

Vegetation of the Intertidal Zone of the Lagoon of Aldabra, with Particular Reference to the Photosynthetic Prokaryotic Communities Author(s): M. Potts and B. A. Whitton Source: *Proceedings of the Royal Society of London. Series B, Biological Sciences*, Vol. 208, No. 1170 (Jun. 23, 1980), pp. 13-55 Published by: <u>The Royal Society</u> Stable URL: <u>http://www.jstor.org/stable/35308</u> Accessed: 24/06/2014 15:52

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*The Royal Society* is collaborating with JSTOR to digitize, preserve and extend access to *Proceedings of the Royal Society of London. Series B, Biological Sciences.* 

http://www.jstor.org

# Vegetation of the intertidal zone of the lagoon of Aldabra, with particular reference to the photosynthetic prokaryotic communities

By M. Potts<sup>†</sup> and B. A. Whitton

Department of Botany, University of Durham, South Road, Durham DH1 3LE, U.K.

> (Communicated by G. E. Fogg, F.R.S.-Received 27 March 1979 – Revised 6 November 1979)

> > [Plates 1 and 2]

An account is given of the blue-green algal and some other communities in the intertidal region of the lagoon at Aldabra Atoll. Data are included on environmental parameters and on standing crop as indicated by chlorophyll *a*. A more detailed study on one species, *Scytonema* sp., includes observations on recolonization over a six-month period.

Visually obvious blue-green algal communities cover about 19% of the intertidal region of the lagoon at Aldabra, being second only to mangroves in importance Other taxa are much less abundant: an approximate estimate for eukaryotic algae indicated that their cover is between one and two orders of magnitude less, while that of marine angiosperms and phototrophic bacteria is still less. The two most abundant species of blue-green alga are Scytonema sp. and Microcoleus chthonoplastes, with the former in the upper zone of the littoral and often also the mid zone, and the latter in the mid zone of most parts of the lagoon and almost everywhere in the lower zone. M. chthonoplastes is most conspicuous along the southern shore, west of Bras Anse du Bois, where it forms an irregular, but almost complete cover over extensive areas of white silt, with the community often showing conspicuous laminations. The most obvious competitors to these two species are Rivularia sp. and Schizothrix calcicola, respectively. An extensive cover of well developed stromatolites occurs only in the southwest part of the lagoon, a region relatively well sheltered and with a tendency for waters to become moderately hypersaline.

In addition to epiliths, endolithic blue-green algae provide an almost complete cover on all intertidal rocks, and recolonize a broken rock surface rapidly, both features showing a marked contrast to terrestrial rocks. It is suggested that grazing animals favour the success of endoliths over epiliths and that it is the synergistic combination of endolithic blue-green algae and grazers which is responsible for biological erosion. The endolith *Mastigocoleus testarum* is exceptional among all the lagoon algae in being the only heterocystous species to occur in the lower zone.

† Present address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306, U.S.A. [Correspondence to the second author.]

[ 13 ]

Communities on the open lagoon shore of Île Picard differ in several ways from those elsewhere; *Scytonema* sp. is more closely restricted to the upper zone; the mid zone is dominated by *Hyella balani* endolithic in sand particles; *Chromatium* is sometimes conspicuous. It seems probable that these phenomena are all due to a predominantly horizontal drainage of mangrove forest water displaced at spring tides, through sediments that are much coarser here than elsewhere on the atoll. Away from Île Picard, visually obvious phototrophic bacteria are mostly restricted to mangrove forests, usually at the sides of creeks, though at Cinq Cases they are sometimes abundant in shallow pools.

#### 1. INTRODUCTION

#### (a) Algal studies on Aldabra

It is well known that blue-green algae (cyanobacteria) tend to be especially successful in calcareous environments and at high temperatures. An atoll therefore seems likely to offer many opportunities for these organisms. Observations made during the Phase VI of the Royal Society Expedition to Aldabra showed that they are abundant in both terrestrial and freshwater environments. As a result, it was decided to make a general survey of the blue-green algae over the whole of the atoll, with accounts of floristic composition, micro-environments, vegetation in which they dominate and features of special interest.

The present paper deals with the intertidal region of the lagoon. Observations are included on phototrophic bacteria and the more frequent eukaryotic algae. Studies of pH and Eh of waters and sediments, coloured sand communities and nitrogen fixation have been published elsewhere (Potts & Whitton 1977, 1979a, b) and are mentioned here only briefly.

#### (b) Intertidal blue-green algae in the tropics

Blue-green algae are widespread, and sometimes abundant, in most marine habitats, except the colder parts of the open ocean (Fogg 1973). There are many records of their occurrence in the intertidal zone of temperate regions, both on rocky shores (Ercegović 1932; le Campion-Alsumard 1969; Little 1973) and in salt marshes (Carter 1933*a*, *b*: Chapman 1960; de Jonge 1976). In recent years it has become increasingly evident that intertidal blue-green algae are particularly abundant in the tropics, sometimes covering extensive. areas. Conover (1962), who worked along the Atlantic and Caribbean coasts of North America, reported that, in the tropics and subtropics, the margins of shoal areas of lagoons support very extensive, thick, vigorously growing blue-green algal mat communities. At higher latitudes, only patches and discontinuous mats occur. In the lower latitudes, the type of lagoon where these mats grow freely is protected by barrier islands and bars. A particularly extensive area of laminated mats was described by Kendall & Skipwith (1968) from the protected flats of a highly saline lagoon in Abu Dhabi; these mats run parallel to the coast for 42 km and have an average width of 2 km

and a thickness of some 30 cm. Other recent studies on subtropical and tropical intertidal algal mats include those of Ginsburg *et al.* (1970), van den Hoek *et al.* (1972), Gunatilaka (1975) and a series of papers in a volume on stromatolites (Walter 1976).

# (c) Taxonomy of blue-green algae

There are so many difficulties in naming blue-green algae that it is essential to give some background to the methods used here. The variability of the organisms has led to fundamentally different approaches to their taxonomy (Komárek 1973). The situation is especially difficult with tropical marine forms, since these have been the subject of relatively few descriptive studies by classical taxonomists. Many authors describing marine communities (see, for example, Degener & Degener 1959) have either restricted identification to the generic level or dumped materials under a name based on Drouet's system (Drouet 1963, 1968, 1973). Unfortunately, this system itself has been changed several times and it is difficult to compare data from one period with that of another; further, Stanier *et al.* (1971) have argued convincingly that the system is determinatively worthless.

Another complication has been introduced by a recent proposal (Stanier *et al.* 1978) that the nomenclature of blue-green algae (or rather, Cyanobacteria) should be transferred from the rules of the International Code of Botanical Nomenclature to that of the International Code of Nomenclature of Bacteria. One of the present authors (B.A.W.) joined in this proposal, and so the retention here of classical botanical methods requires justification. Important (although not essential) aspects of the Bacteriological Code are the use of the type strain and isolation of axenic clonal cultures. It is still difficult to bring blue-green algae into axenic culture, and, with present techniques, it would take many years to survey a whole atoll. The classical approach, based on similarity to morphological descriptions in botanical floras and preserved type materials, permits both much more rapid survey and comparison with previous studies. We realize that by adopting this approach we may often be giving names to forms that are genetically close and probably also the same name to forms that are quite different.

### (d) Aldabra

The four islands of the Aldabra group  $(9^{\circ} 24' \text{ S}, 46^{\circ} 20' \text{ E})$  are formed of coral reefs elevated 5–10 m above present sealevel. Much general information on the atoll is given in the volume edited by Westoll & Stoddart (1971). Climatic data from the Royal Society Research Station (Île Picard) for 1967–74 have been summarized by Stoddart & Mole (1977). The atoll lies in an area of the Indian Ocean with a moderate rainfall, the mean annual value at the station being 940.6 mm. It experiences two main climatic seasons, each of approximately six months duration. The rainy season lasts from November or December to April, and the dry season, from approximately May to October or November. The averages of maximum and minimum monthly temperatures do not rise above

 $31.2^{\circ}$  or fall below 22.1°, respectively. The highest temperature recorded is  $36.3^{\circ}$  and the lowest,  $17.5^{\circ}$ .

The lagoon shores are formed either by undercut limestone or by mangrove communities. The vertical amplitude of the notch on cliffs is 2-2.5 m near the entrances to passes, but decreases to 0.5 m (or less) with decreasing tidal range (Stoddart *et al.* 1971). The northern shore is exposed to windwaves developed across the lagoon by the southeast Trades, and consequently its exposure is rather greater than that of the southern shore (Taylor 1971). The highest cliffs are found on the northern perimeter, and many limestone residuals are visible close to the shore. Shores along Grande Terre (figure 1) tend, for the most part, to slope gently towards the lagoon, but undercut cliffs and rocky hummocks are nevertheless common (Macnae 1971).

The lagoon is extremely shallow, averaging about 3 m, and never exceeding 6 m in depth (Farrow 1971b). The mean spring tidal range of 2.74 m is far greater than the normal for truly oceanic atolls (Farrow & Brander 1971; Wiens 1962). The range is, however, markedly reduced in the lagoon, even near the mouths of the four major channels. The amplitude of spring tides may be a mere 1.2 m only 500 m from a channel mouth (Passe Houareau) where the oceanic range is 3.3 m (Farrow & Brander 1971). Lagoon tide curves are markedly asymmetric and extreme low water corresponds with neap tides. At low neap tides a large area becomes dry and the rock base is sometimes exposed. For its greater part, the floor is very flat, with a slightly depressed area in the centre. Away from the passes, lagoon sediments are relatively shallow. Along the protected southern shore the sediments are normally less than 0.3 m thick, and nowhere in the atoll does sediment thickness exceed 1 m (Farrow 1971b). The sediments are extremely shallow when compared with those of other atolls where carbonate sediments are accumulating, such as Bikini and its nearby atolls (Emery et al. 1954) and Tarawa Atoll (Weber & Woodhead 1972). Three types of lagoon platform were recognized on Aldabra by Farrow (1971b): sandflats, carbonate mudflats and mangrove mudflats, all of which can be distinguished by their crustacean burrows.

There are too few studies to indicate to what extent the lagoon has special climatic features. However, according to Farrow (1971*a*), mean temperatures over the lagoon at spring tides may exceed local air shade temperatures by over  $3 \,^{\circ}$ C, and so very high temperatures may occur here in summer (December). There are a wide range of values of both pH and Eh in lagoon water and sediments (Potts & Whitton 1979*a*). The most clearcut trend is for the Eh values of any water body to be lower the further the body is from the influence of oceanic water, with the lowest values of all occurring in sheltered mangrove creeks. White silts usually show higher values than coloured silts; the mean values of Eh are also higher for white than for coloured silts, but the distinction is less clear than for pH, and some Eh values for white silts are very low. Sands are associated with a wide range of values of Eh. At one site studied in detail (Potts & Whitton 1979*b*), the pH and Eh of sand sediments at 1 cm depth was found to vary markedly during

each 14-day tidal cycle. This was associated apparently with the movement through the sand of mangrove water displaced at spring tides.

Mangroves occur almost all round the lagoon, including on much of the shore with cliffs, being absent only from a few rocky stretches (Macnae 1971), yet nowhere on the atoll is there a complete zonation such as is described for other Indian Ocean islands (Macnae 1968). In some deeper parts of the lagoon, especially the sides of the passes, there is a luxuriant algal vegetation (Price 1971). Of the  $100\,\%$  cover in the region near the western channels, the algae make up about  $65\,\%,$ and the angiosperms 35 %, total cover. Where residual undercut islets are present in these channels, there are shaded environments for benthic algae, including Oscillatoria submembranacea. On the southern shores of the lagoon there are wide, partly intertidal flats, which bear only relatively stunted algal growths, with Enteromorpha the most frequent genus. Price suggested that the poor algal growth may perhaps be due to the effects of high insolation at low tides and of unstable substratum, giving very turbid water at flood tide. Taylor (1971) noted a growth of Lyngbya near the base of the undercut of the cliff at (the lagoon coast of) Dune d'Messe, a site that he regarded as being typical of much of the southern shore. Hughes & Gamble (1977) gave records of eukaryotic algal genera from sites round the lagoon not studied by Price. However, many of the sites that they regarded as intertidal would be treated as sublittoral in the present study, and comments on algal mats deal with periphytic flocs rather than with the communities usually treated as mats by phycologists. Braithwaite et al. (1973) and Braithwaite (1975) give an account of fossil stromatolites. The former authors illustrate recent stromatolites in a high intertidal pool at Cinq Cases, while the latter reports recent stromatolites close to low-water mark in tidal channels at the Takamaka Creeks.

The nitrogen-fixing potential of eight different lagoon intertidal communities on Île Picard has been investigated (Potts & Whitton 1977). When the reduction rates are related to chlorophyll *a* contents of the communities, the maximum rates recorded come in the following order (from high to low): *Hyella balani*, *Scytonema* sp., *Hyella balani* – *Schizothrix* sp., *Calothrix crustacea*, *Rivularia* sp., *Microcoleus chthonoplastes*, *Hyella balani* – purple sulphur bacteria (Chromatiaceae), *Pleurocapsa* – *Chroococcus*.

#### 2. Methods

#### (a) Interpretation of zones on the lagoon shore

For descriptive purposes we have adopted the nomenclature of Womersley & Edmonds (1952). This recognizes a supralittoral zone, littoral zone, sublittoral fringe and upper sublittoral zone; the littoral is divided into upper, mid and lower. Schneider (1976) has provided a chart that compares the various schemes in the literature, including that of J. R. Lewis used by Taylor (1971) in his account of zonation at Aldabra. Taylor's study deals mainly with the outside of the atoll. Zonation in the lagoon at Aldabra is very difficult to recognize. Because of the

behaviour of tides along most of the shore, mean low-water neaps occupy a line lower on the shore than that of mean low-water springs, a feature that contrasts with the generalized scheme of Womersley & Edmonds. In practice, the nearly flat bed of parts of the lagoon makes it very difficult to recognize the lower limits of the littoral, large areas being covered by only a few centimetres of water at low tides. We therefore refer simply to the lower limit of the littoral as mean low water. It corresponds approximately to extreme low-water springs and probably lies slightly above mean low-water neaps. (The gap between these two limits probably gets greater the further from the influence of *passes*.)

