

## Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity

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(Received 17 September 1985; in revised form 27 December 1985; accepted 16 January 1986)

**Abstract**—Studies from a submersible on a seamount off San Salvador (Bahamas) revealed a diverse multilayered macrophyte community, with net productivity levels comparable to shallow water seaweeds although receiving only 1–2% of the light energy available at the surface. Four zonal assemblages occur over the depth range from 81 to 268 m and consist of a *Lobophora*-dominated group (81–90 m), a *Halimeda* assemblage (90–130 m), a *Peyssonnelia* group (130–189 m), and a crustose coralline zone (189–268 m). This deep flora is composed of unique deep-water taxa combined with shallow water forms characteristic of shaded, low-light conditions.

### INTRODUCTION

RECENTLY, a record depth for attached living marine macrophytes was reported (LITTLER *et al.*, 1985a). The discovery was made during an extensive floristic-ecological survey off San Salvador Island, Bahamas with the use of the Harbor Branch Foundation's submersible *Johnson-Sea-Link I*. Detailed findings related to that report, including the presence and productivity of complex deep-water (81–268 m) plant communities, are elaborated in this paper.

Submersibles have greatly expanded our knowledge of distributional limits for marine organisms; however macroalgae have received only incidental attention in the past. For example, crustose red and filamentous green algae were seen by LANG (1974) as deep as 175 m at Discovery Bay, Jamaica. ADEY and MACINTYRE (1973) cite the unpublished observations of J. C. Lang and J. W. Porter for the maximum depths for crustose coralline algae (200 m) on steep Belizean and Bahamian reef walls. Crustose corallines also have been reported growing attached to depths of 250 m at Glover's Reef, Belize (JAMES and GINSBURG, 1979) and at Johnson Atoll, Line Islands (AGEGIAN and ABBOTT, 1985). Even on high-latitude, cold-temperate continental shelves, encrusting algae that coat stable rock substrata have been directly observed (HOOPER, 1985) down to 100 m.

Modern submersibles offer the technology to permit *in situ* measurements of deep-water plant communities in their natural state. To our knowledge, however, no accurate taxonomically documented ecological analysis of plant life below 75 m (GILMARTIN, 1960; LARKUM *et al.*, 1967) has been conducted. Other than our own work (LITTLER *et al.*,

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1985a; JENSEN *et al.*, 1985), the same is true regarding metabolic studies of field-collected macroalgae [although DREW (1969) incubated macroalgae inside a shallow cave simulating the light environment at 130 m].

### Study area

San Salvador Island, located along the eastern margin of the Bahamas (24°02'N, 74°30'W), is about 612 km eastsoutheast of Miami, Florida and 346 km north of Cuba. The island is bordered by a contiguous fringing reef that slopes to a deep fore-reef at depths ranging from 20 to 40 m. Below about 40 m, the reef slope becomes nearly vertical extending to depths far below the level of plant growth. Because such steep slopes are not conducive to the settlement and development of large algal populations, we became intrigued by an uncharted region off the northern tip of the island where more gradual slopes having extensive algal rhodoliths (i.e. coralline algal balls or nodules) were noted by the pilot of the submersible (T. ASKEW, personal communication) during a previous dive.

Fathometer tracings of the area showed a seamount (herein referred to as San Salvador Seamount) to be located 6.5 km north of the island (Fig. 1, 24°13.7'N, 74°29.0'W). The geomorphology and relative proximity of San Salvador Seamount to the island presented a habitat of potential floristic and ecological interest.

## METHODS AND MATERIALS

### Standing stocks

The epibiota was videotaped at right angles to the substratum in a continuous belt format beginning at a depth of 520 m, between the north end of the island and the

