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The marine algae of the Solomon Islands and their place in biotic* reefs.

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Introduction

The Royal Society Expedition to the Solomon Islands aimed at examining the biogeographical relationships between these islands and other island systems of the western tropical Pacific. The marine party also studied intertidal and reef ecology. Comprehensive collections of benthic marine algae were made at the main localities visited (Florida Islands, north-west and south-east Guadalcanal, Matiu Island off the north coast and Batuona and Ulukoro Islands off the south coast of New Georgia, Banika Island in the Russell Islands, and south-east Gizo Island). Additional small collections were obtained from Kolombangara and the north coast of San Cristobal. Habitat notes accompanied each collection and preliminary determinations were made in the field where possible. General ecological observations on the reefs included profiles selected after a preliminary survey of an area. Such profiles (see below) indicate the general situation but are not based on detailed transect work; restricted time and the great variation in distribution of organisms over the reef surface (especially in the moat) rendered isolated detailed transects of limited value.

The marine algal flora of the Solomon Islands has been one of the least known in tropical regions. Setchell (1935) recorded nine species from Malaita Island and also several taxa from Sikaiana Island (in the Stewart Islands, north-east of Malaita Island) and from Bellona Island, south of the Solomon Islands. Levring (1960) recorded a number of species from Rennell Island, near Bellona Island. Otherwise there are only a few scattered records in taxonomic monographs.

TAXONOMIC ACCOUNT

Taxonomic studies are well advanced and it appears that about 220 species of Chlorophyta and Rhodophyta can be credited to the Solomon Islands. The Cyanophyta are well represented also, as free-living forms, epiphytes and within the encrusting corallines, but have not yet been determined. Only a few species appear to be undescribed, but two of these (in the Ceramiaceae and Rhodomelaceae of the Rhodophyta) are probably generically distinct. A full account of the known marine algae of the Solomon Islands will be published later.

Our knowledge of tropical marine algae is far from satisfactory. Many tropical algae are

* As will be seen from this account, and from many other accounts of tropical reefs, coral growth is conspicuous under most conditions of wave action but not under heavy surf. Here, encrusting coralline algae are dominant and basic in reef development, and in calmer areas they are also important as cementing organisms. It thus seems more appropriate to refer to such tropical reefs as 'biotic' reefs than to continue the misleading term 'coral' reefs.

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widely distributed, yet no general account has been published and only two recent monographs (on *Halimeda* and *Turbinaria*) are available. Hence considerable uncertainty exists in many determinations.

BIOGEOGRAPHICAL ASPECTS

Taxonomic uncertainties and lack of widespread and comprehensive collections of tropical algae greatly reduce the value of biogeographical studies. In many cases the biogeography of collectors rather than taxa is recorded and it was noteworthy on the Expedition that the number of algal species collected in an area was related to the number of days spent there.

In number of taxa the Solomon Islands are fairly typical of such an area of islands in the tropics. Their 220 or more species compare with about 240 species from the Marshall Islands. The Siboga Expedition recorded some 600 species from a much larger area (mainly Indonesia). Nearly all of the Solomon Islands species are widely distributed; probably almost one-third are pantropical and over half occur either throughout the tropical Indian and Pacific Oceans or from the Indian Ocean through to the western Pacific Ocean. A few are apparently restricted in their distribution, but further collections from tropical areas may show these species to be more widespread.

The distribution of Sargassum and the encrusting coralline algae deserves further comment.

(1) Sargassum

Only four species were collected in the Solomon Islands. S. cristaefolium C. Agardh (S. duplicatum Bory) was the commonest species, growing on the reef rim under surf conditions. Setchell (1935) recorded two other species from Malaita Island. This contrasts markedly with some 45 species recorded by Reinbold (1913) from the Siboga Expedition collections, even allowing for the greater area and lack of good specific concepts at that time. In the Marshall Islands, however, no species of Sargassum has been recorded by Taylor (1950) or Dawson (1956, 1957). These islands lie within the area of atolls (165° E to 141° W and 16° N to 16° S) from which Sargassum is absent (Doty 1954). While Sargassum may occur only on high islands of igneous origin, there appears to be a distinct decrease in number of species eastwards from the Indonesian region, with the genus being poorly represented in the Solomon Islands.