It often proved almost as difficult to divide the littoral into (sub)zones. As the lagoon is relatively young, conspicuous limestone hummocks and residuals are common; there is thus a complex mosaic of substrata at different heights above low water. Due to the restriction of water flows through *passes*, ponding occurs in some areas, whereas, in others, much of the littoral can remain dry for several days. A transect at  $90^{\circ}$  to the land rim often passes through a wide range of habitats, each with different tidal characteristics. In the present account, horizontal (sub)zones are recognized according to the predominant tidal influence in the particular area. These zones may include residuals that themselves show vertical zonation. For instance, residuals in the lower zone of the littoral may have both mid and upper zones. The upper and sometimes also the mid horizontal zones of the littoral are missing wherever there are undercut cliffs, as occurs along much of the north coast. Recognition of a distinct supralitoral zone was even harder than for the other zones. The term is used for communities that appear intermediate between intertidal and terrestrial ones, and that are probably submerged at the highest tides or are subject to wave action during storms. The top of the vertical notch is not a reliable indicator of the highest tides, because, in some instances, especially on residual islets, a cliff may be submerged completely during high-water springs (Stoddart et al. 1971).

# (b) Surveys and recording of field observations in the lagoon

Observations on the blue-green algae of the atoll have been made during three periods (December 1968 – January 1969 by B.A.W.; November 1972 – June 1973 by B. A. W. (part of the time) and A. Donaldson; and November 1974 – June 1975 by B.A.W. (part of the time) and M.P.). Brief observations on the lagoon were made during the first two visits but detailed ones were made only during the third visit.

Because the lagoon is shallow and tidal events complex, access (by boat) to many parts is possible on only a few days during each lunar cycle, at the time of spring tides. It was essential to collect as many data as possible on one day; as a consequence, in many instances only subjective estimates of percentage cover and relative abundance were made.

The study commenced after prolonged discussion with Seychellois boatmen and brief visits to many different sites. Thirteen locations were then chosen for

# Photosynthetic prokaryotes of Aldabra lagoon

transects across the intertidal (figure 1; table 1). A visually obvious point on the upper part of the shore was used to locate the landward end of the transect. The boat was anchored somewhere in the upper or mid part of the littoral, and the transect studied as the tide fell. Each transect consisted of a strip at 90° from the general line of the land rim and was approximately 10 m wide. In some instances, an exact measurement was made, but usually the width was estimated visually. Sketch maps, photographs, notes and collections were made at intervals, while more detailed records were made for five or more 10 m<sup>2</sup> quadrats along the



FIGURE 1. Aldabra, showing location of transects. Insert shows part of Île Picard. For more detailed map, see Stoddart & Westoll (1979).

transect number	date	lagoon shore	location	grid ref. (at upper end)
1	16.11.74	Île Picard	La Gigi	0610 + 0895
2	18.11.74	Île Picard	La Gigi	0625 + 0907
3	18.11.74	Île Picard	lagoon beach adjacent to Passe Femme	0635 + 0920
4	7.12.74	Île Picard	lagoon beach towards Entre Deux	0650 + 0937
<b>5</b>	12.02.75	Île Malabar	between Île Verte and Perdu Couteau	2705 + 1099
6	10.02.73	Île Malabar	Passe Houareau	3138 + 1187
7	1.03.73	Grande Terre	Cinq Cases	3770 + 0620
8	13.12.74	Grande Terre	Takamaka	3380 + 0673
9	31.01.73	Grande Terre	lagoon landing to Dune Jean-Louis	2623 + 0433
10	29.01.75	Grande Terre	lagoon landing to Dune d'Messe	1858 + 0287
11	13.03.75	Grande Terre	Gros Îlot Cavalier	1120 + 0280
12	27.11.74	Grande Terre	Îles Moustique	9005 + 5250
13	11.12.74	Grande Terre	Petit Cavalier	0810 + 0505

# TABLE 1. DATE AND LOCATION OF TRANSECTS

This content downloaded from 132.248.28.21 on Tue, 24 Jun 2014 15:52:29 PM All use subject to JSTOR Terms and Conditions

transect. These were selected for two different reasons: representatives of large, relatively uniform areas to be crossed by the transect, and visually obvious photosynthetic microbial communities. The data collected for each transect included environmental parameters (see below), subjective estimates of percentage cover of visually obvious photosynthetic communities and 1 cm<sup>2</sup> samples of these communities for studies of specific composition. The 13 transects were all studied during the wet season (table 1); unless stated to the contrary, all environmental data were collected between 10h00 and 16h00; surveys were made during fine weather, with the exception of that of transect 5, which was made after a heavy rain storm.

In addition to these one-day studies, transects on Île Picard were visited at frequent intervals over seven months and many spot visits were made to other parts of the atoll. The distributions of communities in transects 1, 2 and 3 were compared with those of the first surveys, in particular on 4 December 1974, on 8 February 1975, every day from 28 March 1975 to 20 April 1975 (high spring tides, through neaps, springs, neaps and reapproaching springs) and on 28 May 1975. Most regions of the lagoon perimeter were visited at some time. However, neither the lagoon shore of the western end of Île Malabar nor the mangrove forest east of Passe Houareau has been visited by either author. Six-hundredand-four 1 cm<sup>2</sup> samples were collected for detailed microscopic study, of which 177 were taken from transects and the remainder from spot visits. Of the 604, 227 were taken from sediments or limestone surfaces only slightly emergent, while 377 were from cliffs and residuals.

### (c) Environmental parameters

#### (i) Sediments

Samples of the uppermost 2 cm of sediments were collected within each transect from the mid littoral, and also, in a few cases, from other zones (table 2). About ten samples were collected at random and then pooled in a polythene bag open to the air. A subsample sufficient to give approximately 150 g was dried at ambient air temperature. This was passed through a set of four standard sieves to cover the range pore diameters from 2000 to 250  $\mu$ m. The coarser fractions were sieved dry by shaking and agitation, while the finer fractions were washed through with water. The scales and class terms for clastic sediments are those of Wentworth (1922).

#### (ii) Temperature

Most measurements were made with mercury thermometers. For more detailed studies, a copper-constant n thermocouple was used, wired through a 'Galvam' galvanometer: the wire probe had a surface area of only 1 mm<sup>2</sup>; the galvanometer was protected from the sun by a white screen.

#### (iii) Relative humidity

This was measured with the aid of a battery-operated portable psychrometer (Atkins Technical Inc.) with a probe aperture of 1 cm diameter.

# (iv) pH and Eh

Measurements of pH were made of waters and sediments by means of a glass electrode with a 1 M KCl reference electrode. Measurements of Eh (redox potential) were taken with two Pt-Ag/AgCl electrodes with 3 M KCl as a reference. Each of the electrodes was used with a separate, portable meter (Pye Unicam model 293). The precautions taken when measuring both pH and Eh have been discussed in detail by Potts & Whitton (1979*a*).

#### (v) Water chemistry

Provided that the water column was deep enough, samples for analysis were collected at 20 cm depth; if the water was more shallow, the sample was taken half-way between the water surface and the bottom sediment; in a few instances in which only a thin film of water was present, this was removed with a Pasteur pipette. The sample was immediately filtered through a no. 2 Sinta funnel and collected in plastic tubes, which were sealed with wax on return to the research station and stored at -10 °C. After return to the U.K., samples were analysed for Na, K, Mg and Ca, by means of atomic absorption spectrophotometry.

Salinity was measured *in situ* with a portable salinometer (National Institute of Oceanography), and dissolved oxygen with a meter (Lakelands Instrument Co.) and Mackereth electrode; allowance was made for salinity.

# (d) Standing crop

Studies on the standing crop of communities of blue-green algae were carried out at Île Picard near transects 1, 2 and 3. Each community was delimited subjectively and an estimate made of its area. Twenty samples were taken at random (by throwing 10 cm square quadrats), together with four further samples representing apparent maxima. Samples were dried in the shade immediately after collection and stored in polythene bags for return to U.K. for extraction of chlorophyll. Details of storage, extraction of chlorophyll and the reliability of the method are given by Potts & Whitton (1977) and Whitton *et al.* (1979).

#### (e) Taxonomy

The following were especially useful for naming blue-green algae: Bornet & Flahault (1886-88), Geitler (1932), Desikachary (1959), Frémy (1933), le Campion-Alsumard (1969). The choice of names is often rather arbitrary and so forms have sometimes been recorded under taxonomic categories that do not correspond strictly to descriptions in the floras. The conventions used have been developed for a computer recording system (Whitton *et al.* 1978, 1979). These include the

delimitation of some, or all, of the taxonomic categories in certain genera simply on their size ranges. This has been done here for all species of *Aphanocapsa*, *Aphanothece*, *Chroococcus*, *Gloeocapsa*, *Gloeothece*, *Merismopedia* and *Pleurocapsa* and for some species of *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phormidium*, *Scytonema*, *Spirulina* and *Xenococcus*. For *Chroococcus*, the size categories are split further into ones with and without layered sheaths, and, in *Gloeocapsa*, into ones with colourless, yellow/brown or violet sheaths. With the Chroococcales, we have added, for ease of discussion, a classical binomial to each size (and sheath) category, although this conveys no further information about the organism. A specific name has been chosen that corresponds to an original description with a similar, though usually not identical, size range. Where several classical descriptions apply to similar size ranges, the earlier legitimate name has been chosen, even if this refers to a freshwater rather than a marine form (or *vice versa*). These binomials are used in the main text, but the true morphological categories used for coding 'species' are listed together with the binomials in the appendix.

The naming of the three most abundant phototrophic bacteria was based simply on morphological criteria in Bergey's (1974) manual, and therefore remains tentative. The provisional names of the most abundant forms are *Chromatium buderi* Trüper et Jannasch, *Thiocystis violacea* Winogradsky and *Thiospirillum sanguineum* (Ehrenberg) Winogradsky. These are listed only by generic names throughout the rest of the account.

#### 3. Results

#### (a) Sediments

The distribution of sediments from each transect according to size class is summarized in table 2, and a general picture of the main types round the atoll is given in figure 2. The results from each transect may be arranged in order from lowest to highest percentage of sediments in the smallest size class: 2, 3, 1, 6, 7, 5, 12, 13, 4, 8, 11, 10, 9. The first four are from near *passes*; based on their predominant Wentworth size class, they may be termed medium/coarse sands. Among the other transects, pale sediments in general have more material in the smallest size than do brown sediments, but transect 5, with brown sediment, has a similar particle size distribution to transect 12, with pale sediment.

There is considerable range in colour of the surface of the sediments when viewed *en masse*. This results principally from three causes: varying proportions of white carbonate sediment and organic debris from mangrove forest; staining of white sediment as a result of passage of waters from mangrove forest; closely associated microbial communities, especially blue-green algae. In the vicinity of the *passes*, sediments appear overall as very pale yellow. In the area of transect 3, the sands of the upper littoral and supralittoral are white to very pale yellow. Below a beachbar at the level of the sandflat, the sands are darker yellow, probably because mangrove waters drain through the sands here (Potts & Whitton 1979b).

In this area, most of the mid littoral is pale or even dark green due to endolithic blue-green algae in the sediment particles. On moving away from the *passe* (from transect 3 to 4) the sediments change from pale yellow to a much darker colour due to the influence of the mangrove forests of Entre Deux.



FIGURE 2. Types of sediment in areas exposed at extreme low water.

Along much of the north coast, the surface sediments are chocolate brown; in some places, these sediments overlie paler ones. At transect 5, the deep brown sediment overlies dark grey or pale brown sediment. The dark surface materials are apparently derived recently from mangrove forest and are probably subject to frequent resorting at each high tide.

At Cinq Cases (e.g. at transect 7), wide expanses of sediment in the lower and mid littoral are coloured dark brown. On moving from the *Avicennia* parkland into the upper littoral, the sediment changes from brown to grey on the surface and is black below 2 cm depth; the black sediment becomes grey after a short period of exposure to the air. On moving from the supralittoral to the terrestrial, the colour changes again, this time to yellow.

Along most of the south coast, the surface sediments are pale grey or white, although they often appear pale blue when viewed macroscopically, due to the cover of *Microcoleus*. Especially deep, white sediments occur at Bras Anse du Bois (near transect 9). At the large sandflat area between Îles Moustique and Île Esprit, the sand sediment is stabilized by the stratiform stromatolites of *Microcoleus/Schizothrix*, which colour the surface a brilliant orange.

	oucedus		цр	ry mass (% ^	(		tuanimohonn		
transect	in in littoral	> 2000†	2000 - 1000	1000- 500	500-250	< 250	Wentworth (1922) size class	name given visually	colour
Н	mid	12.9	5.12	16.8	38.7	26.5	medium/coarse sand	-	pale yellow
01	mid	5.63	2.91	14.6	64.9	10.9	medium/coarse sand	Manual National Networks	pale yellow
ŝ	mid	0.55	6.46	27.9	51.4	13.7	medium/coarse sand		pale yellow
4	mid	3.40	0.90	2.60	16.1	80.0		fine sand/silt	$\mathbf{brown}$
5	mid	16.3	1.66	2.74	11.2	68.1		silt .	$\mathbf{brown}$
5	lower	6.20	2.40	1.90	15.2	74.3		$\operatorname{silt}$	$\operatorname{brown}$
9	mid	10.8	6.09	12.5	38.3	32.3	medium/coarse sand		pale yellow
7	upper	17.5	6.50	0.90	11.0	55.1		silt	$\mathbf{brown}$
- 2	mid	12.8	4.60	8.20	17.0	57.4		silt	$\operatorname{brown}$
2	lower	16.6	5.30	7.80	14.0	56.3		$\operatorname{silt}$	$\operatorname{brown}$
8	upper	0.67	0.39	0.21	0.74	97.9		silt	white
8	mid	1.94	2.40	0.16	1.20	94.3		silt	white
6	mid	0.42	0.59	1.30	1.33	96.4		silt	white
10	mid	1.22	0.85	1.24	0.69	96.0		silt	white-grey
11	mid	0.67	0.50	0.83	2.60	95.4	Territoria	silt	white-grey
12	mid	6.69	3.48	7.30	13.3	69.2		very fine sand/silt	white-grey
13	mid	1.05	2.06	4.82	14.9	77.2		fine sand/silt	white-
									pale yellow

† Size range/µm.

TABLE 2. FRACTIONATION OF SEDIMENTS FROM LAGOON TRANSECTS

 $\mathbf{24}$ 

# M. Potts and B. A. Whitton

#### (b) Water chemistry

Measurements were taken of salinity and pH, and samples were taken for later analysis of Na, K, Mg and Ca from large pools remaining in the littoral during the surveys of the transects. As only 79 samples were collected, these being insufficient to establish a clear understanding of variation round the lagoon, only a summary of the main observations is given here. (Fuller data are given by Potts (1977).)