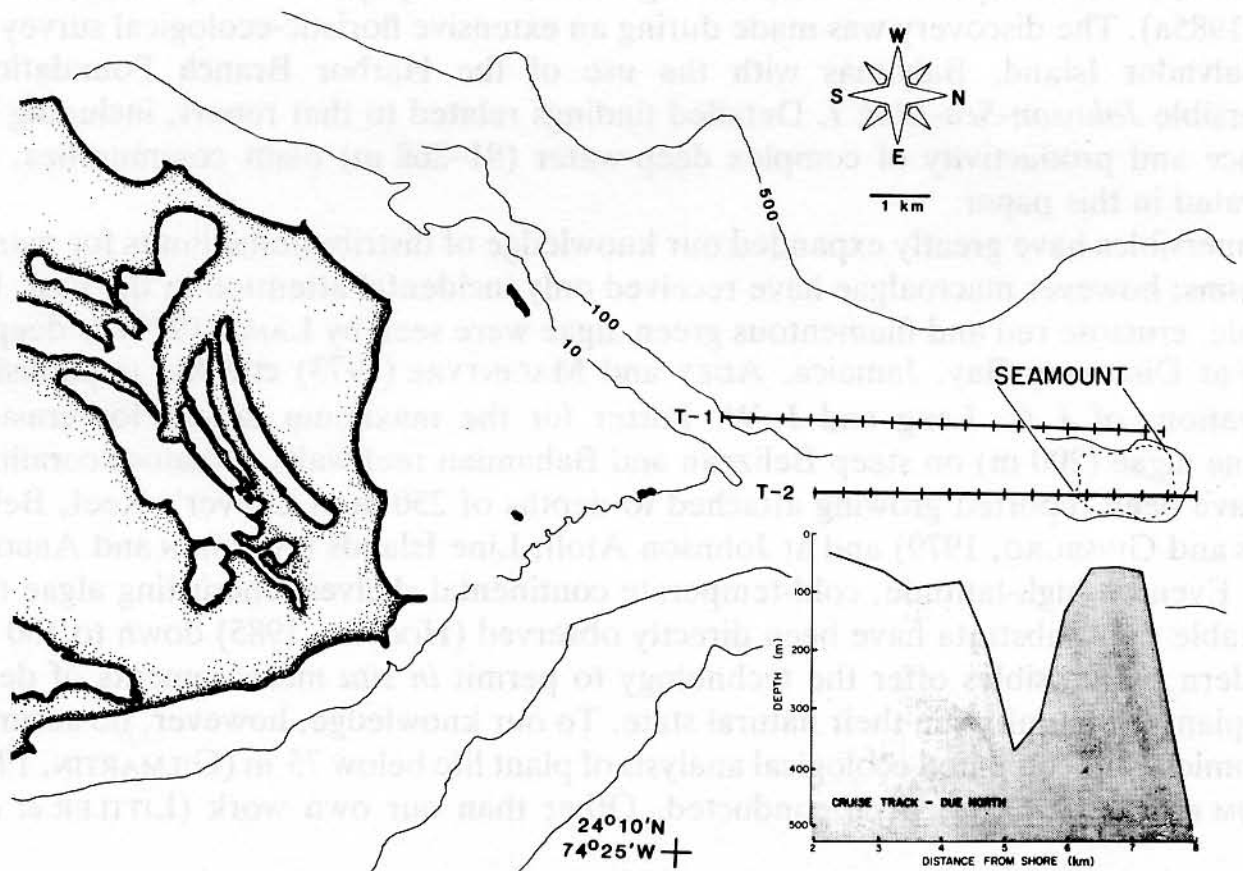


Fig. 1. Fathometer transects used to determine the location and position of San Salvador Seamount. Depth contours are in fathoms (1 fathom = 1.83). Inset is profile of fathometer tracings along T-2 taken by the R.V. *Johnson* from 2.2 to 8.0 km due north of San Salvador Island.

seamount (Fig. 1). A Marine Optical Systems 3000 video camera and two Benthos 372 35-mm cameras, mounted externally on the frame of the *Johnson-Sea-Link I*, recorded the imagery. A 1.0 m long aluminum rod calibrated at 10-cm intervals was mounted externally where it could be positioned in slight contact with the substratum, providing a sample scale and right-angle orientation when framed at the upper edge of the video monitor. The 'video transect' continued along a northward compass heading up the south slope of the submerged mount to the top, a plateau (about 3 km<sup>2</sup>) 81 m in depth. Concurrent detailed field notes and collections were made of the diverse algal taxa. Visual estimates of biotic coverages were updated continuously on a tape recorder and were simultaneously referenced to the video recording in terms of depth and environmental data. The submersible also was equipped with a temperature probe, conductivity meter, and Li-Cor LI-550 printing integrator with a 192 s cosine response light sensor, which were used to record data at specific depth intervals (Fig. 2).

In the laboratory, 86 square quadrats, each 60 × 60 cm (0.36 m<sup>2</sup>), were selected by randomly determined tape distances from throughout the depth range 81–268 m recorded by the continuous, belt-transect, video tape. The various quadrats were projected on a Sony high-resolution video monitor and scored in stop action to gain accurate documentation concerning the distribution and cover of the macrophyte species. Replicate scoring was accomplished by two separate grids of dots on 27 × 35-cm transparent vinyl sheets. A total of 140 point-intercepts were scored per quadrat, being randomly distributed within adjacent 2.0 × 2.0-cm squares on the vinyl sheets. This has

