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Marine Macrophyte Communities on the Reef Flat at Agatti Atoll (Lakshadweep, India)

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The distribution, abundance and standing stock of macrophytes on the intertidal reef flat at Agatti atoll (Lakshadweep, India) were recorded in a total of 1234 quadrats in October 1993 and April 1994. Eighty seven species of macrophytes, including 16 new records, were observed on the different islands. The reef flat at Agatti can be divided into three zones partly correlated with physical factors. The upper zone is characterized by *Thalassia hemprichii*, *Boergesenia forbesii*, *Gracilaria edulis* and *Valoniopsis pachynema*, the middle zone by *Gelidiella acerosa*, *Laurencia papillosa* and *Ceramium* sp., and the lower zone by *Ulva lactuca*, *Turbinaria ornata* and *Codium arabicum*. *Halimeda gracilis* is dominant in both the middle and lower zone. The majority of algae exhibited patchy distributions, with seasonal fluctuations in their abundance. Species diversity increased with distance from the shore while percentage cover and species richness exhibited the reverse trend. Herbivory appeared significant with sea urchins as the major grazers. Algal abundance was reduced to one third in April mainly because of periodicity governed by the monsoon. Macrophyte wet weight standing stock of Agatti reef flat was estimated to be 835 ± 59 t (October 1993) and 686 ± 77 t (April 1994).

Introduction

The Lakshadweep (Laccadive) archipelago comprises 36 coral islands, including atolls, reefs and submerged banks in the Arabian Sea (8°–12°30' N, 71°–74° E, 32 km^2), 300–400 km off the west coast of India. These islands are flat with an elevation of less than two meters. Tidal amplitude ranges from 0.3–1.0 m. Sea surface temperature varies between 28–31 °C while its salinity ranges from 34–37‰. The eastern side of islands is generally characterized by a reef flat of variable width, often with sizable boulders. Lakshadweep has a warm tropical climate (annual air temperature range, 17–38 °C; average daily relative humidity, 70%). The year can be divided into 3 seasons: pre-monsoon (February to May), monsoon (June to September) and post-monsoon (October to January). High temperatures are prevalent during the pre-monsoon season. The annual rainfall of about 150 cm is received mainly during the southwest monsoon season.

The archipelago harbours a diverse marine flora and fauna. Although several studies on the marine macrophytes of Lakshadweep have been undertaken (Barton 1903, Newton 1953, Subbaramaiah *et al.* 1979, Jagtap and Untawale 1984, Untawale and Jagtap 1984, Jagtap 1987), available information is generally qualitative. Quantitative aspects of macrophyte communities have been largely neglected. No information on the diversity of these communities is available, as is the case with many other tropical regions (Bolton 1994). Further, available estimates of algal resources, a prerequisite for commercial use, are inconsistent although recommendations have been made to exploit them for agar, algin and

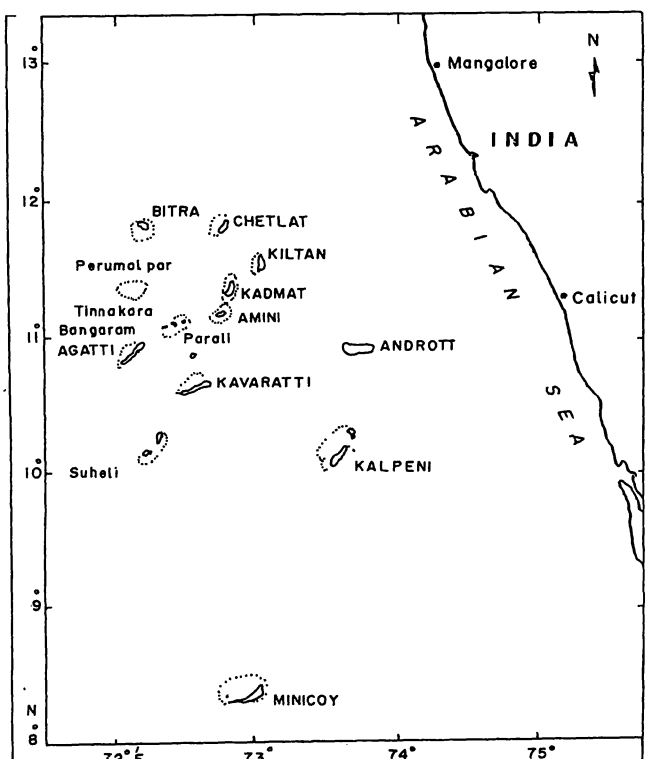

Fig. 1. The Lakshadweep archipelago.

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Table I. Macrophyte species recorded in Lakshadweep.

Phanerogams
  Order Helobiae
    Family Hydrocharitaceae
      Halophila ovalis (R. Brown) Hooker *f.*
      Thalassia hemprichii (Ehrenberg) Ascherson
    Family Potomogetonaceae
      Cymodocea rotundata Ehrenberg *et* Hemprich

