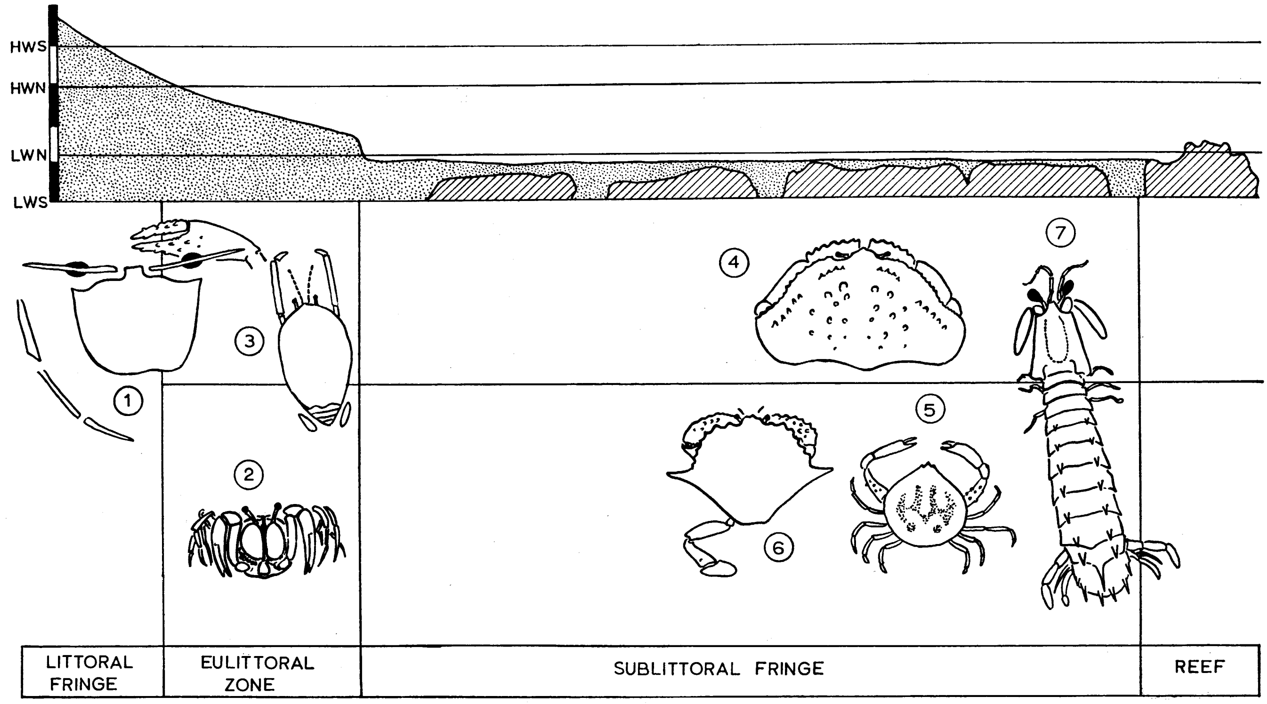


FIGURE 157. Tetel Island, Florida Group. Distribution of burrowing Crustacea and demarcation of their zones on a beach of white coral/foraminifera sand, and a reef flat of silty coral sand. The species represented are:

Littoral fringe: 1. *Ocypode cordimanus*
Eulittoral zone: 2. *Dotilla myctirioides*
3. *Hippa pacifica*

Reef flat (= sublittoral fringe):
4. *Calappa gallus*
5. *Leucosia* sp.
6. *Matuta planipes*
7. *Squilla*, c.f. *oratoria*

there may be first a bed of the amphidestmatid, *Actactodes striata*, then a species of *Donax*, and in some places a *Donax*-like venerid close to *Tawera*, and a *Semele*. It is here alone on the sandy beach that any bivalve is found in beds with great numbers of one species. On the lower shore, the picture is one of very great diversity of species, each with fewer individuals.

Towards the lower edge of the eulittoral zone, especially, it would appear, on 'grey beaches' with finer and more uniform sediments, carnivorous gastropods are plentiful, especially *Terebra hectica*, *T. dimidiata*, *Oliva hispandula* and others, and species of white-shelled *Polinices*. On both white and grey beaches, above and below the water step, the largest contingent of gastropods, out-numbering all the rest in individuals, are the scavenging force of Nassariidae (e.g. species of the genera *Nassarius*, *Plicarcularia*, *Scabronassa*, *Niotha* and others.)

In white beaches towards the wave step there is generally a densely occupied zone of the smoothly ovoid mole-crab, *Hippa pacifica*, a filter feeder during the return of the water-table. Farther up the middle shore may appear the burrow of the small globose soldier

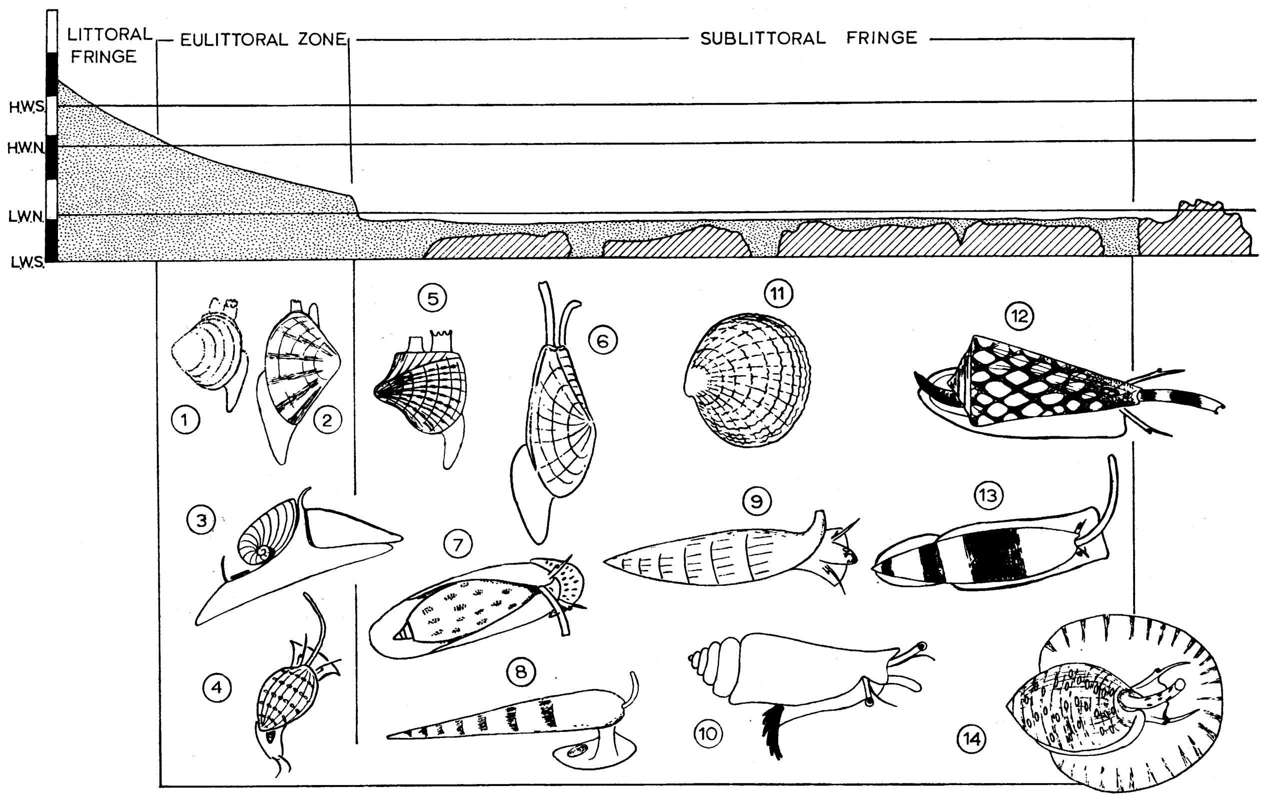


FIGURE 158. Tetel Island, Florida Group. Distribution of burrowing molluscs and demarcation of zones on a beach and reef flat of coral sand. The animals represented are:

Eulittoral zone:
1. *Atactodea striata*
2. *Donax faba*
3. *Polinices pyriformis*
4. *Nassarius globosus*

Sublittoral fringe:
5. *Fragum* (Cardiidae)
6. *Tellinella* sp.
7. *Oliva episcopalis*

Sublittoral fringe:
8. *Terebra hectica*
9. *Rhinoclavis vertagus*
10. *Oostrombus gibberulus*
11. *Codakia tigerina*
12. *Conus marmoreus*
13. *Swainsonia casta*
14. *Quimalia pomum*

crab, *Dotilla myctirioides*, regularly sifting the nutritive content of surface sand. On 'grey beaches' small, fast crabs of the genus *Scopimera* are frequent and numerous. The signs of their activity are unmistakable in the form of large areas of tiny sand-balls lying like lead shot in a broad area round each vertical burrow shaft, and traversed by radial paths.

Tweedie has charmingly described the ecology of habits of these and other tropical sand beach crabs, in a series of contribution from Malayan coasts (see also Tweedie 1936).