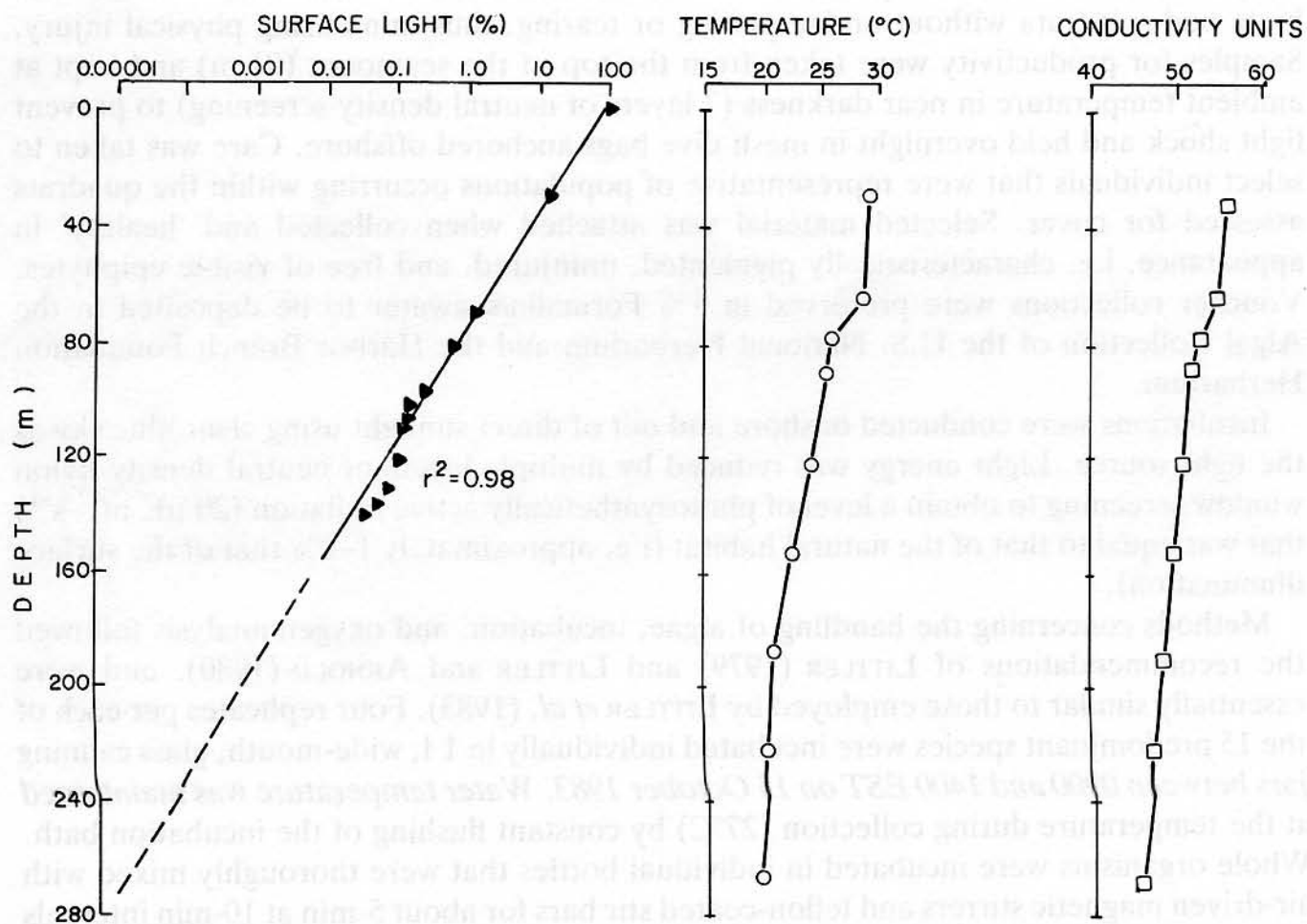


Fig. 2. Left: attenuation (as semi-log plot of % surface irradiance) of photosynthetically active radiation (PAR) recorded at depth, the dashed portion is an extrapolation of the regression line derived from the data. Middle: temperature as a function of depth. Right: conductivity data.

been shown (LITTLER, 1980) to be an appropriate density (e.g. about 0.5 dots per cm<sup>2</sup>) for consistently reproducible estimates of cover. Each stop action video tape quadrat was scored twice by the two different grid arrays that were each positioned without regard to the fields of view to assure unbiased replication. The percent cover values were expressed as the number of 'hits' for each species, divided by the total number of dots contained within the quadrats for each replicate scoring. Reproducibility was consistently high by this technique and seldom varied more than  $\pm 5\%$  for a given taxon. Species not abundant enough to be scored by the replicated grid of point intercepts were assigned an arbitrary cover value of 0.1%.

To characterize natural zonal assemblages over the entire length of the transect in an unbiased manner, the cover data of every species for all quadrats were subjected to hierarchical cluster analyses (flexible sorting, unweighted pair-group method; SMITH, 1976) using the BRAY and CURTIS (1957) percent distance statistic. The product of this analysis, a dendrogram of quadrat assemblages, was then interpreted according to their dominant biota and environmental affinities.

### *Primary productivity*

To complement the photographic and video records, voucher specimens, as well as material for primary productivity experiments, were collected with a manipulator arm outside the submersible. Collections were made throughout the range of macrophyte distributions using a hydraulically operated, Petersen-type, manipulator grab sampler, designed and constructed by the Harbor Branch Foundation. This collector removes biota and substrata without undue pulling or tearing, thus minimizing physical injury. Samples for productivity were taken from the top of the seamount (81 m) and kept at ambient temperature in near darkness (7 layers of neutral density screening) to prevent light shock and held overnight in mesh dive bags anchored offshore. Care was taken to select individuals that were representative of populations occurring within the quadrats assessed for cover. Selected material was attached when collected and 'healthy' in appearance, i.e. characteristically pigmented, uninjured, and free of visible epiphytes. Voucher collections were preserved in 5% Formalin/seawater to be deposited in the Algal Collection of the U.S. National Herbarium and the Harbor Branch Foundation Herbarium.