Cryptogams
  Division Chlorophyta
  Order Ulvales
    Family Ulvaceae
      Enteromorpha clathrata (Roth) Greville
      Ulva lactuca Linnaeus
  Order Cladophorales
    Family Cladophoraceae
      Cladophora vagabunda (Linnaeus) van den Hoek
      **Cladophora prolifera* (Roth) Kuetzing (Andrott)
      Cladophora sp.
      Claetomorpha sp.
  Order Acrosiphonales
    Family Acrosiphoniaceae
      **Spongomorpha* sp. (Andrott)
  Order Dasycladales
    Family Dasycladaceae
      Neomeris annulata Dickie
  Order Siphonocladales
    Family Valoniaceae
      **Chamaedoris auriculata* Boergesen (Agatti)
      Dictyosphaeria cavernosa (Forsskal) Boergesen
      Valonia Aegagropila C. Agardh
      **Valonia utricularis* (Roth) C. Agardh (Agatti, Kiltan)
      Valoniopsis pachynema (Martens) Boergesen
    Family Boodleaceae
      Boodlea composita (Harvey) Brand
    Family Siphonocladaceae
      Boergesenia forbesii (Harvey) Feldmann
      Cladophoropsis sp.
      **Ventricaria ventricosa* (J. Agardh) Olsen *et* J. West (Andrott)
    Family Anadyomenaceae
      Anadyomene stellata (Wulfen) C. Agardh
  Order Bryopsidales
    Family Bryopsidaceae
      Bryopsis plumosa (Hudson) C. Agardh
    Family Caulerpaceae
      **Caulerpa mexicana* Sonder *ex* Kuetzing (Minicoy)
      Caulerpa peltata Lamouroux
      Caulerpa racemosa (Forsskal) J. Agardh
      Caulerpa serrulata (Forsskal) J. Agardh *emend* Boergesen
      Caulerpa sertularioides (Gmelin) Howe
      Caulerpa taxifolia (Vahl) C. Agardh
      Caulerpa sp.
    Family Codiaceae
      Codium arabicum Kuetzing
      Codium sp.
    Family Halimedaceae
      Halimeda gracilis Harvey *ex* J. Agardh
      Halimeda incrassata (Ellis) Lamouroux
      Halimeda opuntia (Linnaeus) Lamouroux
      Halimeda sp.
    Family Udoteaceae
      Avrainvillea ridleyi A. *et* E. S. Gepp
      **Tydemania expeditionis* Weber-van Bosse (Minicoy)
      Udotea sp.
  Division Phaeophyta
  Order Ectocarpales
    Family Ectocarpaceae
      Hincksia breviarticulata (J. Agardh) Silva
      **Hincksia* sp. (Agatti, Andrott, Kadmat)
  Order Dictyotales
    Family Dictyotaceae
      Dictyopteris delicatula Lamouroux
      Dictyota sp.
      **Padina australis* Hauck (Agatti, Andrott)
      Padina tetrastromatica Hauck
  Order Scytosiphonales
    Family Scytosiphonaceae
      Hydroclathrus clathratus (C. Agardh) Howe
  Order Fucales
    Family Sargassaceae
      Sargassum cristaefolium C. Agardh
      Sargassum sp.
      Turbinaria ornata (Turner) J. Agardh

  Division Rhodophyta
  Order Nemaliales
    Family Galaxauraceae
      **Galaxaura filamentosa* Chou (Agatti)
      Galaxaura marginata (Ellis *et* Solander) Lamouroux
      Galaxaura rugosa (Ellis *et* Solander) Lamouroux
    Family Chaetangiaceae
      Actinotrichia fragilis (Forsskal) Boergesen
  Order Bonnemaisoniales
    Family Bonnemaisoniaceae
      Asparagopsis taxifomis (Delile) Trevisan
  Order Gelidiales
    Family Gelidiaceae
      Gelidium sp.
    Family Galidiellaceae
      Gelidiella acerosa (Forsskal) Feldmann *et* Hamel
  Order Corallinales
    Family Corallinaceae
      Jania adhaerens Lamouroux
      Jania capillacea Harvey
      **Jania rubens* (Linnaeus) Lamouroux (Kiltan)
      Crustose coralline algae (unidentified)
  Order Cryptonemiales
    Family Halymeniaceae
      Halymenia venusta Boergesen
  Order Gigartinales
    Family Gymnophocaceae
      Portieria hornemannii (Lyngbye) Silva
    Family Gracilariaceae
      Gracilaria arcuata Zanardini
      Gracilaria edulis (Gmelin) Silva
      **Gracilaria salicornia* (C. Agardh) Dawson (Minicoy)
    Family Solieriaceae
      **Solieria robusta* (Greville) Kylin (Agatti)
    Family Hypneaceae
      Hypnea musciformis (Wulfen) Lamouroux
      Hypnea pannosa J. Agardh
      Hypnea valentiae (Turner) Montagne

Table I. Continued

Order Rhodomeniales
Family Champiaceae
Champia parvula (C. Agardh) Harvey
Family Rhodymeniaceae
Ceratodictyon spongiosum Zanardini
Gelidiopsis intricata (C. Agardh) Vickers
Order Ceramiales
Family Ceramiaceae
**Antithamnion* sp. (Kiltan)
**Ceramium* sp. (Agatti, Andrott, Kadmat)
Spyridia hypnoides (Bory) Papenfuss
Family Dasyaceae
Dictyurus purpurascens Bory
Family Rhodomelaceae
Acanthophora spicifera (Vahl) Boergesen
Chondria dasyphylla (Woodward) C. Agardh
**Laurencia intricata* Lamouroux (Andrott)
Laurencia caraibica Silva
Laurencia obtusa (Hudson) Lamouroux
Laurencia papillosa (C. Agardh) Greville
Leveillea jungermannioides (Hering *et* Martens) Harvey
Polysiphonia sp.

Division Cyanophyta
Order Oscillatoriales
Family Oscillatoriaceae
Lyngbya sp.
Oscillatoria sp.
Phormidium sp.
Symploca sp.

* indicates new distribution records for Lakshadweep. Localities of new records indicated in brackets ().

carrageenin (Subbaramaiah *et al.* 1979, Kaliaperumal *et al.* 1989).

The present paper reports the results of a study on marine macrophytes that is part of a larger ongoing study on the marine fauna and flora of Lakshadweep. We have determined the distribution of the macrophytes, their abundance and standing stock, and the structure and diversity of their communities on the intertidal reef flat at Agatti, one of the atolls. This information will not only help in understanding tropical marine macrophyte reef communities, but it is also useful for their optimal resource management.

Materials and Methods

Field studies were conducted on several islands of the Lakshadweep archipelago (Fig. 1) in March–April and October–November from 1993 to 1995. Intertidal reef flats were surveyed during low tide and lagoons explored using boats and by snorkeling. Representatives of observed macrophyte species were hand picked, preserved in 2% formaldehyde and labelled. Identification was carried out to species level as far as possible. These qualitative surveys served to prepare an inventory of marine macrophytes of Lakshadweep.

In addition, the distribution, abundance and other macrophyte community characteristics were studied at Agatti atoll in October 1993 and April 1994. Sixteen transects were fixed on the reef flat at the eastern side of the atoll at intervals of 500 m (Fig. 2). At each transect a nylon line, marked at 5 m intervals to denote stations was laid, running from the average high tide mark towards the low tide mark and perpendicular to the shore. The 0 m station mark on the line was made to coincide with the average high tide mark. The abundance of macrophytes, in terms of percentage cover as visible from above, was estimated using a 1×1 m quadrat frame subdivided into 100 squares. Percentage cover was estimated at 5 m intervals in duplicate quadrats. Sampling at each transect extended seawards as far as the low tide permitted. In all, 850 quadrats were analyzed in October 1993. Percentage cover was again estimated in April 1994 from 384 quadrats placed at alternate transects (II, IV, VI, VIII, IX, X, XII and XIV) to study temporal variation. Data obtained from all transects were pooled for statistical analyses.

