The deep-water species of *Halimeda* Lamouroux (Halimedaceae, Chlorophyta) from San Salvador Island, Bahamas: species composition, distribution and depth records

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Abstract. Caribbean species of *Halimeda* from the steep slopes of San Salvador Island, Bahamas, were collected along vertical transects between 25 and 255 m, on the northeast, northwest, west, southwest and south sides of the island, using the Harbor Branch Oceanographic Institution's submersible *Johnson Sea Link I*. The characteristics delineating species (segment and utricle size) were assessed for selected species, and the depth and western Atlantic distributions of the species reviewed. *Halimeda copiosa* was found to show a variation of surface utricle diameter with depth, with the deeper plants having 15% larger diameter utricles than the shallower plants. Of the seven species, one variety and one form of *Halimeda* studied from our submersible dive sites, *H. copiosa, H. cryptica* and *H. gracilis* grew to the greatest depths, from 120 to 150-m depths. *H. lacrimosa* var. *globosa* was found growing to 91 m, and *H. tuna* f. *platydisca* and *H. discoidea* to a depth of 73 m. Those of lesser depth, to 61 m, were *H. goreauii, H. tuna* f. *tuna* and *H. lacrimosa* var. *lacrimosa*. These represent substantial increases in depth distribution of the nine taxa found.

Introduction

The benthic marine flora of the Caribbean, in general, has received quite a bit of attention. Investigations by Mazé and Schramm (1878), Murray (1888, 1889), Børgesen (1913–1920) and Taylor (1942, 1960) established the bases for our knowledge of the species composition and distribution of the marine algae of the region. More recent studies by, among others van den Hoek et al. (1978), Price and John (1979), Norris and Bucher (1982), Almodovar and Ballantine (1983), and numerous reports by Taylor (e.g. 1969; Taylor and Abbott 1973) have contributed to the overall understanding of the Caribbean marine flora.

In the Caribbean, with the exception of Howe (1920) and Marshall (1980), little work has been done in Bahamian waters. Further, recent investigators have shown that a diverse and often unique, abundant deepwater flora exists in many regions of the western Atlantic (Cheney and Deyer 1974; Schneider 1974; Oliveira Filho 1976; Oliveira Filho and Quége 1978; Sears and Cooper 1978; Eiseman 1979; Eiseman and Norris 1981; Eiseman and Earle 1983; Littler et al. 1985, 1986).

The general lack of information on the Bahamian marine flora, specifically from deep water, prompted a collaborative research program between the Harbor Branch Oceanographic Institution and the Smithsonian Institution to examine the species composition and distribution of the deep-water algae off San Salvador Island, Bahamas. Some results of our first joint expedition have been reported elsewhere (Littler et al. 1985; Jensen et al. 1985; Littler et al. 1986).

Halimeda is an often dominant, ecologically and geologically important component of the subtropical and tropical reef flora. There are 33 species in the genus (Hillis-Colinvaux 1980; Dong and Tseng 1980; Ballentine 1982, Noble 1986), with 14 species, 4 varieties and 8 forms reported in the subtropical-tropical western Atlantic (Wynne 1986). The present account describes our specimens, and gives the depth, regional distribution, and species composition of the deep-water representatives of the genus *Halimeda* [Bryopsidales (=Caulerpales, see Silva 1982); Halimedaceae [1]] from San Salvador Island, Bahamas.

[1] Silva (1980; see also Nicolson 1981) has recently proposed the name Codiaceae Kützing (1843) for conservation over Halimediaceae Link (1832); both names have nomenclatural priority over Udoteaceae J. Agardh (1887)

Methods

Study site

San Salvador Island is located approximately 600 km ESE of Miami, Florida (24°02′ N, 74°30′ W), along the eastern margin of the Bahama Island chain. San Salvador Island has patchy shallow-water fringe reefs that extend 0.16 to 0.8 km out from the island. At the seaward edge of the patch reefs, the bottom slopes nearly vertically, producing a wall structure with numerous ledges and undercuts, to a depth of 135 to 165 m. Below this, the bottom slopes at a 30- to 60-degree angle to a depth of approximately 225 to 270 m. An indication of the steepness of the slope around the island is the fact that depths in excess of 1000 m can be found approximately 1.5 to 2 km off its coast.

Five locations were selected for sampling, representing the various directional faces of the island (Fig. 1). The sampling sites were Dixon Hill, on the northeast side (24°8.3′ N, 74°26.2′ W; Station 1), Green Cay, on the northwest side (24°8.5′ N, 74°31.2′ W; Station 2), Cockburntown, on the west side (24°3.2′ N, 74°32.6′ W; Station 3), Fernandez Bay, on the southwest side (24°0.9′ N, 74°33.4′ W; Station 4) and French Bay, on the south side (23°56.7′ N, 74°31.3′ W; Station 5) of the island (Fig. 1). These samples were supplemented with incidental samples from the Pinnacle area, north of the island (24°14.0′ N, 74°28.9′ W), and the Northeast point (24°8.4′ W; 74°26.3′ W).

The collections were made with the submersible JOHNSON SEA LINK-I. This four-person submersible is equipped with various instrumentation and pilot controlled equipment, such as a manipulator arm with Petersen style grab sampler and a suction collection device, a rotating bin system for segregation of samples, a Benthos 35-mm color still camera with strobe, Sony color video camera (3/4″), current meter, conductivity-temperature-depth meter, sonar, and ship to submersible communicator.