(i) The three lowest values for salinity were recorded in transects 5, 6 and 7. For instance, the salinity of pools in the upper and mid littoral of transect 7 was  $21.7 \pm 1.6\%$  (n = 12).

(ii) Salinity values equal to or greater than those of oceanic water were recorded along the south coast. For instance, the salinity of pools in the upper and mid littoral of transect 8 was  $41.4 \pm 6.1\%$  (n = 13).

(iii) The ranges, for all transects, in the mean values of parameters recorded for each transect were: salinity, 21.7-47.3%; pH, 7.1-8.9; [Na], 6936-15770 mg l<sup>-1</sup>; [K], 255-290 mg l<sup>-1</sup>; [Mg], 888-1792 mg l<sup>-1</sup>; [Ca], 292-603 mg l<sup>-1</sup>.

In addition to the studies of the transects, 13 samples were taken from inland tidal pools on Île Picard. Their average composition quite closely resembles that of oceanic water: salinity, 35.6%; [Na],  $10680 \pm 176 \text{ mg } l^{-1}$ ; [K],  $368 \pm 49 \text{ mg } l^{-1}$ ; [Mg],  $1318 \pm 197 \text{ mg } l^{-1}$ ; [Ca],  $423 \pm 60 \text{ mg } l^{-1}$ .

(iv) Although no measurements of sulphide were made, there were sufficiently obvious differences in the  $H_2S$  odour to indicate marked differences in sulphide levels at the surface of the sediments. Even without disturbing the sediments, the odour was strong in several parts of Île Picard; at La Gigi beach this occurred for a few days at spring tides; a similar odour occurred near Entre Deux, although here it was apparently more persistent through the tidal cycle. Elsewhere in the lagoon intertidal, a strong odour was noted only when the sediments were disturbed; this was the situation on parts of the northern shore (e.g. transect 5) and Cinq Cases region. Along the southern shore, disturbed sediments had usually only a slight odour or none at all.

# (c) Flora

A list of blue-green algal species from the lagoon intertidal is given in the appendix, together with brief taxonomic notes. A fuller account of morphology and distribution round the atoll is given by Potts (1977). Details of the most abundant eukaryotic algae are included in the present text.

#### (d) Transects

The results of the transects are summarized in table 3. The repeat visits to transects 1, 2 and 3 showed that the distribution, limits and features of most communities changed very little during the seven months of the survey.

# TABLE 3. SUMMARY OF DATA FOR THE LITTORAL ZONE OF INDIVIDUAL TRANSECTS

(The lists of phototrophic bacteria and algae refer to the dominants of visually recognizable communities, a dominant being regarded as a species forming at least one-third of the biomass of a community. Where two species in the community each constitute at least one-third of the total, these are bracketed together in the list. The digit given for each community represents a

transect	extent to which typical	general features: geomorphology, tide, mangroves	upper	
1	typical of area adjacent to Passe Femme	<pre>mangroves; sandflat (ca. 55 m); no cliff; creek entrance in low zone; sand bar+dunes surround area; tidal lag ca. 30 min</pre>	Scytonema sp. Microcoleus chthonoplastes Calothrix crustacea	4 3
2	typical only of a small area	mangroves; sandflat (ca. 250 m); mangroves + sand dunes surround area forming 'horse- shoe' shape; coral debris on sandflat	Scytonema sp. Calothrix contarenii Pleurocapsa fuliginosa Schizothrix calcicola Calothrix contarenii Entophysalis granulosa Pleurocapsa fuliginosa	4 2 2 2
3	typical of long stretch of lagoon beach	sandflat, long sand bar parallel to coast; tall cliff; coral debris over extensive area; mangroves abundant in lower zone; large residuals in sublittoral	Scytonema sp. Calothrix contarenii *Pleurocapsa fuliginosa *Hormathonema violaceonigrum	3 3 2 2
4	typical of long stretch of lagoon coast towards Entre Deux	sandflat adjacent to wide creek; low cliff with mangroves; exposed limestone and ponding of water; 0.3 m standing water in creek at neaps	$\left.\begin{array}{l} Calothrir\ scopulorum\\ Microcoleus\ chthonoplastes\\ Vaucheria\ sp.\\ Lyngbya\ confervoides\\ Spirulina\ sp.\ >\ 2\ \leqslant\ 4\ \mu m\\ ^*Hyella\ balani\\ ^*Hormathonema\ violaceonigrum\\ ^*Pleurocapsa\ fuliginosa\\ \end{array}\right\}$	3 2 2 2 3 2 2 2
5	typical of long stretch of lagoon coast off Île Malabar	mudflat + mangroves; cliff 2 m above mudflat; numerous residuals close to shore; drifts of sediment in hummocks; residuals offshore; exposed for ca. 2 h at low tide, tidal advance rapid		

subjective estimate of visually obvious cover within a subzone, with the following scale:  $2 > 0.1 \le 1\%$ ;  $3 > 1 \le 10\%$ ; 4 > 10%. Records for the non-photosynthetic *Beggiatoa* are included with those for phototrophic bacteria and algae. \* Community on substrata emergent above usual level, such as on limestone residual or mangroves.)

photosynthetic	bacterial + algal	vegetation
----------------	-------------------	------------

mid		lower	ì	ecological notes
Hyella balani Scytonema sp. pennate diatoms	3 2 2	Microcoleus chthonoplastes Chromatium	2 2	dominant mangroves Rhizophora + Bruguiera; no visually photosynthetic communities on beach bar; H <sub>2</sub> S smell in lower zone; Thalassodendron + Cymodocea meadows in sublittoral; Ocypode burrows in Scytonema zone
Scytonema sp. Hyella balani	3 3	Microcoleus chthonoplastes Chromatium	2 2	dominant mangroves Bruguiera + Avicennia; Scytonema over cemented silt; Thalassodendron + Thalassia in sublittoral; Ocypode burrows in Scytonema zone
Hyella balani Chromatium sp. pennate diatoms Phormidium sp. $> 2 \le 4 \ \mu m$ (Beggiatoa sp.) Monostroma sp.	4 3 2 2 2	Hyella balani pennate diatoms Chromatium Spyridia filamentosa *Mastigocoleus testarum	3 3 3 2	dominant mangroves $Avicennia$ ; $H_2S$ smell over area and pink Chromatium associated with pools; Thalassia + Thalasso- dendron + Halodule in sublittoral
Hyella balani Chromatium *Solentia stratosa	3 3 2	Spirulina labrynthiformis Microcoleus chthonoplastes Lyngbya confervoides (Beggiatoa sp.) Spyridia filamentosa Bostrychia tenella	3 3 2 2 2	dominant mangroves Rhizophora; prominent epiphytic algae on man- grove roots; Ulva sp.+ Graciloria+Halodule+ Syringodium in sublittoral
Vaucheria sp. Scytonema sp. Scytonema sp. Microcoleus chthonoplastes Microcoleus chthonoplastes Lyngbya confervoides Pleurocapsa fuliginosa *Hyella balani *Solentia stratosa *Brachytrichia sp.	4 - 4 3 2 2 2 2 2	Spirulina subsalsa Thiospirillum Microcoleus chthonoplastes pennate diatoms Boodleopsis sp. Bostrychia tenella Rhizoclonium sp. Heterosiphonia sp. *Hyella balani *Solentia stratosa *Phormidium submembranaceus	3 3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	dominant mangroves Bruguiera, Rhizophora; Caulerpa + Halimeda + Cladophora in sublittoral; Uca spp. burrows visible in sediments

transec	extent to which t typical	general features: geomorphology, tide, mangroves	upper	
6	only of an area adjacent to Passe Houreau	flat pavé area, thin sediment cover; sediment mainly in shallow depressions; small cliff in extreme upper supralittoral adjacent to <i>Cocos</i> scrub with <i>Nostoc</i>	Scytonema sp. Lyngbya aestuarii Pleurocapsa fuliginosa Pleurocapsa fuliginosa *Hyella balani Tolypothrix byssoidea	3 2 3 3
7	typical of a wide area	mudflat; Avicennia portland in lower zone; depressions filled with sediment; small cliff; in low zone; long lag in tides; rapid tidal advance ca. $0.3 \text{ m s}^{-1}$	Calothrix scopulorum Microcoleus chthonoplastes Calothrix scopulorum Entophysalis granulosa Dichothrix rupicola Lyngbya majuscula *Entophysalis granulosa *Tolypothrix byssoidea	4 3 3 3 2 2
8	typical of creek areas and entrance in coastline	mudflat; low irregular limestone cliff; hummocks in upper zone; land rim ca. 0.5 m above mudflat; low density mangrove forest; deeper sediments associated with creek	$ \begin{array}{l} Scytonema {\rm sp.} \\ Scytonema {\rm sp.} \\ Chroococccus spelaeus \\ Lyngbya aestuarii \\ Lyngbya confervoides \\ Pleurocapsa {\rm sp.} > 4 \leq 8 \ \mu m \\ ^*Brachytrichia {\rm sp.} \\ ^*Entophysalis granulosa \end{array} $	4 4 3 3 2
9	typical of long stretch of coast	mudflat; medium cliff with hummocks creek lined by mangroves forming a corridor; 3.5 h lag in tides; sediment banks at side of creek; white silt at bottom of creek 50 cm deep	Schizothrix calcicola Lyngbya confervoides Rhizoclonium sp. *Brachytrichia sp. *Pleurocapsa fuliginosa *Hormathonema violaceonigrum	3 3 2 2 2
10	typical of lagoon coast of Grande Terre	mudflat; tall undercut cliff; hummocks close to shore; soluted base of lagoon floor; 2-2.5 h lag in tides; no upper zone		
11	typical of southwest coast of Grande Terre	mudflat; several large residuals close to shore; lagoon floor visible; at low tide 3-4 cm water over much of area; 2 h lag in tides	Scytonema sp. *Pleurocapsa fuliginosa	$2 \\ 2$
12	no comparable area elsewhere in lagoon	mudflat merging into sandflat; mangroves lining 'mini'-lagoon in upper zone; thick forest; lithified gypsum crusts in upper zone; extensive sandflat between Îles Moustique and Île Esprit	Scytonema sp. Entophysalis granulosa Entophysalis granulosa Pleurocapsa fuliginosa Scytonema sp. Microcoleus chthonoplastes	4 3 3 3
13	typical of this stretch of coast	mudflat; tall mangrove forest; sand beach in upper zone; irregular and jagged limestone bottom visible in many places	Scytonema sp. Microcoleus chthonoplastes Lyngbya martensiana	3 2 2

photosynthetic bacterial + algal vegetation

$\sim$	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~			
mid Phormidium sp. > $2 \leq 4 \mu m$	3	lower Schizothrix calcicola	2	ecological notes <i>Rhizophora</i> in thin line at
(Beggiatoa sp.) Scytonema sp.	$\frac{3}{2}$	Lyngbya confervoides Aphanocapsa grevillei	$2 \\ 2$	side of pavé; <i>Thalasso-</i> <i>dendron</i> in sublittoral
Aphanocapsa montana Microcoleus chthonoplastes Scytonema sp. Thiocystis Calothrix pulvinata *Hyella balani	3 2 2 2	Thiocystis (Beggiatoa sp.)	2 2	Avicennia parkland 'unique' at Cinq Cases; Lumnitzera in sublittoral; many Terebralia in lower zone
Rivularia sp. A (Beggiatoa sp.) Microcoleus chthonoplastes Entophysalis granulosa *Hyella balani *Solentia stratosa	$\left. \begin{array}{c} 3 \\ 3 \\ 3 \\ 3 \\ 2 \end{array} \right\}$	Microcoleus chthonoplastes Lyngbya confervoides Microcoleus chthonoplastes Lyngbya pusilla (Beggiatoa sp.) Cladophora sp. *Mastigocoleus testarum	$\left. \begin{array}{c} 3 \\ 3 \\ 3 \\ 2 \\ 2 \end{array} \right.$	dominant mangroves Rhizophora + Avicennia; Cladophora 'balls' in creek; Cymodocea in sublittoral; Terebralia on silt
Schizothrix calcicola Schizothrix arenaria Vaucheria sp. Rhizoclonium sp. *Scytonema sp.	3 3 3	$Microcoleus\ chthonoplastes$	3	many Uca spp.
Rivularia sp. A Scytonema sp. Schizothrix calcicola Microcoleus chthonoplastes *Solentia stratosa *Hyella balani *Placoma vesiculosa *Pleurocapsa sp. > 4 ≤ 8 μm	4 4 3 2 2 2 2 2	Microcoleus chthonoplastes Schizothrix calcicola	3	dominant mangroves Rhizophora + Avicennia; few Terebralia
Microcoleus chthonoplastes Phormidium sp. 'stromatolite' Rivularia sp. A *Solentia stratosa *Phormidium sp. > 4 ≤ 6 µm *Hyella balani *Lyngbya martensiana	3 3 2 2 2 2 2 2	Microcoleus chthonoplastes Lyngbya confervoides	4 2	many dead and fallen mangroves; Avicennia dominant; Phormidium sp. forming purple globular stromatolites
Microcoleos chthonoplastes Schizothrix calcicola Hyella balani	4 2 2	Microcoleus chthonoplastes Schizothrix calcicola	4	dominant mangroves Rhizophora + Bruguiera; Microcoleus chthonoplastes; Schizothrix calcicola community forming orange stratiform stromatolites
Microcoleus chthonoplastes (Beggiatoa sp.) *Hyella balani	${3 \atop {3} \atop {2}}$	Microcoleus chthonoplastes Lyngbya digueti Microcoleus chthonoplastes	} 4 4	dominant mangroves Bruguiera; Terebralia present

#### Changes that are apparently a regular feature of each tidal cycle

(i) During high spring tides, the *Scytonema* community appears as a relatively flat, olive-green mat, remaining damp from one tide through to the next. During long periods without tidal cover, the mat breaks into polygonal crusts.

(ii) Pink growths of phototrophic bacteria are much more obvious when the sand is exposed at springs than at neaps. This is evident both at the sides of creeks and over large areas of beach in transect 3. This phenomenon is described in detail by Potts & Whitton (1979b).

# Changes independent of regular tidal events and probably associated with animal excreta

(iii) Aphanothece microscopica frequently forms yellow-green patches around rat droppings on La Gigi beach and at least occasionally elsewhere.

(iv) A community dominated by *Hydrocoleum* sp. was noted in transect 1 on 28 March 1975. It formed a pale green film over the surface of sand hummocks at the sides of a creek, but disappeared at the end of these spring tides, and was not recorded again. Rat droppings occurred in the vicinity.