(2) The encrusting corallines

In the Solomon Islands, the widespread Indian and Pacific Ocean reef-building *Porolithon onkodes* (Heydrich) Foslie is most important, but other species of this genus are apparently absent. Together with *P. onkodes*, *P. gardineri* (Foslie) Foslie is of prime importance in the Marshall Islands (Taylor 1950), where *P. craspedium* (Foslie) Foslie also occurs; on Indian Ocean atolls such as the Maldive Islands and Chagos Archipelago, *P. craspedium* is codominant with *P. onkodes*, while *P. gardineri* is of lesser importance (Foslie 1903). Both *P. gardineri* and *P. craspedium* are branched species occurring on the rim under strong surf. Neither of these species was collected in the Solomon Islands, nor during the Siboga Expedition. Both are characteristic of heavy surf, and it is possible that suitable conditions

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do not occur in the Solomon Islands and Indonesia; alternatively, perhaps sufficiently rough habitats were not visited.

Neogoniolithon frutescens (Foslie) Setchell & Mason is a common alga in the moat area of Pacific atolls, in Indonesia, and is present on Indian Ocean atolls. However, it was not collected in the Solomon Islands. Another common alga of the Indian Ocean and Indonesia, Lithothamnium fruticulosum (Kuetzing) Foslie was also not found in the Solomon Islands. This is possibly because it is a deeper sublittoral alga, and suitable habitats were not examined in the Solomon Islands.

Within the Solomon Islands, there is little variation in the species composition of similar habitats in the islands visited by the Expedition. The apparent absence of a species from a locality is of little consequence, since it was seldom possible to locate and survey the great variety of microhabitats at any one locality. Apparently restricted distributions are illustrated by species in the following two microhabitats.

- (1) The underside of table-Acropora corals, where a distinctive flora usually occurs in complete shade. This includes Coelarthrum boergesenii W. v. Bosse, Erythrocolon podagricum J. Agardh, Rhodymenia anastomosans W. v. Bosse, Champia viellardii Kuetzing and Dictyopteris repens (Okamura) Boergesen, all of which are rare elsewhere.
- (2) Deep, heavily shaded pools at the rear of the outer reef on Matiu Island, connected to deep water under the reef and subject to surges even at low tide. These pools contain a number of species not found elsewhere—e.g. Halymenia dilata Zan., Carpopeltis?, Polyopes lingulatus (Harvey) Schmitz?, Neogoniolithon megalocystum Foslie?, Peyssonnelia sp.nov.? and Dasyphila plumaroides Yendo. Similar habitats were not seen elsewhere.

ECOLOGICAL ASPECTS

The broader aspects of the algal ecology of the Solomon Islands reefs are discussed below, followed by a brief outline of the more distinctive features and problems. Detailed accounts for the localities visited await completion of the taxonomic work, and integration of these with the zoological account will be considered later.

The prime factor in the ecology of biotic reefs is clearly the degree of wave action, this being inter-related with topography and aspect. Where wave action is slight to moderate the widest fringing reefs occur, commonly with either sand-debris beach at their rear or sand-mud areas of mangroves when near rivers. In such cases the eulittoral zone is poorly represented since little of the reef surface is emergent at low tide and few obvious organisms occur on the sand or mud at the reef rear (see, however, Challis 1969). Under conditions of heavy wave action the reef is usually narrower, and commonly rock at the reef rear permits a more distinctive zonation within the eulittoral.

The following examples illustrate reef ecology under varying degrees of wave action.

(1) Calm localities (figure 126) with a wide moat area (100 to 300 m), slightly raised rim area dominated by corals, and backed by sandy beach or sand-mud flats with 'sea-grass' beds (Thalassia, Enhalus) and mangroves near streams, e.g. Tetel Island (Florida Islands) and Komimbo (north-west Guadalcanal). The common mangroves are species of Avicennia, Rhizophora and Bruguiera, but the Bostrychia-Caloglossa algal flora usually associated with them in other tropical areas was not found in the Solomon Islands. The reef rim is

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characterized by corals and an apparent lack of coralline algae, though the latter are present as cementing organisms. Corals are also present in the moat area, though limited in variety of taxa.

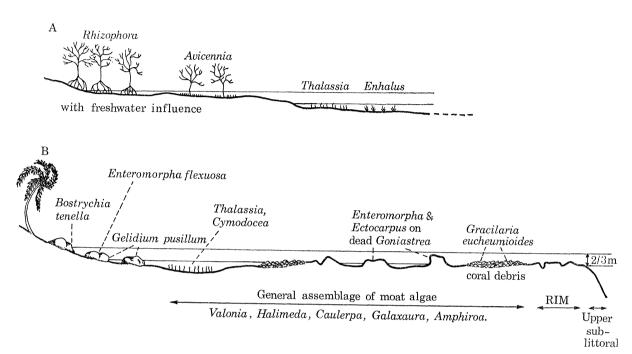


Figure 126. General transect of a reef under calm conditions (e.g. Komimbo on Guadalcanal); A, shoreward part of reef near a river mouth, with mangroves present; B, reef away from freshwater influence. Width of reef about 200 m.