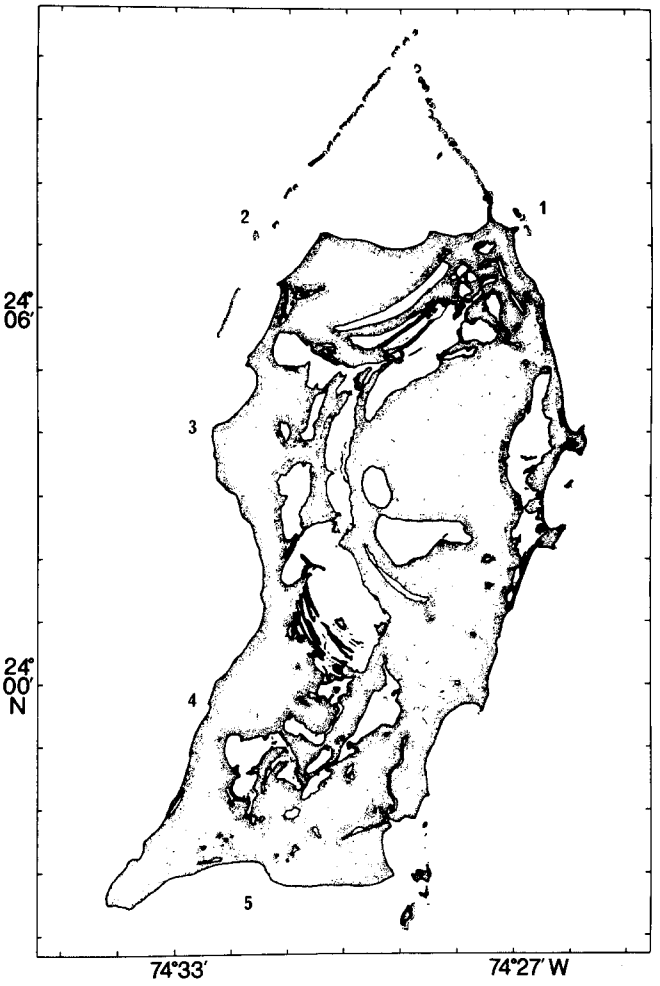

Fig. 1. Map of San Salvador Island, Bahamas, showing the sampling stations around the island: *1* Dixon Hill, *2* Green Cay, *3* Cockburntown, *4* Fernandez Bay, *5* French Bay

Samples were collected at 15.2-m (50-ft) intervals along vertical transects at each sampling station, starting at the bottom of algal growth (usually above 250-m depth) and ending at the top of the wall structure. Samples were preserved in 5% buffered Formalin/seawater and returned to the lab for identification. Specimens are deposited in the Algal Collection of the U.S. National Herbarium (US) of the Smithsonian Institution and the Harbor Branch Oceanographic Institution Herbarium (HBFH).

Morphometrics

Two species were chosen for a detailed assessment of utricle size, each quantified for a different question. The utricle size and structure of *Halimeda tuna* f. *tuna* was examined to test if significant variation existed between the San Salvador Island samples, and those of *Halimeda tuna* known from elsewhere in the Caribbean and in the Mediterranean. This evaluation was conducted owing to a lack of fit of utricle characteristics of the San Salvador Island specimens when compared to illustrations and descriptions given by Hillis-Colinvaux (1980). To determine if a variation existed, three specimens from San Salvador were arbitrarily selected for utricle size determination. Three segments from each of these plants were hand sectioned after decalcification in 10% HCl, and 50 surface utricles, haphazardly selected, were measured for length and width. The length and width of supporting utricles were also measured. These measurements were compared with the published utricle size dimensions of Hillis-Colinvaux (1980) for *H. tuna*. The utricle organization of the San Salvador specimens was compared with the utricle organization of specimens of *H. tuna* from the Mediterranean Sea (type locality for *H. tuna*).

The second species examined, *Halimeda copiosa,* was selected to test if there were any significant differences between utricle sizes of the plants with depth. To determine this, the length and width of 150 surface utricles were measured in each of three plants (50 utricles/segment; three segments/plant) from 76 m and in three plants collected between 122 to 132 m. The Kruskal-Wallis test was used to test if significant differences existed within each depth group (i.e., segment to segment and plant to plant variation) and between each of the two depth groups.

Results

Our study revealed nine taxa, representing seven species of the genus *Halimeda,* in the San Salvador samples. The *Halimeda* species present in the deep-water flora and

Table 1. Species present and depth range at the five sampling stations around San Salvador Island (depths in meters). DH = Dixon Hill, GC = Green Cay, CT = Cockburntown, FNB = Fernandez Bay, FRB = French Bay

Species	Stations				
	DH	GC	CT	FNB	FRB
H. copiosa	61–152	76–91	108–122	107–137	61–91
H. cryptica	61–152	76–91	70–107	61–152	107
H. discoidea		73			61
H. goreauii			29		61
H. gracilis	61–152	107	61–107	107	76–122
H. lacrimosa var. *lacrimosa*				61	
H. lacrimosa var. *globosa*	37–152		61–70		61
H. tuna f. *tuna*		70–76	100		
H. tuna f. *platydisca*					61–70