# Change for which there is no obvious explanation

(v) There was a slight increase throughout the survey period in the area dominated by *Microcoleus chthonoplastes* at the sides of a creek in the lower littoral.

# (e) Vegetation of the lagoon intertidal

The following generalized description is based on the transects (table 3), including results from  $1 \text{ cm}^2$  samples, and on spot visits. It deals with all photosynthetic organisms except mangroves. Both here and elsewhere in the text (but not in figures 5–14), the lagoon sites on the shore are considered in a clockwise direction, starting with Île Picard. Figure 3 gives an impression of where the most important dominants are especially abundant. Estimates of areas occupied by various taxa are given in §4.

# (i) Sediments and low rock surfaces outside mangrove forest

Upper littoral. The most obvious organism at most sites is Scytonema sp. This forms thick mats on relatively well drained substrata, including mangrove roots, emergent limestone, medium/coarse sand on Île Picard (figure 5, plate 1) and sands and shallow silts elsewhere; it appears to avoid silts, except where these form a layer only a few centimetres deep over limestone. Scytonema often occurs in close association with other species, such as Calothrix spp. and Microcoleus chthonoplastes (table 3).

Visually obvious growths of other organisms are much more restricted. *M. chthonoplastes* is dominant in a few small areas, while *Schizothrix calcicola* is dominant along parts of the south coast. Occasional dominants include *Lyngbya* 

aestuarii, L. confervoides, Calothrix scopulorum and Dichothrix rupicola, although the last is abundant only at Cinq Cases (figure 6, plate 1). Other frequent species are listed in table 4.

Mid littoral. Scytonema sp. is often abundant in this (sub)zone as well, although it is more closely restricted to well drained substrata (figure 12, plate 2). In view of the difficulty of establishing comparable limits at different sites, the lower limit is uncertain. It does, however, seem clear that this alga is more or less restricted to the upper intertidal at the south end of Île Picard (transects 1, 2, 3).

Among other species, there is obvious variation in their relative development in different parts of the lagoon. Hyella balani, endolithic in sand particles, colours part of the beach (figure 9, plate 1) pale green on Île Picard, with the most obvious green layer usually below the superficial sediments; beneath this occurs a pink Chromatium layer. No conspicuous mats or colourations at all were found during a brief visit to Île Polymnie. Vaucheria sp. is abundant along parts of the shore of the north coast and occasional on the southeast coat. The most abundant species along most of the south is *Microcoleus chthonoplastes* (figures 10, plate 1; 11 and 13, plate 2). This forms occasional films on flat sediments near transect 8 and a denser cover near creeks, but further west it sometimes forms an almost complete cover, which breaks up into polygons on drying. Occasionally, mats of M. chthonoplastes include a purple or pink layer of phototrophic bacteria at a depth of about 2-5 mm (e.g., in some areas near Takamaka and Petit Cavalier); sometimes, also, an orange layer lies between the upper green of the *Microcoleus* and the lower pink layer; usually, however, both orange and pink layers are absent. Scytonema sp. is frequent on slightly elevated sediments or limestone surfaces near transect 8, but further west Rivularia sp. A (figure 8, plate 1) becomes of increasing importance in this microhabitat. Large areas of well developed stromatolites (Microcoleus chthonoplastes/Schizothrix calcicola; Phormidium sp.) were found in only two areas of the mid littoral, the sites of the two types being quite near together  $(\S 3f)$ .

Lower littoral. Microcoleus chthonoplastes is the most frequent blue-green algal species almost everywhere, but eukaryotic algae and marine angiosperms may also be frequent towards the bottom of this zone. The distribution of *M. chthonoplastes* is somewhat patchy on the north and east sides of the lagoon. From transect 9 westwards, it is very abundant. Where this alga forms a thick cover on Île Picard (near transect 2) it grows over a conspicuous pink layer of *Chromatium*. Such an obvious pink layer was recorded beneath *Microcoleus* elsewhere only occasionally on the southern shore (see above). Schizothrix calcicola is perhaps more abundant in this zone than in the mid littoral, forming crusts pink in colour due to pigmented sheaths. The laminated stromatolites, between Îles Moustique and Île Esprit being dominated jointly by this species and by *Microcoleus* chthonoplastes, were just as abundant in this zone as in the mid littoral. Brown patches on the sediments due to pennate diatoms are sometimes conspicuous in the lower littoral, especially where a shallow layer of water remains at low tide.

The central 'lagoonal' area of Îles Moustique is covered with a community not found elsewhere on the atoll. The water here is relatively hypersaline and the sediments are exclusively white. Much of the surface is completely flat and is undergoing lithification associated with precipitation of gypsum and aragonite. This crust can, however, be broken easily with a hammer. The surface appears grey or even black due to *Hormathonema violaceo-nigrum*. Pale yellow colonies of *Entophysalis granulosa* frequently emerge several millimetres from the crust, and at a depth of about 3 mm inside the crust is a bright green layer composed principally of *Pleurocapsa fuliginosa*. A continuous layer of white sediment separates



FIGURE 3. Distribution of important dominants in subzones of the littoral around the lagoon (upper subzone is missing in some regions because of the presence of cliffs); d., diatoms; Dx, Dichothrix rupicola; H., Hyella balani; L., Lyngbya confervoides; M., Microcoleus chthonoplastes; M/Sx, Microcoleus/Schizothrix stromatolite; p., phototrophic bacteria; Ph., Phormidium stromatolite; R., Rivularia sp. A; S., Scytonema sp.; Sx, Schizothrix calcicola; V., Vaucheria sp.

This content downloaded from 132.248.28.21 on Tue, 24 Jun 2014 15:52:29 PM All use subject to JSTOR Terms and Conditions the superficial black layer completely from the green layer. Some of the *Pleurocapsa* colonies appear to be undergoing calcification.

#### (ii) Mangrove forest

Records for mangrove forest where transects pass through this community are included in table 3. Blue-green algal growths are sparse on sediments, although there are occasional patches of *Microcoleus chthonoplastes*. Pink colorations

# TABLE 4. DISTRIBUTION OF THE MORE COMMON NON-ENDOLITHIC BLUE-GREEN ALGAE IN SUBZONES OF THE LAGOON LITTORAL

	$\mathbf{upper}$	$\mathbf{mid}$	$\mathbf{lower}$
Aphanocapsa grevillei	+		
Calothrix contarenii	+		
C. crustacea	+		
C. scopulorum	+		
Chroococcus spelaeus	+		
Dichothrix rupicola	+		
Entophysalis granulosa	+		
Lyngbya aestuarii	+	+	
L. confervoides	+	+	+
L. digueti			+
L. majuscula			+
L. martensiana		+	+
L. pusilla		+	+
Microcoleus chthonoplastes	+	+	+
Oscillatoria nigro-viridis		+	+
Placoma vesiculosa	+		
Pleurocapsa fuliginosa	+		
Rivularia sp. A	+	+	
Schizothrix arenaria	+	+1	+
S. calcicola	+	+	+
Scytonema sp.	+	+	
Spirulina subsalsa			+

Species are included for each subzone if their overall abundance is estimated to be three or more on a five-point scale (see text).

frequently occur at the sides of creeks inside or bordering mangrove forest on Île Picard and sometimes elsewhere. At Cinq Cases, phototrophic bacteria in the upper intertidal sometimes colour the water body of small pools pink; this is the only area on the atoll where these bacteria form planktonic 'blooms' rather than remain at the interface between sediments and water.

Algae are much more abundant on surfaces above the level of the sediments. Exposed limestones have apparently a complete cover of blue-green algae, though mostly endoliths and thin films rather than thick mats. There are sometimes also, in the mid and lower zones, obvious growths of eukaryotic algae. Prop roots of *Rhizophora* and *Bruguiera* and pneumatophores of *Avicennia* often have a visually

Vol. 208. B

2

obvious algal cover. Where prop roots reach a level corresponding with the upper zone of the littoral, *Scytonema* sp. often covers the upper part of the root. Near Entre Deux (Île Picard) *Rhizophora* roots near the top of the lower zone show the following zonation, from top to bottom: *Monostroma* sp., *Calothrix scopulorum*, *Spirulina subtilissima*, with *Gracilaria* sp. and *Vaucheria* sp. on the sediment.

## (iii) Cliffs and emergent limestone surfaces

Data from the  $1 \text{ cm}^2$  samples are summarized in table 5, while a profile of one particular cliff is shown in figure 4a. A colour zonation is usually evident on exposed rock surfaces, typically appearing light grey at the bottom, pale to darker yellow-brown in the central area and black on top; these colours are at least partly due to the different dominant endoliths. Endoliths form an almost complete cover in the superficial layer of limestone within the lagoon, which is submerged intermittently and which is free of overlying sediment. Epilithic algae are also frequent, usually consisting, in open situations, of blue-green algae only, but with filamentous red or green algae becoming more frequent in shaded situations or nearer low water. A striking feature of the intertidal rocks is the speed with which a grazed or broken surface becomes recolonized. A surface exposed in the mid littoral usually becomes recolonized to an extent that it is visually indistinguishable from its surroundings within three to four weeks.

Most endolithic growths appear green or blue-green, although the colour is sometimes masked near the surface by yellow-brown or deep violet sheath pigments. Sometimes, cell colour seen with the light microscope does, however, suggest that the species are capable of producing phycoerythrin. *Hyella* may sometimes be grey or violet and *Mastigocoleus testarum* may be pink-grey.

#### (iv) Supralittoral

Species of blue-green algae typical of terrestrial surfaces become more frequent here, especially *Tolypothrix byssoidea*. Other taxa absent or rare in the upper subzone of the littoral but that occur in the supralittoral of some parts of the atoll include angiosperms (especially *Pemphis acidula* and *Lumnitzera racemosa*), the fern *Acrostichum aureum* and lichens. The last were noted at Île Esprit and Bassin Lebine ( $\S3(e)$ , v), two areas where phosphate-rich rocks occur.

# (v) Tidal pools

These are depressions in the terrestrial limestone, often some metres across with a subterranean connection to the sea or to the lagoon or possibly to both. They are especially frequent in the Bassin Cabri area of Île Picard, where a large pool was chosen for more detailed study (see below). The smaller tidal pools are subject to a more marked influence from rainfall and probably also from nutrient run-off from the land than is the main body of the lagoon. Dark brown films occur in the bottom of many of the depressions, typically over the limestone at the side,

CTS (THREE CLIFFS, TWO LARGE RESIDUALS	ON ÎLE PICARD
VERTICAL TRANSE	THE LOWER ZONE
<b>JE SPECIES ON FIVE V</b>	EMERGENT FROM 1
ABLE 5. DISTRIBUTION C	

species Tolypothrix byssoidea Pleurocapsa fuliginosa Entophysalis granulosa #Hormathonema violaceo-nigrum *Brachytrichia sp. *Hyella balami *Solentia stratosa Lyngbya confervoides Oscillatoria nigro-viridis Phormidium Sp. > 4 ≤ 8 µm	$\left(\begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 $	6. + + + + + • • • • • •	1         1				$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	ight/			₽ · · · · · + + + + + +	6	2 2		8 + + . + +	0,	9	[ • · · · · · · · · · · · · · · · · · ·
Lyngoya martensiana L. majuscula Smirulina subsala	•••			 					 + + •	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
operation success *Mastigocoleus testarum Microcoleus chthonoplastes	· · ·			 					 	+ + +	+ + +	+ + +	+ + +	- + +	- + +	- + +	- + +	- + +
				*	$\operatorname{End}$	olith												

Only species recorded with an abundance of two or more on a five-point scale (see §2b) on at least one of the five transects are included, i.e., rare species are excluded.

# Photosynthetic prokaryotes of Aldabra lagoon

35

2-**2** 



FIGURE 4. Vertical zonation on limestone surfaces of Île Picard: (a) cliff of residual islet, La Gigi; (b) cliff of inland tidal depression, Bassin Cabri; (c) residual in Bassin Lebine. Location of species in diagram indicates where they are most abundant; epiliths are shown on the outside of the rock, endoliths on the inside. Scale bars, 1 m; e.h.w.s., extreme high water springs. where there is a small accumulation of sediment. The dominant here is Oscillatoria nigro-viridis. Dark blue-green growths of Lyngbya majuscula are also often conspicuous towards the base of the depressions; unlike Oscillatoria nigro-viridis, this alga forms flocs in the water column when the pools are filled, although the filaments lie over the sediment or limestone when the pools are empty.

Bassin Lebine is the largest tidal inland pool on Île Picard, with a close, but underground, connection with the main body of the lagoon. At low tide the rock base is exposed, except for an area about 12 m in diameter at the western side, where a pool forms adjacent to the connection to the lagoon. The dominant blue-green algal community has no exact parallel elsewhere.

The main floor of the pool, with dimensions of  $30 \text{ m} \times 50 \text{ m}$ , has an extremely smooth surface; there is a slight drop towards the eastern end. The surrounding rocks are heavily eroded and pitted, elevated some 2 m above the base of the pool. Large pinnacles and champignon residuals occur in the centre of the pool.

The bottom of the pool is covered with a thin layer of silt, ranging from 1 to 6 cm in depth. Towards the western side, this is pale yellow, with numerous *Cardisoma* burrows. The rest of the silt is green, with a slightly gelatinous texture, and is often aggregated into small crumbs. Some areas of the green silt dry to form polygons, but most remain as a loose, crumbly structure. Much of the silt consists either of live unicellular blue-green algae or sheaths and other dead remains of former cells. The dominant forms are *Pleurocapsa* and *Chroococcus*. The bacterium *Achromatium* is also frequent. This community is heavily grazed by cerethids and small species of *Littorina*, and the component of the silt that obviously consists of former blue-green algae is apparently material that has passed one or more times through their digestive systems. Under the silt, endolithic *Hyella balani* is abundant. However, some areas are deep pink when viewed from above; microscopy showed that a small unicell dominates here (§3(g), iii).

Changes in pH and Eh in the *Pleurocapsa-Chroococcus* silt were followed from 08h45 to 14h00 on a moderately sunny day (8 March 1975). This included a period of standing water, followed by exposure and then rewetting by the incoming tide. The pH showed little variation; apart from a drop to pH 7.5 for a short period, it remained in the range 7.8-8.1. Values of Eh showed greater changes, but were always comparatively high, mostly in the range  $Eh_7 = +200$  to +300 mV; the lowest values were associated with the incoming tidal waters.