Common moat algae are Valonia fastigiata Harvey, V. ventricosa J. Agardh, Boodlea composita (Harvey) Brand, Struvea anastomosans (Harvey) Picc. and Grunow, Caulerpa spp., Chlorodesmis comosa Harvey & Bailey, Halimeda spp., Dictyota friabilis Setchell, Padina commersonii Bory, Actinotrichia fragilis (Forssk.) Boerg., Galaxaura spp., Peyssonnelia spp., Amphiroa foliacea Lamx., A. fragilissima (L.) Lamx., Halymenia durvillaei Bory, Gracilaria salicornia (C. Ag.) Dawson, Gelidiopsis intricata (C. Ag.) Vickers, Hypnea nidulans Setchell, Champia parvula (C. Ag.) Harvey, C. vieillardii, Tolypiocladia glomerulata (C. Ag.) Schmitz, Acanthophora spicifera (Vahl) Boerg., and Laurencia spp.

2. Moderate wave action localities (figure 127) with waves 0.50 to 1 m high at most times, e.g. Mamara and Kukum on north-west Guadalcanal. Here the reef is narrower (10 to 20 m) and the rim is characterized by crustose corallines (especially Lithophyllum moluccense Foslie) together with a diversity of corals. Neogoniolithon myriocarpon (Foslie) Setchell & Mason, and Porolithon onkodes to a lesser extent, also occur on the rim and are the main algae responsible for consolidation of the reef. Within the moat, corals (often dead) are the most conspicuous organisms, and the algal flora is similar to that of calmer reefs.

Intertidal rock is often present at the reef rear and permits the patchy development of mat algae such as *Gelidium*, *Sphacelaria* and *Enteromorpha*. Where a rock is subject to wave splash at medium to high tide, *Porolithon onkodes* commonly occurs as a very thin crust.

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3. Heavy wave action localities* on 'weather coasts' facing south-east (figure 128). Here Porolithon onkodes is the dominant organism of the rim and corals are virtually absent under the constant surf. The main debris-cementing organism is Neogoniolithon myriocarpon, together with Porolithon onkodes.

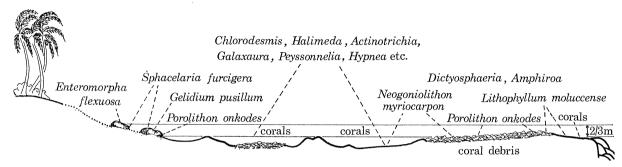


Figure 127. General transect of a reef subject to moderate wave-action (e.g. Mamara on Guadalcanal). Width of reef about 30 m.

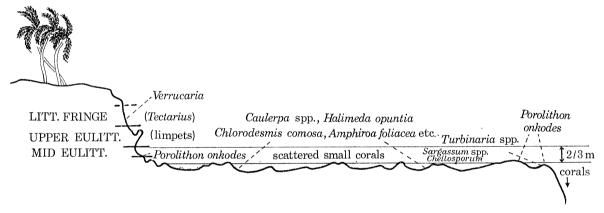


Figure 128. General transect of a 'weather coast' reef subject to strong wave-action (e.g. Sifola on Banika Island in the Russell Islands). Width of reef about 25 m.

While many of the moat-algae of calmer places are present, the usual absence of sand patches prevents the occurrence of stipe-forming species of *Halimeda* and of other species dependent on a sandy bottom. Other rough-water algae become conspicuous, especially near low tide level—e.g. *Chondria armata* (Kuetzing) Okamura, *Martensia flabelliformis* Harvey, *Ectocarpus breviarticulatus* J. Agardh, *Turbinaria* spp., *Sargassum cristaefolium*.

Corals in the moat are usually small and scattered, and largely confined to deeper pools and protected areas.

Rock at the reef rear shows fairly typical zonation, with animals (molluscs, chitons, etc.) much more conspicuous than algae. However, *Gelidium pusillum* (Stackh.) Le Jolis, *Bostrychia tenella* (Vahl) J. Agardh, *Feldmannia indica* (Sonder) Pap. & Chihara and bluegreen algae occur as thin mats or tufts, best developed in shaded areas.

* The term 'exposed' is deliberately avoided since it has been applied to both coasts subject to rough seas and to reefs or organisms exposed to the air during low tide; in the latter case, the zone (and organisms in it) are referred to as 'emergent'.

