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The Distribution, Abundance, and Communities of Deepwater Hawaiian Crustose Corallinaceae (Rhodophyta, Cryptonemiales)[1]

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ABSTRACT: Two deepwater (8–28 m) areas studied off Oahu, Hawaii, are remarkably similar in the kinds and order of importance of calcareous producer organisms. *Hydrolithon breviclavium* is primary at the Maile deep area (25-percent cover) as well as at Waikiki (37-percent cover). At Maile *H. reinboldii* (7-percent cover) ranks second in relative importance; however, at Waikiki *Tenarea tessellatum* (5-percent cover) and corals (3-percent cover) are so abundant at the stations below 20 m that they surpass *H. reinboldii* (2 percent) in total cover. Corals (2-percent cover) and *T. tessellatum* (1-percent cover) rank third and fourth, respectively, as important builders in the Maile deep area. At Waikiki, when density and frequency are considered with the cover values, corals are second in importance followed by *H. reinboldii* and *T. tessellatum*. The deepwater crustose Corallinaceae (38-percent mean cover) overshadow all other calcareous organisms in terms of standing stock and also seem to have more biological influence than do the other limestone producers.

THERE ARE no previous assessments of crustose coralline standing stocks from tropical deep waters (below 3 m); consequently, there has existed a general unawareness of the roles of these algae beyond the fringing reef. The production (Littler, unpublished) and ecology (Littler, in press) of Hawaiian fringing reef builders will be reported and some of the ecological factors operative in the *Porolithon* ridge are now reasonably well understood (Littler and Doty, unpublished). However, the only published data on tropical crustose corallines below a depth of several meters have resulted from collections obtained by dredging (e.g., David, Halligan, and Finckh 1904; Setchell 1926; Skottsberg 1943; Lemoine 1940).

The present study is concerned with the distribution, abundance, and community structure of Hawaiian crustose Corallinaceae beyond the *Porolithon* ridge over a depth range from 8 to 28 meters. The first of the two deepwater areas examined (Fig. 1) is the zone directly seaward from the Waikiki fringing reef. This area was sampled at stations 1 (8 m deep), 2 (13 m), 3 (20 m), 4 (20 m), 5 (21 m), 6 (23 m), and 7 (28 m), which ranged from 0.6 km to 1.7 km offshore. The seven stations investigated through this zone are thought to be representative because other areas examined, at the same depth off Oahu Island, appear to be quite comparable. The other deepwater area investigated (Fig. 1) lies approximately 1.5 km seaward of the town of Maile and off leeward Oahu Island. The Maile sites selected for study are three stations that have been studied extensively (McVey 1970) in respect to their fishery ecology. These are referred to hereafter as station A (12 m deep), station B (18 m deep), and station C (27 m deep). These three stations are likewise thought to be representative, by reason of their similarity, to other regions of Oahu at the same depths.

METHODS AND MATERIALS

Because reliable techniques for measuring crustose coralline standing stocks were lacking, special methods were devised during this study. Among these is a photographimetric technique, which I have described and evaluated (1971*b*). Additionally, notes were recorded on an underwater tape recorder to alleviate potential taxonomic difficulties encountered in the photoquadrats.