Scytonema sp. forms mats along the perimeter of the depression on horizontal or gently sloping surfaces. Rivularia sp. also occurs on rocks and light-coloured mud, but is largely restricted to two small areas. Lyngbya majuscula, L. confervoides, Microcoleus chthonoplastes, Spirulina and various eukaryotic algae (Bostrychia, Valonia, Vaucheria, Ulva) are present along the base of the undercut for most of the perimeter and also of the residuals in the centre of the pool (figure 4c).

#### (f) Mats, crusts and stromatolites

As will be evident from  $\S3(e)$ , i, there exists a range of mat and crust communities. Most of those species listed in table 6 bind sediments, and, in at least some instances trap sediments suspended in the water. However, large areas of well developed laminated structures, with obvious potential for preservation, were found in only two areas. *Phormidium* sp., forming purple globular stromatolites up to 3 cm in diameter, is abundant at Gros Îlot Cavalier; it is closely associated with the surrounding crust of *Microcoleus chthonoplastes*. Slightly to the west, between Îles Moustique and Île Esprit, *M. chthonoplastes* and *Schizothrix calicola* together form laminated stromatolites emergent some 10 cm above the general level of the surrounding substratum. Some of these occur in an area where the sediments show ripple marks indicative of moderate tidal scour.

A photograph of recent stromatolites (Braithwaite et al. 1973, figure 39) at Cinq Cases was mentioned in  $\S1$ . Other observations made by these authors are included here as they concern important structures missed in our study. J. D. Taylor (personal communication) reports that recent stromatolites are occasional in parts of the supralittoral at Cinq Cases (above the mangrove forest); they are either hemispherical structures up to about 2 cm in diameter or more extensive crusts. Laminated oncolites reaching about 6 cm in diameter also occur here. Quite different stromatolites were noted in one small area at Takamaka in the upper zone. From Taylor's description it seems likely that these include Microcoleus. C. J. R. Braithwaite (personal communication) gives further information about the stromatolites close to low-water mark at Takamaka Creeks mentioned in his 1975 paper. 'These occur on shores of creeks northwest of Cinq Cases camp. They lie within channels and are most common in areas of good circulation, particularly in channel constrictions. Their upward growth is limited by low water mark. Laminated coatings occur on pebbles, *Terebralia* shells and exposed rock surfaces, the latter with a distinctive ridge and runnel microtopography. They apparently consist of layers of filamentous algae binding sandy sediment. The surfaces are sometimes smooth, sometimes papillose. Some crusts are up to 2 cm thick and appear to be forming at present.' From sections loaned by Braithwaite, it seems almost certain that *Microcoleus* is a key organism in the formation of these structures.

#### (g) Biology of selected taxa

## (i) Scytonema sp.

This is abundant in sheltered, well drained areas of the upper and parts of the mid littoral zones (§3(e), i). It is occasionally also present on surfaces emergent in the lower zone; it then occurs only on the uppermost part of such surfaces. Features of the mats growing by transects 1 and 2 are summarized in table 7; estimates of standing crop (chlorophyll a) are included in table 8. Data on standing crop in table 8 refer to small areas with complete cover; data in table 9 refer to



- FIGURE 5. Transect 1: upper zone free of photosynthetic organisms and mid zone with mats of *Scytonema*.
- FIGURE 6. Transect 7: upper zone at limit of Avicennia parkland; marine photosynthetic microbial communities here dominated by Calothrix scopulorum and Dichothrix rupicola.
- FIGURE 7. Oncolite of Scytonema from mid zone, mangrove forest, Île Picard.
- FIGURE 8. Transect 10, mid zone: hemispherical colonies of *Rivularia* sp. A and mixed community of *Rivularia* and *Scytonema*.
- FIGURE 9. Near transect 3, mid zone: crab burrow and faeces in area of sand green with Hyella balani.
- FIGURE 10. Transect 10, mid to low zones: carbonate silt with crust of *Microcoleus chthonoplastes*, pale blue when viewed macroscopically.

(Facing p. 38)



- FIGURE 11. Transect 13, mid zone, with upper zone in background: knee roots of Bruguiera capped by Scytonema; Microcoleus chthonoplastes abundant on sediments here.
- FIGURE 12. Transect 8, mid zone: Scytonema abundant on exposed rock, absent from all but the shallowest silts.
- FIGURE 13. Transect 13, mid zone: Microcoleus chthonoplastes and Beggiatoa abundant on sediments here.
- FIGURE 14. Transect 7, mid zone: Avicennia parkland; Microcoleus chthonoplastes, Thiocystis and Beggiatoa abundant here.

TABLE 6. MATS, CRUSTS AND STROMATOLITES: SUMMARY OF THE MORE IMPORTANT COMMUNITIES IN THE LAGOON LITTORAL, ARRANGED IN APPROXIMATE ORDER OF EXTENT OF COVER

species	$\mathbf{morphology}$	area	comments
Microcoleus chthonoplastes	(i) thick crusts, pale blue when viewed macro- scopically, binding white silts	mid and lower zones of much of south shore	—
	<ul><li>(ii) bright green polygons up to 20 cm diameter, laminated, 2–3 cm thick</li></ul>	mid zone, near Takamaka	adjacent to creeks with <i>Cladophora</i> balls; <i>Cerithium</i> spp., <i>Uca</i> spp.
<i>Scytonema</i> sp.	(i) mats and crusts, former sometimes laminated, binding sands and both carbonate and mangrove silts	upper zone of most of lagoon shore	often with Micro- coleus chthonoplastes; disturbed by burrows of Ocypode
	<ul> <li>(ii) scoured crust, up to</li> <li>10 cm in relief, over</li> <li>substratum of</li> <li>comented sand</li> </ul>	one sandflat area in upper zone, Île Picard	disturbed by Ocypode, Birgus latro and Cerithium
	<ul> <li>(iii) oncolites usually reaching 5 cm diameter, but sometimes 10–15 cm;</li> <li>binding mangrove silts,</li> <li>laminations sometimes obvious</li> </ul>	depressions in lime- stone in one area of upper zone, Île Picard	
Schizothrix calcicola	deep pink crusts over exposed limestone and white silt	all zones mainly on south shore	in upper zone, often with Lyngbya confervoides; Cerithium, Uca spp.
<i>Rivularia</i> sp. A	hemispherical colonies reaching 15 mm diameter, not calcified, binding carbonate silts	west end of south shore, especially in mid zone	disturbed by Uca spp.
Microcoleus chthonoplastes + Schizothrix calcicola	stratiform stromatolites, pink–orange when viewed macroscopically, with fine sand abundant in sediment	large sandflat near Île Moustique	polychaetes
Phormidium sp.	hemispherical or subglobose stromatolites, purple when viewed macroscopically, 2–3 cm diameter, laminated, with white silt sediment	mid intertidal at Gros Îlot Cavalier	
Dichothrix rupicola	'blistered' mats over dark anaerobic sediments	upper zone at Cinq cases, in depressions	giant tortoise disturbs silts here
Calothrix crustacea	black, smooth crusts, laminated, binding medium/coarse sand	upper zone, Île Picard	Ocypode burrows

(Details of other stromatolites noted only by Braithwaite (1975) not included here; see \$3f).

# TABLE 7. SUMMARY OF FEATURES OF MATS NEAR TRANSECTS 1 AND 2(ÎLE PICARD, LA GIGI BEACH)

(Data for (3) taken from Potts & Whitton (1977); data for (10) based on one day (29 March 1975, high springs); data for (12) based on one day study (12 May 1975, sunny, three days after rain).)

	feature	n	data
(1)	chl. $a/(\mu g \text{ cm}^{-2})$ (small areas with 100 % cover)	69	25.6–338, $\bar{x} = 236$ , s.d. = $\pm 98.6$
(2)	phaeophytin $a$ as percentage of (phaeophytin $a + \text{chl. } a$ )	48	$2.4{-}57\%,ar{x}=28.9\%$
(3)	C,H, reduction assay for	8	light: $0.0015-0.0074 \text{ nm C}_{2}H_{4} (\mu \text{g chl. } a)^{-1} \text{min}^{-1}$
. ,	nitrogen fixation at 10h00-11h00	(separate experiments)	dark: 0.00076–0.0020 nm $\tilde{C}_2 H_4 (\mu g \text{ chl. } a)^{-1} \min^{-1}$
(4)	polyphosphate granules (shown by $(NH_4)_2S + Pb$ staining)		never observed
(5)	wetting by lagoon or rain water		site on figure 5: lagoon water about $10-13\%$ year, rain water $3-5\%$ year
(6)	Eh, sediments under mats	200	$-66 \text{ to } +275 \text{ mV}, \ \bar{x} = +130 \text{ mV}$
(7)	pH, sediments under mats	200	7.1–9.3, $\bar{x} = 8.4$
(8)	Eh, surrounding water	100	$+120 \text{ to } +278 \text{ mV}, \ \bar{x} = +187 \text{ mV}$
(9)	pH, surrounding water	100	7.8–9.3, $\bar{x} = 8.6$
(10)	$O_2$ , surrounding water	21	3.9–5.6 mg l <sup>-1</sup> ; minimum recorded (= $52.5 \%$ , 28.1 °C)
(11)	temperature of mat surface over 24 h, 18.03.75	47	24.5–42.2 °C, $\bar{x} = 29.8$ °C
(12)	r.h. immediately above mat	42	minimum of $64\%$ at $33.3$ °C (3 h after exposure; r.h. above mat is then $14\%$ less than at high tide); 1 m above mat; in contrast r.h. immediately above moist mats may be greater than at 1 m

Abbreviations: chl., chlorophyll; s.d., standard deviation; r.h., relative humidity.

# TABLE 8. STANDING CROP OF SEVEN COMMUNITIES ON ÎLE PICARD

(Data obtained by throwing  $100 \text{ cm}^2$  quadrats within areas  $(10-100 \text{ m}^2)$  delimited subjectively. (Breaks in the surface may be included, so the maximum standing crop within small areas may be considerably higher.))

	ופוופון		$\frac{\text{standing crop}}{(\mu \text{g chl. } a) \text{ cm}^{-2}}$		
species	appearance	location	'n	$ar{x}$	s.d.
Scytonema sp.	thick mat	tidal pool	<b>24</b>	159	74.4
Scytonema sp.	thick mat	transect 2	<b>24</b>	73.8	44.5
Calothrix crustacea, Microcoleus	thin crust	tränsect 1; creek	24	37.2	26.1
Hyella balani	endolithic in sand	transect 3	24	27.6	8.0
Hyella balani	endolithic in sand	transect 5	5	25.9	3.8
Phormidium molle	thick crust	transect 3	•	25.9	6.4
Hyella balani, Scytonema sp.	$ ext{thin crust}$	transect $3$		7.6	6.8

n, Number of samples;  $\bar{x}$ , mean; s.d., standard deviation.

larger areas of mature mat, which include crab burrows and other gaps. This species is widespread on the outside of the atoll, but is restricted to short tufts associated with pockets of sediment in rock depressions.

The lower parts of mats consist of sheaths of dead filaments. The mats bind sediments. In parts of the mat shown in figure 5, there is a zoned arrangement of particles with and without old sheath material.



FIGURE 15. General views of some of the dominant blue-green algae on sediments (a-c) and diagrams of widespread forms on cliffs and residuals (d-g): (a) Scytonema sp. from transect 1, showing alternation of layer of old sheaths with sand; (b) Schizothrix gracilis from Gros Îlot Cavalier, section through dry globular stromatolite; (c) Microcoleus chthonoplastes - Schizothrix calcicola from Îles Moustique, section of stratiform stromatolite; (d) Entophysalis granulosa; (e) Solentia stratosa; (f) Hyella balani; (g) Mastigo-coleus testarum.

In an area of Île Picard sheltered but only partly shaded by mangrove forest, the alga grows as free 'pebbles'; in at least some instances they show obvious laminations; so they may be regarded as oncolites (figure 7, plate 1). The oncolites are derived from pieces of mat, usually overlying rock, that become detached and are eventually deposited in particular areas by tidal action. Initially, these oncolites move around with each tide and are sometimes turned over, such that algal mat develops on all surfaces. Larger oncolites (table 6) are probably moved very little.

The appearance of the *Scytonema* sp. community on Île Picard differs yet again over a wide area of sandflat crossed by transect 2. It grows as a turf or individual tufts of filaments over the surface of hummocks and domes reaching 10 cm height. The hummocks themselves are made up of cemented sand and can be broken easily. This area contains many small fragments of coral debris. In

contrast to other parts of La Gigi beach, much of the sediment between the hummocks is free of *Scytonema*. When viewed from a distance, the whole area suggests one that has been both scoured and subject to deposition of storm debris. Nevertheless, the general appearance was similar in 1968 and 1975.

# TABLE 9. REGENERATION OVER 25 WEEKS OF SCYTONEMA SP.AT TRANSECT 2, ÎLE PICARD

(Relative abundance of species in five  $1 \text{ cm}^2$  samples taken at random on each occasion; a five-point abundance scale was used.)

	weeks						
	before						
species	experimen	nt 1	2	4	10	22	25
Aphanocapsa grevillei	1		1		3	3	<b>2</b>
Aphanothece microscopica					4	2	1
Calothrix scopulorum	3		1	-		4	3
Chroococcus turicensis	1				1	<b>2</b>	2
Dermocarpa olivacea		4	—	2		3	2
Entophysalis granulosa	1		4			<b>2</b>	$^{2}$
Gloeothece palea					<b>5</b>	1	
Hormathonema violaceo-nigrum	4		<b>5</b>			4	$^{2}$
Hyella balani			<b>2</b>			3	3
Lyngbya aestuarii	-			1		3	1
L. digueti			1			<b>2</b>	3
L. martensiana				<b>5</b>	<b>2</b>	<b>2</b>	3
L. pusilla			1			-	1
Microcoleus chthonoplastes	1		—		<b>2</b>	3	4
pennate diatoms			1	<b>2</b>		<b>2</b>	<b>2</b>
Pleurocapsa crepidinum	2	3	1	-		3	3
P. fuliginosa	_	<b>5</b>	—	—	3	3	3
Radaisia epiphytica		<b>2</b>	1	—		1	1
Schizothrix calcicola	2		_	3		<b>2</b>	<b>2</b>
Scytonema sp.	5		1	<b>2</b>	1	4	<b>5</b>

There is no indication that *Scytonema* sp. shows any seasonal or other periodic change other than that associated with the tidal cycle  $(\S 3d)$ . Its behaviour at the site shown in figure 5 has been studied in some detail. Its distribution was very similar during each of the three different periods when the atoll was studied. The upper limit of the community here is sharp; the zone on the shore above is virtually free of photosynthetic organisms. Development of the mature community is slow. Breaks in the mat formed by ghost crabs (Ocypode) show no rapid recolonization. At the beginning of the wet season, 1 m<sup>2</sup> areas here and in an opening in the mangrove forest by transect 2 were cleared of alga. It took six months for Scytonema sp. to become the dominant alga, and, even then, the growths were much less than those in a mature mat (table 9). All the other species found in the community, six months old, listed in table 7 may at times be found in fully mature mats, but only Microcoleus chthonoplastes and to a lesser extent Calothrix scopulorum and Hormathonema violaceo-nigrum are abundant in such mats. Epiphytes (Xenococcus, Dermocarpa) are sometimes frequent, though this is more marked on filaments growing on the oceanic shore.