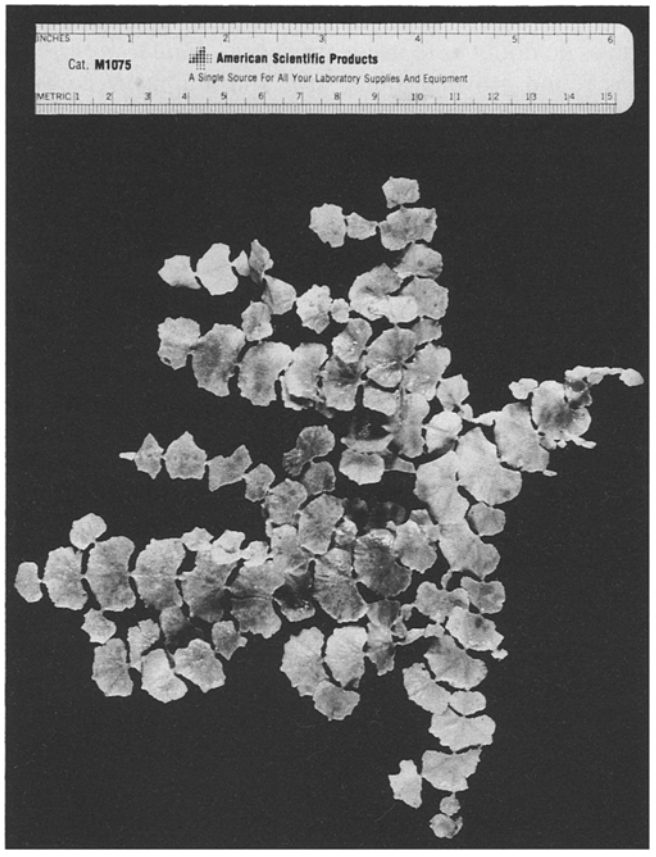

Fig. 2. Habit of *Halimeda copiosa*

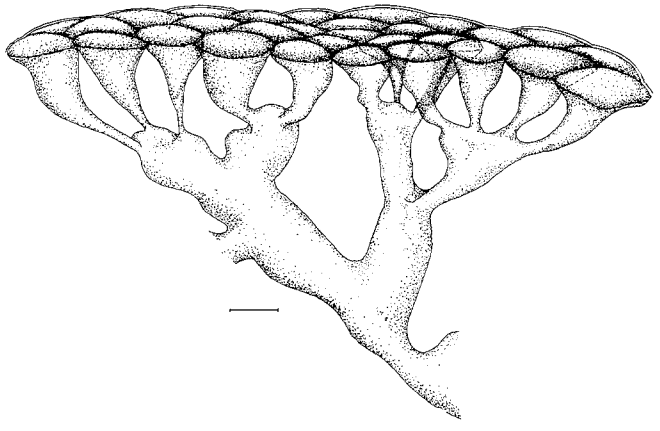

Fig. 3. Utricle structure of *Halimeda copiosa*

Table 2. Surface utricle variation in *Halimeda copiosa* with depth

	Width (μm)	Length (μm)
76 m		
Mean	29.5	39.9
s. d.	4.0	6.9
122 m		
Mean	33.8	37.2
s. d.	5.4	7.2
Kruskal-Wallis H =	10.7	101.4
Significance level	< 0.001	< 0.001

their depth range at each sampling station are summarized in Table 1. These species are listed below with descriptions based on our Bahamian specimens, their local distribution and references to their western Atlantic distribution. Of the nine taxa, two species, *H. gracilis* and *H. cryptica* have not previously been reported from the Bahamas. The voucher specimens for the photosynthesis and calcification studies of Jensen et al. (1985) are reported in this study.

Halimeda copiosa Goreau et Graham 1967:433

The Bahamian deep-water plants are up to 40 cm long, from a single holdfast. The plant is di-trichotomously branched in a single plane. Segments are depressed ovate to transversely oblong, often dorsally convex (Fig. 2). The segment size varies from 7 to 15 mm wide and 5 to 11 mm long. Utricles in 2–3 series (Fig. 3), surface utricles 18 to 50 μm wide (mean = 33 μm) and 18.5 to 79 μm long (mean = 38 μm). Subsurface utricles were 18 to 43 μm wide (mean = 30 μm) and 28 to 74 μm long (mean = 41 μm).

Reported distribution. San Salvador Island: Pinnacle (no of island), Northeast Pt., Dixon Hill, Green Cay, Cockburntown, French Bay. Caribbean: Bahamas (Bula Meyer 1982); Belize (Norris and Bucher 1982); Curaçao (Colinvaux 1968, 1969); Jamaica (Goreau and Graham 1967); Netherland Antilles (van den Hoek et al. 1978); Puerto Rico (Ballantine 1982; Almodovar and Ballantine 1983); Venezuela (Bula Meyer 1982; Diaz-Piferrer 1970; Colombia (Bula Meyer 1982).

Remarks. Our plants agree very well with the descriptions and illustrations of Goreau and Graham (1967) and Hillis-Colinvaux (1980). While utricle sizes fit into the ranges given by the above authors, significant differences in utricle size were found with depth. The variances found were still within the reported range for this species. Results of the comparison of the utricle sizes of deep and shallow water plants (Table 2) show the deeper specimens to have a significantly larger surface utricle diameter (mean = 33.8 μm) than the shallower plants (mean = 29.5 μm). *Halimeda copiosa* was the most common *Halimeda* in the deep-water algae community off San Salvador Island. This species was collected between 61 and 152 m at the various stations around the island. This represents a substantial increase in the known depth range of this plant.

Specimens studied. San Salvador Island: Pinnacle, north of island, 18 Oct. 1983, J. Norris, D. Liberatore & S. Blair, 76 m, No. JSLI-1493-4; Northeast Point, 10 Oct. 1983, D. Liberatore, S. Blair & J. Norris, 91 m, No. JSLI-1480-2; Green Cay, 14 Oct. 1983, S. Blair, P. Jensen and D. Liberatore, 76.3 m, No. JSLI-1486-31, and 91.6 m, No. JSLI-1486-28; Dixon Hill, 11 Oct. 1983, D. Liberatore, S. Blair & R. Gibson, 61 m, No. JSLI-1481-48;

French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1483-12; Cockburntown, 18 Oct. 1983, J. Norris & S. Blair, 29.3 m, No. JSLI-1494-28.

Halimeda cryptica Colinvaux et Graham 1964:5

Plants to 10 cm long from a single small holdfast, with moderate to heavy calcification, and light green to off-white (cream) color. Branching di-trichotomous (Fig. 4). Segments depressed ovate to shallowly trilobed in the lower and middle portions of the plant, and rhombic to tranversely elliptic in the upper portion. Cortex of two to three layers of utricles. The segments small, 2 to 8 mm (mean = 4 mm) wide and 2 to 5 mm (mean = 4 mm) long, with a distinctive (after decalcification) uniaxial construction. Surface utricles 45–60 μm wide, 50–65 μm long.

Reported distribution. San Salvador Island: Pinnacle, Dixon Hill, Green Cay, Cockburntown, French Bay. Caribbean: Jamaica (Colinvaux and Graham 1964; Goreau and Goreau 1973; McConnell and Colinvaux 1967; Moore et al. 1976); Puerto Rico (Ballantine 1982; Almodovar and Ballantine 1983).