The step that bounds the middle shore at the wave-break line is an interesting and distinctive habitat with a varied interstitial fauna; Challis (1969*a*) has discussed its biology at some length in a separate paper. The richest interstitial fauna at this level is to be found in 'white beaches' where the particles are of coarse grade, clean and relatively mobile. At every wave break water pours over the surface and seeps freely down into the sand through extensive interspaces. There is normally rather little energy in the form of wave wash translated to the upper beach, and the step and the 'middle shore' immediately above it tends to remain stable in storms. The interstitial spaces are kept cool, well aerated and no doubt receive a constant renewal of detrital food. In places under stronger wave attack, as on 'grey beaches' in the absence of sheltering reefs, the mobile wave-break step may reach well up into the middle shore, and the firmly compacted sands of this area may give place to an expanse of coarse, shifting sand. The step appears to be a classical habitat of the type first thoroughly described by Delamare-Deboutteville (1960) for interstitial fauna (see Swedmark 1964). Challis has found at this level in the Solomon Islands a rich population, of which the prominent life forms are illustrated in his separate paper (p. 517).

Soft flats of the lower shore

Beyond the wave-break step, the character of the shore changes greatly. The sediments no longer form sloped beaches, but grey flats of silty sand, generally with a wide extent to seaward and enclosed within the shelter of a reef at the line of breaking surf. The soil particle spectrum tends to be rather broad, with a predominance of silt and fine sand, and also much coarse rubble and gravel. These flats are left briefly emersed only at low water of spring tides. The sediments are always below the level of the water table, and at low spring tides pools and sheets of standing water may be left temporarily isolated, sometimes warming to high mid-day temperatures of 35 °C. Ecologically, these flats constitute the 'lower shore' and are to be referred to as a sub-littoral fringe. Though the plants and animals are never—properly speaking—left dry between tides, conditions of life may at such periods be very different from those of water with unimpeded circulation from wave action; large parts of the flat may take on at low tides the character of an extensive tepid pool, no more than a few inches deep.

The physiognomy of the lower beach flats varies considerably from place to place.

(i) In the cleanest situations, amidst reefs with good circulation, there may be flats of almost pure, coarse white sand, or of finely comminuted, powdery coral debris.

(ii) More often the flats may be dull greyish white in hue, with a high content of silt and organic remains; they are generally strewn with large coral rubble, and may lie as only a thin veneer upon a basement of coral rock beneath.

(iii) With greater shelter and further accumulation of silt, such areas may develop green swards of sea-grass. On shallow banks of sand a few inches raised, so as to be briefly emersed at most tides, sparse *Thalassia hemprichii* and *Cymodocea rotundata* will intermingle with scattered boulders and finger rubble. Much less frequent and confined to places where

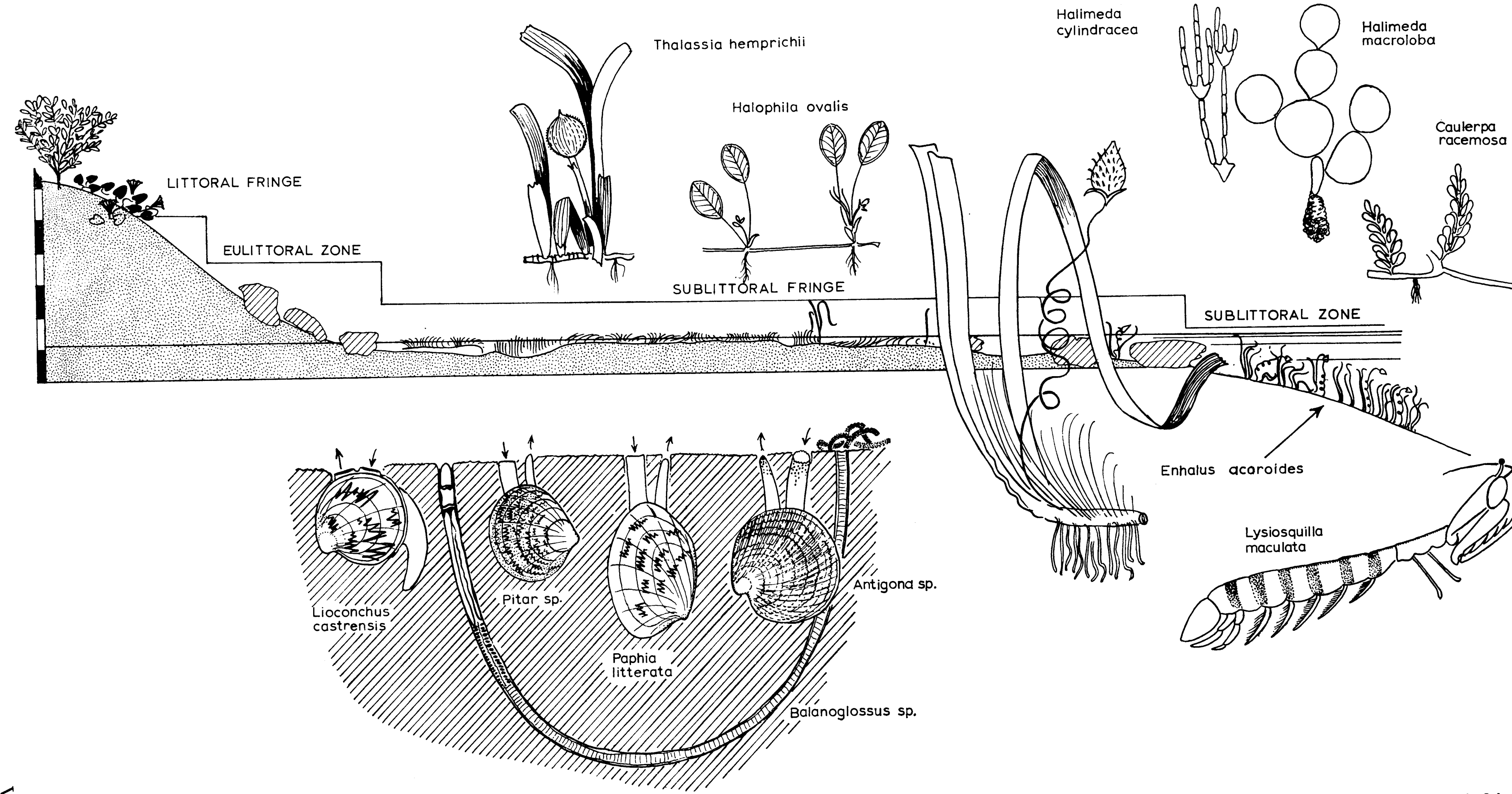


FIGURE 159. The plants and animals of silty sand-flats in sheltered conditions. The upper profile shows the demarcation of zones, with the littoral fringe preceded by a maritime zone with *Scaevola sericea* and *Ipomaea pes-caprae*. The common species of sea-grass are represented, together with three forms of green algae frequently contributing to the vegetation of sea-grass flats. Below are shown four characteristic bivalves *in situ* with *Balanoglossus* sp., and the large low-tidal stomatopod, *Lysiosquilla maculata*.

standing water is constant, are the other marine monocotyledons, *Halophila ovalis*, and (scattered between tides but predominantly subtidal) the much larger *Enhalus acoroides*.

(iv) In permanent standing water pools, often reaching high temperatures, *Thalassia* thickens to a dense dark green sward, often covering wide areas. It carries a rich faunule of *Marginopora* and other discoid Formanifera, an orange brown *Nerita*, the small white cowry *Monetaria annularis*, and a slender, well-camouflaged pipe-fish *Siphonostoma typhle*.

(v) On the low-tidal flats, a green algal cover may develop, including the *Halimeda* species, *H. cylindracea* (closest to the landward), *H. simulans* and *H. opuntia*, attached to sand strewn basement rock. Lower still may appear the scrambling *Caulerpa racemosa* var. *macrophysa*. In tepid pools without dense sea grass, the brown alga *Padina commersonii* may grow, attached to small stones or pieces of hard rubble. The inconspicuous but widespread algae prominent on finger rubble would collectively form a long list. The Chlorophyceae include *Dictyosphaeria cavernosa*, *Valonia fastigiata*, *Neomeris van-bosseae*, *Struvea anastomans* and *Boodleya composita*. The commonest brown species is *Dictyota friabilis*, and among the reds *Hypnea nidulans* and *Gelidiopsis intricata*, *Gelidiella lubrica* and the larger *Galaxaura acuminata*. The familiar cementing species of the rubble is *Neogoniolithon myriocarpon* (see Womersley & Bailey 1969).

(vi) In the greatest shelter, as in protected moats, the silty sand may carry, as well as small *Rhizophora stylosa* striplings, a carpet of the green alga *Avrainvillea erecta*, with upright several-planed thalli, resembling little flags of green baize.

For burrowing and surface-living animals, the soft flats of the lower shore are the richest and most diversely rewarding collecting ground. Sampled either by systematic sieving in shallow water, or by wading across the flats at night with a Tilley lamp, the profusion of species reduces concise description to tabloid form.

TABLE 34. BURROWING FAUNA OF SANDFLATS IN THE SUBLITTORAL FRINGE

(*a*) **Crustacea.** Burrowing crabs include Portunidae (*Ovalipes*, *Charybdis* and *Portunus* species), and (very commonly *Calappa gallus*, *Leucosia* aff. *rhomboidalis* and *Matuta* aff. *planipes*). The specialized brachyuran *Albunea* was found *in situ* in fine grey sands. The commonest of any burrowing crustacean was a pale, 1 in. long *Callianassa*. The stomatopods are represented by the large *Lysiosquilla maculata*, towards low water spring on sea grass beds, and smaller *Squilla* species of which *S. oratoria* is the commonest.

(*b*) **Bivalvia.** The principal burrowing bivalves are Cardiacea: *Vasticardium* spp., *Laevicardium*, *Fragum* and *Trigoniocardium*, as well as the somewhat uncommon *Corculum*. In cleaner sand beaches occur *Codakia tigrina*, *Tellinella staurella*, and other *Tellina*, *Gari* and *Fabulina* species. In siltier ground are a large *Scutarcopagia* sp., *Lioconcha castrensis*, *L. fastigiata*, *Antigona* sp., *Gafrarium* sp., *Glycodontia marica*, *Antigona* sp., and anchored by byssus threads to fine rubble, a small *Atrina*.