Detailed zonation studies on Matiu Island

The visit to Matiu Island gave the opportunity for a more detailed study of zonation, based on a 24 h tidal survey. On the outer side the island faces very deep water (Stoddart 1969 b, this Discussion) with a narrow reef and intertidal rock rising steeply, subject to heavy wave surge and shaded in part by overhanging trees. At the western end, the island has a much broader reef, and on the inner side of the island conditions are calm and subject to only slight wave action at low tide. The substratum here is mostly firm mud, gently sloping and usually shaded in the upper intertidal region by overhanging trees. Algae are inconspicuous except under the tree shade; those in the lower eulittoral and sublittoral are small and mostly film-like, covering the mud or dead coral.

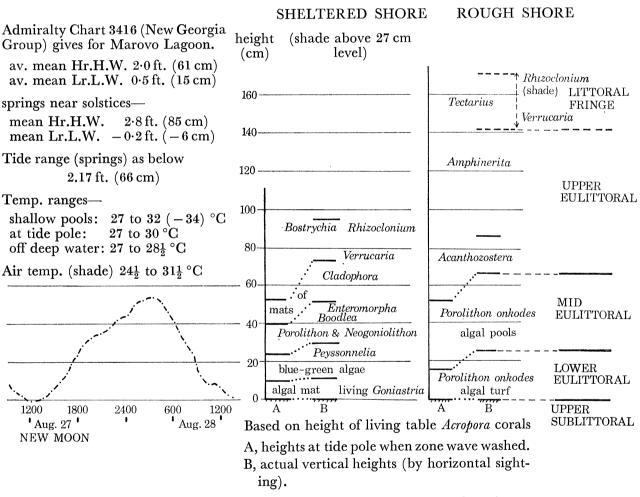


FIGURE 129. Zonation studies on Matiu Island, New Georgia.

Figure 129 gives the basic tidal data, temperatures and zonation related to tidal and wave-wash levels, for areas subject to heavy wave surge, and for calm areas on the sheltered side of Matiu Island. The heights given are based on the level of living table—Acropora corals; this appears to correspond to the low tide level.

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Distinct zonation* occurs on the outer, rougher coast, and the organisms characterizing zones are comparable to zone dominants elsewhere in the world—e.g. the littorinid *Tectarius pagodus* conspicuous in the littoral fringe, the nerite gastropod *Amphinerita polita* in the upper eulittoral above a zone of the chiton *Acanthozostera gemmata* and the crustose *Porolithon onkodes* or mat-like algae in the mid and lower zones of the eulittoral. The upper sublittoral is coral dominated, with *Porolithon* and *Neogoniolithon myriocarpon* as encrusting and cementing organisms.

On the sheltered side of the island the zonation is less well marked, and only the more conspicuous algae are included in the diagram. Mats of Chlorophyta are prominent in the upper zones, and encrusting corallines, *Peyssonnelia* and blue green algae in the lower zones. The *Bostrychia–Rhizoclonium–Verrucaria*† zone is best regarded as the littoral fringe.

Some ecological features and problems

- 1. Zonation of a fairly typical pattern is well marked where intertidal rock or other suitable substrate occurs, as has been found elsewhere in the tropics (Doty 1967; Endean, Kenny & Stephenson 1956; Lawson 1955; Southward 1958, p. 157). This occurs mainly where wave action is moderate to strong, and on calmer coasts the presence of sloping sandy or muddy areas at the rear of reefs, in the mid and upper intertidal regions, prevents conspicuous zonation of organisms.
- 2. The relative importance of corals and coralline algae. Although corals are prominent in most areas of clean water and slight to moderate water movement, crustose coralline algae are dominant under strong surf conditions and important under less rough conditions. This conforms with the pattern of most tropical reefs (Ladd 1961; Marshall 1931; Yonge 1940, p. 374).

In the Solomon Islands, two species of coralline algae are of great importance. *Porolithon onkodes* is the main organism of the reef rim under surf conditions, and also occurs elsewhere as a cementing organism. The most important cementing species, however, is *Neogoniolithon myriocarpon*, both in the moat where it welds coral debris into a solid mass and also near the rim (especially where shaded) where it may form smooth masses several cm across. Both species occur down to a depth of 30 m. Under moderate wave action, *Litho-phyllum moluccense* is conspicuous on the rim, together with corals.

No species of the genus *Lithothamnium* is of any consequence on the reefs studied in the Solomon Islands, and in fact the genus appears to be quite rare. This situation has been found elsewhere (Taylor 1950, p. 124) and it is evident that the rim should not be referred to as the 'lithothamnium rim' as it has usually been named, but the '*Porolithon* rim'.

Other encrusting red algae (not Corallinaceae) are common in the moat and in crevices in the rim, and probably play a small part in holding debris together. The commonest of these belong to the genus *Peyssonnelia*.