Incubations were conducted onshore and out of direct sunlight using clear blue sky as the light source. Light energy was reduced by multiple layers of neutral density nylon window screening to obtain a level of photosynthetically active radiation ( $20 \mu\text{E m}^{-2} \text{s}^{-1}$ ) that was equal to that of the natural habitat (i.e. approximately 1–2% that of the surface illumination).

Methods concerning the handling of algae, incubation, and oxygen analysis followed the recommendations of LITTLER (1979) and LITTLER and ARNOLD (1980), and were essentially similar to those employed by LITTLER *et al.* (1983). Four replicates per each of the 15 predominant species were incubated individually in 1 l, wide-mouth, glass canning jars between 0900 and 1400 EST on 15 October 1983. Water temperature was maintained at the temperature during collection (27°C) by constant flushing of the incubation bath. Whole organisms were incubated in individual bottles that were thoroughly mixed with air-driven magnetic stirrers and teflon-coated stir bars for about 5 min at 10-min intervals to disrupt any metabolically induced diffusion gradients. The water used was collected

just prior to the experiments, filtered through a nanoplankton net (10  $\mu\text{m}$  pore size), then vigorously poured between buckets to bring the oxygen level to ambient saturation.

Net productivity was measured to within 1.0  $\mu\text{M O}_2 \text{ l}^{-1}$  by means of an Orbisphere Model 2610 oxygen analyzer, and calculated as milligrams carbon fixed per unit of thallus organic dry weight (or square meter of thallus area) per hour, assuming a photosynthetic quotient of 1.00. The two-dimensional plant cover (i.e. planar area intercepting the light) per square meter of substratum in conjunction with individual production rates per square meter of planar thallus area were multiplied to estimate the contribution of each abundant macrophyte to overall community production on the seamount plateau.

Net apparent photosynthesis was measured for four of the macrophyte species ( $n = 4$ ) by using the  $^{14}\text{C}$  and  $\text{O}_2$  methods simultaneously. There was no significant difference between the two techniques ( $P < 0.05$ , Student Newman-Keuls multiple range test) and the mean rates were remarkably close (see also JENSEN *et al.*, 1985).

Throughout the experiments, the average thallus concentration per volume of water did not exceed 0.04 dry g  $\text{l}^{-1}$ , except in the case of the lower-producing calcareous algae, where approximately 10 times this amount was used.

## RESULTS

### *Standing stocks*

Profiles of physical data for the seamount (Fig. 2) indicated a photon flux density characteristic of that for the clearest of oceanic water (i.e. Type I oceanic water, JERLOV, 1970), while temperature and conductivity decreased at fairly constant rates with more abrupt declines near the plateau.

The cluster analysis (Fig. 3) revealed four general algal zones grouped as a function of depth on San Salvador Seamount. Several quadrats, which clustered within a given group at a relatively low coefficient of similarity (e.g. 3–244 in Fig. 3), deviated in abundance levels but not in dominant species. The lower plant zone is characterized by a crustose coralline alga along with sparse patches of a rock-boring micro-filamentous rhodophyte that extends from 268 m upward to 189 m. The crustose coralline reaches up to 10.2% cover at 244 m and is the predominant organism and the only macrophyte between 210 and 268 m in depth. Coralline algae (several species) maintain an average of 6.8% cover to the top of the seamount. At 210 m, the rock-boring green alga *Ostreobium* sp. appears in trace amounts and maintains a mean cover of 5.8% to the top of the seamount. Below 268 m, encrusting sponges are the major cover organisms down to at least 520 m.

Above 189 m, an assemblage (Fig. 3) dominated by another red algal crust, *Peyssonnelia* sp., continues to 130 m. *Peyssonnelia* sp. appears abruptly (4.5% cover) and averages 12.4% cover to the seamount top, with a peak abundance of 52.1% in one sample at 157 m. In the *Peyssonnelia* group there also are two frondose Chlorophyta, *Johnson-sea-linkia profunda* and an undescribed palmelloid gelatinous species, unique to deep waters, that begin at 157 m in considerable abundance. *Johnson-sea-linkia* is restricted to below 113 m on San Salvador Seamount.

Upward from the *Peyssonnelia* assemblage, a distinct *Halimeda* group (Fig. 3) is predominant, consisting mainly of four species of the articulated green calcareous genus *Halimeda* (*H. copiosa*, *H. cryptica*, *H. discoidea*, *H. lacrimosa* var. *globosa*). *Halimeda copiosa* dominates the zone from 117 to 130 m and is abundant to the top of the mount with an overall cover of 19.8% (maximum cover of 39.1% in one sample).