#### (ii) Chromatiaceae

Pink colourations at the surface of sediments, due to phototrophic bacteria, are quite frequent in some areas of mangrove forest. They are usually most obvious at the sides of creeks, but, at Cinq Cases, they sometimes colour the whole water body of small shallow pools ( $\S3(e)$ , i). Crimson films over the surface of mangrove mud in mid and lower littoral *Avicennia* 'parkland' at Cinq Cases are dominated by *Thiocystis* (figure 14); all other phototrophic bacterial populations (with the possible exception of cells discussed in  $\S3(g)$ , iii, were dominated by *Chromatium*, with cells identified as *Thiospirillum* sometimes being frequent.

The greater surface cover of phototrophic bacteria on Île Picard at spring tides than at neaps has already been mentioned (§3*d*). As most sites away from Île Picard were visited at spring tides, it is possible that these bacteria may also be less conspicuous elsewhere at other times in the tidal cycle. The conspicuous development of pink colourations due to *Chromatium* occurs also on the sandy shore at the oceanic side of Île Picard (just north of the research station). The *Chromatium* cover here occurs at spring tides and is associated with a strong odour of H<sub>2</sub>S; the extent of its development, however, appears to vary more from one period of spring tides to another here than in the lagoon.

A distinct pink layer of phototrophic bacteria beneath a layer of blue-green algae is found only occasionally. In the lagoon, the overlying dominant is apparently always *Microcoleus chthonoplastes*. Phototrophic bacteria are also evident at several inland, non-tidal, brackish pools, associated with other species of Oscillatoriaceae.

## (iii) Pink unicells

Pink colourations inside rocks were found at three sites, one inside the lagoon, one in the supralittoral on the outside of the atoll, and one near a freshwater pool (W2: see Donaldson & Whitton 1977*a*, *b*). As mentioned in §3(*e*), iii, part of the rock floor of Bassin Lebine appears pink when the superficial green silt is removed, and this pink is almost certainly due to groups of small cells about 1.8  $\mu$ m in diameter. The pink colorations at the other two sites were visible only on breaking open the rock; so it is possible that similar colorations are widespread elsewhere. They are, however, certainly absent from most rocks. Although the supralittoral material is not from the lagoon, it was studied in most detail and will be described here.

The pink colonies are spherical, reaching about 0.5 mm in diameter, and are frequent at a depth of about 2 mm in the upper part of the limestone overhang by the research station. The colonies are gelatinous *in situ*, though they eventually become leathery when broken rocks are left to dry. The cells are spherical, are typically  $1.7-2.0 \ \mu$ m in diameter and appear pale green to colourless at high magnification; they lack sulphur granules; the cells have a thin colourless sheath; they are embedded in communal mucilage. The taxonomic status of this organism

is not clear. Electron micrographs show an ultrastructure similar to that of coccoid blue-green algae such as *Aphanocapsa*. Attempts to make the cells fluoresce failed, although cells of four blue-green algal species (*Aphanocapsa concharum*, *A. montana*, *Entophysalis granulosa*, *Pleurocapsa fuliginosa*) taken from the adjacent rock surface and stored for the same period (18 months) all showed strong red light fluorescence when exposed to a blue light source at 490 nm. Similar results were obtained after the rock had been incubated in sea water for three days at  $32^{\circ}$  (and 3000 lx).

#### (iv) Beggiatoa

Occasional Beggiatoa filaments were noted in many mixed communities of blue-green algae overlying sediments, especially those with Microcoleus, Schizothrix and Spirulina. Sometimes Beggiatoa formed a visually conspicuous cover. It was noted in several places at La Gigi beach to form a thin white film overlying a Spirulina film. At Cinq Cases, it occurred in similar areas to those with a Thiocystis cover, forming thin white films over the surface of the brown mud, usually in some standing water.

# (v) Cladophora

Besides the more typical forms, this occurs as distinctive balls 3-5 cm in diameter on the bed of the creek at Takamaka; in general appearance they resemble less tightly packed versions of the freshwater balls formed by *C. aegagropila* known from temperate regions. Each ball is associated with one empty cerethid gasteropod shell.

#### 4. Discussion

In the lagoon intertidal, two groups of photosynthetic organisms are far more successful than any others: mangroves and blue-green algae. Price's (1971) comment about poor algal growths along the southern shore applies only to the sublittoral fringe. It may be helpful to give rough estimates of the relative cover of the various groups. The areas of different parts of the atoll are listed in table 10. Perhaps 30 % (or 9.6 km<sup>2</sup>) of the lagoon intertidal outside the mangrove forest has a visually obvious cover of blue-green algae; this is 40% of the area covered by mangrove forest. As the blue-green algal cover within denser parts of mangrove forest is restricted largely to roots and exposed limestone surfaces, its total contribution in all mangrove forests is probably less than 1 km<sup>2</sup>; this gives an estimate for the total blue-green algal cover within the lagoon intertidal of about 19%. The areas covered by other groups are much less. Within mangrove forest, the cover of eukaryotic algae is probably of a similar order to that of blue-green algae, but, in the intertidal outside the forest, their cover is between one and two orders of magnitude less. Outside the forest eukaryotic algae are least frequent in the upper littoral and become increasingly frequent towards the bottom of the

# Photosynthetic prokaryotes of Aldabra lagoon

lower littoral. The cover of marine angiosperms is probably still less. Although they form extensive beds in the sublittoral near the *passes*, in the intertidal, they are restricted to the bottom of the lower littoral and to more or less permanent pools higher up the shore. Other photosynthetic groups give still less cover. Estimates for the Chromatiaceae are particularly difficult. The pink colourations catch the eye easily, but the boundaries of the communities tend to be ill-defined and, at least on Île Picard, vary with the tidal cycle. Their cover at the surface is perhaps three orders of magnitude less than that of the blue–green algae.

# TABLE 10. AREAS OF DIFFERENT REGIONS OF THE ATOLL

(Aerial photographs used in estimates are the 1:25000 Ordnance Survey (P.M. SEY) published in 1969.)

	$area/km^2$	source of data
atoll, including reef ridge	365	Stoddart et al (1971)
outer intertidal	31	our interpretation of width of intertidal (365 m), given by Stoddart <i>et al.</i> (1971), and total land rim (93 km), by Taylor & Way (1976)
land, including mangrove limits indicated by Stoddart (1971)	155	Stoddart et al. (1971)
mangroves; includes areas with only partial cover, but excludes freshwater	23	our estimate, based on Stoddart (1971) map and aerial photos
land above high water (i.e., excluding mangroves)	132	calculated from above
lagoon, including mangroves	203	calculated from above
lagoon, excluding mangroves	180	calculated from above; Farrow (1971b) gives a slightly different value (184 km²)
lagoon surface outside mangroves, exposed at extreme low water neaps (very approximate)	32	our estimate, based on aerial photos and field observation
blue–green algal cover on lagoon sediments outside mangroves (very <b>approximate)</b>	9.6	our estimate, based on field observation

The contrast between the rarity of well developed blue-green algal mats on sediments inside dense mangrove forest and their abundance outside is striking. It seems unlikely that the difference in light regime is the most important factor. Areas of relatively well illuminated sediment inside forest usually lack obvious blue-green algal cover. Nevertheless, in much more shaded parts of the forest, there are almost always blue-green algal growths on limestone surfaces and often also on prop roots. The high levels of organic matter in the sediments may perhaps favour heavy grazing by molluscs and direct competition from heterotrophic microorganisms.

For some of the more abundant algal species and communities, it is possible to generalize about the factors favouring their development. With the exception of the endolith Mastigocoleus testarum, heterocystous species are restricted to upper and mid zones. Scytonema sp. is by far the most abundant. Its substratum is usually relatively well drained ( $\S3(g)$ , i) and the Eh of any associated sediments is relatively high (mostly > 0 mV and often > +100 mV (Potts & Whitton 1979*a*). At the top of its vertical range, wetting by rain water becomes of quantitative importance as compared with submergence by the tide (table 8), and nitrogen relatively high (mostly > 0 mV and often > +100 mV (Potts & Whitton 1979*a*)). Rates of nitrogen fixation for mature mats are low in comparison with those for some other blue-green algae on lagoon sediments when expressed per unit of chlorophyll, although not so per unit area (Potts & Whitton 1977). The alga in the mature mat has a relatively high proportion of phaeophytin a (table 7) as compared with other lagoon blue-green algae (unpublished data). At the sites on Ile Picard studied in most detail ( $\S3(q)$ , i), it appears to form a climax community, which takes many months to redevelop if removed (table 9).

The community the physical environment of which most closely resembles that dominated by *Scytonema* sp. (figure 12) is that dominated by *Rivularia* sp. A (figure 8). It did not prove possible to differentiate between their environments on criteria of length of exposure, type of substratum or drainage. *Rivularia* is most abundant along the western parts of the main south coast and in Bassin Lebine on Île Picard; it is absent near any of the *passes*. A possible explanation is that lagoon water chemistry may influence competitive success. In the only atoll lagoon of which the water chemistry has been studied in detail, that of Canton Island, the levels of phosphate steadily decreased with distance away from the single *passe* bringing in oceanic water (Smith & Jokiel 1978).

The *Microcoleus chthonoplastes* community is frequent over fine sediments in the mid and lower littoral, but no obvious factor can be suggested that might explain its much greater abundance on the western end of the southern shore. Similarly, there is no obvious hypothesis that might explain why *Schizothrix calcicola*, rather than *Microcoleus chthonoplastes*, sometimes forms the surface crust. The environment in the 'lagoonal' area at Île Moustique, where the *Entophysalis granulosa – Pleurocapsa fuliginosa* community occurs, appears to be very similar to that of the *Entophysalis* community described from Baja California by Horodyski & Vonder Haar (1975). At both sites, precipitation of gypsum and aragonite leads to the formation of a smooth crust. Although Horodyski & Vonder Haar do not mention *Pleurocapsa*, several of their photographs suggest that this alga also forms part of the community in Baja California. A hypothesis that may explain the localized abundance of *Vaucheria* sp. is that it occurs where sediments are influenced by freshwater draining off terrestrial limestones after heavy rain.

It is not clear what are the factors favouring the development of the *Pleurocapsa* – *Aphanocapsa* community at Bassin Lebine. To judge from the conspicuous animal activity, algal growth rates must be high to compensate for grazing. No evidence

for nitrogen-fixing activity was found (Potts & Whitton 1977). The relatively constant pH on a sunny day suggests that respiratory release of  $CO_2$  compensates for much of the  $CO_2$  taken up in photosynthesis. In view of the loose structure of the silt and the high values of Eh indicated by an electrode, the source of  $H_2S$  for *Achromatium* is obscure. Perhaps  $H_2S$ -rich water or cells are transported from the main lagoon or a side-arm of the pool overlying dark anaerobic mud, or anaerobic micelles develop inside the crumbs of silt. Such microniches favouring sulphate reduction alongside others favouring sulphide oxidation are known from Denmark (Jørgensen 1977).

A variety of different laminated structures resulting from blue-green algal activities is found within the lagoon (table 6). The laminations in the communities along the south coast are apparently associated with a daily (or possibly tidal) cycle of changes. However, the conspicuous lamination in some communities dominated by *Scytonema* sp. and by *Calothrix crustacea* on Île Picard sands perhaps results from the deposition of particles during the occasional storm. There appear to be no previous records of the hemispherical to near globular purple stromatolites of *Phormidium* sp., nor of large *Scytonema* oncolites.

The growing stromatolites provide records from further away from a large land body than any previous ones (see Awramik *et al.* 1978) and are the first for an atoll. When compared with stromatolites from other intertidal localities such as Shark Bay (Playford & Cockbain 1976), however, those on Aldabra are local and relatively thin. The present land rim of Aldabra was breached about 4000–5000 B.P. (Braithwaite *et al.* 1973), yet the structures found in the present survey seem unlikely to be more than a few years old, if as much. Nevertheless, there are indications that stromatolites were once more widespread on Aldabra. In the southeast of the atoll, 1 km inland, there are extensive mamillated surfaces, with stromatolites ranging from a few centimetres up to 20 and 30 cm in diameter, with composite structures reaching 50 cm in height. It has, however, not been possible to recognize in sections any biological component (C. J. R. Braithwaite, personal communication). These structures occupy an area of several thousand square metres, and may represent some geologically fairly recent event, such as a lowering of sealevel (Braithwaite *et al.* 1973).

The main areas of growing stromatolites are apparently in the southwest of the lagoon. Both areas are well away from any *passe* and are in the parts of the lagoon least likely to suffer storm damage. Waters tend to be slightly hypersaline here. The intertidal is wide, and most of the stromatolites are developing well away from mangrove forest. None of these factors explain why stromatolites are not equally abundant on the southern shore east of the area where they do occur. A possible explanation for the localized occurrence of the *Microcoleus/Schizothrix* stromatolites is that they are growing in an area of moderate tidal scour.

The distribution of blue-green algae on limestones in the lagoon at Aldabra appears to have a more distinct zonation (table 5) than do those on the limestone coasts in the northern Adriatic Sea, as indicated by Schneider's (1976, p. 55) table.

Mastigocoleus testarum was found near the base of cliffs on Aldabra, whereas Schneider reported its presence in the grey zone of the supralittoral and its abundance in the yellow-brown and white zones of the eulittoral (approximately the upper and mid littoral of the present study). The difference may lie in the presence of deep pools in the limestone of the Adriatic, allowing a marked range of microenvironments within each zone. Schneider found M. testarum at the bottom of a pool, where the Eh of the water was -560 mV. This and its situation low on the shore at Aldabra together suggest a role for the heterocysts of this alga different from that of other blue-green algae.