(*c*) **Mesogastropoda.** The sand-burrowing Naticidae include *Polinices melanostoma* and other species, and the broad, distinctively flattened *Sinum laevigatum*. Of the Cerithiidae there are *Cerithium aluco*, *C. nodulosum* and *Rhinoclavis vertagus*. The most frequent strombid, and one the commonest of sand-flat gastropods is *Oostrombus gibberulus*; also burrowing in sand are *Conomurex luhuanus* and the thin, streamlined *Terebellum terebellum*. More characteristic of the sand surface are the strombids *Lambis lambis* and *Strombus lentiginosus*. The tun-shells are represented by *Cadus perdix*, *Tonna costata*, and *Quimalea pomum*, the helmets by the oddly ornamented *Distortio anus* and the cassids by small *Casmaria* species and occasional specimens of the huge *Cassis cornuta* on reef flat sands.

(*d*) **Neogastropoda.** Along series of smooth fusiform burrowing carnivores include the Olividae (*O. episcopalis*, *O. carneola*, *O. sericea*); Mitridae (*Mitra mitra*, *M. episcopalis*, *Vexillum* spp., *Strigatella* sp., *Swainsonia olivaeformis*, *S. casta*), and Volutidae (*Voluta rutila*, *Pterygia* sp.). *Harpa gracilis* and *Fasciolaria*

TABLE 34 (*cont.*)

trapezium are occasionally taken, and there is always a wealth of Nassariidae. In addition to several turrid species, the Toxoglossa are represented by numerous cones (*Lithoconus punctatus, L. litteratus, Conus marmoreus, Virgiconus lividus* and *Leptoconus generalis* are commonest, with *Dendroconus striatus* and *Gastridium geographus* not infrequent), and the Terebridae form a wide assemblage: small yellowish brown, *Cinguloterebra* and *Noditerebra* spp., and the large, distinctive *Terebra maculata, T. nodulosum, T. hectica, T. subulata, T. dimidiata, T. guttata* and *T. areolata.*

(*e*) **Echinodermata.** The burrowing holothurians include both plumpish Cucumariidae embedded in coarse rubble, and Synaptidae, much more slender and definitively vermiform. The primitive starfish *Archaster typicus* lies just below the surface sand. There are sand-burrowing cphiuroids, a cake-urchin *Clypeaster* and a long-spined heart urchin *Lovenia.*

(*f*) '**Worms**'. Errant burrowing polychaetes appear to play a smaller part than in temperate sand-flats, though the Clyceridae, Ariciidae and Nereidae have many species. Common in coarser sand is the densely bristled *Eurythoe complanata.* The Echiuroidea include species of *Echiurus* and *Thalassema*, and the Sipunculoidea are widely exemplified in *Sipunculus* and *Aspidosiphon.* Nemerteans are very numerous, though too often, in the present state of taxonomy, indeterminable.

(*g*) **Brachiopoda.** A small and very abundant *Lingula*, a centimetre in shell length.

(*h*) **Hemichordata.** Two proboscis worms, a *Balanoglossus* 6 in. or more long, brick red and yellow, and a scarcer much larger yellow *Balanoglossus*, as thick as a finger.

Of all the fauna of the exposed surface of soft flats, the holothurians deserve special mention. They are of large size and offer examples of several families. The Holothuriidae are smooth and black, and the Stichopodidae dark and stiffly papillose. The largest and most distinctive of all stichopodids is *Thelonotas ananas* closely beset with rubbery and overlapping bifid papillae. The largest and most peculiar of the Apoda is the synaptid *Opheodesoma grisea*, common on sea-grass flats, especially with *Enhalus acoroides*; over 1 m long and $1\frac{1}{2}$ in. in diameter it is thin-skinned, alternatively wholly flaccid or tensely inflated with seawater.

ENCLOSED SHORES; ESTUARIES AND CHANNELS

The shores of estuaries and harbours are formed under conditions of small or no wave action, with constant deposition of sediments derived from land run-off. They show a different transect profile from mobile shores on more open coasts, in that there is no sharp threshold between the beach and the lower flats in the form of a wave-break step; nor is the intertidal part of the shore generally so greatly prolonged as with reef-enclosed sandy flats. Turbidity from land-derived sediments almost precludes the growth of coral at the seaward fringe, although where a profile drops off at a steep edge to uncover a hard basement, *Porites* c.f. *lutea* nodules, or even small micro-atolls may appear. The intertidal flat is either bare of vegetation, or—where there is some admixture of sand—may support a vegetation of *Halimeda* species (especially *cylindracea* and *macroloba*) as well as *Caulerpa racemosa* to the seaward edge.

To the landward, extensive fringing swamps of mangroves almost invariably develop. The front rampart at the water's edge is nearly always of low or medium-sized *Rhizophora*, with the line of the lowermost foliage just reached by high water spring tides, and a thick complex of arched roots and struts exposed at low water. Behind the *Rhizophora*, a maritime forest of *Bruguiera* species presents a higher canopy, these mangroves replacing the fringe of *Barringtonia*, *Terminalia*, *Cocos*, etc., normal on more open shores.

We may look first at the areas of mud or muddy sand lying sometimes in front of the mangrove line, or at the head of waterways secluded from the main channels of tidal flow. These are regularly immersed and emersed by the daily tide, and may be held to constitute an eulittoral zone. Beyond this zone lies the softer, semifluid-mud, sometimes only

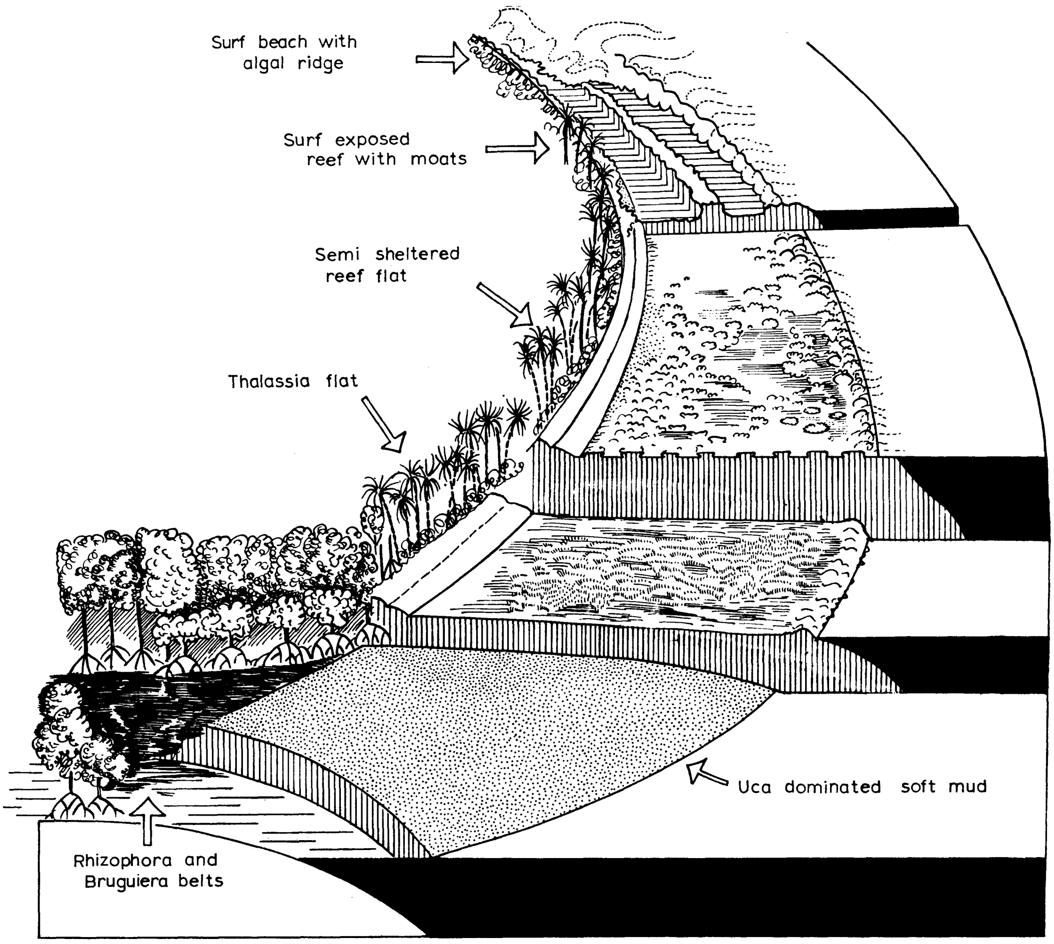


FIGURE 160. Schematic view of full sequence of Solomon Islands shores, surf-swept coral bench in maximal exposure; through coral reef with moats; wider fringing reef with coral boulders; seagrass flat; and estuarine mudflats in maximal shelter.

with difficulty walkable, of a sublittoral fringe. The sediments of the eulittoral zone are however firm and rather well-compacted; they are the characteristic domain of fiddler crabs or Ucidae which are here able to maintain stable burrows and permanent systems of shallow warrens. Highly distinctive of intertidal mudflats, these crabs exist in huge numbers of individuals, sometimes densely parcelling out the shore between several species. These may be combined in a mosaic of different colonies at a single locality. Observation is easy as the fiddlers emerge sideways from their oblique burrows and scuttle over the whole flat. Colonies of different species can be distinguished at a distance by the bright colours of the carapace and of the chelae with which the males aggressively confront each