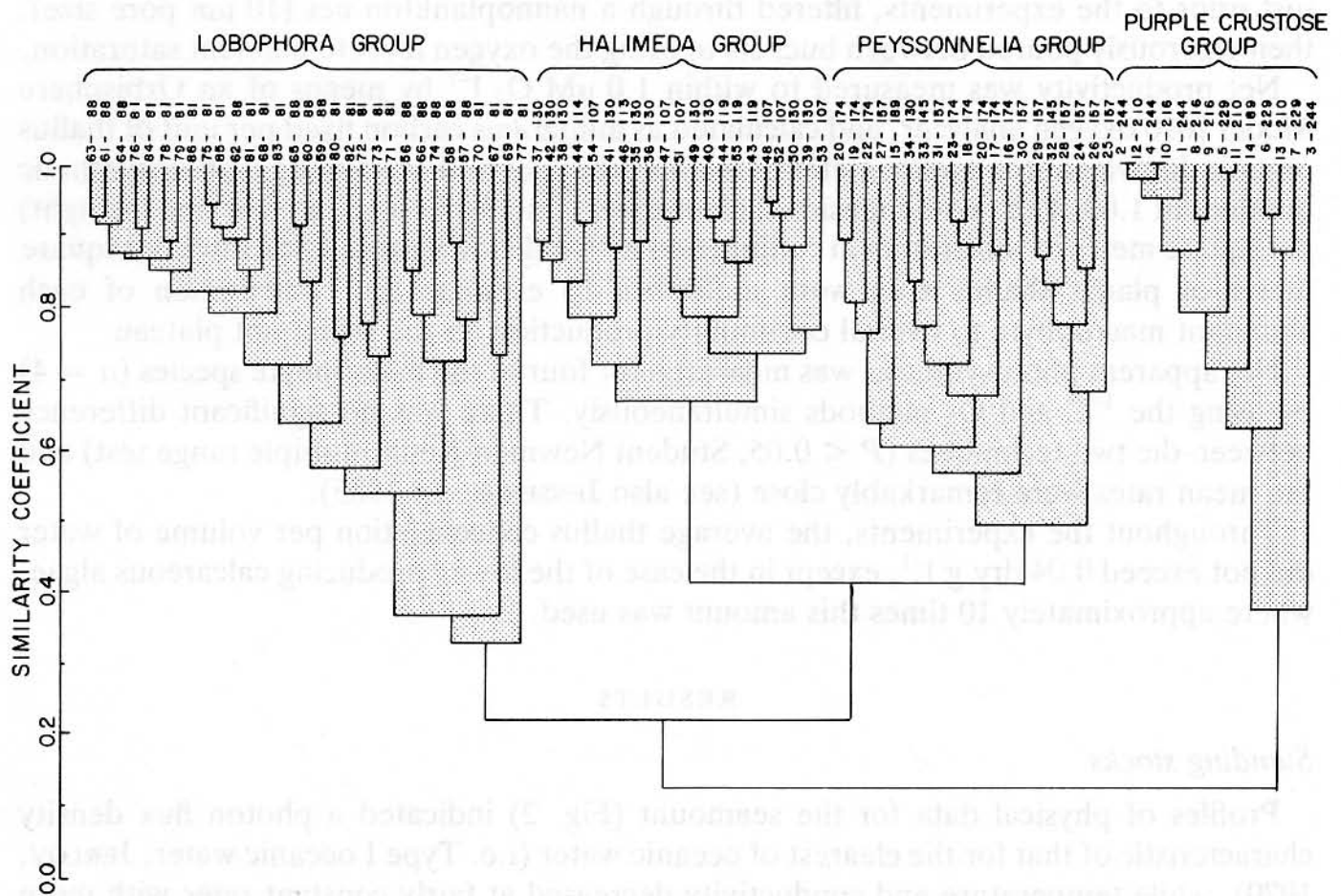


Fig. 3. Differential dendrogram display based on cluster analysis of the percentage cover data of macroalgal species for all 86 quadrats (labeled by depth in meters). Dominant cover organisms in each cluster group are given.

Above the *Halimeda* zone, a complex four-layered assemblage, the *Lobophora* group (Fig. 3), begins at 90 m and is dominated by the fan-shaped brown alga *Lobophora variegata* (54.6% mean cover). At times this species covers up to 100% of a secondary substratum comprised of irregularly shaped coralline rhodoliths.

The plateau region of the mount begins at 81 m and contains a rich, multilayered, macroalgal community with an underlying bed of rhodoliths composed of various crustose coralline algae (8.3% mean cover), *Peyssonnelia* sp. (6.3%), the encrusting foraminiferan *Gypsina* sp. in association with *Ostreobium* (5.4%), and various rock boring sponges. Upon this living secondary substratum, *Lobophora variegata* dominates (59.4%). Overlying this second living layer is a tertiary canopy formed by patches of *Dictyota divaricata* (8.9% mean cover), *Caulerpa peltata* (5.5%), an exceptionally large undescribed species of *Cladophora* (0.1%), and the undescribed palmelloid green alga (0.4%). The uppermost canopy of large macroalgae includes *Kallymenia westii* (4.6% cover), *Halimeda copiosa* (6.2%), *H. discoidea* (4.5%), occasional individual thalli of *Stypopodium zonale*, and new species of *Titanophora* sp. (BUCHER and NORRIS, submitted) and *Wrangelia*.

Our video scoring method did not permit moving canopy layers aside to quantify understory; however, we did estimate that total planar algal cover (understory and canopies) exceeded 100%, reaching at least 160% for much of the approximately 3-km<sup>2</sup> plateau. Diversity of plant life is exceptionally high with many small Rhodophyta

(including undescribed members of the Rhodomelaceae and Delesseriaceae) being epiphytic on the large algae.