Macrophyte standing stock was estimated using %cover-biomass (wet weight) conversion factors. To obtain the factors, each macrophyte species with a percentage cover of 1 to 5% of the quadrat was collected, preserved separately and later, rinsed, blotted

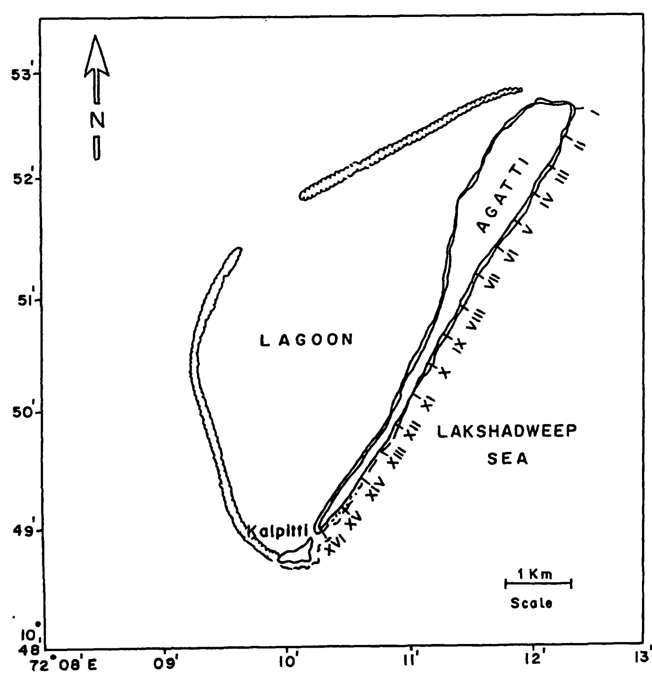

Fig. 2. Map of Agatti atoll indicating the location of transects.

and weighed. At least three samples were obtained for each species and mean factors computed. The macrophyte standing stock (wet weight) for the 150 m belt transect along the entire eastern coast of Agatti (6.5 km) was thus estimated using mean percentage cover data. The biomass of rare species was not estimated as their contributions were considered negligible. The biomass of crustose coralline algae was also not estimated. Methods used in this study enable assessment of macrophyte biomass from a large number of quadrats and avoid destructive collection and disturbance to the ecosystem.

The zonation pattern of the macrophyte community was analyzed by subjecting the pooled transect data to cluster analysis (Clifford and Stephenson 1977). The percentage cover data was normalized using arcsine transformation (Figs 3, 4). Unlike the log transformation which compresses values to a narrow range, this transformation compresses middle values, stretching out values at both extremes of the scale. It is appropriate for percentage data (Sokal and Rohlf 1981). The Bray-Curtis dissimilarity index between pairs of stations was computed using normalized percentage cover data to obtain the dissimilarity matrix and stations were clustered using the group average linkage method (Clifford and Stephenson 1977). In the resulting dendrograms (Fig. 5), stations harbouring similar macrophytes formed clusters, enabling the subdivision of the reef flat into different zones.

The mean percentage cover with 95% confidence limits of each species along with other community

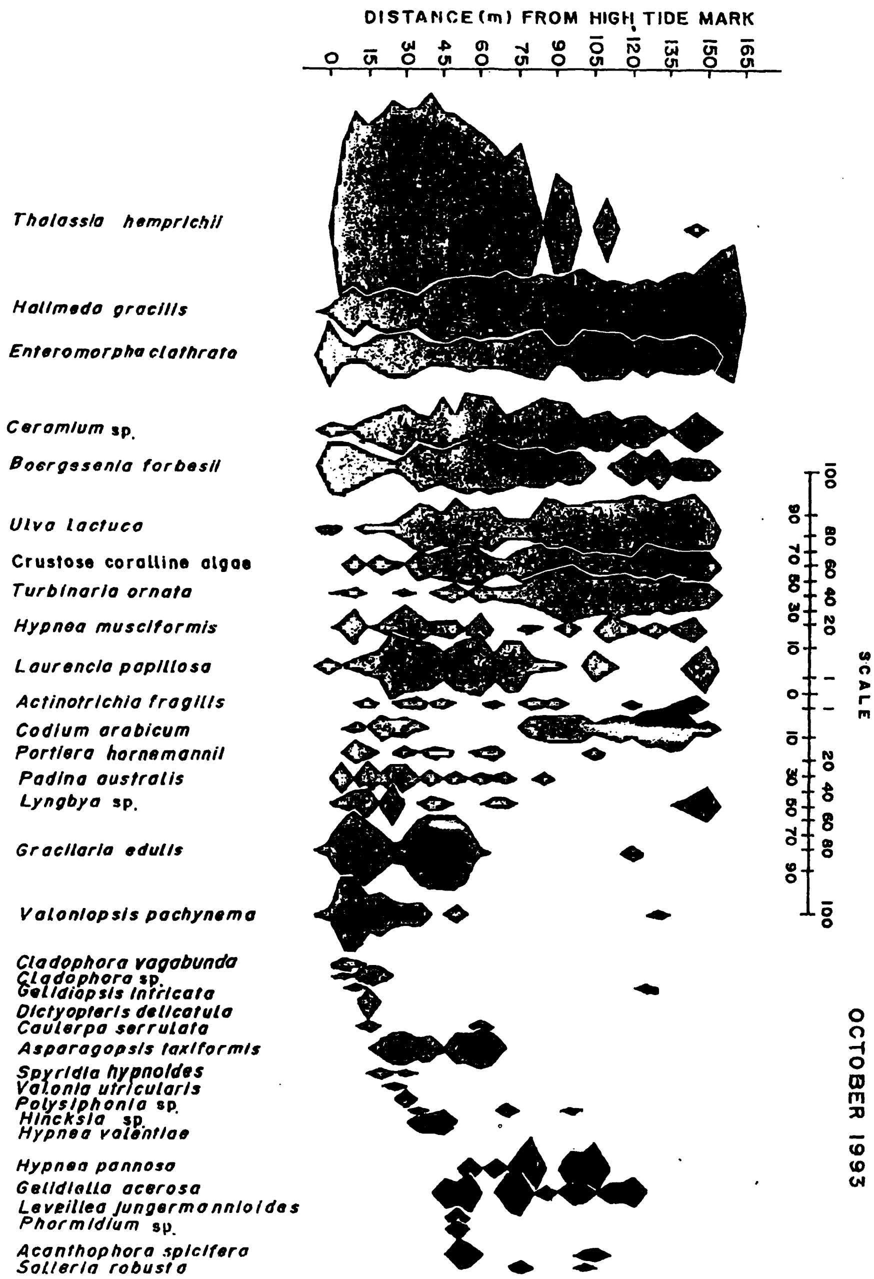

Fig. 3. Kite diagram illustrating the abundance (% cover) and distribution of macrophytes on the Agatti reef flat in October 1993.

characteristics as well as their percentage occurrence in quadrats (%Q) for each zone and for each period were computed. The latter value indicates the commonness of the species on the reef flat. The number of species was taken as an index of species richness. The Shannon-Wiener species diversity index (H'), expressed in bits, and evenness (J) were calculated (Pielou 1975). This index incorporates species richness and evenness of occurrence and has been widely used in community ecology. The diversity index is zero when only one species is present and increases with species richness and evenness. The evenness index ranges from 0–1, representing maximum and minimum dominance respectively.