163

164

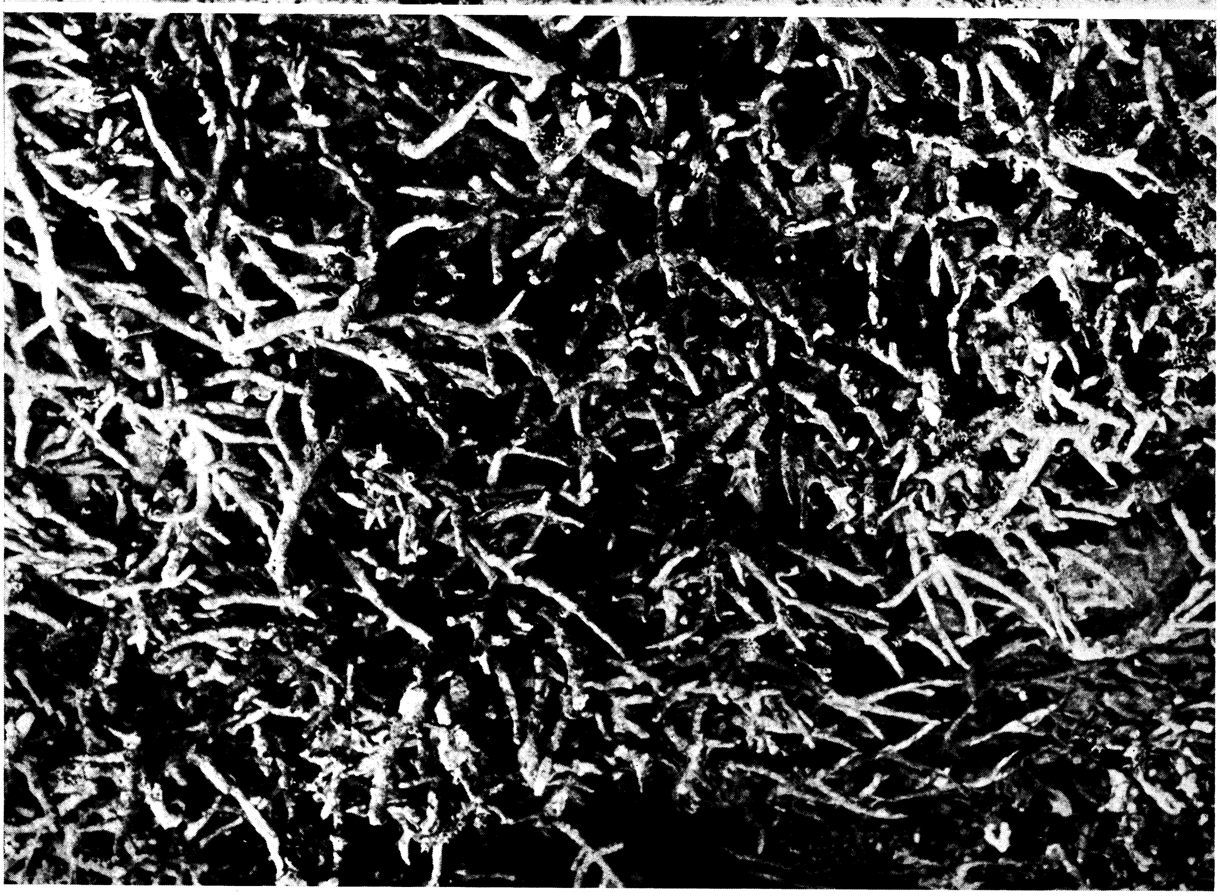
Tulagi, Florida group

FIGURE 163. A.K. *Maroro* at anchor, with a rubble flat and sheltered reef partly emersed at low tide in the foreground.

FIGURE 164. Paruru Reef, Marau Sound, east Guadalcanal. Rubble flat and sheltered reef, with boulder jetty at low water.

(*Facing p.* 508)

165

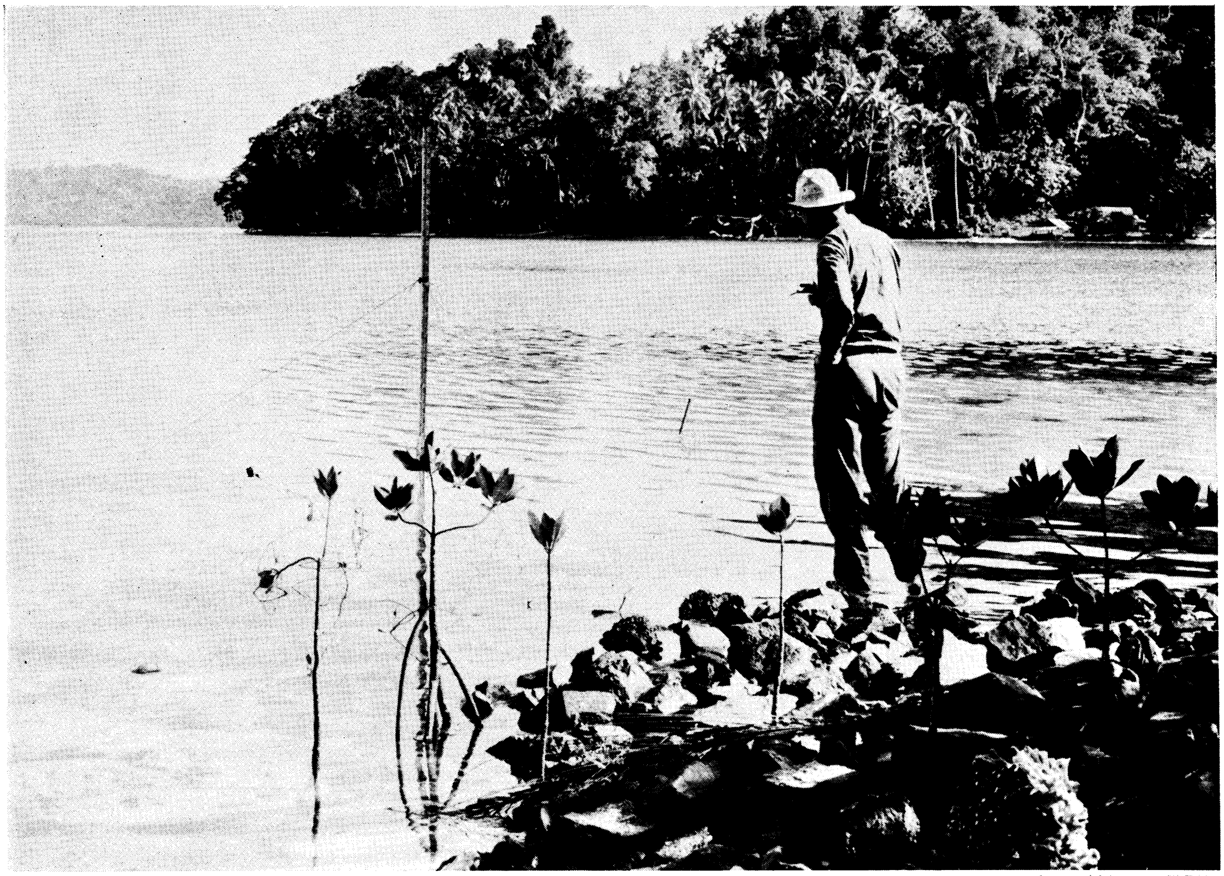


166

Tulagi, Florida group

Figure 165. A typical reef flat with *Porites* nodules, loose *Acropora* and broken rubble, emersed at low water.

Figure 166. *Acropora rubble,* cemented with calcareous algae, on a sheltered reef flat emersed between tides.



167

168

FIGURE 167. Tetel Island, Sandfly Passage, Florida group. The working site on shore, with the tide pole.

FIGURE 168. Tetel Island, Sandfly Passage, Florida group. *Thalassina anomala* mounds in the supratidal area.