### Primary productivity

To compare the dominant species in terms of their functional-form groups (LITTLER and LITTLER, 1984), and their net apparent photosynthetic performances, species were taken from populations growing at 81 m on the plateau of the seamount and incubated at simulated *in situ* light levels (Table 1). The two sheet-like species, *Dictyota divaricata* (7.12 mg C fixed g<sup>-1</sup> organic dry wt h<sup>-1</sup>) and *Kallymenia westii* (3.23 mg C), showed the highest rates. The three encrusting forms [crustose coralline (0.43 mg C), *Peyssonnelia* sp. (0.43 mg C), and *Ostreobium* sp. (0.39 mg C)] tended to have relatively low productivities. Coarsely branched forms, thick leathery/rubbery taxa, and jointed calcareous species had intermediate rates, with the exceptions of the two strictly deep-water forms, palmelloid green alga (0.14 mg C) and *Johnson-sea-linkia profunda* (0.30 mg C), which showed exceptionally low production rates.

Total macrophyte cover on top of the seamount averaged 99.2% with a mean overall productivity of 0.066 g C m<sup>-2</sup> h<sup>-1</sup>. In terms of productivity per square meter of thallus planar area (Table 2), the sheet-like *Dictyota divaricata* was highest (0.14 g C m<sup>-2</sup> h<sup>-1</sup>) followed by crustose coralline algae (0.10). Production per unit of substratum on the

Table 1. Productivity (as mg C fixed per gram organic dry weight per hour) of the dominant taxa by form group from 81 m; as compared to previously reported values (from LITTLER et al., 1983) for common shallow Caribbean species incubated at 1500  $\mu\text{E m}^{-2} \text{s}^{-1}$

Species	Productivity ±S.D.	Range of previous values (species measured)
Sheet group		2.89–13.39
<i>Dictyota divaricata</i> Lamouroux	7.12 ± 1.74	(3)
<i>Kallymenia westii</i> Ganesan	3.23 ± 1.08	
Coarsely branched group		0.87–10.20
Undescribed <i>Titanophora</i> sp.	1.40 ± 0.55	(15)
<i>Caulerpa peltata</i> Lamouroux	0.75 ± 0.20	
<i>Johnson-sea-linkia profunda</i> Earle & Eiseman	0.30 ± 0.01	
Thick leathery/rubbery group		1.08–3.24
<i>Lobophora variegata</i> (Lamour.) Womersley	2.64 ± 0.43	(9)
<i>Styopodium zonale</i> (Lamour.) Papenf.	1.69 ± 0.66	
Palmelloid green	0.14 ± 0.07	
Jointed calcareous group		0.77–2.06
<i>Halimeda copiosa</i> Goreau & Graham	2.38 ± 0.42	(7)
<i>Halimeda lacrimosa</i> Howe var. <i>globosa</i> Dawes	1.70 ± 0.05	
<i>Halimeda cryptica</i> Colinvaux & Graham	1.53 ± 0.60	
<i>Halimeda discoidea</i> Decaisne	1.21 ± 0.16	
Crustose group		0.10–0.32
Crustose coralline	0.43 ± 0.05	(4)
<i>Peyssonnelia</i> sp.	0.43 ± 0.11	
<i>Ostreobium</i> sp.	0.39 ± 0.17	

Table 2. The major contributors of community cover (%) and primary productivity ( $\text{g C m}^{-2} \text{h}^{-1}$ ) on top (81 m deep) of the seamount

Dominant taxa	Mean % cover	Productivity per $\text{m}^2$ of thallus	Productivity per $\text{m}^2$ of substratum
<i>Lobophora variegata</i>	57.9	0.06	0.035
<i>Dictyota divaricata</i>	5.9	0.14	0.008
Crustose coralline algae	6.9	0.10	0.007
<i>Peyssonnelia</i> sp.	8.3	0.06	0.005
<i>Halimeda copiosa</i>	8.1	0.06	0.005
<i>Kallymenia westii</i>	3.1	0.07	0.002
<i>Ostreobium</i> sp.	4.6	0.03	0.001
<i>Caulerpa peltata</i>	3.7	0.03	0.001
Palmelloid green	0.4	0.01	<0.001
<i>Halimeda discoidea</i>	0.3	0.02	<0.001
Total	99.2	—	0.066

seamount plateau was dominated by *Lobophora variegata* which provided 58.3% of the total plant cover and 53.0% of the community productivity. Nine other less abundant but common species contributed the remainder (Table 2).

#### DISCUSSION

The zonal pattern observed (Fig. 3), i.e. reds > greens > browns with increasing depth, is quite similar to that recorded (LARKUM *et al.*, 1967) on the south coast of Malta (Jerlov Type II water) and also postulated by DRING (1981) for 'clear-blue' deep waters. Off Malta, the shallower zone to 15 m is dominated by brown algae; green algae (mainly *Halimeda*) are then most abundant down to 75 m, and red algae (particularly *Peyssonnelia* and *Lithophyllum*) dominate below the 80–90 m transitional depth.