A *t*-test (Sokal and Rohlf 1981) was applied to cover/biomass values of each species as well as total algae/macrophytes to analyze differences between the two sampling periods.

Results

Physical characteristics

The intertidal reef flat at Agatti is narrow towards the northern end and extends up to approximately 170 m. This reef flat is bordered by a sloping coralline sandy stretch, 5–10 m in width and extending above the average high tide mark. At transect VI and XIII concrete tetrapods, laid in the lower part of this stretch to check erosion, served as a substratum for sessile organisms and hiding places for mobile organisms. Beyond this sandy stretch, the substratum is compacted into coralline sandstone and is heterogeneous with a mosaic of tide pools, sandy patches, live coral colonies and a few coralline boulders. Sandy patches were sometimes stabilized into a firmer substratum by seagrass roots with hardly any visible seagrass blades. Considering islands in Laksh-

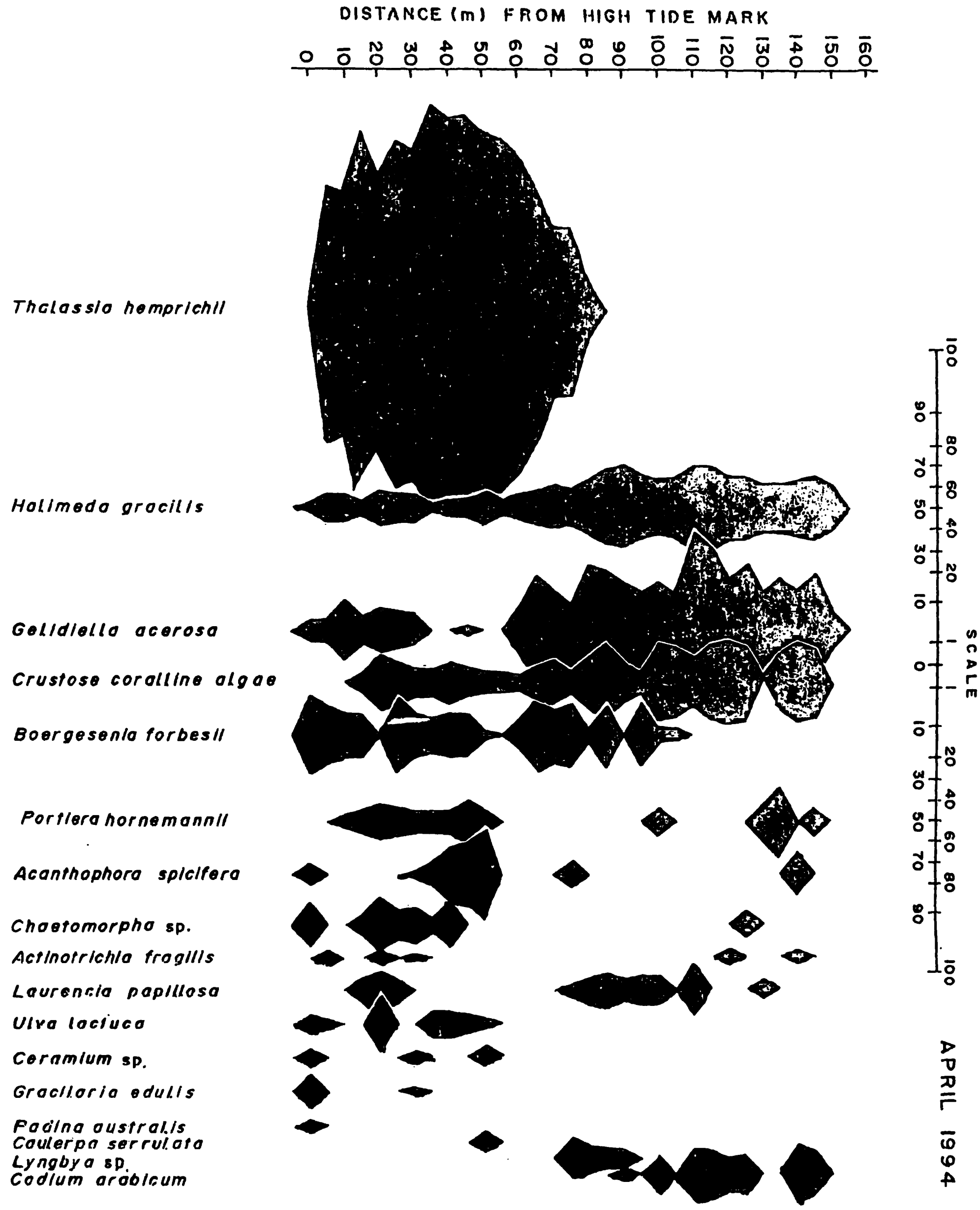

Fig. 4. Kite diagram illustrating the abundance (% cover) and distribution of macrophytes on the Agatti reef flat in April 1994.

adweep, the reef flat is wide enabling observations for a considerable distance during low spring tides. Beyond the reef flat is an approximately 10 m wide slightly elevated strip, comprising small to medium sized coral boulders, which gradually slopes downwards for about 100 m and descends steeply thereafter.

Biological characteristics

Eighty seven macrophyte species, including 16 new records, were recorded during the surveys (Table I). Green algae, particularly *Halimeda gracilis*, were the most abundant, followed by red and brown algae. Most macrophyte species were recorded at all islands. Localities of new records are indicated in Table I. Algae were recorded not only on the coral substrata but also on sand. These include *Enteromorpha clathrata*, *Ulva lactuca*, *Chaetomorpha* sp., *Boergesenia forbesii*, *Caulerpa serrulata*, *Halimeda gracilis*, *Padina australis*, *Gelidiella acerosa*, *Ceramium* sp., *Laurencia papillosa* and *Acanthophora spicifera*.