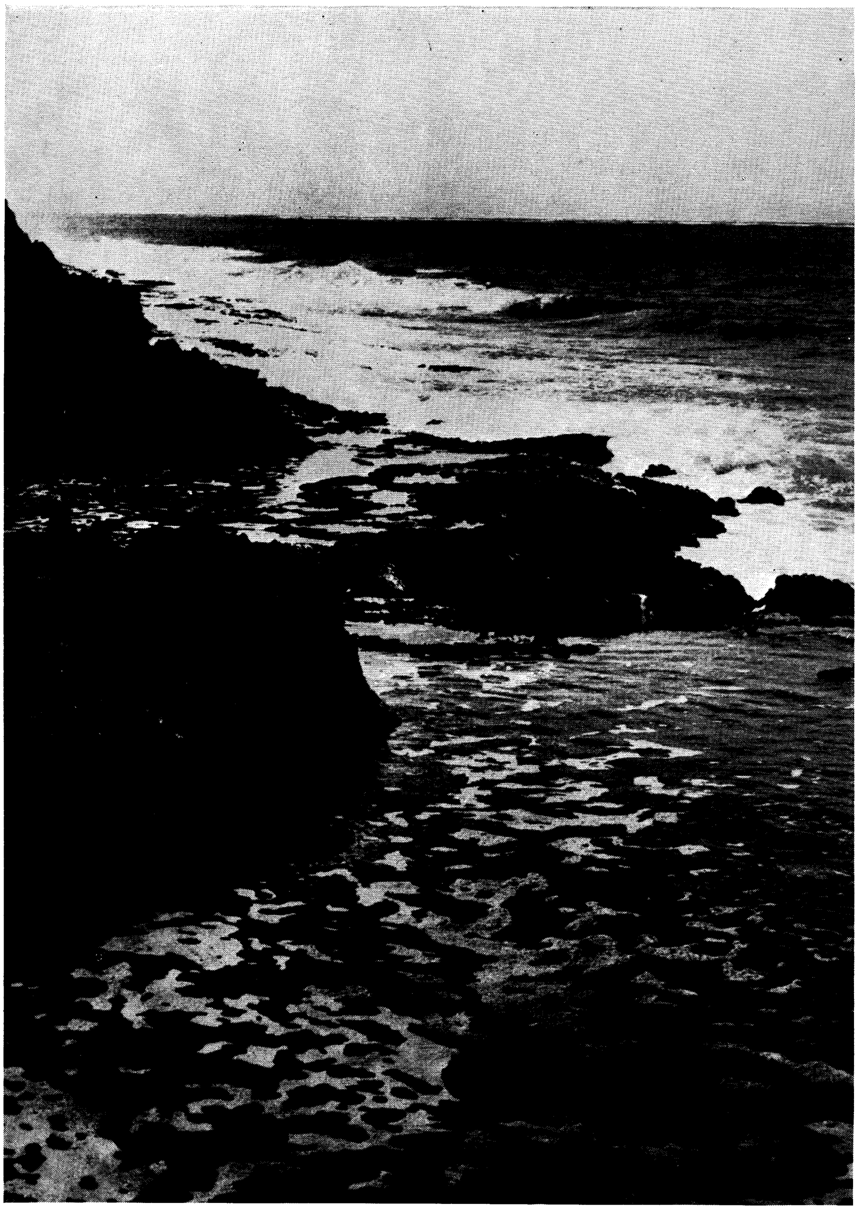


FIGURE 169. Banika Island, Russell group. Surf-washed bench on the southern weather coast near the point of maximal exposure.

other or signal to the females. Our own list of Solomon Islands ucids, undoubtedly by no means exhaustive, runs to some 20 species, each with a distinctive and attractive colour combination in the 'chic' adornment of carapace and chelae.

The zone of soft mud below the ucid territory, entitled on our present scheme to the designation of a 'sublittoral fringe', is frequented by polychaete worms. Gibbs records (personal communication) from one such typical locality, a common capitellid, probably *Dasybranchus caducus*, a nereid and a species of *Marphysa*. Where the substratum is firm enough, it is penetrated by long straight shafts of phascolosomid worms; or by shorter bottle-shaped chambers occupied by a thalassemid echiuroid. A large species of *Callianassa* constructs spacious shafts of wider calibre, reaching a finger's width (figure 161).

The mudbanks of estuaries may be in some places fringed by a narrow, sloped beach of coarser textured greyish or brown sand. Here the chief crabs are grapsids and sesarmids living under leaf litter. There is sometimes an upper eulittoral zone where shallow-burrowing bivalves exist alongside the maritime earthworm, *Pontodrilus matsuchimensis*, elsewhere discussed by Lee (1969). Ellobiid gastropods are here and higher up abundant, generally species of *Melampus* at or above high-water mark, while the larger and thoroughly terrestrial *Pythia pantherina* is to be found on tree boughs and among forest litter a considerable distance inland.

Around most estuarine shores the firm thicket of the strut-roots of *Rhizophora* drops straight to the water-line or borders upon very soft mud. Where there has been much delta-building, we find the mangrove swamp of the maritime zone and sublittoral fringe very prolonged. The mangrove is indeed an entity that resists classification in terms of a vertical zonation scheme. A *Rhizophora* tree cuts across several levels. The base of its trunk will carry rock oysters (*Crassostrea*) and *Isognomon*, both bivalves characteristic of the middle eulittoral; above these may be a scatter of barnacles, *Chthamalus* sp. marking an upper eulittoral. The littoral fringe is represented by the large thin-shelled littorine, *Melarhaphe scabra*, living upon *Rhizophora* foliage. The ecological status of *Rhizophora* must be regarded as one of co-adaptation of two realms, one below the foliage level that is intermittently marine, save in respect of aerial respiration by special pneumatophores, and the other permanently aerial, with atmospheric photosynthesis.

The trees and shrubs called 'mangrove' belong of course not to a single taxon, but constitute a life form with certain characters acquired in common, such as aerial roots and viviparous embryos, and adaptations to 'physiological drought', developed in a number of families independently. The Solomon Islands trees that may be grouped ecologically as mangroves fall into at least five families (see van Steenis 1958) and table 35. These are the Rhizophoraceae, Sonneratiaceae, Avicenniaceae, Combretaceae, and Aegicerataceae.

In figure 161 we have shown schematically the development of a mangrove formation in relation to tide level upon muddy as well as semi-sandy shores and beaches fringes. Further distribution data are cited in table 35. The *Rhizophora* species, especially *R. mucronata* always form the rampart farthest to the seaward edge the lower reaches of their strut roots carry a displaced benthos marking them as corresponding to an upper and middle eulittoral. *R. mucronata* is submerged at high tides right up to the foliage line. Above approximately high water of neap tides, the root systems of *R. apiculata* arch widely over

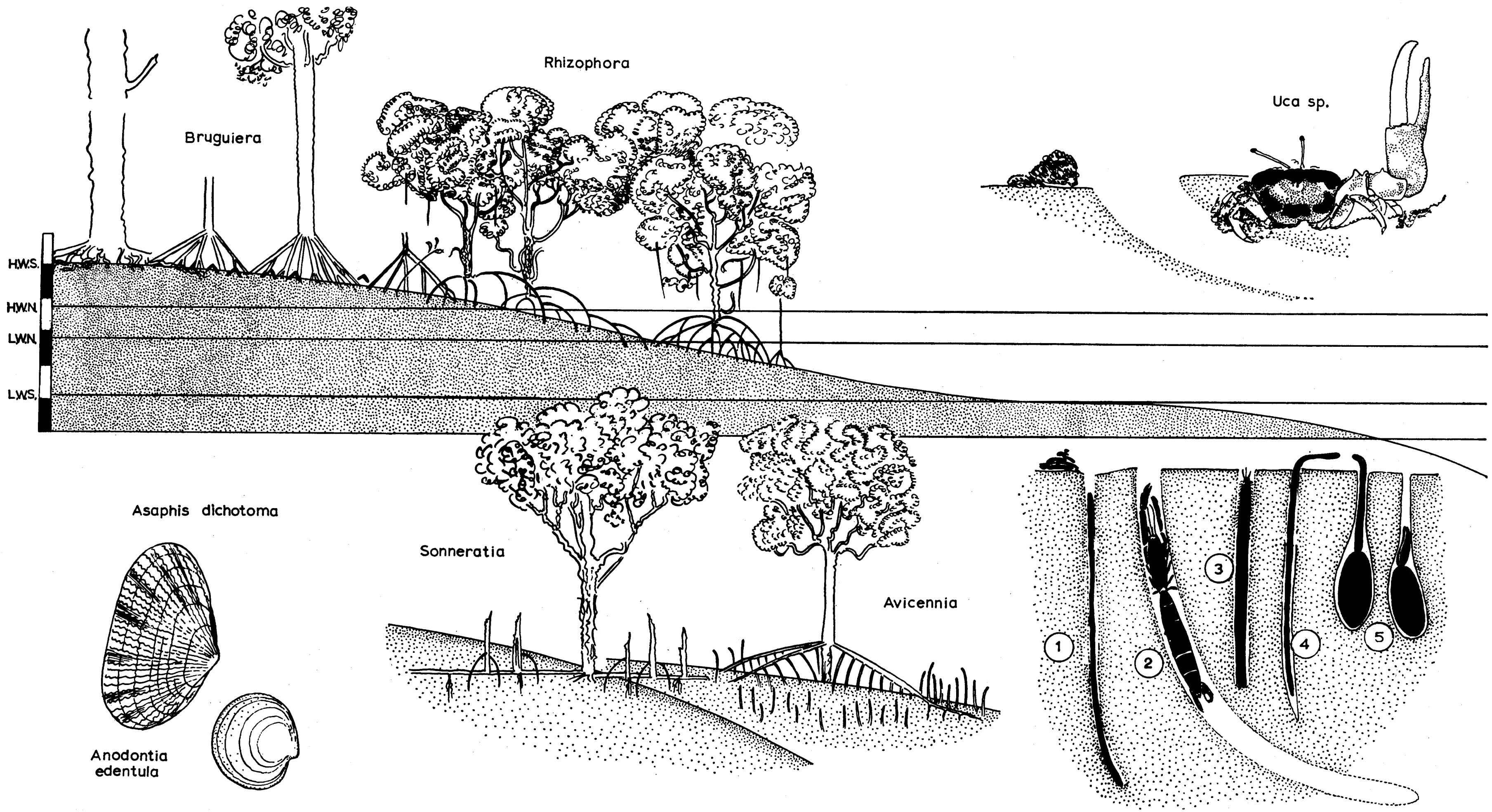


FIGURE 161. Profile of a muddy estuarine shore, fringed by a mangrove formation with *Bruguiera* to landward and *Rhizophora* (sometimes *R. mucronata* and *R. apiculata*) together along the water-line. Illustrated below are the distinctive root and pneumatophore systems of the mangroves *Sonneratia griffithii* and *Avicennia officinalis*, both trees found solitary or in small clumps where there is an admixture of sandier beach. The two bivalves to the left are highly characteristic of such a habitat. The portion of the mud-bank to seaward is dominated by a rich diversity of Ucidae, or beckoning crabs. Towards low water mark a number of burrowing animals are highly typical: 1, a capitellid worm; 2, a *Callianassa*; 3, *Marphysa* sp.; 4, a sipunculoid; 5, a *Thalassema* species.