There is some confusion in the literature concerning maximum depth records for frondose algae. For example, BOLD and WYNNE (1985, p. 301) report attached collections to 220 m. However, R. W. Cook (HBF), the lockout diver who collected the frondose *Lobophora variegata* referred to in BOLD and WYNNE (1985), recalls (personal communication) that these specimens were from 214 m deep but adrift over a sandy substratum (see also LINK, 1973, p. 178). It is our belief that these taxa do not actively colonize and grow much below 100 m, based on extensive observations of attached algae from submersibles throughout the Bahamas and Belize from 1980 to 1985. Another exceptionally deep record for a healthy fertile frondose alga, *Sargassum hawaiiensis* Doty and Newhouse, was obtained (DEWREEDE and JONES, 1973) in a shrimp trawl off Molokai'i, Hawaii. A number of whole thalli attached to shell fragments were taken at 200 m, but DEWREEDE and JONES (1973) indicate that this material could have been swept down from shallower depths by currents. Other deep dredging records for frondose seaweeds include specimens from the interval 200–250 m over soft bottoms in the Adriatic Sea (ERCEGOVIC, 1960), between 183 and 366 m at Funafuti Atoll (DAVID *et al.*, 1904), just below 100 m near Dry Tortugas, Florida (TAYLOR, 1928; HUMM, 1956) and fleshy algae to 105 m in Hawaii (DOTY *et al.*, 1974). The deepest frondose alga directly observed and collected on bedrock is *Johnson-sea-linkia profunda* at approximately 200 m from San Salvador Island. We documented a deeper zonal pattern for *J. profunda* (113–157 m) than previously reported by EISEMAN and EARLE (1983), who found it mainly in



the interval between 60 and 120 m. The zone of *Halimeda* spp. dominance (90–130 m, Fig. 3) also represents a considerable extension of the maximum depth range reported for this genus at Funafuti Atoll (37–82 m, DAVID *et al.*, 1904) and at Jamaica (<98 m, LANG, 1974). Our Bahamian material represents the deepest (268 m) macrophyte population directly observed, photographed, and collected (LITTLER *et al.*, 1985a) growing *in situ* on primary basement substratum. There is also a microfilamentous rock-boring rhodophyte down to at least 268 m on San Salvador Seamount.

The San Salvador Island region presents an excellent system in which to study deep-water algal ecological processes, such as the little known phenomenon of rhodolith formation. Unattached spherical coralline rhodoliths have been collected abundantly in continental shelf samples to 200 m (ADEY and MACINTYRE, 1973). We videotaped and collected (unpublished data) large concentrations of such rhodolith balls on the westward (downcurrent) slope of the seamount on a subsequent dive from *Johnson-Sea-Link I*. These are living and clearly have spilled down from the top of the mount, possibly due to occasional strong currents or storm turbulence. As a working hypothesis, it appears that sponges and other boring organisms weaken and cut off the irregularly sized and shaped coralline fragments which are abundant beneath the *Lobophora* and other frondose algae on top of the seamount. Hypothetically, such living fragments comprise rhodolith 'nuclei' that continue to grow into characteristic round nodules as they are carried slowly down the slope into deeper water.

The apparent net photosynthetic performances of the deep-water macroalgal populations under natural light levels is of interest if we are to understand their potential contribution to community metabolism. As an initial study, collections of the 15 major species on the plateau were brought to the surface and incubated onshore. A potential problem in our productivity measurements is that incubations were conducted at *in situ* photosynthetically active light energies (PAR) but not light qualities. The neutral density screening used to reduce intensity does so without preference to wavelength unlike seawater (Jerlov Type I) which absorbs preferentially the red and ultra-violet ends of the spectrum. Any effects of this methodological artifact can be argued; DRING (1971), RAMUS and VAN DER MEER (1983), and DREW (1983) concluded that reduction in light quantity has the same effect on photosynthesis as increase in depth. In addition, the light source we used was clear blue skies (and not direct sunlight), which more closely simulated the natural spectrum. Light was measured as PAR (400–700 nm) and quality does not affect quantity when PAR is compared. In other words, PAR at depth was equal to the PAR used in our incubations.

The most interesting finding for the majority of the deep-water species investigated was that their apparent photosynthetic rates are not dramatically lower than those of shallow water members of the same form groups (Table 1; LITTLER and ARNOLD, 1982; LITTLER *et al.*, 1983; LITTLER and LITTLER, 1984). This is significant because all were incubated at only  $20 \mu\text{E m}^{-2} \text{s}^{-1}$  (1–2% of the maximum surface light), strongly implicating mechanisms for efficient utilization of low photon fluxes. This light level was formerly thought (RYTHER, 1956; PARSONS *et al.*, 1977) to approximate the physiological compensation point for marine plants, i.e. where photosynthesis and respiration are equivalent. The photosynthetic rates of the 15 predominant taxa, as documented here (and also indicated by their observed abundances), are well above the compensation point at this intensity. Their prolific standing stocks at considerably lower light intensities further suggests an efficient utilization of available light energies.

