What local and large-scale mechanisms, if any, account for the anomalous heat content during those years in which El Niño conditions do not occur?

Local mechanisms, especially the stratification and the vertical mixing of heat downward, below the mixed layer, play a crucial role in coupling Castle Lake to long-term interannual variation. For a small lake, local meteorological and topographic conditions might be expected to predominate; however, these local effects are most strong in surface waters, not below the mixed layer where the effects we report are observed (*19*). Our study also suggests that there are significant effects from El Niño and the Southern Oscillation in temperate latitudes away from oceanic and coastal areas where it has been best studied (*2, 20*).

Important ecological processes in Castle Lake may also be controlled by the interaction of surface meteorological forcing and vertical mixing. Goldman and de Amezaga (*4*) suggest that annual primary productivity is a function of the amount of precipitation because nutrients and algae are washed out of the lake during years with high runoff. Moreover, in 1975, a year with a late thaw and low productivity, the lake did not mix completely (overturn) in spring (*4*) and thus did not fully renew the upper euphotic zone with nutrients. In contrast, Castle Lake mixed completely to the bottom in 1976, a year with an early thaw and high productivity. Finally, during 1983, when the lake stayed frozen until 6 July and the maximum heat content was 4 standard deviations below normal, the primary productivity during the summer was only 25 percent of normal. Other quantities that can be measured in terrestrial systems, some ecological in nature and thus related to precipitation or other meteorological parameters, show significant year-to-year variations. These may also have a strong link to large-scale phenomena, just as interannual variations in Castle Lake are linked to El Niño and the Southern Oscillation.

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10. The amount of thermal energy stored in the lake during the period from the date of minimum heat content (that is, the date of minimum average temperature, taken to be 4°C) to the date of maximum average temperature, usually in August. This is commonly called the Birgean heat budget. G. E. Hutchinson, *A Treatise on Limnology* (Wiley, New York, 1957), vol. 1, p. 492.
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12. Snowfall data for Mount Shasta City, approximately 10 km from Castle Lake, were obtained from the National Climatic Data Center, Asheville, N.C. 28801.
13. Anomalous is defined as greater than 1 standard deviation above or below the 20-year mean. The year 1982 to 1983 is excluded because of its extreme values of snowfall and heat content (*2*). Experimental errors associated with the measurement of temperature lead to an error in estimation of the maximum heat content that is at most 10 percent of the year-to-year variation and thus negligible.
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Deepest Known Plant Life Discovered on an Uncharted Seamount

Abstract. *The discovery of abundant autotrophic macrophytes living below 200 meters indicates their importance to primary productivity, food webs, sedimentary processes, and as reef builders in clear oceanic waters. Estimates concerning minimum light levels for macroalgal photosynthesis and macrophytic contributions to the biology and geology of tropical insular and continental borderlands must now be revised.*

A record depth (268 m) for living marine macrophytes was directly determined during a survey of the flora of San Salvadore Island, Bahamas, with the use of the Harbor Branch Foundation's submersible Johnson-Sea-Link I (JSLI). It had been thought (*1*) that plant life could not develop below about 200 m because of low light intensity.

Until recently, scientists had available for study only fragmentary samples of deep-sea plant life collected by dredgings taken with hooks, nets, buckets, chains, chisels with hemp tangles, or trawls. Because of problems in accurately determining the sampling site and whether specimens were attached or broken free and carried to depth secondarily, results obtained from these remote methods are inherently imprecise.

The deepest recorded frondose seaweeds were dredged below 100 m off Florida (*2*) and 200 m near Hawaii (*3*). A chisel-edged drill containing hemp tan-

Table 1. Attenuation (as a percentage of surface irradiance) of photosynthetically active radiation, conductivity, temperature, and approximate upper or lower plant zonal limits.

Depth (m)	Conductivity (μmho/cm^2)	Temperature (°C)	Radiation (μE m^{-2} sec^{-1})	Light attenuation	Zonal limits
0	55.3	29.1	1500.00 to 1700.00	100.00	
37	55.4	29.9	208.00 to 238.00	14.92	
71	54.6	29.0	19.05 to 21.59	1.27	
83	53.5	25.8	13.35 to 15.13	0.89	*Lobophora*, lower (88 m)
97	52.9	25.8	7.35 to 8.33	0.49	
100			5.25 to 5.95	0.35	
104			3.75 to 4.25	0.25	
107	52.2	24.7	2.85 to 3.23	0.19	
116			2.25 to 2.55	0.15	*Johnson-sea-linkia*, upper (113 m)
128	51.7	24.6	1.35 to 1.53	0.09	
134			1.20 to 1.36	0.08	*Halimeda*, lower (130 m)
137	51.4	23.6	0.75 to 0.85	0.05	Palmelloid green, *Johnson-sea-linkia*, lower (157 m) *Peyssonnelia*, lower (189 m)
210	48.4	20.6	0.013 to 0.015*	0.0009*	*Ostreobium*, lower (210 m)
268	47.2	19.0	0.007 to 0.009*	0.0005*	Crustose coralline, lower (268 m)

*Extrapolated from the attenuation plot.

gles (*4*) was used to collect living, freshly fractured samples of crustose coralline algae somewhere between 183 and 366 m (*5*) on the seaward, nearly vertical, outer slope of the reef at Funafuti Atoll.