The most abundant macrophyte was the seagrass, *Thalassia hemprichii* (Figs 3, 4), which formed extensive meadows in the nearshore region at most transects, particularly XIV to XVI. At Transect XI, an abundance of decaying seagrasses was observed piled ashore. Several algae were associated with these seagrass beds, including *Lyngbya* sp., *Oscillatoria* sp. and *Phormidium* sp. (blue green algae); *Ulva lactuca*

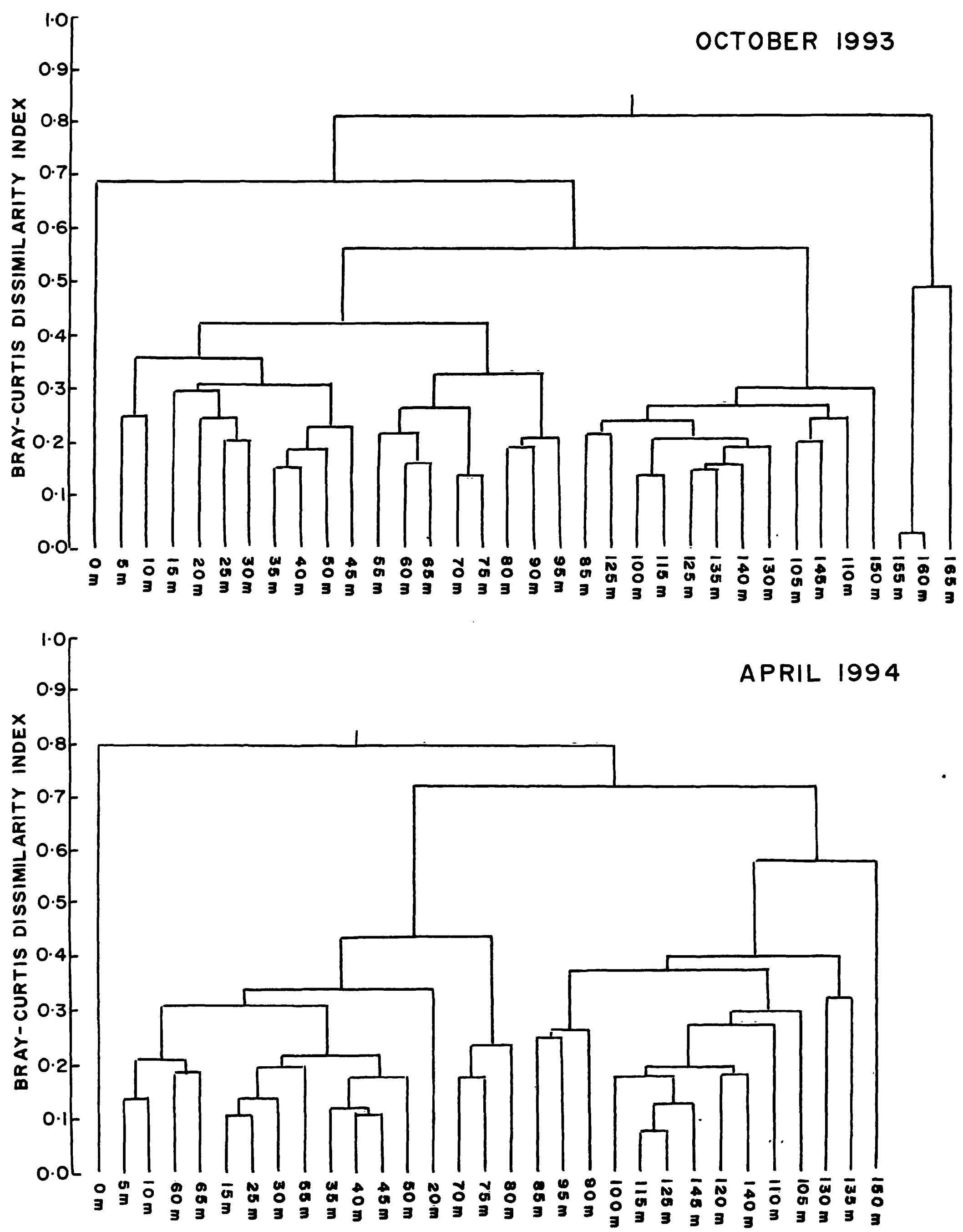

Fig. 5. Dendrograms illustrating macrophyte similarities between stations on the reef flat at Agatti in October 1993 and April 1994.

and *Chaetomorpha* sp. (green algae) and *Hypnea musciformis*, *H. valentiae*, *Spyridia hypnoides*, *Leveillea jungermannioides*, *Gracilaria edulis* and *Laurencia papillosa* (red algae). Many small epiphytic algae, unidentified, were also observed on blades of seagrasses. These seagrass beds also sheltered a large number of faunal groups.

Though some algal species were distributed along almost the entire width of the reef flat, many species exhibited restricted distributions which varied seasonally (Figs 3, 4). Analysis of floral similarities between stations suggested that clusters resulted on the basis of distance from the average high tide mark (Fig. 5). Three clusters were discerned corresponding

Table II. Mean percentage cover (± S. E.) of common macrophytes at Agatti in October 1993.

	Upper reef flat		Middle reef flat		Lower reef flat	
	(0–45 m)	%Q	(50–95 m)	%Q	(100–145 m)	%Q
No. of quadrats	316		278		228	
Seagrass						
Thalassia hemprichii	46.6 ± 5.3	51.9	26.6 ± 5.0	30.9	0.5 ± 0.8	1.3
Chlorophyta						
Enteromorpha clathrata	1.6 ± 0.7	15.5	1.2 ± 0.5	12.2	1.8 ± 0.7	14.9
Ulva lactuca	0.8 ± 0.5	8.2	2.4 ± 1.3	11.2	4.6 ± 2.0	11.8
Valoniopsis pachynema	2.0 ± 1.3	7.9	*	0.7	*	0.4
Boergesenia forbesii	1.7 ± 0.7	22.2	2.3 ± 0.7	25.2	0.6 ± 0.4	8.8
Codium arabicum	0.2 ± 0.1	2.5	0.3 ± 0.1	6.1	1.0 ± 0.5	15.4
Halimeda gracilis	1.4 ± 0.4	26.6	5.9 ± 0.9	66.2	6.4 ± 1.3	60.1
Phaeophyta						
Turbinaria ornata	*	2.2	0.8 ± 0.5	10.4	1.7 ± 0.7	16.2
Rhodophyta						
Gelidiella acerosa	0.1 ± 0.1	0.6	0.8 ± 0.6	3.6	0.3 ± 0.2	2.6
Portieria hornemannii	0.1 ± 0.1	1.9	*	1.1	*	0.4
Gracilaria edulis	3.9 ± 1.7	20.3	1.1 ± 1.2	1.8	*	0.4
Ceramium sp.	1.4 ± 0.9	9.5	3.7 ± 1.6	13.7	0.9 ± 0.5	9.2
Laurencia papillosa	1.7 ± 0.9	7.0	1.8 ± 1.0	7.2	0.2 ± 0.2	3.9
Acanthophora spicifera	–	–	0.2 ± 0.2	1.4	*	1.3

* mean cover ‹ 0.1%

Table III. Mean percentage cover (± S. E.) of common macrophytes at Agatti in April 1994.