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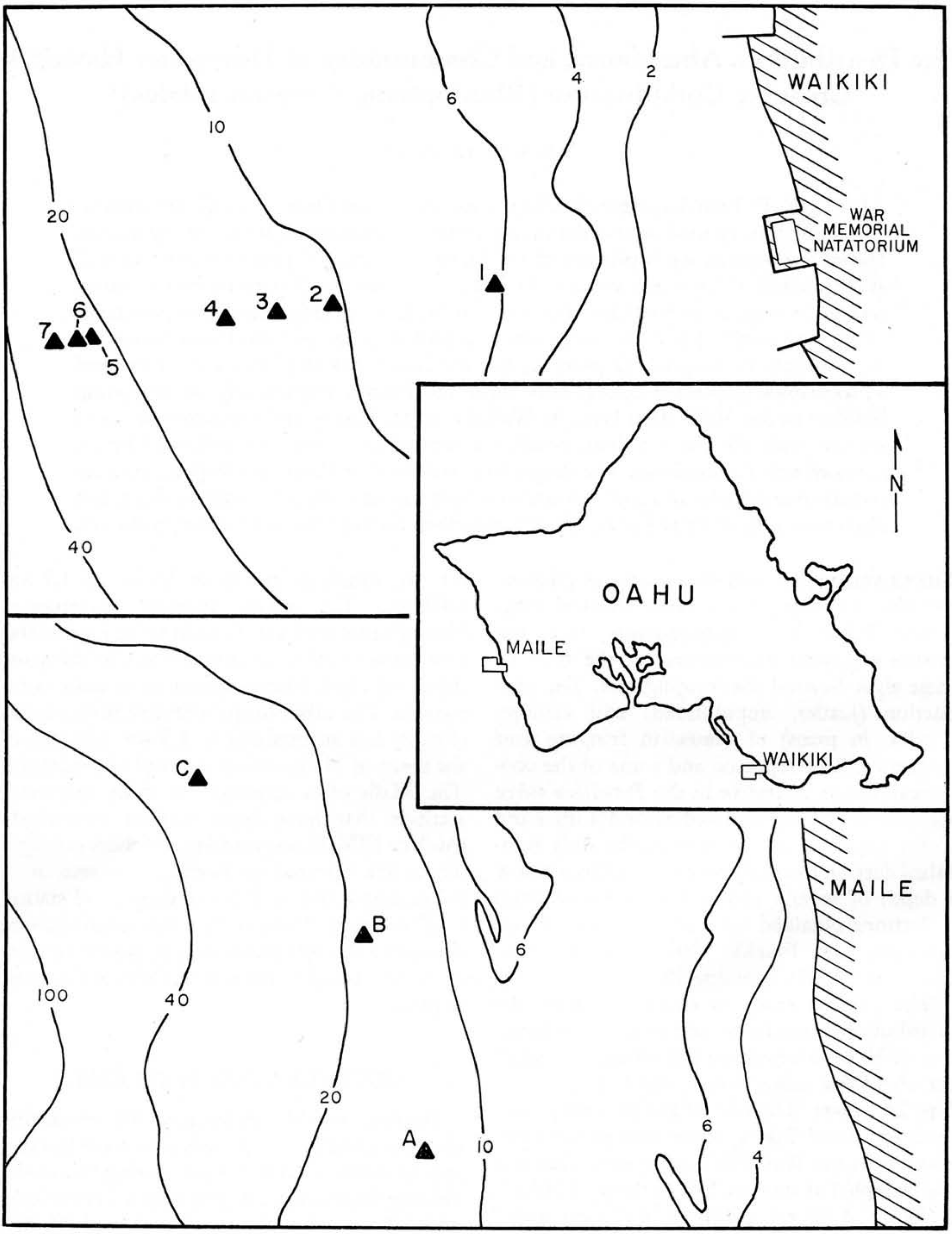

FIG. 1. Map of Oahu Island showing the location of the stations sampled at Waikiki (numbered 1 to 7) and a Maile (lettered A to C). Depth contours are in meters.