Direct observations from submersibles are much more precise when documented by voucher collections; however, published accounts are few and critical voucher specimens are mostly lacking. Crustose red and filamentous green algae are reported (*6*) as deep as 175 m in Jamaica. Also, unattached coralline algal balls (termed rhodoliths or nodules) have been collected abundantly in continental shelf samples to 200 m (*7*), although they are thought (*8*) to develop actively only in depths above 70 m. Submersible sightings (*9*) of a crustose coralline as deep as 250 m have been reported at Glover's Reef, Belize.

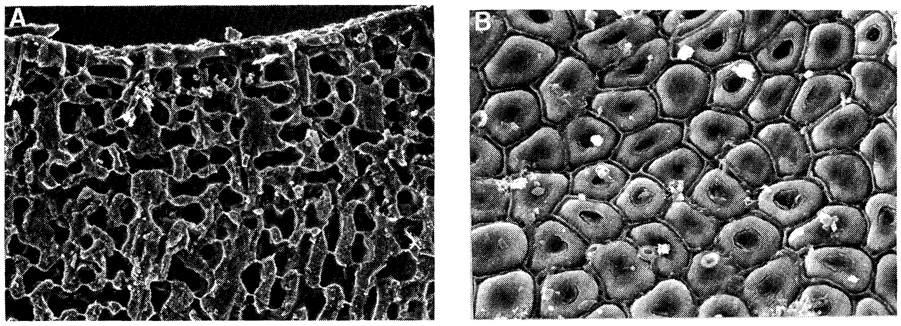

Fig. 1. Scanning electron micrograph of the purple crustose coralline in (A) sectional (×450) and (B) surface views (×800). Lateral walls and intercellular regions are heavily calcified (calcite).

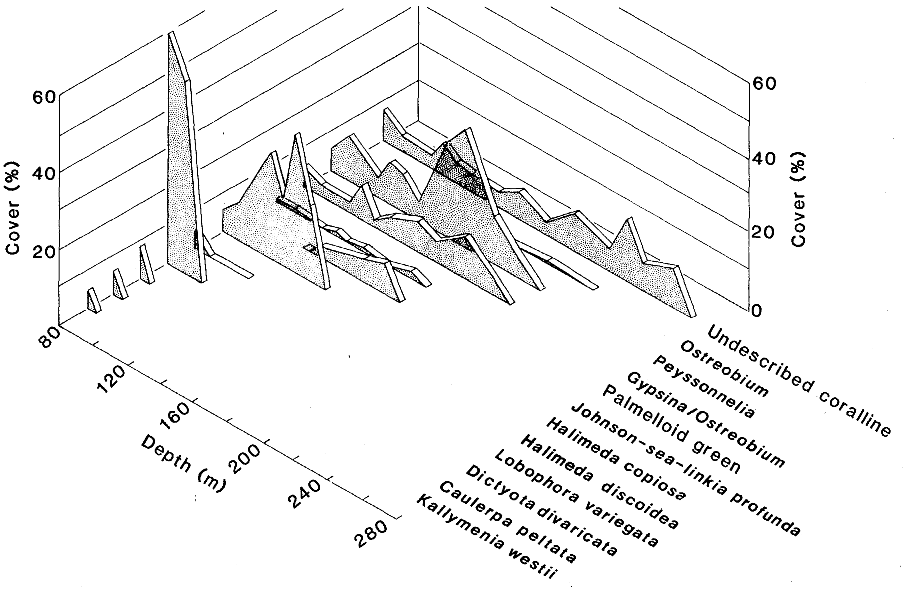

Fig. 2. Distribution and abundance patterns of the major plant cover.

Data concerning the most basic aspects of distribution and abundance patterns are elusive if not impossible to obtain with the use of remote dredging techniques. Yet, most of our knowledge of deepwater macroalgal distribution and depth limits is based on samples obtained by these techniques. Research submersibles such as the two Johnson-Sea-Link submersibles enable scientists to have unprecedented working access underwater. They are being used for a wide range of studies that are providing new data on the ecology and distribution of deepwater plants (*9–12*).

While conducting algal surveys from JSLI off the northern border of San Salvadore Island during October 1983, our group discovered an uncharted seamount. A crustose member of the division Rhodophyta was found in abundance growing attached at a depth of 268 m. A videotape transect and still photographs were made at right angles to the substratum along a transect extending from the limit of observed light penetration (520 m) to the top of the submerged mount, which forms a flat plateau (~1 km^2) approximately 81 m below the surface. To gain accurate, complete documentation concerning the distribution and cover of conspicuous species, a grid was superimposed on the video screen in the laboratory and appropriate counts, measurements, and permanent records were made at random intervals. A total of 86 quadrats, each 60 by 60 cm (0.36 m^2), was assessed in this manner. 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.