- 3. The biology of Porolithon merits investigation in view of its fundamental importance in reef development. While P. onkodes is the most widespread tropical species, and apparently
- * Zonation nomenclature used here is that adopted by Lewis (1961), which is basically similar to that of Womersley & Edmonds (1952).
 - † This black encrusting film is not fully determined, and may in some areas consist of blue-green algae.

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always present on Indian and Pacific Ocean reefs, other species also occur on the rim of atolls. The genus is characterized by horizontally arranged plates of larger cells, which have been called 'heterocysts' in most accounts but more recently have been referred to as 'megacells' (Lee 1967). Another genus (*Neogoniolithon*), usually found in less rough habitats than *Porolithon*, has 'heterocysts' arranged singly or in vertical rows.

These 'heterocysts' are superficially similar in appearance to those of blue-green algae, in that they are larger cells with thicker walls than adjacent cells. Since the heterocyst-forming groups of Cyanophyta are able to fix nitrogen (Stewart 1966, p. 64) it would be of interest to examine *Porolithon* for comparable activity.

4. Dead coral and Lithophyllum on the reef surface. During the visit of the Expedition, dead coral (mainly Acropora) was a feature of many reefs subject to slight to moderate surf (e.g. in Sandfly Passage in the Florida Islands and at Mamara, Kukum and Marau Sound on Guadalcanal). This coral occurred from some 12 to 15 cm above to just below low tide level, in the moat area and near the rim, and was often accompanied by dead Lithophyllum moluccense. Both coral and alga appeared to have been quite recently killed, since there were no signs of breakdown of the colonies nor of growth of other organisms on them.

Death of large areas of coral has been reported previously from many areas, and has usually been ascribed to storm deluges covering the sea with a layer of fresh water (Hedley 1925; Slack-Smith 1959). The effect on reef organisms is particularly damaging if this occurs during low tide. Heavy rainfall over a short period is common in the Solomon Islands and could be a frequent cause of damage when coincident with low tide. Near river mouths the effect may be greater, though reefs here are usually less well developed.

While fresh water may have caused the death of both coral and alga on the Solomon Islands reefs, the height at which they had been growing is both pertinent and not satisfactorily explained. The *Acropora* coral in particular was mostly emergent, by up to 15 cm, at low tides during the time of the Expedition (July to October), and appeared to have grown at a distinctly higher level than existing live coral. Corals can survive only slight emergence, and growth which occurs during seasonal high tides is commonly killed during low tides at other times of the year (Yonge 1940, p. 364).

During winter (the period of the Expedition) the low tide in the Solomon Islands occurs during the day, whereas in summer the low tide is during the night. A similar tidal pattern is reported for the northern Queensland coast (Fairbridge & Teichert 1948, p. 71). Also, the mean sea level in the Solomon Islands is lower in winter than in summer (Stoddart 1969 a; Honiara tide tables). Consequently, reef organisms are subject to greater day-time emergence (probably by 10 to 20 cm) during the winter with greater desiccation or rain influence in this period of the year.

The rate of growth of coralline algae is little known, while that of corals amounts to only a few cm per year and in some cases may be spasmodic (Yonge 1940, pp. 372, 373). From the size of both the dead *Acropora* colonies (to 10 cm high) and the *Lithophyllum moluccense*, it seems unlikely that growth over a single season of high water level and subsequent death was involved, especially as there was no indication that this had occurred more than once.

Emergence of reefs due to very recent earth movements has been recorded (Marshall, Richards & Walkom 1925; Ladd 1961) and might have occurred in the tectonically active

Solomon Islands (Stoddart 1969a). Whether coral death in the Solomon Islands might be the result of such a process is uncertain, but it is apparently unlikely since death of the *Acropora* and *Lithophyllum* was widespread, occurring on different islands, yet did not apply generally to other corals or coralline algae at a lower level on the reefs.

Conclusions

The marine algae of the Solomon Islands will be comparatively well known as a result of this Expedition, and their biogeography and aspects of their ecology will be better understood. However, it must be stressed that tropical marine (plant) biology is, and will be, seriously handicapped until a great deal more taxonomic work is accomplished, especially work at a generic monograph level. Until this is done, little progress in biogeography can be made. Any stimulus that can be given to such studies will be most worthwhile.

We are grateful to the Royal Society of London for the opportunity to take part in the Expedition, to the Expedition leader, Professor E. J. H. Corner, F.R.S., and to members of the Marine Party for stimulating discussions. Professor E. J. Morton identified the zoning animals mentioned in the account. Financial aid was given by the Science and Industry Endowment Fund, C.S.I.R.O., Australia.

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