As endoliths usually grow beneath a layer of epiliths, it is surprising that pink colours due to presence of phycoerythrin are not more frequent. Only the groups of pink unicells  $(\S 3(g), iii)$  show a distinct pink colour when viewed macroscopically. Their taxonomic status remains uncertain. Ercegović (Geitler 1932) has described *Aphanocapsa endolithica* as sometimes violet. The lack of fluorescence shown by the Aldabra population studied suggests that at least some pink cells might be phototrophic bacteria instead. There are apparently no records of endolithic phototrophic bacteria.

The contrast between the behaviour of blue-green algae on limestone surfaces in the intertidal (§3(c), iii) and in terrestrial environments of Aldabra is striking. In the former, endoliths are abundant and recolonization of bared surfaces is rapid; in the latter, the opposite is true (Whitton & Donaldson 1979). Experimental studies of le Campion-Alsumard (1975), on colonization of calcite in the Mediterranean, also indicate relatively quick growth. Within four weeks, *Hyella caespitosa* had penetrated down to 50  $\mu$ m and, after three months, colonization by endolithic and epilithic algae and fungi had approached its maximum. Golubić (1973) concluded that, in the intertidal zone of areas with carbonate rocks, the distribution of endolithic algae is controlled mainly by water supply. However, it does not seem clear just how the supply of water influences the growth of endoliths selectively over epiliths.

The grazing activities of animals also differ between intertidal and terrestrial environments. A range of species on Aldabra remove the superficial layer of rock in the intertidal (Taylor & Way 1976), but grazing on terrestrial rock surfaces appears largely to be restricted to small animals unlikely to disrupt the rock surface. The removal of superficial rock in the intertidal by grazing may be expected to favour the growth of endoliths; the innermost part of a boring filament will remain after grazing and, with the removal of epilithic competitors, rapid growth of the endolith will be favoured. That endolithic blue-green algae are capable of high metabolic activity is indicated by studies of nitrogen fixation by communities at Île Picard (Potts & Whitton 1977). *Hyella balani* in sand particles showed the highest rates expressed per unit of chlorophyll.

Experiments by Trudgill (1972) suggested that, within sheltered shore notches at Aldabra, a rate of surface erosion of 1 mm per year is caused by a combination of abrasion and physical action (40%), solution (10%), and biological action

(50%). The biological contribution in the lagoon is, however, probably less, especially in peaty mangrove areas (Trudgill 1976). A study of grazing by chitons (*Acanthopleura brevispinosa*) (Taylor & Way 1976) led the authors to conclude that chitons contribute a mean of 3.4% and a maximum of 7.6% towards biological erosion. Chitons take in the deeper endolithic algae, with penetration of 0.5-1 mm, but echinoids and crabs take in the shallower and epilithic algae (Trudgill 1976). Blue-green algae are known also to be important agents of erosion in some circumstances, and, for *Hormathonema*, it has been shown that excavation is a distinctive chemical process (Alexandersson 1975). It may, therefore, be the synergistic combination of endoliths and grazers that is especially effective in bringing about biological erosion. It would be of interest to test the effects of excluding at least the larger grazers from an area of rock for a year to see if there is not only an increase in epiliths but also a decrease in endoliths.

Accounts of blue-green algae from other atoll lagoons are few. The most extensive list is from Raroia (Newhouse 1954), where Calothrix, Entophysalis, *Rivularia* and *Schizothrix* are frequent in the lagoon intertidal; there is no mention of abundant covers of *Microcoleus* or *Scytonema*. Brief observations by B.A.W. (in 1973) of the upper and mid subzones of the lagoon shore of the north island of Farquhar, Indian Ocean, indicated that the blue-green algal cover is less there than on Aldabra. It seems likely that the blue-green algal vegetation of the lagoon intertidal at Aldabra is more extensive than that of most other atolls. Not only would the physical features of the lagoon  $(\S1d)$  seem especially favourable, but the presence of mangrove forest may also be important. Although blue-green algal growths are restricted inside the forest, it is likely that the forest favours growths in the adjacent shore. This is almost certainly the situation on Ile Picard, where anaerobic, low Eh waters are apparently displaced through the sediments at each spring tide. It seems likely that reduced oxygen and Eh levels are general phenomena in the vicinity of mangrove forest, and that phosphate enrichment may also occur as the result of dissolution of limestones by the forest (Trudgill 1976). Atolls where the natural vegetation has been replaced by plantations are likely to have a reduced blue-green algal cover in the intertidal.

While blue-green algae may prove to be more abundant in the lagoon intertidal of Aldabra than in that of most other atolls, they are evidently less so than in some other regions, such as parts of the Persian Gulf (Kendall & Skipwith 1968), Baja California (Horodyski *et al.* 1979), and, at least as far as stromatolites are concerned, Shark Bay, Australia, (Playford & Cockbain 1976) and Freshwater Creek, Andros (Monty 1972). Nevertheless, many of the communities at Aldabra are similar to those elsewhere. *Scytonema*, *Microcoleus* and *Schizothrix* are the three genera quoted most frequently from areas with thick mat and stromatolite communities (see Golubic 1976). The similarity of the *Entophysalis – Hormathonema – Pleurocapsa* community at Îles Moustique to that in the Baja California has already been mentioned. Differences between Aldabra and elsewhere include not only the absence of stromatolites round much of the lagoon, but also the

restricted development of Lyngbya aestuarii. Nowhere does it become the dominant of extensive mats as it does in Baja California (Horodyski 1977), and Gulf of Elat, Aqaba (Potts 1979). In a comparison of the stromatolite flora of three areas, Golubic & Awramik (1974) included among the commoner genera Gardnerula, a genus apparently absent from Aldabra.

This project was made possible by research grants from the Natural Environment Research Council and by the support of Professor T. S. Westoll, Dr D. R. Stoddart and the other members of the Aldabra Research Committee of the Royal Society. D. J. H. Griffin and L. U. Mole of the Royal Society London staff helped solve many administrative problems. The Aldabra Research Station was invaluable for laboratory studies during the two later studies. Thanks are due to: Dr D. J. Bellamy, the leader of the Phase VI expedition; the Seychellois staff, with their extensive knowledge of the lagoon, especially to George LaRue, Harry Charles and Mazarin; D. Johnston, Dr V. W. Spaull, Dr I. R. Swingland, and F. Topliffe, for other aid on the atoll; Dr A. Donaldson, for much helpful discussion; Dr C. J. R. Braithwaite and Dr J. D. Taylor, for unpublished data on stromatolites. J. W. Simon and T. Brett provided valuable assistance in Durham.

#### REFERENCES

- Alexandersson, E. T. 1973 Marks of unknown carbonate-decomposing organelles in cyanophyte borings. Nature, Lond. 254, 237–238.
- Awramik, S. M., Cloud, P. & Gebelein, C. D. 1978 Biogeologic relationships of ancient stromatolites and modern analogs. In *Environmental biogeochemistry and geomicrobiology*, vol. 3 (ed. W. E. Krumbein). Ann Arbor: Ann Arbor Science.
- Bergey, D. H. 1974 Bergey's manual of determinative bacteriology (8th edn, ed. R. E. Buchanan & N. E. Gibbons). Baltimore: Williams & Wilkins.
- Bornet, E. & Flahault, C. 1886–8 Révision des Nostacacées héterocystées. Annls Sci. nat. A (7) 3, 323–381; 4, 343–373; 5, 31–129; 7, 177–262.
- Braithwaite, C. J. R. 1975 Petrology of palaeosols and other terrestrial sediments on Aldabra, Western Indian Ocean. *Phil. Trans. R. Soc. Lond.* B **273**, 1–32.
- Braithwaite, C. J. R., Taylor, J. D. & Kennedy, W. J. 1973 The evolution of an atoll: the depositional and erosional history of Aldabra. *Phil. Trans. R. Soc. Lond. B* 266, 307-340.
- Carter, N. 1933*a* A comparative study of the alga flora of two salt marshes. Part II. J. *Ecol.* 21, 128–208.
- Carter, N. 1933b A comparative study of the alga flora of two salt marshes. Part III. J. Ecol. 21, 385-403.
- Chapman, V. J. 1960 The plant ecology of Scolt Head Island. In Scolt Head Island (ed. J. A. Stears), pp. 85–163. Cambridge: W. Heffer.
- Degener, O. & Degener, I. 1959 Canton Island, South Pacific (resurvey of 1958). Atoll Res. Bull. 64, 1-24.
- de Jonge, V. 1976 Algal vegetations on salt-marshes along the western Dutch Wadden Sea. Netherlands J. Sea Res. 10, 262-283.
- Desikachary, T. O. 1959 Cyanophyta. New Delhi: Indian Council of Agricultural Research.
- Drouet, F. 1963 Ecophenes of Schizothrix calcicola. Proc. Acad. nat. Sci. Philad. 115, 261-281.
- Drouet, F. 1968 Revision of the classification of the Oscillatoriaceae. Monogr. Acad. nat. Sci. Philad. 16, 1-341.

- Drouet, F. 1973 Revision of the Nostocaceae with spherical trichomes. New York: Hafner Press.
- Emery, K. O., Tracey, J. I. & Ladd, H. S. 1954 Geology of Bikini and nearby Atolls. U.S. geol. Surv. prof. Pap. no. A 260.
- Ercegović, A. 1932 Études écologiques et sociologiques des cyanophycées lithophytes de la côte yougoslave de l'Adriatique. Rad jugosl. Akad. Znan. Umjetn. 244, 129–220.
- Farrow, G. E. 1971a The climate of Aldabra Atoll. Phil. Trans R. Soc. Lond. B 260, 67–92.
  Farrow, G. E. 1971b Back-reef and lagoonal environments of Aldabra Atoll, distinguished by their crustacean burrows. Symp. zool. Soc. Lond. 28, 455–500.
- Farrow, G. E. & Brander, K. M. 1971 Tidal studies on Aldabra. *Phil. Trans. R. Soc. Lond.* B 260, 93-122.
- Fogg, G. E. 1973 Physiology and ecology of marine blue-green algae. In *The biology of blue-green algae* (ed. N. G. Carr & B. A. Whitton), pp. 368-378. Oxford: Blackwell.
- Frémy, P. 1933 Cyanophycées des côtes d'Europe. Mém. Soc. natn. Sci. nat. math. Cherbourg no. 41.
- Geitler, L. 1932 Cyanophyceae. L. Rabenhorst's Kryptogamen-Flora, vol. 14. Leipzig: Akademische Verlagsgellellshaft.
- Ginsburg, R. B., Bricker, O. P., Wanless, H. R. & Garrett, P. 1970 Exposure index and sedimentology structures of a Bahama tidal flat. *Geol. Soc. Am., Abstr. Prog.* 2 (7), 744-745.
- Golubić, S. 1973 The relationship between blue-green algae and carbonate deposits. In: The biology of blue-green algae (ed. N. G. Carr & B. A. Whitton), pp. 434-472. Oxford: Blackwell.
- Golubic, S. 1976 Taxonomy of extant stromatolite-building cyanophytes. In *Stromatolites* (ed. M. R. Walter), pp. 113–126. Amsterdam, Oxford and New York: Elsevier.
- Golubic, S. & Awramik, S. M. 1974 Microbial comparison of stromatolite environments; Shark Bay, Persian Gulf and the Bahamas. Geol. Soc. Am., Abstr. Prog. 6 (7), 759–760.
- Gunatilaka, A. 1975 Some aspects of the biology and sedimentology of laminated algal mats from Mannar Lagoon, northwest Ceylon. *Sedim. Geol.* 14, 275–300.
- Horodyski, R. J. 1977 Lyngbya mats at Laguna Mormona, Baja California, Mexico: comparison with proterozoic stromatolites. J. sedim. Petr. 47, 1305-1320.
- Horodyski, R. J., Bloeser, B. & Vonder Haar, S. P. 1980 Laminated algal mats from a coastal lagoon, Laguna Mormona, Baja California. J. sedim. Petr. (In the press).
- Horodyski, R. J. & Vonder Haar, S. P. 1975 Recent calcareous stromatolites from Laguna Mormona (Baja California) Mexico. J. sedim. Petr. 45, 894–906.
- Hughes, R. N. & Gamble, J. C. 1977 A quantitative survey of the biota of intertidal soft substrata on Aldabra Atoll, Indian Ocean. *Phil. Trans. R. Soc. Lond.* B 279, 327–355.
- Jørgensen, B. B. 1977 Bacterial sulfate reduction within reduced microniches of oxidized marine sediments. Mar. Biol. 41, 7–17.
- Kendall, C. G. St. C. & Skipwith, F. P. d'E. 1968 Recent algal mats of a Persian Gulf lagoon. J. sedim. Petr. 38, 1040-1058.
- Komárek, J. 1973 Prospects for taxonomic development. In The biology of the blue-green algae (ed. N. G. Carr & B. A. Whitton), pp. 482–486. Oxford: Blackwell.
- le Campion-Alsumard, T. 1969 Contribution à l'étude des cyanophycées lithophytes des étages supralittoral et mediolittoral (Région de Marseille). Tethys 1, 119–172.
- le Campion-Alsumard, T. 1975 Étude expérimentale de la colonisation d'éclats de calcite par les cyanophycées endolithes marines. Cah. Biol. mar. 16, 177-185.
- Little, M. G. 1973 The zonation of marine supra-littoral blue-green algae. Br. phycol. J. 8, 47-50.
- MacNae, W. 1968 A general account of the flora and fauna of mangrove swamps and forests in the Indo-West Pacific region. *Adv. mar. Biol.* 6, 73–270.
- McNae, W. 1971 Mangroves on Aldabra. Phil. Trans. R. Soc. Lond. B 260, 237-248.
- Monty, C. L. V. 1972 Recent algal stromatolitic deposits, Andros Island, Bahamas. Preliminary report. Geol. Rdsch. 61, 742-783.
- Newhouse, J. 1954 Ecological and floristic notes on the Myxophyta of Raroia. Atoll Res. Bull. 33, 42-54.