Productivity rates reported for shallow carbonate reef systems range from 0.06 to 0.72 g C m<sup>-2</sup> of substratum h<sup>-1</sup> (approximated from daily rates) as follows: intertidal, blue-green algal dominated substrata at Enewetak Atoll = 0.06–0.22 g C m<sup>-2</sup> h<sup>-1</sup> (BAKUS, 1967), macroalgal dominated habitats in the Canary Islands = 0.15–0.30 (JOHNSTON, 1969), photosynthetic coral and algal turfs at Enewetak = 0.16–0.72 (SMITH, 1973), a coralline algal dominated fringing reef in French Polynesia = 0.38 (SOURNIA, 1976), and fore- and back-reef algal turf systems = 0.5–0.7 (BRAWLEY and ADEY, 1977). The mean rate for the seamount plateau, 0.066 (Table 2) falls within the lower end of this range. We conclude that deep-water macroalgal communities, although receiving as little as 1–2% of the energy available to shallow water communities, produce at rates comparable to some shallow reef systems, but lower than most seagrass beds (LITTLER *et al.*, 1985b) or typical carbonate reef-flat habitats.

The only other study (DREW, 1969) of photosynthesis in deep-water algae indicated extremely high photosynthetic efficiencies, i.e. photosynthetic rates did not decrease with depth as rapidly as ambient light intensity (also noted by DREW and LARKUM, 1967). The proportion of photosynthetically active radiation (PAR) converted to chemical energy in photosynthesis (DREW, 1969) increased from about 2% near the surface to over 50% near the extinction depth (*sensu* SEARS and COOPER, 1978) at 70–100 m deep. It is significant that other physiological processes (i.e. calcification) for the four deep-water *Halimeda* species (JENSEN *et al.*, 1985) also showed comparable rates to those reported BOROWITZKA and LARKUM, 1976; LITTLER *et al.*, 1983, 1985b) for shallow forms of the genus. The production values for the crustose group, on a gram dry-weight basis, are lower than those reported for many other primary producers. It is the high percent cover and associated high biomass that makes these algae significant producers of organic carbon and carbonates on an area basis. The unique palmelloid green alga was the lowest producer on the seamount, probably due to the relative paucity of photosynthetic cells which are separated widely within its extensive gelatinous organic matrix.

Previous estimates of compensation depths in the sea have been disproportionately influenced by a preponderance of biological oceanographic programs focused on phytoplankton productivity. Because phytoplankton are passively carried upward and downward by advective and convective currents, specialized adaptations to extremely low light energy may not have been widely selected over evolutionary time (PLATT *et al.*, 1983). Unlike phytoplankton, it is impossible to find an attached benthic plant at its physiological compensation point, which by definition must be at light levels below its extinction depth (the ecological term for the maximum depth limit *sensu* SEARS and COOPER, 1978). It may be safely assumed that the deepest macrobenthic plant zone with which we are dealing (210–268 m) is never exposed to light >0.0015–0.027  $\mu\text{E m}^{-2} \text{s}^{-1}$ . With an attenuation of 0.00005–0.0009% (to be conservative) at the lower limits of the observed algal growth, the surface intensity would have to be 3000  $\mu\text{E m}^{-2} \text{s}^{-1}$  to obtain an *in situ* value of 0.0015–0.027  $\mu\text{E m}^{-2} \text{s}^{-1}$ . Even this 'upper' light limit is well below the lowest compensation intensity ( $I_c$ ) levels reported for phytoplankton [ $I_c$  equivalent to 5.98–1.38  $\mu\text{E m}^{-2} \text{s}^{-1}$  (PLATT *et al.*, 1983), 1.38  $\mu\text{E m}^{-2} \text{s}^{-1}$  (BUNT *et al.*, 1966), 0.046  $\mu\text{E m}^{-2} \text{s}^{-1}$  (MORGAN and KALFF, 1975 in PLATT *et al.*, 1983)]. The fact that encrusting algae are actively growing (indicated by new cell divisions) in considerable abundance at such low energy levels suggests adaptation to this extreme light regime; i.e. adaptation in the evolutionary sense, as opposed to acclimation [a shorter-term adjustment of physiological systems (PLATT *et al.*, 1982)] that may be responsible for the variation of photosyn-

thetic parameters shown by phytoplankton. Therefore, it is not surprising that concepts based on studies of the more generalist phytoplankton guild would not be applicable to benthic algae, which apparently have evolved photosynthetic light utilization efficiencies that are at least two to three orders of magnitude greater than primary producers exposed to near-surface light environments. As more plant specialists gain access to deep-sea communities, the role of benthic algae will become clearer and new botanical theories and concepts based on *in situ* research will replace older ones derived from shipboard studies and remote sensing.

*Acknowledgements*—We thank D. T. Gerace for his hospitality at the College Center of the Finger Lakes Bahamian Field Station. Gratitude is extended to R. A. Gibson and P. R. Jensen for field assistance and K. E. Bucher for taxonomic expertise. We appreciate the continuous encouragement of our colleague, M. D. Hanisak (HBF). This study would not have been possible without the combined talents of the R.V. *Johnson* ship crew and the *Johnson-Sea-Link I* submersible crew. In particular, the skill and expertise of T. Askew (HBF) in piloting the submersible and his prior knowledge of the seamount proved to be instrumental. This study is Contribution 489 of the Harbor Branch Foundation (HBF) and Contribution 150 of the Smithsonian Marine Station at Link Port, Florida.

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