TABLE 35. ECOLOGY AND OCCURRENCE OF MANGROVES IN THE SOLOMON ISLANDS

family and species	substrate	tide level and ecology	shelter	localities where studied
RHIZOPHORACEAE				
Rhizophora mucronata	deep soft mud	inundated up to foliage line at all tides	land-locked inlets	common throughout the Protectorate
R. apiculata	soft or consolidated mud	inundated at normal high tides	lagoons and estuaries or behind reef shelter	widespread; especially developed at South Spit, Marau Sound, Guadalcanal
R. stylosa	consolidated sand or fine rubble	inundated at normal high tides	beaches, facing open sea semi-solitary	locally common. Marau Sound; Banika Is.
Bruguiera sexangula	consolidated delta soils	inundated at spring tides	coastal trees at back of sheltered inlets	common throughout
B. gymnorhiza	well-consolidated terrestrial soils	inundated only at equinoctial tides	in protected coastal forest	common throughout
SONNERATIACEAE				
Sonneratia griffithii	sandy ground, bordering beaches or river mouths	inundated by medium high tides	moderately protected beaches	spotwise throughout the Protectorate
COMBRETACEAE				
Lumnitzera littorea	consolidated ground at back of *Bruguiera*	seldom or never inundated	mangrove swamps and tidal rivers	Marau Sound delta forest
AVICENNIACEAE				
Avicennia alba	sandy ground, often beach-fringing behind *R. stylosa*	inundated by medium high tides	beaches of only moderate shelter	Marau Sound, Guadalcanal
A. officinalis	consolidated sandy mud	inundated at medium high tides	estuaries	Sandfly Passage, Florida Group
A. intermedia	consolidated sandy ground	inundated by medium high tides	moderate shelter	Komimbo Bay, Guadalcanal
AEGICERATACEAE				
Aegiceras corniculatum	consolidated sandy ground	inundated by exceptional tides	moderate shelter	Marau Sound, Florida Group

the mud in what may—on the evidence of the fauna—be held to constitute a littoral fringe They harbour bivalves and crabs, especially certain fast-running seasarmids and a specialized low-pitched neritid attaching firmly to the bark. Beyond the domain of *Rhizophora*, a higher canopy of *Bruguiera* species is established, with pure stands of these tree mangroves upon firm, easily walkable muds. These areas are seldom inundated by the tides; the substratum is black and anaerobic, though in places with evident aeration from burrowing crabs and molluscs. The *Bruguiera* pneumatophores have a characteristic irregular hoop-shape or a kneed triangular form. Two *Bruguiera* species, *B. sexangula* and *B. gymnorhiza*, were found. Mingled with these, or sometimes replacing them to landward may be tall trees of *Lumnitzera littorea*, sometimes reaching many hundreds of yards inland, or stretching along a delta plain. The whole area of *Bruguiera* and *Lumnitzera*, once the cordon of *Rhizophora* roots is passed, forms a forest with a stablized floor, open and freely penetrable.

Several species of mangrove may appear in small numbers, isolated from forests or thickets. Of these, *Rhizophora stylosa* is found most commonly on a sandy or muddy shoreline, seldom forming a close community. In the littoral fringe of sandy beaches, common mangroves, single or in small stands, are *Avicennia alba*, *A. intermedia* and *A. officinalis*, distinguished by the long, flexible pneumatophores, and *Sonneratia griffithii*, a larger leafed tree, with shorter, strong spike-like pneumatophores. *Aegiceras corniculatum* is another semi-solitary tree of this community.

The animals characteristic of *Bruguiera* swamps may burrow rather deeply in mud, as do several of the bivalves, or lie loosely at the surface, especially under blocks of strewn or impacted coral or log debris. In the softer mud may be found numerous bivalves: the thin shelled globose *Anodontia edentula*; the venerids *Pitar*, and *Lioconcha* spp., *Gafrarium tumidum*; the tellinaceans *Macoma*, *Scutarcopagia* and the long-siphoned *Asaphis dichotoma*. Among the loose surface cover appear the several aerially breathing species of gastropods and crabs. Of the snails the prosobranchs (Cerithiidae) and the pulmonates (Ellobiidae) take the pre-eminence. The former include the long, trailing *Terebralia palustris* and *Cerithidea obtusata*. The largest of the ellobiids is *Cassidula mustelina*, accompanied by two species of *Melampus* and an *Auriculastra* living under loose or mud-embedded logs. The related *Pythia pantherina* is entirely terrestrial, living in maritime bush behind the mangrove fringe. The Ellobiidae as a whole form a prolific series of early pulmonates, characteristically centred in mangrove and estuarine reaches, and also in intertidal rock crevices. Another gastropod group with a large tropical terrestrial and also freshwater contingent is the Neritidae, represented in the streams of mangrove deltas by species of *Clithon* and *Vittina* and by a small very common *Septaria*, found on smooth boulder surfaces—or, more commonly in deltas, on water-logged empty coconut shells.

The crabs of the mangrove flats include a wide assortment of sesarmids, grapsids and portunids under loose cover. In softer and sticky mud the heavy portunid *Scylla serrata* burrows. Land Brachyura (*Cardisoma*) abound on stiffer terrestrial mud and clay; the land hermit *Coenobita perlata* is found on cleaner, semi-sandy fringes, replacing here the smaller *C. rugosa* which lives farther down in the littoral fringe. The coconut crab, *Birgus latro* is a thoroughly terrestrial anomuran, still common enough on small less-frequented islets. A characteristic anomuran in areas of stiff mud, well above the tidal reach, is the 10 in. long,

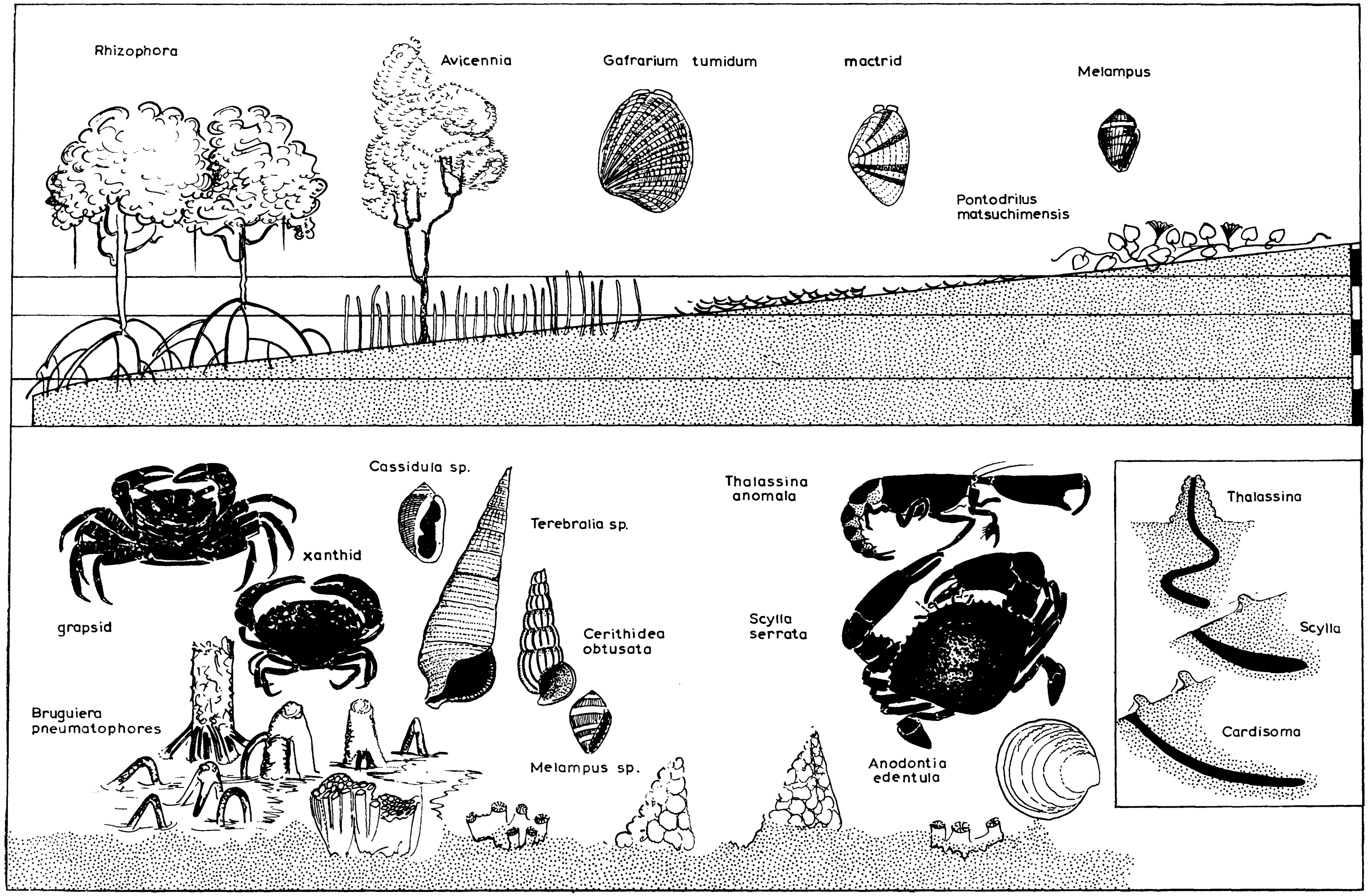


FIGURE 162. Soft shores under maximal shelter. (Above): west Guadalcanal—a sand beach bounded to seaward by an expanse of soft mud. The characteristic mangrove at the mud level is *Rhizophora mucronata*, with *Avicennia intermedia* on higher sandy ground. The sandy upper beach is fringed with *Ipomaea pes-caprae*. The beach litter of leaves and other stranded material is characterized by a *Melampus* species and a little lower down, where leaves lie on sand by a high level mactrid bivalve in great abundance and the worm, *Pontodrilus matsuchimensis* as discussed by Lee (1968). (Below): east Guadalcanal—the consolidated mud and clay floor of a *Bruguirea* maritime forest showing the characteristic molluscs and crustaceans with schemata of their burrows. To the left are represented *Bruguiera* kneed pneumatophores, and embedded coral blocks, and in the centre the conical mounds of *Thalassina anomala*.

so-called mud-lobster *Thalassina anomala*; its deep descending burrows are provided with conical mounds like oast-houses at their entry. Johnson (1961) has contributed a short note on its ecology, but much of its life and habits remain obscure.