- Playford, P. E. & Cockbain, A. E. 1976 Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia. In *Stromatolites* (ed. M. R. Walter), pp. 389–411. Amsterdam, Oxford and New York: Elsevier.
- Potts, M. 1979 Nitrogen fixation (acetylene reduction) associated with communities of heterocystous and non-heterocystous blue-green algae on mangrove forests of Sinai. *Oecologia* 39, 359-373.
- Potts, M. & Whitton, B. A. 1977 Nitrogen fixation by blue-green algal communities in the intertidal zone of the lagoon of Aldabra Atoll. Oecologia 27, 275-283.
- Potts, M. & Whitton, B. A. 1979*a* pH and Eh on Aldabra Atoll. 1. Comparison of marine and freshwater environments. *Hydrobiologia* 67, 11–17.
- Potts, M. & Whitton, B. A. 1979 b pH and Eh on Aldabra Atoll. 2. Intertidal photosynthetic microbial communities showing zonation. *Hydrobiologia* 67, 99–106.
- Price, J. H. 1971 The shallow sublittoral marine ecology of Aldabra. *Phil. Trans. R. Soc. Lond. B* 260, 123-172.
- Schneider, J. 1976 Biological and inorganic factors in the destruction of limestone coasts. Contr. Sedimentol. 6, 1-112.
- Smith, S. V. & Jokiel, P. L. 1978 Water composition and biogeochemical gradients in the Canton Atoll lagoon. Atoll Res. Bull. 221, 15-53.
- Stanier, R. Y., Kunisawa, R., Mandel, M. & Cohen-Bazire, G. 1971 Purification and properties of unicellular blue-green algae (Order Chroococcales). Bact. Rev. 35, 171-205.
- Stanier, R. Y., Sistrom, W. R., Hansen, T. A., Whitton, B. A., Castenholz, R. W., Pfennig, N., Gorlenko, V. N., Kondratieva, E. N., Eimhjellen, K. E., Whittenbury, R., Gherna, R. L. & Trüper, H. G. 1978 Proposal to place nomenclature of cyanobacteria (bluegreen algae) under the rules of the International Code of Nomenclature of Bacteria. *Int. J. syst. Bact.* 28, 335–336.
- Stoddart, D. R. 1971 Place names of Aldabra. Phil. Trans. R. Soc. Lond. B 260, 631-632+map.
- Stoddart, D. R. & Mole, L. U. 1977 Climate of Aldabra Atoll. Atoll Res. Bull. 202, 1-27.
- Stoddart, D. R., Taylor, J. D., Fosbert, F. R. & Farrow, G. E. 1971 Geomorphology of Aldabra Atoll. *Phil. Trans. R. Soc. Lond.* B 260, 31–66.
- Stoddart, D. R. & Westoll, T. S. 1979 The terrestrial ecology of Aldabra. Phil. Trans. R. Soc. Lond. B 286, 1–263.
- Taylor, J. D. & Way, K. 1976 Erosive activities of chitons at Aldabra Atoll. J. sedim. Petr. 46, 974–977.
- Trudgill, S. T. 1972 Process studies of limestone erosion in littoral and terrestrial environments, with special reference to Aldabra Atoll, Indian Ocean. Ph.D. Thesis, University of Bristol.
- Trudgill, S. T. 1976 The marine erosion of limestones on Aldabra Atoll, Indian Ocean. Z. Geomorph. Supplement Bd. 26, 164-200.
- van den Hoek, C., Colijn, F., Cortel-Breeman, A. H. & Wanders, J. B. W. 1972 Algal vegetation types along the shores of inner bays and lagoons of Curacao, and of the lagoon Lac (Bonaire), Netherlands Antilles. Verh. K. ned. Akad. Wet. 61 (2), 1-72.
- Walter, M. R. (ed.) 1976 Stromatolites. Amsterdam, Oxford and New York: Elsevier.
- Walter, M. R., Golubic, S. & Preiss, W. V. 1973 Recent stromatolites from hydromagnesite and aragonite depositing lakes near the Coorong Lagoon, South Australia. J. sedim. Petr. 43, 1021–1030.
- Weber, J. N. & Woodhead, M. J. 1972 Carbonate lagoon and beach sediments of Tarawa Atoll, Gilbert Islands. *Atoll Res. Bull.* 157, 1–27.
- Wentworth, C. K. 1922 A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392.
- Westoll, T. S. & Stoddart, D. R. (eds) 1971 A Discussion on the results of the Royal Society expedition to Aldabra 1967–68. *Phil. Trans. R. Soc. Lond.* B 260, 1–654.
- Whitton, B. A. 1971 Terrestrial and freshwater algae of Aldabra. *Phil. Trans. R. Soc. Lond.* B 260, 249-255.
- Whitton, B. A., Diaz, B. M. & Holmes, N. T. H. 1979 A computer orientated numerical coding system for algae. Br. phycol. J. 14, 353-360.

- Whitton, B. A. & Donaldson, A. 1980 Algal vegetation of terrestrial and freshwater environments on Aldabra Atoll. (In preparation.)
- Whitton, B. A., Donaldson, A. & Potts, M. 1979 Nitrogen fixation by Nostoc colonies in terrestrial environments of Aldabra Atoll, Indian Ocean. *Phycologia* 18, 278–287.
- Whitton, B. A., Holmes, N. T. H. & Sinclair, C. 1978 A coded list of 1000 freshwater algae of the British Isles. Water Archive Manual Series, no. 3. Reading: Department of the Environment.
- Wiens, H. J. 1962 Atoll environment and ecology. New Haven and London: Yale University Press.
- Womersley, H. B. S. & Edmonds, S. J. 1958 A general account of the intertidal ecology of South Australian coasts. Aust. J. mar. fresh wat. Res. 9, 217-260.

#### APPENDIX

1. Blue-green algae from lagoon intertidal

taxonomic category used for recording data (see  $\S2$ )

Aphanocapsa >  $1 \leq 2 \mu m$ Aphanocapsa >  $2 \leq 4 \ \mu m$ Aphanocapsa >  $4 \leq 6 \,\mu\text{m}$ Aphanocapsa >  $6 \leq 8 \,\mu\text{m}$ Aphanothece  $\leq 2 \mu m$  $A phanothece > 2 \leq 4 \ \mu m$ Aphanothece >  $4 \leq 6 \,\mu\text{m}$ Brachytrichia sp. Calothrix aeruginea (Kütz.) Thuret C. confervicola (Roth.) Ag. C. contarenii (Zanardini) Bornet et Flahault C. crustacea Thuret C. pulvinata Ag. C. scopulorum Weber et Mohr Chlorogloea conferta (Kütz.) Setchell et Gardner Chroococcus >  $6 \leq 8 \mu m$ , sheath striated Chrococcus >  $8 \leq 16 \,\mu\text{m}$ , sheath striated Chroococcus >  $16 \leq 32 \mu m$ , sheath striated Chroococcus > 32, sheath striated Chrococcus  $\leq 4 \,\mu\text{m}$ , sheath not striated Chroococcus > 4  $\leq$  6 µm, sheath not striated Chroococcus >  $6 \leq 8 \mu m$ , sheath not striated Chroococcus >  $8 \leq 16 \,\mu\text{m}$ , sheath not striated Chroococcus >  $16 \leq 32 \mu m$ , sheath not striated  $Chroococcus > 32 \ \mu m$ Chroococcopsis gigantea Geitler Dalmatella buaensis Ercegović Dermocarpa hemisphaerica Setchell et Gardner D. leibleiniae (Reinsch) Bornet et Thuret D. olivacea (Reinsch) Tilden D. sphaerica Setchell et Gardner Dermocarpa sp. Dichothrix rupicola Collins Entophysalis granulosa Kütz. yellow/brown  $Gloeocapsa > 4 \leq 6 \mu m$ , sheath colourless, not striated  $Gloeocapsa > 6 \ \mu m$ , sheath colourless, not striated

suitable binomial where size width used for primary records (§2)

A. concharum Hansgirg
A. montana Cramer
A. grevillei (Hass.) Rabenhorst
A. roeseana de Bary
A. saxicola Nägeli
A. microspora (Menegh.) Rabenhorst
A. microscopica Nägeli

- C. schizodermaticus West
- C. turqidus (Kütz.) Nägeli
- C. westii (West) Boye-Peterson
- C. macrococcus (Kütz.) Rabenhorst
- C. minor (Kütz.) Nägeli
- C. minutus (Kütz.) Nägeli
- C. membraninus (Menegh.) Nägeli
- C. turicensis (Nägeli) Hansgirg
- C. spelaeus Ercegović
- Chroococcus sp. (no suitable binomial)

G. atrata (Turp.) Kütz. G. crepidinum Thuret  $Gloeocapsa > 2 \leq 4 \mu m$ , sheath yellow-brown  $Gloeocapsa > 4 \leq 6 \,\mu\text{m}$ , sheath orange/red/violet  $Gloeocapsa > 6 \leq 8 \mu m$ , sheath orange/red/violet Gloeothece >  $2 \leq 4 \ \mu m$ Hormathonema epilithicum Ercegović Hormathonema violaceo-nigrum Ercegović  $Hydrocoleum > 6 \leq 8 \ \mu m$ Hyella balani Lehmann Isactis sp. Johannesbaptistia pellucida (Dickie) Taylor et Drouet Lyngbya aestuarii Liebmann ex Gomont L. allorgei Frémy L. confervoides Ag. ex Gomont L. digueti Gomont L. epiphytica Hieronymus L. kuetzingii Schmidle L. limnetica Lemmermann L. majuscula Harvey ex Gomont, >  $16 \leq 32 \,\mu\text{m}$ L. majuscula Harvey ex Gomont,  $> 32 \mu m$ L. martensiana Meneghini ex Gomont L. nordgardhii Wille L. pusilla (Rabenhorst) Hansgirg Lyngbya >  $1 \leq 2 \mu m$ Mastigocoleus testarum Merismopedia < 1  $\mu m$ Merismopedia >  $1 \leq 2 \mu m$ Merismopedia >  $2 \leq 4 \, \mu m$ Merismopedia >  $4 \leq 6 \,\mu\text{m}$ Merismopedia >  $6 \leq 8 \, \mu m$ Microcoleus chthonoplastes Thuret ex Gomont M. tenerrimus Gomont  $Microcoleus < 2 \ \mu m$  $Microcoleus > 2 \leqslant 4 \ \mu m$  $Microcoleus > 4 \leq 8 \,\mu\text{m}$  $Microcoleus > 8 \ \mu m$ Microcystis reinboldii (Richter) Forti Nodularia spumigena Mertens Oncoby sa rivularis (Kütz.) Meneghini Oscillatoria nigro-viridis Thwaites ex Gomont Phormidium >  $2 \leq 4 \mu m$ Phormidium >  $4 \leq 6 \,\mu\text{m}$ 

*Phormidium* >  $6 \leq 8 \,\mu\text{m}$ Phormidium sp., stromatolite Placoma vesticulosa Schousb. Plectonema battersii Plectonema nostocorum Plectonema notatum Plectonema terebrans Plectonema sp.  $Pleurocapsa > 4 \leq 8 \,\mu m$  $Pleurocapsa > 8 \leq 16 \,\mu m$  $Pleurocapsa > 16 \, \mu m$ Radaisia epiphytica Setchell et Gardner Rivularia sp. A Schizothrix arenaria (Berk.) Gomont S. calcicola (Ag.) Gomont S. minuta (Hansgirg) Forti

G. dermochroa Nägeli
G. alpina (Nägeli) emend. Brand
G. sanguinea (Ag.) Kütz.
G. palea (Kütz.) Rabenhorst
Hydrocoleum sp.

M. warmingiana Lagerh.
M. tenuissima Lemmermann
M. punctata Meyen
M. glauca (Ehrenberg) Nägeli
M. littoralis (Oersted) Rabenhorst

Microcoleus sp. Microcoleus sp. Microcoleus sp. Microcoleus sp.

P. molle (Kütz.) Gomont
P. submembranaceum (Ard. et Straff) Gomont
Phormidium sp.

P. fuliginosa Hauck P. crepidinum Collins Pleurocapsa sp.

# 54

Soguerrea spi	
Solentia intricata Ercegović	
S. stratosa Ercegović	
Spirilina subsalsa Oerst.	
$\bar{Spirulina} > 1 \leq 2 \ \mu m$	S. labrynthiformis (Meneghini) Gomont
Spirulina > $2 \leq 4 \ \mu m$	
Synechococcus > $6 \leq 8 \mu\text{m}$	S. brunneolus Rabenhorst
Tolypothrix byssoidea (Berk.) Kirchner	
$Xenococcus > 2 \leq 4 \ \mu m$	X. laysanensis Lemmermann
$Xenococcus > 4 \leq 6 \ \mu m$	X. kerneri Hansgirg
$Xenococcus > 6 \leq 8 \ \mu m$	X. schousbei Thuret
$Xenococcus > 8 \le 16 \mu\text{m}$	X. cladophorae (Tilden) Setchell et Gardner
$Xenococcus > 16 \ \mu m$	X. chaetomorphae Setchell et Gardner

2. Species found only in lagoon plankton

Nodularia harveyana Thuret Trichodesmium erythraeum Ehrenberg ex Gomont

#### 3. Taxonomic notes on dominants for which it was difficult to allocate binomial

#### Rivularia sp. A

Scutonema sn

Shiny, black, hemispherical colonies, reaching diameter of 8-12 mm; colonies not confluent, solid, slight to moderate calcification. Trichome width near base,  $8.8-15.0 \mu m$ , cells longer than broad; heterocyst wider than basal cell; sheath  $2-4 \mu m$  wide, not lamellate. Typically occurs on this layer of silt overlying slightly elevated limestone surfaces, often dominant (see §3(e), i).

#### Scytonema sp.

Thallus forming dark olive-green mats, which are often extensive. Filaments of the mature mat densely entangled below, irregularly bent or curved; erect filaments of mature mats usually 5–7.5 mm, mostly aggregated into small tufts. Trichomes with cells broader than long, typically  $20-25 \ \mu m \times 5-10 \ \mu m$ , often slightly constricted; filaments typically  $30-34 \ \mu m$  away from the tip, sometimes reaching  $38 \ \mu m$ . Heterocysts rectangular, shorter or longer than broad, up to  $25 \ \mu m$  long. Apex of trichome usually only slightly tapered, and with apical cell rounded; however, the trichomes occasionally taper more strongly and the terminal few cells take on the shape of a nipple. Sheath of filaments in mature mat brown, laminated, not diverging; apex of trichome usually emergent from sheath.

This alga is larger than any other marine species in this genus. It differs from S. siculum Borzi not only in the much greater width of the trichome, but also in the relatively narrow sheath and the shape of both vegetative cells and heterocysts. The closest freshwater species is probably S. crustaceum Ag., but the latter differs in its narrower trichomes (only  $6-8 \mu m$  in the original description), the presence of a diverging sheath and the different cell shapes, especially the heterocysts.

Similar populations occur also on pneumatophores at Ras Muhammad, Sinai, and on sediment at Andros Is., Bahamas (observations of M.P. and B.A.W., respectively), though it is less abundant in these two areas than on Aldabra. S. Golubic (personal communication) reports that mats of similar alga occur in the Persian Gulf and that he is preparing a paper on its taxonomy.