	Upper reef flat		Middle reef flat		Lower reef flat	
	(0–45 m)	%Q	(50–95 m)	%Q	(100–145 m)	%Q
No. of quadrats	160		142		72	
Seagrass						
Thalassia hemprichii	49.3 ± 7.4	56.9	26.4 ± 7.1	33.1	–	–
Chlorophyta						
Ulva lactuca	0.4 ± 0.5	5.6	*	0.7	–	–
Chaetomorpha sp.	0.6 ± 0.4	8.1	–	–	*	1.4
Boergesenia forbesii	1.6 ± 0.8	21.9	1.2 ± 0.8	11.3	*	2.8
Codium arabicum	–	–	*	0.7	0.9 ± 0.6	13.9
Halimeda gracilis	0.3 ± 0.2	13.1	3.8 ± 1.1	43.7	3.1 ± 1.0	50.0
Rhodophyta						
Gelidiella acerosa	0.6 ± 0.5	6.9	4.2 ± 2.0	23.9	7.8 ± 3.5	37.5
Portieria hornemannii	0.3 ± 0.2	8.1	*	1.4	0.5 ± 0.4	11.1
Gracilaria edulis	0.1 ± 0.2	1.3	–	–	–	–
Ceramium sp.	*	1.3	*	0.7	–	–
Laurencia papillosa	0.2 ± 0.2	3.1	0.2 ± 0.1	6.3	0.3 ± 0.3	6.9
Acanthophora spicifera	0.5 ± 0.6	3.8	0.6 ± 0.8	2.8	0.1 ± 0.1	2.8

* mean cover < 0.1%

to 3 zones: an upper reef flat (0–45 m), middle reef flat (50–95 m) and lower reef flat (100–145 m). The clusters were very well defined, particularly during October 1993. The 0 m station was omitted from the clusters because nearly all quadrats at this station were bare. In October 1993, the 155 m–165 m stations formed a separate cluster probably because of the small number of quadrats analyzed at these stations. Similarly, in April 1994, the 150 m station was isolated for a similar reason.

The abundance of common macrophytes in these zones are presented in Tables II and III. The seagrass, *Thalassia hemprichii*, was dominant in the upper and middle reef flat. *Boergesenia forbesii*, *Gracilaria edulis* and *Valoniopsis pachynema* were dominant in the upper reef flat while *Gelidiella acerosa*, *Laurencia papillosa* and *Ceramium* sp. were abundant in the middle reef flat. *Ulva lactuca*, *Turbinaria ornata* and *Codium arabicum* were dominant in the lower reef flat. *Halimeda gracilis* was dominant in both the middle and lower reef flat.

There was a decrease in macrophyte species richness and percentage cover in successive zones with increasing distance from the shore (Fig. 6). Species diversity showed the reverse trend due to decreased abundance and dominance of the seagrass. The decrease in evenness values in successive zones can also be attributed to the decreasing dominance of seagrasses.

Temporal variation in the distribution and abundance of macrophytes, particularly algae, was observed. In the intervening period no storm/cyclone was reported in the study area. There was no statistically significant difference in seagrass cover (Table IV). Several algae, however, exhibited significant variation in abundance. Some species such as *Chaetomorpha* sp., *Gelidiella acerosa*, *Portieria hornemannii* and *Acanthophora spicifera* were significantly more abundant in April 1994. During this period, some algal species such as *Enteromorpha clathrata*, *Ulva lactuca*, *Halimeda gracilis*, *Turbinaria ornata*, *Gracilaria edulis*, *Ceramium* sp. and *Laurencia papillosa* became significantly much more restricted in distribution as well as abundance. In April 1994, the number of macrophyte species recorded in quadrats decreased from 34 to 17. Species richness, diversity and percentage cover of algae were lower in April 1994 compared to October 1993. Macrophyte biomass in October 1993 was higher than that observed in April 1994. Considering only algae, the increase was approximately three times and statistically significant ($t = 8.04$, 1232 df, $P < 0.001$). Re-analysis of the October 1993 data