Remarks. The segment sizes recorded for the San Salvador plants are smaller than those reported by Colinvaux and Graham (1964) and Hillis-Colinvaux (1980). However, the unique uniaxial construction of this species leaves no doubt as to its identification. *Halimeda cryptica* was found growing along with and among *H. copiosa,* though much less commonly. This is in contrast to what has been described for the areas off Jamaica (Goreau and Goreau 1973; Moore et al. 1976). *Halimeda cryptica* was collected off San Salvador between 61 and 152 m. This represents a 50 m increase in its depth range. These specimens represent the first record of *H. cryptica* for the Bahamas.

Specimens studied. San Salvador Island: French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 174 m, No. JSLI-1483-57, 91 m, No. JSLI-1483-38; 61 m, No. JSLI-1483-11; Dixon Hill, 11 Oct. 1983, S. Blair, D. Liberatore & R. Gibson, 91 m, No. JSLI-1481-95, 76 m, No. JSLI-1481-71; and 61 m, No. JSLI-1481-56; Pinnacle, north of island, 12 Oct. 1983, M. Littler, T. Askew & D. Littler, 73 m, No. JSLI-1482-7; Green Cay, 14 Oct. 1983, S. Blair, D. Liberatore, P. Jensen, 91 m, No. JSLI-1486-8; 76 m, No. JSLI-1486-34; Cockburntown, 18 Oct. 1983, J. Norris, S. Blair & D. Liberatore, 85 m, No. JSLI-1494-2.

Halimeda discoidea Decaisne 1842:91

Plants 7 to 15 cm long, attached by a much reduced single basal segment. Segments thick, lightly calcified, discoid

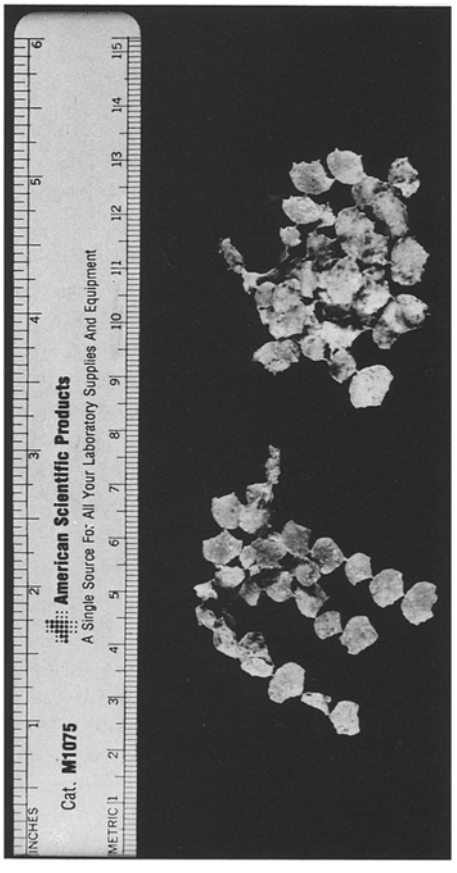

Fig. 4. Habit of *Halimeda cryptica*

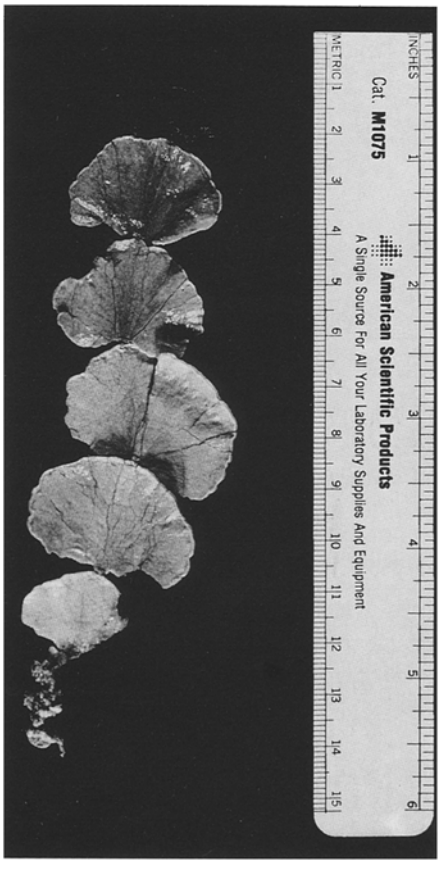

Fig. 5. Habit of *Halimeda discoidea*

to slightly reniform with smaller segments often cuneate to subcuneate (Fig. 5). Segments 7 to 35 mm wide (mean = 21 mm), 14 to 19 mm long (mean = 16 mm). Upper segments 14 to 40 mm wide (mean = 23 mm) and 11 to 27 mm long (mean = 18 mm). Cortex of 2–3 layers of utricles, with the surface utricles 30–50 μm diam. Subsurface utricles characteristically large 90–150+ μm diam.

Reported distribution. San Salvador Island: Pinnacle, French Bay. Caribbean: Antigua, St. Lucia (Taylor 1962a, b); Bahamas (Howe 1920; Taylor 1960); Belize (Norris and Bucher 1982); Brazil (Joly 1953; Oliveira Filho 1977); Cuba (Howe 1918; Taylor 1960); Florida (Taylor 1960; Mathieson and Dawes 1975; McConnell and Colinvaux 1967; Woelkerling 1976); Jamaica (Taylor 1960); Colombia (Taylor 1960); Nicaragua (Phillips et al. 1982); Panama (Earle 1972; Taylor 1960); Puerto Rico (Almodovar and Ballantine 1983; Taylor 1960); Sombrero Is. (Odgen et al. 1985); Venezuela (Taylor 1976); Virgin Islands (Taylor 1960).

Remarks. The majority of the specimens we collected would agree with the habit described for *H. discoidea* f. *platyloba* Børgesen (1911); however, most specimens showed both large and small segment sizes. Because of this gradient of segment size, the authors did not feel subspecific recognition appropriate. This species was collected between 61 and 73 m, being found on the lesser slopes near the top of the "wall" structure. The depth range of the San Salvador samples represents an increase in the known depth range for this species.