It is a pleasure to acknowledge the debt to all the members of the Marine Party for their 5 months' comradeship and close collaboration, to Professor Corner, Leader of the Expedition, for the inspiration and powers of leadership by which the whole venture was carried through, as also to Mr George Hemmen, Administrative Officer, for his cheerful and sustaining help, during our 5 months in the field. Of those members in charge of particular aspects the senior author would record his gratitude to Professor H. B. S. Womersley, whose detailed assistance with the algae is responsible for the precision of nomenclature that rightly deserved acknowledgement at many points in this paper; Dr D. A. Stoddart for his comprehensive guidance and help with geographical problems and general surveying, and Dr Steven Wainwright for his expert guidance to us all in coral biology and systematics.

After our return to Auckland, Professor V. J. Chapman gave us much help with the identification of the mangrove species.

For personal assistance and hospitality in the Solomon Islands the Marine Party would single out here its debt—among many others—to Mr J. C. Grover, O.B.E., Mr Jan Schenk, Mr Ole Torling and Mr Ian Gower.

Finally both authors are grateful to the University of Auckland for its generous grant of leave and financial support and to the Golden Kiwi Scientific Grants Committee in New Zealand for a large grant towards equipment and travelling expenses.

References (Morton & Challis)

Ballantine, W. J. 1961*a* Population dynamics of *Patella vulgata* and other limpets. University of London, Ph.D. thesis.

Ballantine, W. J. 1961*b* A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies* **1**, no. 3.

Bergquist, P. L. 1959 A statistical approach to the ecology of *Hormosira banksii*. *Botanica Mar.* **1**, 12, 22–48.

Bergquist, P. L. 1957 *Some factors in brown algal zonation*. University of Auckland, M.Sc. thesis.

Challis, D. A. 1969*a* An interstitial fauna transect of a Solomon Islands sand beach. *Phil. Trans.* B **255**, 517–526. (This Discussion.)

Challis, D. A. 1969*b* An ecological account of the marine interstitial opistobranchs of the British Solomon Islands Protectorate. *Phil. Trans.* B **255**, 527–539. (This Discussion.)

Dahl, E. 1953 Some aspects of the fauna and zonation of sandy beaches. *Oikos* **4** (1), 1–27.

Dales, R. P. 1957 *Commensalism*. In (ed. Hedgpeth, J. W.), *Geol. Soc. Am. Mem.* no. 67, **1**, 391–412.

Darwin, C. 1842 *The structure and distribution of coral reefs*. London. 214 pp.

Delamare-Deboutteville, C. 1960 *Biologie des eaux souterraines littorales et contienentales*, 740 pp. Paris: Hermann.

Gibbs, P. E. 1969 Aspects of Polychaete ecology with particular reference to commensalism. *Phil. Trans.* B **255**, 443–458. (This Discussion.)

Glynne Williams, J. & Hobart, J. 1953 Studies on the crevice fauna of a selected shore in Anglesey. *Proc. Zool. Soc. Lond.* **122**, 797–824.

Guppy, H. B. 1886 Notes on the character and mode of formation of the coral reefs of the Solomon Islands. *Proc. roy. Soc. Edinb.* **13**, 857–904.

Hiatt, R. W. & Strasburg, D. W. 1960 Ecology relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* **30**, 65–127.

Hiro, F. 1937 Studies on the animals inhabiting coral reefs. I. *Hapalocarcinus* and *Cryptochirus. Palao trop. biol. Stn Stud.* **1**, 137–154.

Hopkins, S. H. 1957 Parasitism. In (Hedgpeth, J. W., ed.), *Geol. Soc. Am. Mem.* no. 67, **1**, 413–428.

Johns, P. M. 1960 *Chiton pelliserpentis* (Mollusca Amphineura): a study in the taxonomy of a species in relation to its breeding biology and ecology. M.Sc. thesis, University of Canterbury, Christchurch, N.Z.

Johnson, D. S. 1961 The food and feeding of the mud-lobster, *Thalassina anomala. Crustaceana* **2**, 325–326.

Knudsen, J. W. 1967 *Trapezia and Tetralia* (Decapoda, Brachyura, Xanthidae) as obligate ectoparasites of pocilloporid and acroporid corals. *Pacif. Sci.* **21**, 51–57.

Kensler, C. R. 1967 Desiccation resistance of intertidal crevice species as a factor in their zonation. *J. Anim. Ecol.* **36** (2), 391–406.

Lee, K. R. 1969 Earthworms of the British Solomon Islands Protectorate. *Phil. Trans.* B, **255**, 345–354. (This Discussion.)

Lewis, J. R. 1953 The ecology of rocky shores round Anglesey. *Proc. Zool. Soc. Lond.* **123**, 481–549.

Lewis, J. R. 1961 The littoral zone on rocky shores—a biological or physical entity? *Oikos* **12**, 280–301.

Lewis, J. R. 1964 *The ecology of rocky shores*. London.

Marshall, N. B. 1965 *The biology of fishes*. London.

Miller, M. C. 1969 The habits and habitats of the opisthobranch molluscs of the British Solomon Islands. *Phil. Trans.* B **255**, 541–548. (This Discussion.)

Morton, J. E. 1954 The crevice faunas of the upper intertidal zone at Wembury. *J. mar. biol. Ass. U.K.* **33**, 187–224.

Morton, J. E. 1956 The tidal rhythm and action of the digestive system of the lamellibranch *Lasaea rubra. J. mar. biol. Ass. U.K.* **35**, 563–586.

Morton, J. E., Boney, A. D. & Corner, E. D. S. 1957 The adaptations of *Lasaea rubra* a small intertidal lamellibranch. *J. mar. biol. Ass. U.K.* **36**, 383–405.

Morton, J. E. & Miller, M. C. 1968 *The New Zealand sea shore*. London: Collins. 638 pp.

Potts, F. A. 1915 *Hapalocarcinus*, the gall-forming crab, with some notes on the related genus *Cryptochirus. Papers Dep. mar. Biol. Carnegie Instn Wash.* **8**, 33–69.

Sargent, M. C. & Austin, T. S. 1954 Biologic economy of coral reefs. *U.S. Geol. Survey, Prof. Pap.* 260 E, 293–300.

Stephenson, T. A. 1953 The world between tide marks. In (ed. Marshall, S. M. and Orr, A. P.), *Essays in marine biology*. Edinburgh: Oliver & Boyd, pp. 73–100.

Stephenson, T. A. 1943 The causes of the vertical and horizontal distribution of organisms between tide-marks in South Africa. *Proc. Linn. Soc. Lond.* **154**, 219–232.

Stephenson, T. A. & Stephenson, Anne 1949 The universal features of zonation on rocky shores. *J. Ecol.* **37**, 289–305.

Stephenson, T. A., Tandy, A. G. & Spender, M. 1931 The structure and ecology of Low Isles and other reefs. *Scient. Rep. Gt Barrier Reef Exped.* 1928–29. (Brit. Mus. N.H.), **3** (2), pp. 17–112.

Stoddart, D. R. 1969*a* Geomorphology of Solomon Islands coral reefs. *Phil. Trans.* B **255**, 355–382. (This Discussion.)

Stoddart, D. R. 1969*b* Geomorphology of the Marovo elevated barrier reef, New Georgia. *Phil. Trans.* B **255**, 383–402. (This Discussion.)

Stoddart, D. R. 1969*c* Sand cays of eastern Guadalcanal. *Phil. Trans.* B **255**, 403–432. (This Discussion.)

Stoddart, D. R. & Cann, J. R. 1965 The nature and origin of beach rock. *J. sedim Petrol.* **35** (1), 243–247.

Swedmark, B. 1964 The interstitial fauna of marine sand. *Biol. Rev.* **39**, 1–42.

Tweedie, M. W. F. 1936 On the crabs of the family Grapsidae in the collection of the Raffles Museum. *Bull. Raffles Mus.* no. 12.

van Steenis, C. G. G. J. (ed.) 1958 *Flora Malesiana*, ser. 1. *Spermatophyta* **5**.

Verwey, J. 1930 Coral Reef Studies. I. The symbiosis between damsel-fishes and sea anemones in Batavia Bay. *Treubia* **12** (3–4), 305–366.

Wells, G. P. 1949 The behaviour of *Arenicola marina* L. in sand and the role of spontaneous activity cycles. *J. mar. biol. Ass. U.K.* **28**, 465–478.

Wells, J. W. 1957 *Coral Reefs.* In (Hedgpeth, J. W., ed.) *Geol. Soc. Am. Mem.* 67, **1**.

Womersley, H. B. S. & Bailey, A. 1969 The marine algae of the Solomon Islands and their place in biotic reefs. *Phil. Trans.* B **255**, 433–442. (This Discussion.)

Womersley, H. B. S. & Edmonds, S. J. 1952 Marine coastal zonation in southern Australia in relation to a general scheme of classification. *J. Ecol.* **40**, 84–90.