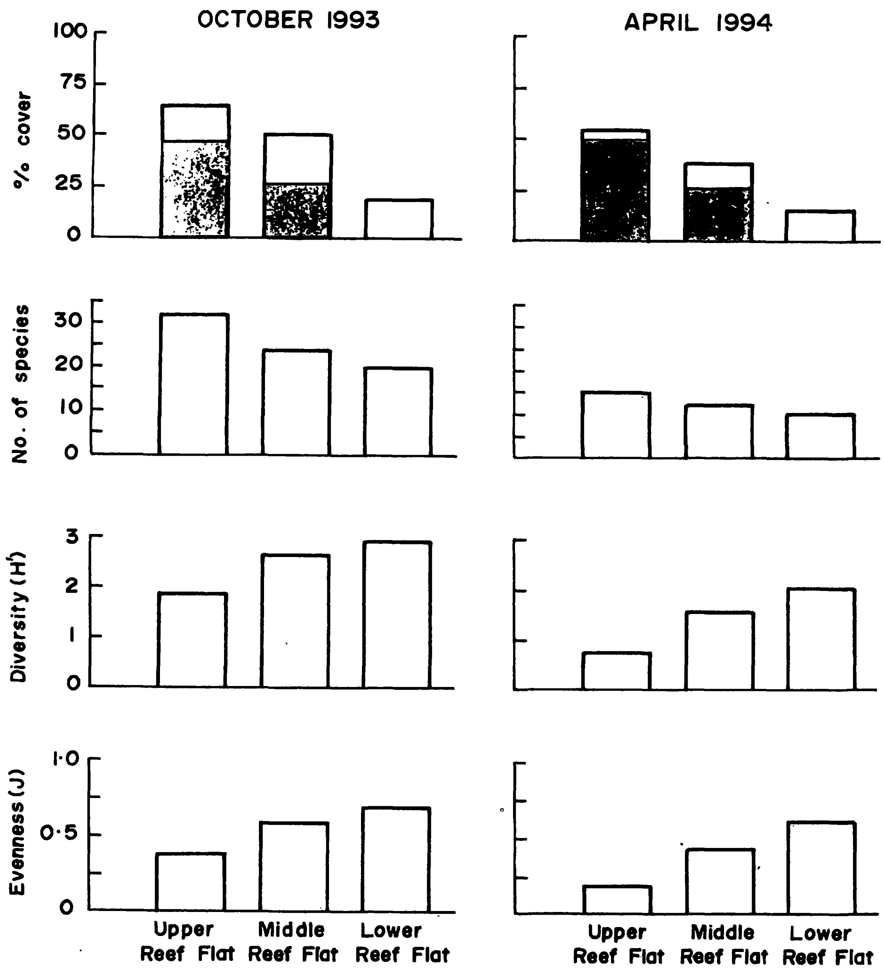

Fig. 6. Macrophyte community characteristics of the reef flat at Agatti in October 1993 and April 1994. The darkened bars denote the % cover of *Thalassia hemprichii.*

by considering only transects sampled in April 1994 did not significantly alter the results.

Discussion

Sixteen algal species are reported from Lakshadweep for the first time in this study. These species have however been recorded elsewhere along the Indian coast (Krishnamurthy and Joshi 1970, Untawale *et al.* 1983).

Macrophyte community characteristics such as percentage cover, species diversity and evenness can be correlated with distance from the shore. The subdivision of the intertidal reef flat into 3 zones can be

Table IV. Mean percentage cover (± S. E.) and total standing stock of macrophytes at Agatti.

	October 1993			April 1994			*t* value (1232 df)
	Mean % Cover	%Q	Biomass (t)	Mean % Cover	%Q	Biomass (t)	
No. of quadrats	850			384			
Seagrass							
Thalassia hemprichii	26.2 ± 2.9	29.8	474.0 ± 51.9	30.3 ± 4.5	35.9	547.5 ± 80.6	1.53 n. s.
Chlorophyta							
Enteromorpha clathrata	1.5 ± 0.4	14.1	20.5 ± 4.8	–	–	–	5.61***
Ulva lactuca	2.4 ± 0.7	10.1	26.8 ± 8.1	0.2 ± 0.2	2.6	2.0 ± 2.4	4.03***
Cladophora vagabunda	×	0.4	+	–	–	–	–
Cladophora sp.	×	0.5	+	–	–	–	–
Chaetomorpha sp.	–	–	–	0.3 ± 0.2	3.6	2.6 ± 1.8	4.20***
Valoniopsis pachynema	0.8 ± 0.5	3.3	1.8 ± 1.2	–	–	–	2.01*
Valonia utricularis	×	0.1	+	–	–	–	–
Boergesenia forbesii	1.6 ± 0.4	19.2	38.9 ± 8.8	1.1 ± 0.5	13.8	28.6 ± 11.1	1.34 n. s.
Caulerpa serrulata	×	0.4	+	×	0.3	+	–
Codium arabicum	0.4 ± 0.1	7.3	11.8 ± 4.1	0.2 ± 0.1	2.9	5.1 ± 3.4	2.05*
Halimeda gracilis	4.6 ± 0.6	50.2	145.1 ± 18.4	2.2 ± 0.5	31.5	67.9 ± 15.2	5.19***
Phaeophyta							
Hincksia sp.	×	0.4	+	–	–	–	–
Dictyopteris delicatula	0.1 ± 0.1	0.1	1.8 ± 3.6	–	–	–	0.67 n. s.
Padina australis	0.2 ± 0.1	2.4	3.3 ± 2.1	×	0.3	0.1 ± 0.2	2.08*
Turbinaria ornata	0.8 ± 0.3	9.1	25.5 ± 8.8	–	–	–	3.84***
Rhodophyta							
Actinotrichia fragilis	×	1.5	0.7 ± 0.6	×	1.3	0.3 ± 0.3	0.87 n. s.
Asparagopsis taxiformis	0.3 ± 0.2	2.0	5.3 ± 2.9	–	–	–	2.37*
Gelidiella acerosa	0.4 ± 0.2	2.1	1.9 ± 1.1	3.3 ± 1.0	19.3	17.3 ± 5.5	7.50***
Gelidiopsis intricata	×	0.2	+	–	–	–	–
Portieria hornemannii	0.1 ± 0.1	1.2	0.6 ± 0.6	0.2 ± 0.1	6.0	2.8 ± 1.5	3.05**
Gracilaria edulis	1.8 ± 0.7	8.2	24.2 ± 9.9	×	0.5	0.5 ± 0.9	3.16**
Solieria robusta	×	0.4	+	–	–	–	–
Hypnea musciformis	0.3 ± 0.2	2.9	1.7 ± 0.9	–	–	–	2.44*
Hypnea valentiae	0.1 ± 0.1	0.7	0.7 ± 0.6	–	–	–	1.58 n. s.
Hypnea pannosa	0.5 ± 0.4	1.2	3.3 ± 2.5	–	–	–	1.76 n. s.
Ceramium sp.	2.0 ± 0.6	10.8	7.8 ± 2.5	×	0.8	0.1 ± 0.1	4.06***
Spyridia hypnoides	×	0.2	+	–	–	–	–
Laurencia papillosa	1.3 ± 0.5	6.5	35.1 ± 12.8	0.2 ± 0.1	4.9	5.6 ± 2.9	3.01**
Acanthophora spicifera	0.1 ± 0.1	0.8	0.6 ± 0.5	0.4 ± 0.4	3.1	4.2 ± 3.7	2.72**
Polysiphonia sp.	×	0.1	+	–	–	–	–
Leveillea jungermannioides	×	0.1	+	–	–	–	–
Crustose coralline algae	0.9 ± 0.2	10.0	+	1.1 ± 0.3	16.7	+	1.13 n. s.
Cyanophyta							
Lyngbya sp.	0.2 ± 0.2	1.9	3.7 ± 2.6	0.1 ± 0.1	1.6	1.1 ± 1.0	1.30 n. s.
Phormidium sp.	×	0.2	+	–	–	–	–
Total macrophytes	46.5 ± 3.3		835.4 ± 59.2	39.6 ± 4.2		685.6 ± 77.3	2.37*
Number of species	34			17			
Diversity (H')	2.61			1.43			
Evenness (J)	0.51			0.35			