Specimens studied. San Salvador Island: Pinnacle, north of island, 18 Oct. 1983, J. Norris, D. Liberatore & S. Blair, 76 m, No. JLSI-1493-11; French Bay, 13 Oct. 1983, S. Blair, R. Gibson, D. Liberatore, 61 m, No. JSLI-1483-8.

Halimeda goreauii Taylor 1962 b:173

Plants small in size (< 10 cm), attached by a single basal segment. Lower segments trident, often ribbed and the trident tips cylindrical. Upper segments more variable, from trident to flattened trilobed. Segments small, 1.5 to 3.5 mm wide by 1.5 to 3.5 mm long.

Reported distribution. San Salvador Island: Cockburntown, French Bay. Caribbean: Bahamas, Belize (Norris and Bucher 1982); Colombia (Bula Meyer 1982); Cuba (Suarez 1973); Jamaica (Taylor 1962 b; McConnell and Colinvaux 1967; Moore et al. 1976; Bula Meyer 1982); Puerto Rico (Almodovar and Blomquist 1965).

Remarks. This small species of *Halimeda* was not common on the fore reef slope around San Salvador. It was more commonly seen beneath ledges and coral heads in the shallow-water patch reefs surrounding the island. The plant agrees well with Taylor's (1962 b) description and the illustration in Hillis-Colinvaux (1980). The segment size is slightly smaller, but there is little doubt as to the identification of this species.

Specimens studied. San Salvador Island: French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1583-14, and No. JSLI-1483-22; Cockburntown, 18 Oct. 1983, J. Norris & S. Blair, 29.3 m, No. JSLI-1494-25.

Halimeda gracilis Harvey ex J. Agardh 1887:82

Plants sprawling, decumbent, to 15 cm long. Holdfast initially from a single basal segment, but adventitious holdfasts may occur. Segments moderately to heavily calcified, 7–15 mm wide and 5–10 mm long (Fig. 6). The segment shape is reniform to subcuneate, with a glossy surface and slightly undulated margin.

Reported distribution. San Salvador Island: Dixon Hill, Fernandez Bay, French Bay. Caribbean: Barbados, Jamaica, Virgin Islands (Taylor 1960); Cuba (Suarez 1973); Florida (Taylor 1960; Woelkerling 1976); Puerto Rico (Ballantine 1982; Almodovar and Ballantine 1983; Taylor 1960); Brazil (Oliveira Filho 1977).

Remarks. Halimeda gracilis was most commonly found intermixed with *H. copiosa*. Although collected from all five stations, this species was not as common a compo-

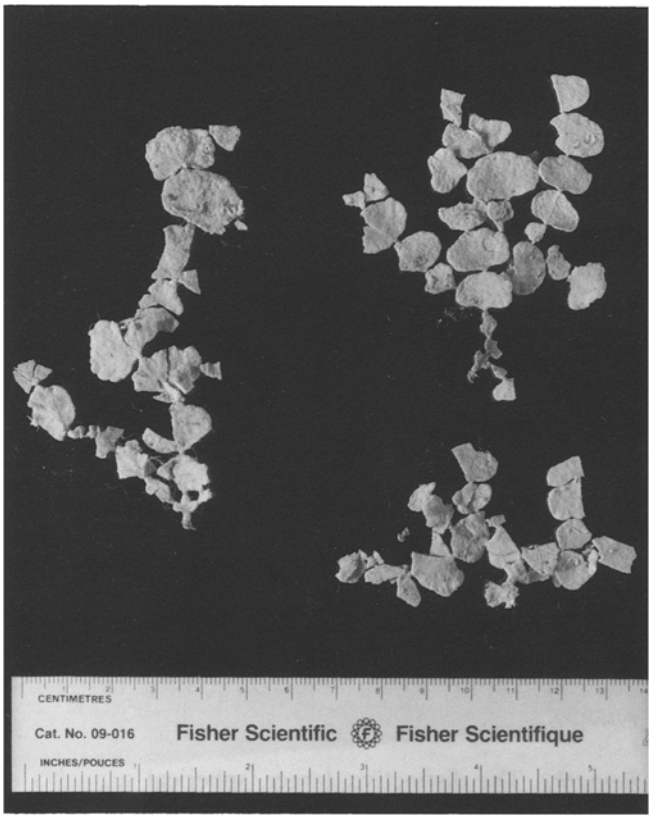

Fig. 6. Habit of *Halimeda gracilis*

nent of the deepwater *Halimeda* flora as the latter species. *Halimeda gracilis* was collected between 61 m and 122 m during this investigation and represents a substantial increase in the known depth distribution of this species. This is the first record of *H. gracilis* from the Bahamas.

Specimens studied. San Salvador Island: French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 91.4 m, No. JSLI-1483-39; Dixon Hill, 11 Oct. 1983, J. Norris. S. Blair & D. Liberatore, 61 m, No. JSLI-1481-47, and 91.4 m, No. JSLI-1481-96; Fernandez Bay, 14 Oct. 1983, M. Littler, R. Gibson & D. Liberatore, 70 m, No. JSLI-1485-11; and 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1484-41.

Halimeda lacrimosa Howe 1909:93 var. *lacrimosa*

Plants lax, irregularly branched, repent to partially erect, to 24 mm long. Segments hollow, obovoid to pyriform, 1 to 3(−5) mm diam.; heavily calcified and easily broken upon drying.

Reported distribution. San Salvador Island: Fernandez Bay. Caribbean: Bahamas (Howe 1909, 1920; Taylor 1960; Dawes and Humm 1969); Cuba (Howe 1918; Taylor 1960); Florida (Dawes et al. 1967).

Remarks. Halimeda lacrimosa var. *lacrimosa* is the smaller of the known varieties, with obovoid, subglobose or pyriform segments, <5 mm in diameter. Previously reported from low-intertidal to a depth of 20 m, our specimens extend the known depth to 61 m.

Specimen studied. San Salvador Island: Fernandez Bay, 13 Oct. 1983, S. Blair, D. Liberatore & R. Gibson, 61 m, No. JSLI-1484-55.