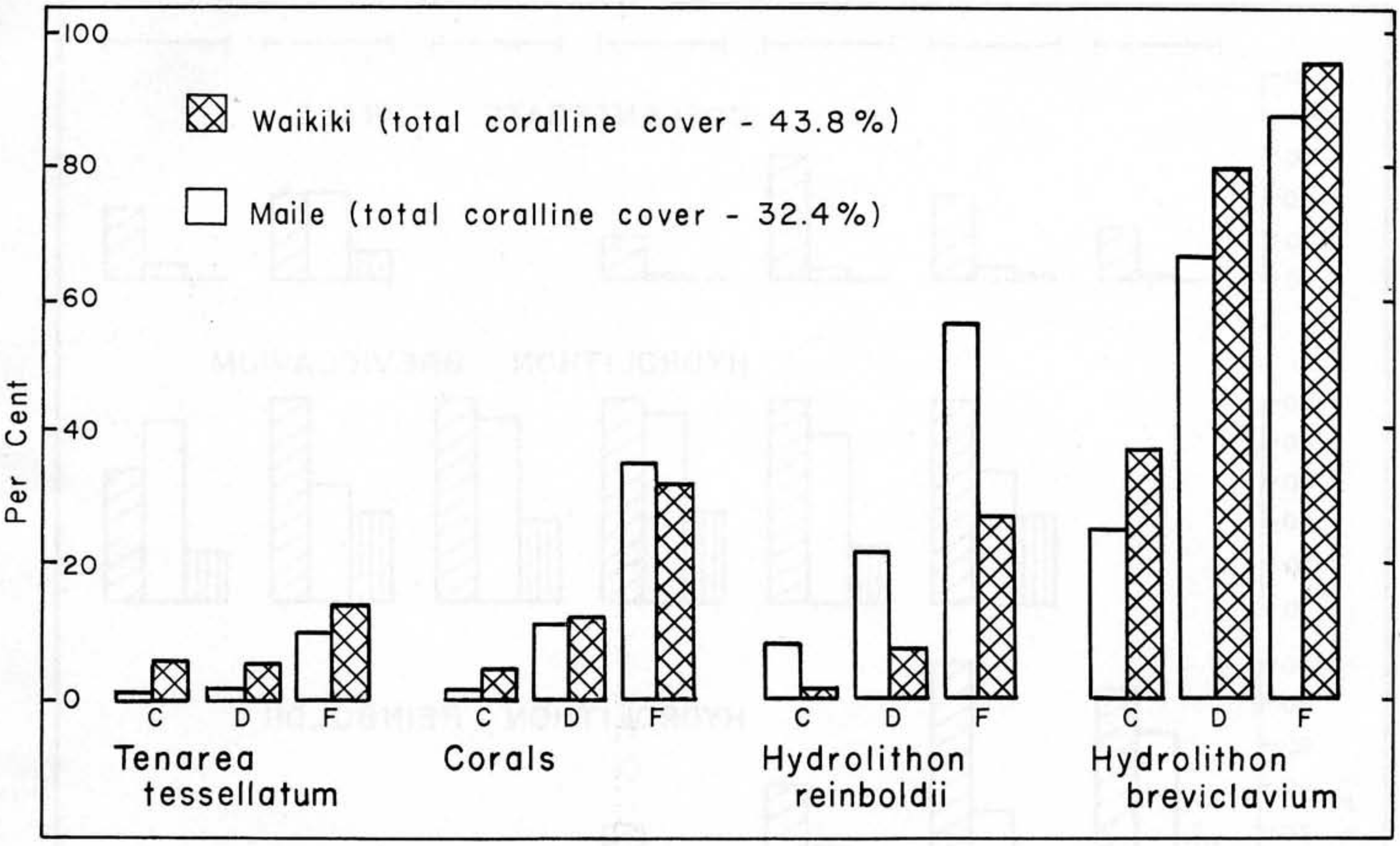

FIG. 2. The mean standing-stock values of the major reef builders over the whole study area at Waikiki and at Maile. For each organism, cover (C) is on the left, relative density (D) in the middle, and frequency (F) on the right.

The Maile area was sampled on 22 November 1968. Stations A and B were each surveyed and approximately 10 random photosamples were taken in each. On 24 November 1968 another set of ring-throw photos was taken at station C and at station B. The Waikiki area was sampled on 14 February 1969. A transect series of photosamples was completed directly seaward of the Waikiki War Memorial Natatorium. Methods and materials were identical to those used on 22 November 1968 at Maile.

RESULTS

VARIATIONS IN COVER

At depths of 8 to 28 m coralline algae comprise 43.8 percent of the cover off Waikiki and 32.4 percent of that off Maile. In both habitats the rest of the bottom is mostly dead reef, sand, and rubble. At Waikiki (Fig. 2) *Hydrolithon breviclavium* is followed primary by *Tenarea tessellatum*, coelenterate corals, and *H. reinboldii*. At Maile (Fig. 2) *H. breviclavium* also is primary in mean cover, but *H. reinboldii* and corals surpass *T. tessellatum*.