× mean cover < 0.1% + biomass not estimated *** P < 0.001 ** P < 0.01 * P < 0.05 n. s. not significant partly correlated with the gradient of physical factors such as temperature, desiccation and irradiation. The upper reef flat is characterized by beds of the seagrass, *Thalassia hemprichii*, with its associated algal species as well as faunal groups and can be delineated as a separate habitat. The dominant alga in this zone was *Gracilaria edulis* in October 1993 and *Boergesenia forbesii* in April 1994. Though harsh physical factors prevail in this zone during low tides, the moist seagrass beds offer shelter to their inhabitants and act as a refuge from desiccation. The dominant algae of the middle reef flat differed from those of the lower reef flat except for *Halimeda gracilis* which was abundant in both zones (see Tables II, III). The high standard error values recorded despite large sample size, indicate the high degree of patchiness exhibited by the majority of macrophytes, particularly algae. The absence of some species in quadrats in April 1994 could thus be partly attributed to their scarcity and patchy distribution. Patchiness could probably be a result of grazing and competition for space and light. Decrease in macrophyte abundance with increasing distance from the shore in coral reefs has been correlated with the abundance of herbivores (Miller 1982, Hay 1985). Thus, while the distribution of algae in the upper reef flat is governed by physical factors, those in the middle and lower reef flat appear to be controlled by biological factors.

Observations on temporal differences in abundance suggest seasonality. Along the Indian coast, many algal species, both annuals and perennials, exhibit maximum growth from October to December and degenerate from December/January onwards due to desiccation, depending on the tidal regime. This seasonal periodicity is governed by the monsoon during which there is intense wave action and turbidity (Svedelius 1906, Umamaheshwararao and Sreeramulu 1964, Murthy *et al.* 1978). In the monsoon-influenced Lakshadweep, it is wave action and desiccation that are the probable causes of algal periodicity as turbidity adversely affects corals. Effects of the high temperatures prevailing during the pre-monsoon season in the upper reef flat are mitigated by the moist seagrass beds.

The distribution of algae in tropical reef communities is determined by biological factors such as competition and grazing as well as physical factors such as wave action, irradiance, temperature and nutrient levels (Littler and Littler 1988, Luning 1990). Algal abundance depends on growth rate and mortality rate. Decrease in algal abundance can be attributed to natural mortality and herbivory. Though grazing rates of the large number of herbivores on the reef flat at Agatti have not been quantified, it appears that herbivory is significant. Furthermore, it is not known whether grazing is seasonal. Perhaps the effects of herbivory on algal abundance in October are not striking due to maximum algal growth rates and they become apparent in April due to the additional effects of desiccation. This question needs to be addressed in future experimental studies. Herbivory has been considered to play a primary role in determining the distribution of algae in coral reefs (Stephenson and Searles 1960, Samarco 1980, Lubchenco and Gaines 1981, Hay 1984). It has been reported to be intense on coral reefs, where grazers often consume 50−100% of total plant production (Hatcher and Larkum 1983, Carpenter 1986), more so than in any other marine habitat.

The grazers observed on the intertidal reef flat at Agatti atoll as well as elsewhere in Lakshadweep are the sea urchins, *Tripneustes gratilla* (Linnaeus), *Toxopneustes pileolus* (Lamarck), *Echinothrix* spp. and the herbivorous reef fishes *Abudefduf* spp., *Dascyllus* spp., *Chaetodon* spp. and juveniles of *Acantharus* spp., *Callyodon* sp. and *Leptoscarus* sp. Among these, sea urchins could be considered as dominant. They were abundant in the middle and lower reef flat. Mol-

Table V. Comparison of standing stock algal estimates (t) at Agatti reef flat.

Source	Subbaramaiah *et al.* (1979)#	Kaliaperumal *et al.* (1989)*	Present study	
Period of study	Jan−Mar '77	Jan−Mar '87	October 1993	April 1994
Boergesenia forbesii	2.3	+	38.9 ± 8.8	28.6 ± 11.1
Halimeda gracilis	112.0 − 301.5	+	145.1 ± 18.4	67.9 ± 15.2
Turbinaria ornata	−	768.1	25.5 ± 8.8	−
Gelidiella acerosa	98.7 − 164.2	6.3	1.9 ± 1.1	17.3 ± 5.5
Portieria hornemannii	6.0	+	0.6 ± 0.6	2.8 ± 1.5
Gracilaria edulis	−	415.3	24.2 ± 9.9	0.5 ± 0.9
Laurencia papillosa	8.8 − 83.3	+	35.1 ± 12.8	5.6 ± 2.9
Total algal biomass	283.8 − 738.9 763.2 − 2137.7*	3836.8	361.4 ± 29.2	138.1 ± 22.7
Number of species	11	37	34	17

lower and upper limits of estimates * includes reef and lagoon biomass + data not available

luscs such as *Aplysia* sp., *Nerita* spp. and *Littorina* spp. were not abundant and constituted minor grazers. One group of omnivores, the sea cucumbers (holothurians), appears to have been overlooked by many investigators. These animals were distributed over the entire reef flat. The ecological role of holothurians has not been elucidated (Bakus 1973, Kerr *et al.* 1993). During the present study, dissection of common holothurians, such as *Holothuria* spp. and *Actinopyga* spp., revealed remnants of algal fragments, particularly *Halimeda* sp., among the sediment deposit in the gut. The calcified green alga, *Halimeda* sp., has been considered unpalatable to herbivores due to the presence of secondary metabolites (Hay 1984) but it is likely that these chemicals do not deter omnivorous holothurians.

Lastly, we consider exploitation of algal resources at Agatti. Standing stock estimates are given in Table V. The present estimates are close to those of Subbaramaiah *et al.* (1979) though their values have a very large range, presumably due to the small sample size. Estimates by Kaliaperumal *et al.* (1989) appear to be high. The present study reveals that estimates vary from season to season, and hence a proper assessment of resources can be arrived at only after analysing annual algal biomass production and ascertaining peak production periods. Threats to reef communities due to resource utilization is well documented (Littler and Littler 1988). Harvesting of algal resources can lead to a decline in herbivore populations, resulting in a decrease in the overall biodiversity of the reef flat. The grazing requirements of hervibores in the reef would thus need to be assessed. This assessment is essential to prevent overexploitation of natural resources and for the proper management of the fragile coral reef ecosystem.

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