Halimeda lacrimosa var. *globosa* Dawes et Humm ex Dawes 1980:142

Plants straggling, more or less decumbent, branches free, to 15 to 25 cm long (Fig. 7). Initially attached by a single holdfast but capable of developing adventitious holdfasts. Segments hollow, mostly spherical, some tear shaped, 3 to 8(−9) mm diam. and heavily calcified. Although the segments are heavily calcified, they are very brittle and easily crushed or broken. Cortex of two to three layers, produced by lateral branches of the medullary filaments.

Reported distribution. San Salvador Island: Northeast Point, Dixon Hill, Cockburntown, Fernandez Bay, French Bay. Caribbean: Bahamas (Dawes and Humm 1969).

Remarks. The distinctive, larger, spherical segments of this variety distinguishes it from *H. lacrimosa* var. *lacrimosa* (Dawes and Humm 1969) and makes this form

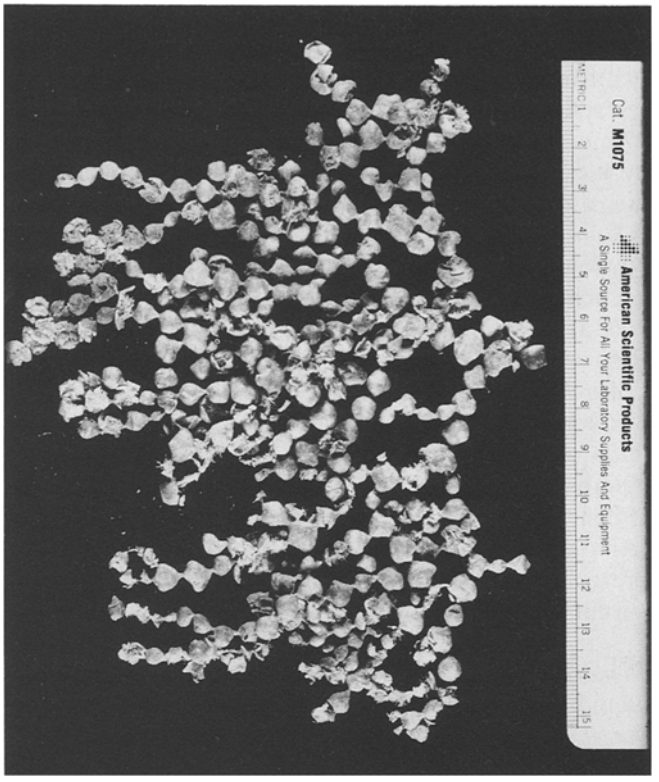

Fig. 7. Habit of *Halimeda lacrimosa* var. *globosa*

one of the most striking *Halimeda* species. Although previously considered a diminutive plant (<10 cm long, Dawes and Humm 1969; Dawes 1980), with mostly spherical segments to 10 mm diam., *H. lacrimosa* var. *globosa* can be found in large decumbent clusters, 15 to 25 cm long, in the deeper waters off San Salvador. This taxa was found between 37 and 91 m at various locations around San Salvador Island. The previous reports of small plants have been from much shallower depths, 1 to 10 m (Dawes and Humm 1969). The finding of larger plants than previously reported and at greater depths off San Salvador may indicate that this plant is better adapted to the moderate to low light conditions found in the deeper waters.

Specimens studied. San Salvador Island: Northeast Point, 10 Oct. 1983, S. Blair, D. Liberatore & J. Norris, 91 m, No. JSLI-1480-1; Dixon Hill, 11 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1481-50, and 37.5 m, No. JSLI-1481-107; French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1483-1; Fernandez Bay, 14 Oct. 1983, M. Littler, R. Gibson & D. Liberatore, 70.2 m, No. JSLI-1485-1; Cockburntown, 18 Oct. 1983, J. Norris, S. Blair & D. Liberatore, 61–67 m, No. JSLI-1494-21 a.

Halimeda tuna (Ellis et Solander) Lamouroux 1812:186 f. *tuna*

Plants to 20–25 cm, erect from a single holdfast. Segments below compressed to irregularly cylindrical, pro-