Hydrolithon breviclavium (Fig. 3) appeared in samples off Waikiki at the 13-m station most often as loose aggregates and less often as saxicolous crusts. This species is by far the most abundant deep form (up to 45.2-percent cover) and is surpassed only at station 7 (28 m deep) by *Tenarea tessellatum*. *T. tessellatum* seems restricted to deeper water (Fig. 3) and becomes more abundant as depth increases. Coral colonies are generally small and occur in low abundance (Fig. 3) except for a 10-m-wide band of nearly 100 percent *Porites compressa*. The coral band is parallel to shore and 23 m deep where slope of the bottom becomes steep. *Hydrolithon reinboldii* occurs in the study area off Waikiki but decreases in abundance as depth increases; it was absent from the samples below 20 m.

The same general trends were noted (Fig. 4) at the Maile stations. However, total coralline cover is about 11 percent greater off Waikiki than at Maile. *Hydrolithon breviclavium* (Fig. 4) also dominates at Maile but generally covers

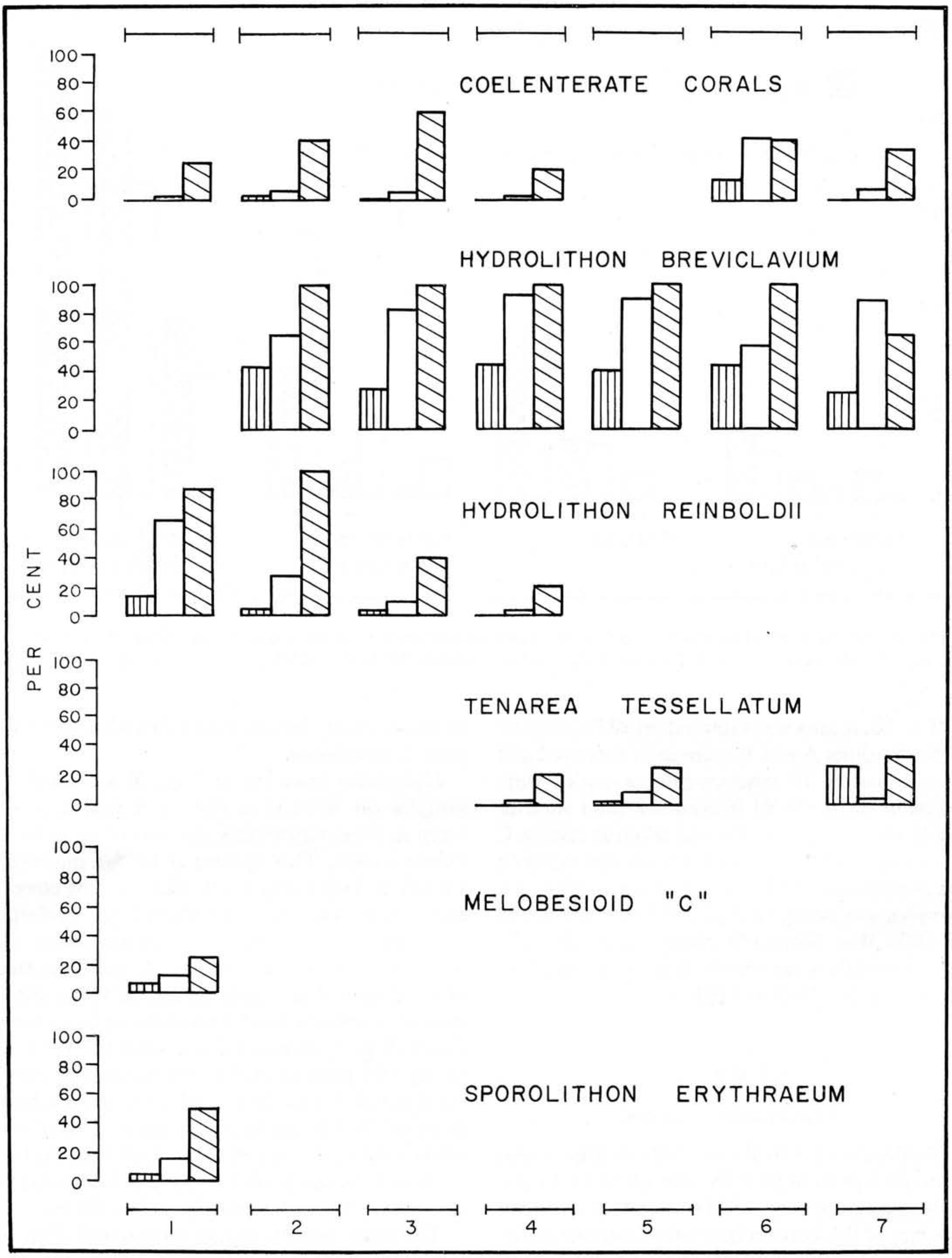

FIG. 3. The standing stocks of major builders along a transect seaward of the Waikiki fringing reef. In each histogram cover is given by the left column, relative density by the middle column, and frequency by the right column. Numbers 1 to 7 on the ordinate are station numbers.