Videotaping, still photography, and collecting were done and physical measurements were made beginning at a depth of 520 m in the trench between the seamount and the island and progressed due north up onto the top of the plateau. The photon flux density (Table 1) was characteristic of that for the clearest of oceanic water [that is, type I oceanic water (*13*)], while temperature and conductivity decreased at fairly constant rates with more abrupt declines near the top of the seamount.

Community complexity and spatial heterogeneity increase markedly with decreasing depth. Encrusting sponges are most common on the substratum from 520 up to 268 m. However, above this depth, patches of an undescribed, purple, crustose, coralline alga (Fig. 1) appear abruptly (Fig. 2 and Table 1). This coralline represents the deepest known macrophyte population directly observed, photographed, and collected that is growing in situ on primary basement substratum. The purple crustose coralline reaches up to 10.2 percent cover at 244 m and maintains an average of 6.8 percent cover to the top of San Salvador Seamount (Fig. 2). It is the predominant organism and the only macrophyte between 210 and 268 m. At 210 m, the green rock-boring alga *Ostreobium* sp. becomes present in trace amounts. Beginning at 189 m, another crustose rhodophyte, *Peyssonnelia* sp., occurs abundantly (12.4 percent mean cover). Two Chlorophyta (*Johnson-sealinkia profunda* and an undescribed gelatinous genus), which are present only in deep waters, appear at 157 m in considerable abundance. The articulated, calcareous green alga, *Halimeda copiosa*, dominates the zone from 117 to 130 m. From 88 m upward, the fan-shaped brown alga *Lobophora variegata* appears as a sharply delimited dominant (59.4 percent mean cover), at times covering up to 100 percent of the substratum.

The top of the mount contains a multilayered rich community (Fig. 2) beginning with an assemblage of upper canopy plants such as *Kallymenia westii* (4.6 percent mean cover), *Halimeda copiosa* (6.2 percent), *H. discoidea* (4.5 percent), and occasional individual thalli of *Titanophora* sp. These species overlie a secondary canopy formed by *Dictyota divaricata* (8.9 percent), *Caulerpa peltata* (5.5 percent), *Microdictyon* sp., and the undescribed palmelloid (gelatinous) green alga (0.4 percent). Beneath these, *Lobophora variegata* dominates (59.4 percent) over an underlying bed of rhodoliths formed by interactions between corallines, *Peyssonnelia* sp., *Ostreobium*, and various rock-boring sponges. Our video-scoring method did not permit moving upper layers aside to quantify understory; however, we did estimate that total algal cover reached at least 160 percent over much of the 1-km^2 plateau. Diversity of plant life is exceptionally high, with many undescribed small Rhodophyta being epiphytic on the larger algae.

Although we have documented a new depth record for plant life, there is still a question of whether this macrophyte is autotrophic. To investigate this, collections of the undescribed crustose coralline were brought to the surface and incubated on shore under simulated in situ conditions of photosynthetically active light energy, temperature, and water movement. Incubations (*14*) took place out of direct sunlight with clear blue sky as the light source, reduced by layers of nylon screening to obtain a level of photosynthetically active radiation (20 μE m^{-2} sec^{-1}) approximately 1 percent that of the surface illumination (*15*).

The net apparent photosynthetic rate of the purple crustose coralline under these conditions was 0.43 mg of carbon fixed per gram of organic dry weight per hour, clearly establishing the autotrophic competency of the plant. In fact, this rate compares quite favorably with those determined for shallow-water crustose corallines from the southwest coast of North America (0.55 mg of carbon) (*16*), the Gulf of California (0.52 mg of carbon) (*17*), and elsewhere in the Caribbean (0.20 mg of carbon) (*14*), although the San Salvadore seamount material received only 1 percent of the light energy available to the shallow-water forms.

The discovery of macrophytic algae at these depths allows a reevaluation of minimum light levels (Table 1) required for benthic macroalgae. The generally accepted level for the compensation point (the light intensity at which photosynthesis equals respiration—that is, no net growth) is 1 percent of the maximum surface intensity (*15*). Lüning and Dring (*18*) correlated the lower limits of macroalgal growth with light levels equivalent to 0.05 to 0.10 percent of the peak surface irradiance. We found the 0.05 percent level to correspond with the lower limit of fleshy algae (that is, *Johnson-sea-linkia profunda*). However, the amount of light at 268 m (Table 1) is approximately 0.0005 percent of the surface value. This is equivalent to a photon flux of only 0.015 to 0.025 $\mu E\ m^{-2}\ sec^{-1}$ during full sunlight at its maximum zenith.

We suggest that the great abundance of macroalgae in this previously unknown deep-sea realm underscores their potential widespread importance to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical oceans. Estimates concerning macrophyte contributions to insular and continental borderlands must now be increased.

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