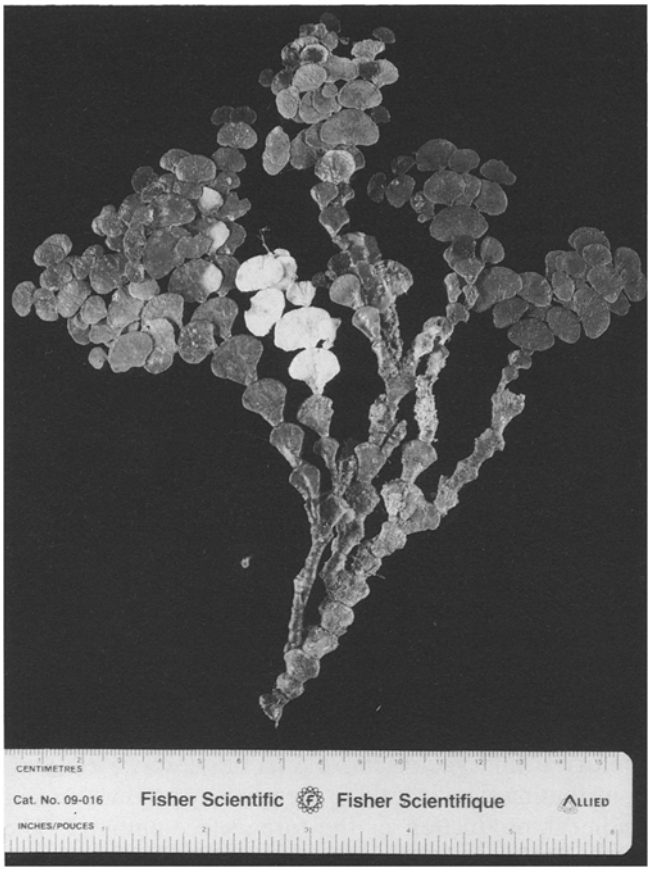

Fig. 8. Habit of *Halimeda tuna* f. *tuna*

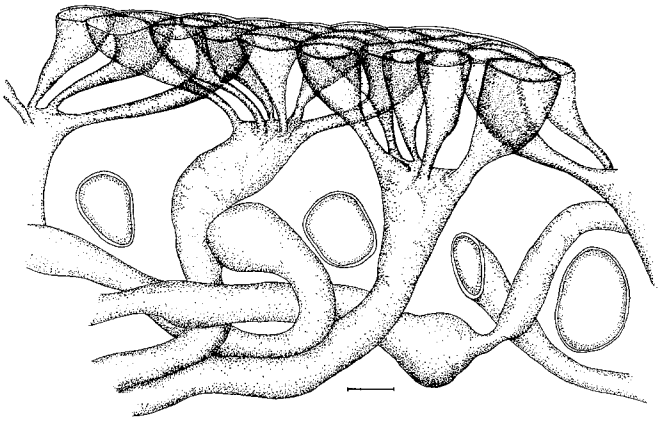

Fig. 9. Utricle structure of Bahamian *Halimeda tuna* plants

ducing a stalk-like structure; above subcuneate, reniform to discoid (Fig. 8). Segments 3.5 to 13 mm wide (mean = 8 mm), and 4 to 13 mm long (mean = 7 mm); lightly to moderately calcified. Cortex of two layers (rarely three) of utricles (Fig. 9); the surface utricles are 18 to 61 μm wide (mean = 33 μm) and 18 to 104 μm long (mean = 47 μm). Subsurface utricles are not notably inflated and are 15 to 67 μm wide (mean = 36 μm).

Reported distribution. San Salvador Island: Pinnacle, Cockburntown, Fernandez Bay. Caribbean: Antigua (Price and John 1979); Bahamas (Howe 1920; Taylor 1960); Barbados (Taylor 1960); Belize (Taylor 1960; Norris and Bucher 1982); Bermuda (Taylor 1969); Brazil (Oliveira Filho 1977); Caicos Island (Taylor 1960); Columbia (Taylor 1960); Costa Rica (Dawson 1962; Wellington 1974); Cuba (Howe 1918; Taylor 1960); Florida (Taylor 1960; Woelkerling 1976); Guadeloupe (Taylor 1960); Isla San Andres (Kapraun 1972); Jamaica (McConnell and Colinvaux 1967); St. Kitts, Nevis (Taylor 1969); Nicaragua (Phillips et al. 1982); Panama (Taylor 1960, Earle 1972); Puerto Rico (Taylor 1960; Almodovar and Ballantine 1983); St. Croix (Connor and Adey 1977); St. Eustatius (Vroman 1968); Sombrero Is. (Ogden et al. 1985); Venezuela (Diaz-Piferrer 1970; Taylor 1976).

Remarks. There was a certain degree of confusion regarding the appropriate placement of this name on the specimens from San Salvador. The overall habit and segment sizes corresponded well to *H. tuna*; however, there was a substantial difference between the cortical utricle organization of the specimens from San Salvador and the illustrations and descriptions of Hillis-Colinvaux (1980) for *H. tuna*. Specifically, Hillis-Colinvaux (1980, p. 122) states this species has two to four layers of utricles, and illustrates (Hillis-Colinvaux 1980, Fig. 20) a cortical structure regularly with three utricle layers and subsurface utricles slightly to obviously inflated. The specimens from San Salvador Island showed two layers of utricles (very rarely three) and no inflation of the subsurface utricles (Fig. 9). The ranges of utricle sizes of the San Salvador specimens (see above) are at the low end or lower than those reported for *H. tuna* by Hillis-Colinvaux (1980). Examination of specimens of *H. tuna* (US), from the type locality ("...in the Mediterranean Sea"; Ellis and Solander 1786:111) showed them to have two layers of cortical utricles and to be indistinguishable from our San Salvador specimens. Further, Barton (1901 as "f. *typica*"), albeit a single utricle series, illustrates only two layers of utricles for this species. Thus, after examination of material from the type region, it is without reservation that we identify the San Salvador specimens as *H. tuna* f. *tuna*. The illustration presented herein (Fig. 9) appears more representative of Caribbean *H. tuna* f. *tuna* than that shown by Hillis-Colinvaux (1980, Fig. 20).

Specimens studied. San Salvador Island: Fernandez Bay, 14 Oct. 1983, M. Littler, R. Gibson & D. Liberatore, 70 m, No. JSLI-1485-19; Pinnacle, north of island, 18 Oct. 1983, J. Norris, D. Liberatore & S. Blair, 73 m, No. JSLI-1493-15; Cockburntown, 18 Oct. 1983, S. Blair, J. Norris & D. Liberatore, 20 m, No. JSLI-1494-46.

Halimeda tuna f. *platydisca* (Decaisne) Barton 1901:14

Plants to 15 cm tall, attached by a single holdfast. Segments discoid 14 to 28 mm wide and 10 to 20 mm long with an erose margin (Fig. 10); lowest segments much re-

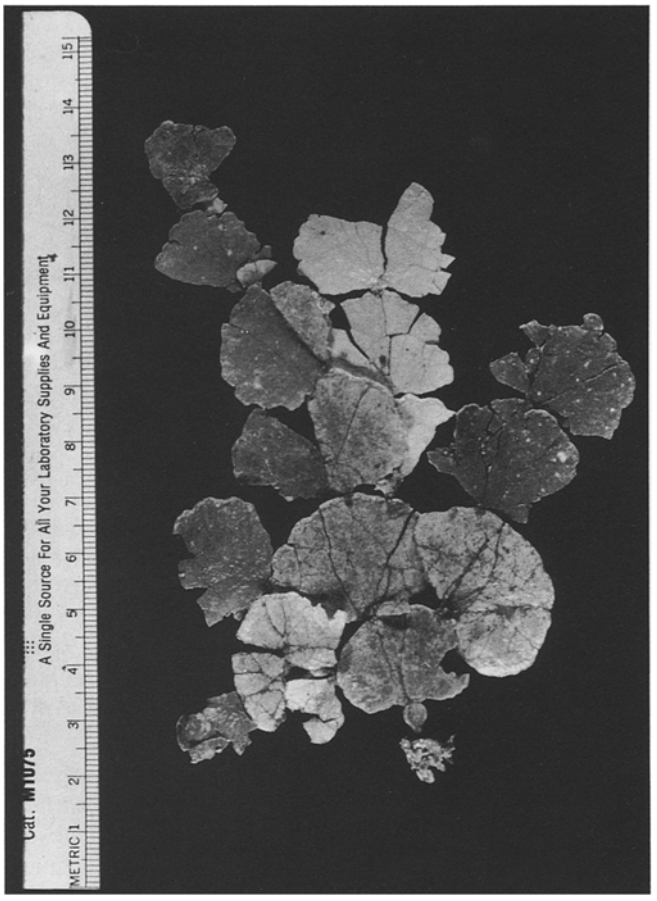

Fig. 10. Habit of *Halimeda tuna* f. *platydisca*

duced. Calcification moderately heavy, the segments thin and brittle on drying.