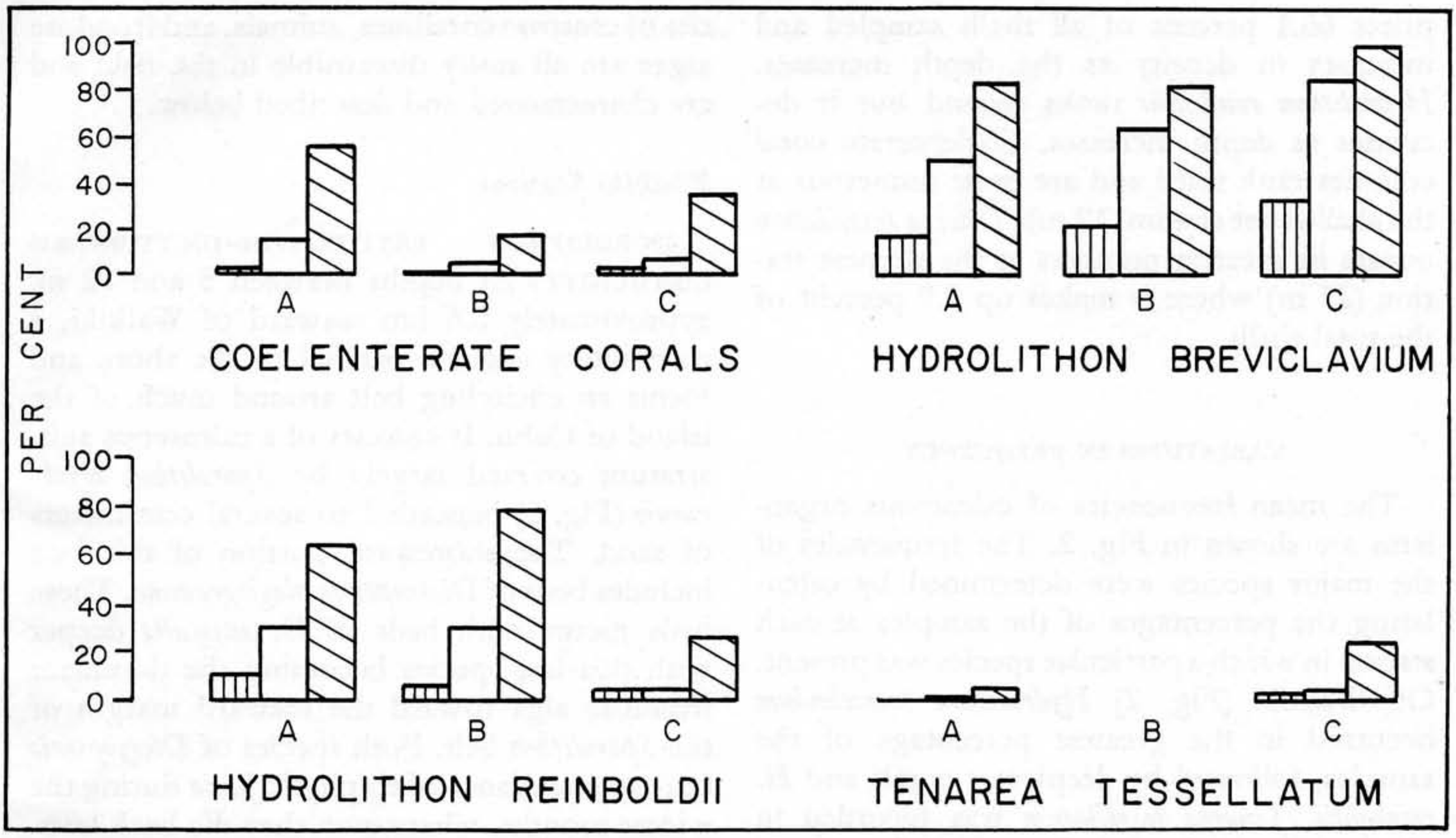

FIG. 4. The standing stocks of major builders seaward of Maile (stations A, B, and C). In each histogram, cover is given by the left column, relative density by the middle column, and frequency by the right column.

less than at Waikiki and increases markedly at the deepest station (27 m). In both study areas *Tenarea tessellatum* is notably more abundant at the deeper stations (Figs. 3 and 4). *Hydrolithon reinboldii* decreases with increasing depth at both Waikiki and Maile, but grows deeper at Maile. At Maile (Fig. 4), *H. reinboldii* and corals exceed *T. tessellatum* in total area covered; the reverse is true at Waikiki (Fig. 3).

VARIATIONS IN RELATIVE DENSITY

The mean relative densities of the major reef builders are presented in Figs. 2, 3, and 4. Relative densities of individuals of each species were calculated for each station as a percentage of the total thalli and coral colonies sampled. At Waikiki (Fig. 2) *Hydrolithon breviclavium* is primary in relative density followed by coelenterate coral colonies and *H. reinboldii*. *Tenarea tessellatum* contributes the least relative density of saxicolous organisms. At Maile (Fig. 2) *H. breviclavium* also shows the highest relative density and makes up 66.1 percent of the thalli sampled. *Hydrolithon reinboldii* has the second highest relative density, corals rank third, and *T. tessellatum* contributes the least number of individuals of the important species.

The standing stocks of the major reef builders at Waikiki are shown in Fig. 3. *Hydrolithon breviclavium* comprises about 90 percent of the total thalli at the 20-m depth, decreases at the 23-m depth, but increases to 88.9 percent relative density at the 28-m depth. *Tenarea tessellatum* thalli (Fig. 3) are found in low numbers (2.5-percent mean density) and only below 20 m deep beyond 1.0 km offshore. Thalli of this species were absent from the samples taken at depths of 23 meters. Coelenterate corals (Fig. 3) occur sporadically and generally in low numbers with a slight peak in the number of colonies (10.6-percent mean density) in the area just seaward of the fringing reef. Corals decrease at the 20-m depths and then reach an abrupt maximum (41.7-percent density) at 23 m deep where *Porites compressa* forms a belt parallel to the shore. *Hydrolithon reinboldii* decreases rapidly in relative density from depths of 8 m with increasing depth and eventually disappears at 23 m deep.

At Maile (Fig. 4) *Hydrolithon breviclavium* comprises 66.1 percent of all thalli sampled and increases in density as the depth increases. *Hydrolithon reinboldii* ranks second but it decreases as depth increases. Coelenterate coral colonies rank third and are most numerous at the shallowest station (12 m). *Tenarea tessellatum* occurs in greatest numbers at the deepest station (27 m) where it makes up 3.9 percent of the total thalli.

VARIATIONS IN FREQUENCY

The mean frequencies of calcareous organisms are shown in Fig. 2. The frequencies of the major species were determined by calculating the percentages of the samples at each station in which a particular species was present. Off Waikiki (Fig. 2) *Hydrolithon breviclavium* occurred in the greatest percentage of the samples, followed by deepwater corals and *H. reinboldii*. *Tenarea tessellatum* was recorded in 13.0 percent of the samples. At Maile (Fig. 2) *H. breviclavium* was present in 87.7 percent of all samples. Next ranking in frequency was *H. reinboldii* followed by corals and *T. tessellatum*.