Yonge, C. M. 1930 Studies on the physiology of corals. I. Feeding mechanisms and food. *Scient. Rep. Gt Barrier Reef Exped.* 1928–29 (Brit. Mus. N.H.), **1** (2), 14–57.

Yonge, C. M. 1940 The biology of reef-building corals. *Scient. Rep. Gt Barrier Reef Exped.* 1928–29. (Brit. Mus. N.H.), **1** (13), 353–391.

Yonge, C. M. 1949 *The sea-shore.* (The New Naturalist) London: Collins. 311 pp.

Yonge, C. M. 1955 Adaptation to rock-boring in *Botula* and *Lithophaga* (Lamellibranchia, Mytilidae) with a discussion on the evolution of this habit. *Q. Jl microsc. Sci.* **96**, 385–410.

Yonge, C. M. 1968 Living corals. *Proc. Roy. Soc.* B **169**, 329–344.

163

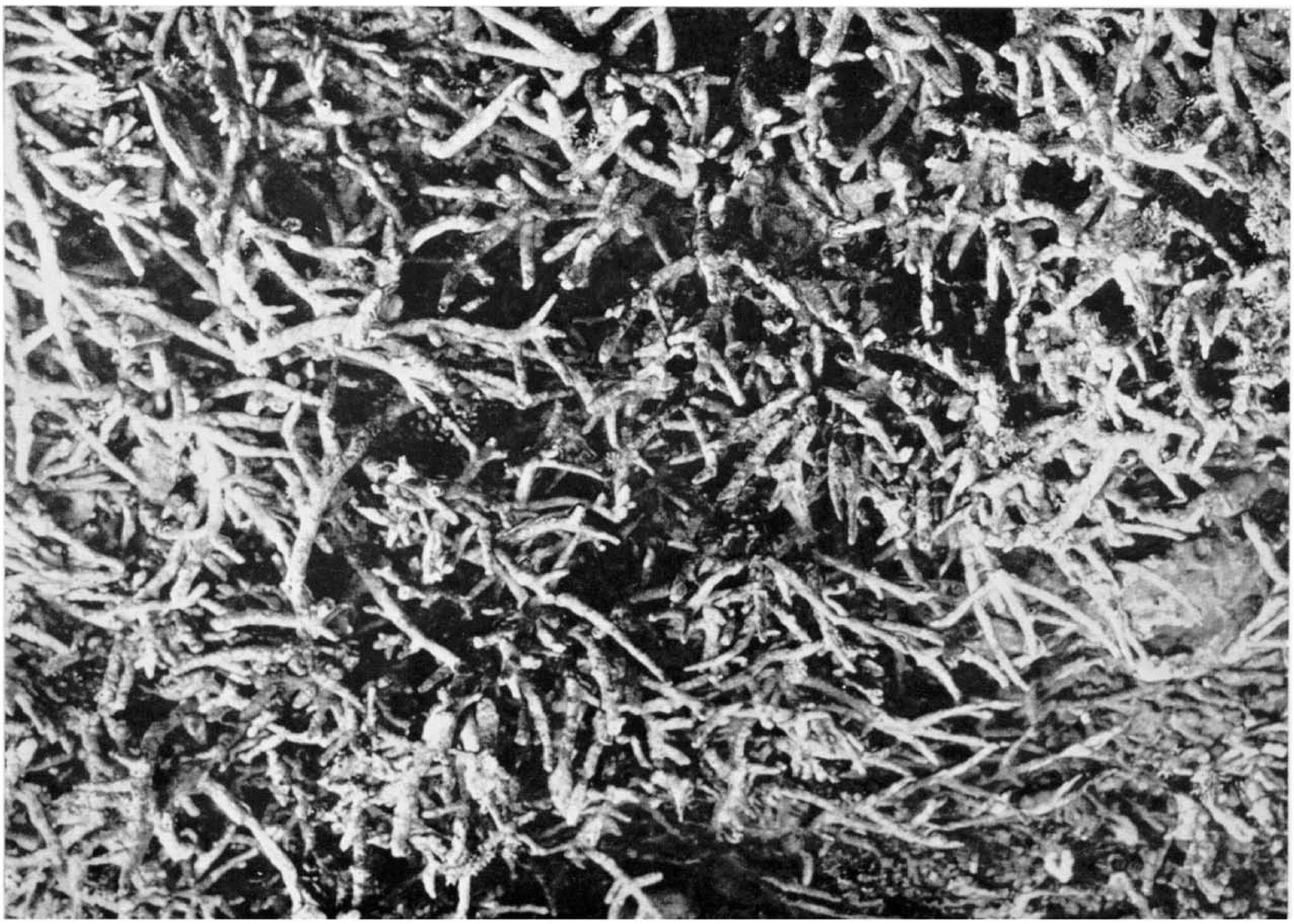
164

Tulagi, Florida group

FIGURE 163. A.K. *Maroro* at anchor, with a rubble flat and sheltered reef partly emersed at low tide in the foreground.

FIGURE 164. Paruru Reef, Marau Sound, east Guadalcanal. Rubble flat and sheltered reef, with boulder jetty at low water.

165

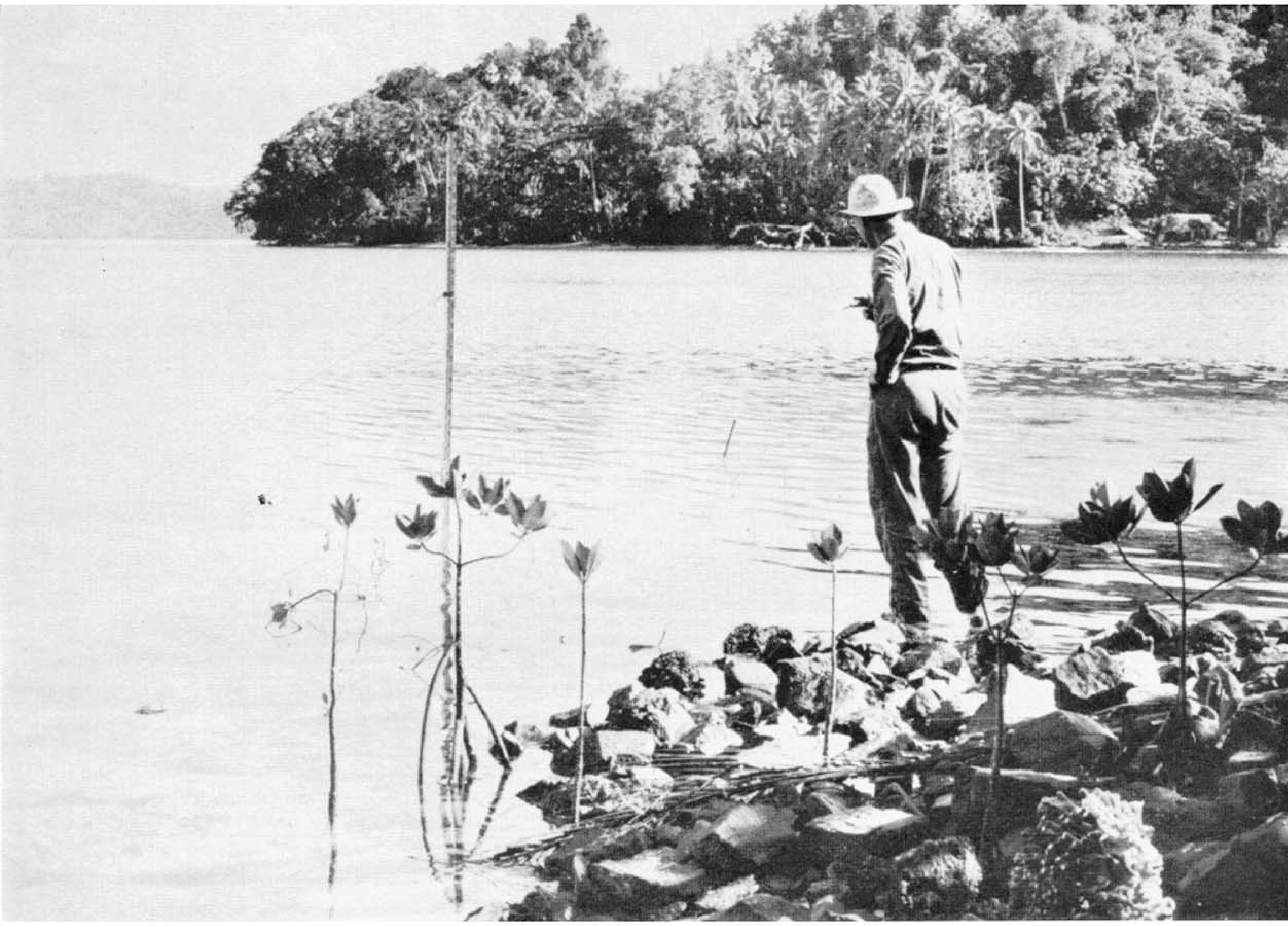


166

Tulagi, Florida group

FIGURE 165. A typical reef flat with *Porites* nodules, loose *Acropora* and broken rubble, emersed at low water.

FIGURE 166. *Acropora rubble*, cemented with calcareous algae, on a sheltered reef flat emersed between tides.



167

168

FIGURE 167. Tetel Island, Sandfly Passage, Florida group. The working site on shore, with the tide pole.

FIGURE 168. Tetel Island, Sandfly Passage, Florida group. *Thalassina anomala* mounds in the supratidal area.

FIGURE 169. Banika Island, Russell group. Surf-washed bench on the southern weather coast near the point of maximal exposure.