Distribution. San Salvador Island: French Bay. Caribbean: Florida (Taylor 1928, 1960); Guadeloupe (Mazé and Schramm 1878); Virgin Islands (Børgesen 1913).

Remarks. This taxon was collected between 61 m and 70 m. General habit of *H. tuna* f. *platydisca* is similar to that of *H. discoidea* var. *platyloba*; however, the utricular organization can be used to easily separate the two taxa. Taylor (1960) reports this form as "seldom" dredged ... but found to a depth of 32–80 m". Our collections suggest it may be more common in deep water than previously recognized.

Specimens studied. San Salvador Island: French Bay, 13 Oct. 1983, S. Blair, R. Gibson & D. Liberatore, 61 m, No. JSLI-1483-3a, and No. JSLI-1483b; 22 Oct. 1982, S. Blair, R. Gibson & M. Flake, 70 m, No. JSLI-1298-1.

Discussion

All taxa except *H. tuna* f. *tuna* were present French Bay. Three of the nine taxa, *Halimeda copiosa, H. cryptica* and *H. gracilis,* were found at all sampling sites; these same species showed the deepest overall depth ranges (Table 1).

The *Halimeda* taxa found can be divided into three groups on the basis of their depth ranges. The first group, *H. goreauii, H. discoidea, H. lacrimosa* var. *lacrimosa* and *H. tuna* f. *platydisca,* was shallowest, found above 73 m. This group also showed the most restricted distribution around the island, with the former two species being collected at only two locations, and the later two species at one station (Table 1).

The second group, *H. lacrimosa* var. *globosa* and *H. tuna* f. *tuna,* showed an intermediate depth range, being found between 37 and 100 m. These species were collected from three of the five sampling locations (Table 1).

The third group, *Halimeda copiosa, H. cryptica* and *H. gracilis,* were the deepest and had the broadest depth range, being found between 20 to 152 m. Each of the species in this group were found at all five sampling locations (Table 1). This group contains the dominant component of the deep-water *Halimeda* flora. *Halimeda copiosa* was seen to be (personal observation) the most abundant *Halimeda* in deep water around San Salvador.

The deep-water *Halimeda* species have an important biological and geological role in the deep-water flora, contributing significantly to the primary production and sediment production of the fore-reef community. The role of *Halimeda* in carbonate sediment production within a Bahama coral reef environment was investigated by Hoskin et al. (1986). This investigation documented the importance of *Halimeda* in the production of sediments in the fore-reef and deep-water communities. *Halimeda* fragments were found to constitute between 32% and 63% (by volume) of the sand fractions of surficial sediments. Although the specific percentage contribution of *Halimeda copiosa* to the sediment production has not been calculated, its abundance on the fore-reef slope around San Salvador Island indicates that this species plays a significant role in the production of carbonate sediments. A similar role for *Halimeda* is hypothesized for the Pacific species found off Enewetak Atoll (Hillis-Colinvaux 1986). Although a dominant species was not identified, it points to the global importance of *Halimeda* in carbonate sediment production within tropical reef systems.

Jensen et al. (1985) studied production rates for four of the deep-water species, *Halimeda copiosa, H. cryptica, H. discoidea* and *H. lacrimosa* var. *globosa.* The rates varied, ranging from 0.04 to 0.24 mg C g dry wt^{-1} h^{-1}, but are comparable to those reported for shallow-water species. This suggests a higher efficiency in the deep-water *Halimeda* species and attests to the role of *Halimeda* species in the primary productions in the deep-water benthic community.

Mariani Columbo and Orsenigo (1977) have documented utricle size variation with depth (range 0.5 to 6.0 m) for *Halimeda tuna.* Because of the depth range through which our *Halimeda* samples were found (i.e., 61

to 152 m for *H. copiosa* and *H. cryptica*), *H. copiosa* was examined to determine if its utricle size varied, as had been documented for *H. tuna*. No significant differences were found between plants from the same depth; however, highly significant differences were determined between the two depth groups (Table 2). The difference between the mean surface utricle diameter was less for *H. copiosa* (i.e., 4.3 μm) than that found for *H. tuna* (9.3 μm) by Mariani Columbo and Orsenigo (1977).

The ecological significance of this variation is hypothesized to be that an increase in the surface area of the utricle would allow a larger surface area for light capture in habitats with lower light levels (i.e., deep water). The 4.3-μm difference in diameter can be roughly estimated to increase the surface area of the utricle by 25%. This could be a sizable increase in available potential area for light capture.

To summarize, nine taxa of *Halimeda* have thus far been collected off San Salvador Island in the Bahamas. The lower depth limit of the species recorded here represent significant increases in the known depth range of the taxa. The *Halimeda* species form an abundant assemblage through much of their range on the wall structure (fore-reef slope) off San Salvador Island and is considered to contribute significantly to the primary production of the deep-water benthic community and sediment production. The dominant species of *Halimeda* observed in the deep-water flora off San Salvador Island was *Halimeda copiosa*. *Halimeda copiosa* exhibits plasticity in its utricle dimensions, increasing with depth, which has been associated with decreased light levels, and is thought to be an adaptation by the alga to increase the light capturing capacity of the plant's surface.

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