At Waikiki (Fig. 3) *Hydrolithon breviclavium* appeared in all samples over a depth range of 13 to 23 meters. *Tenarea tessellatum* (Fig. 3) occurred in samples at depths of 20 and 21 m, was absent from the samples at 23 m, and reached a peak frequency at 28 m deep. Coral colonies (Fig. 3), although small, were included in 2.0 percent of the total number of samples. Corals reach two peaks in frequency, one at 20 m deep, the other at 23 m where *Porites compressa* is abundant. Off Waikiki, at depths of 13 m, *H. reinboldii* occurred in all of the samples. From there it decreased in frequency and was absent from samples below depths of 21 meters.

At Maile (Fig. 4) *Hydrolithon breviclavium* and *Tenarea tessellatum* occur most frequently at 27 m, whereas the corals reach a maximum at 12 meters. *Hydrolithon reinboldii* shows a peak frequency at 18 m deep.

VARIATIONS IN COMMUNITY STRUCTURE

The term "community" as used here refers to those aggregations of organisms that characteristically occurred together. These communities of crustose corallines, animals, and frondose algae are all easily discernible in the field and are characterized and described below.

Waikiki Stations

SPOROLITHON ERYTHRAEUM-DICTYOPTERIS COMMUNITY: At depths between 8 and 12 m, approximately 0.6 km seaward of Waikiki, a community extends parallel to the shore and forms an encircling belt around much of the island of Oahu. It consists of a calcareous substratum covered largely by *Sporolithon erythraeum* (Fig. 3) beneath 1 to several centimeters of sand. The shoreward portion of this belt includes beds of *Dictyopteris plagiogramma*. These beds merge with beds of *D. australis* deeper with this last species becoming the dominant frondose alga toward the seaward margin of the *Sporolithon* belt. Both species of *Dictyopteris* bear an abundance of epiphytic *Jania* during the winter months, whereupon they die back leaving only portions of the stipe and holdfast. *Hydrolithon reinboldii* is also a member of the community, forming extensive crusts on outcroppings and dead coral heads, and melobesioid "C" (Littler 1971*a*, appendix C) is abundant beneath ledges. Numerous tunicates extend from beneath the layer of sand and *Gymnothorax* was the only fish commonly seen in this area.

HYDROLITHON BREVICLAVIUM-HYDROLITHON REINBOLDII COMMUNITY: Seaward of the *S. erythraeum-Dictyopteris* community, *Hydrolithon* is the major paver of the calcareous substratum. *Hydrolithon breviclavium* occurs both as saxicolous crusts and as round aggregates that lie scattered over this zone (13 to 20 m). It increases (Fig. 3) and *H. reinboldii* decreases in cover, density, and frequency between depths of 13 to 20 meters. *Tenarea tessellatum* (Fig. 3) also increases as depth increases below 13 meters. Attached to the crustose corallines and dead reef, beneath a thin layer of silt and sand, are *Lyngbya*, *Halymenia*, *Amansia*, *Padina*, *Neomeris*, *Herposiphonia*, *Halimeda*, *Dictyota*, and *Peyssonellia*. Various species of sea urchins are common in this area.

HYDROLITHON BREVICLAVIUM CRUST COMMUNITY: At depths of 21 m the bottom is very uniform and pavementlike. Crusts of *Hydrolithon breviclavium* and *Tenarea tessellatum* are present but here the slope is too steep to retain loose aggregates and only sand is found in the depressions.

PORITES COMPRESSA-HYDROLITHON BREVICLAVIUM COMMUNITY: Near the 23-m-deep station at Waikiki two distinctive belts parallel the shore. These belts may extend around much of leeward Oahu Island because similar zones were observed seaward of the 27 m station at Maile, some 45 km to the west. The deeper of these belts (Fig. 3) is composed almost entirely of *Porites compressa* and is approximately 25 m wide. Only the distal portions of the branches of this coral are living; *Hydrolithon breviclavium* and *Peyssonellia* encrust the dead lower portions.

HYDROLITHON BREVICLAVIUM AGGREGATE COMMUNITY: The *Porites compressa-Hydrolithon breviclavium* community, by acting as a dam, creates a shallower, 21-m-deep, zone approximately 10 m wide shoreward of station 6 at Waikiki. This zone (Fig. 3) consists of rounded aggregates of *H. breviclavium* that have piled up against the branches of the preceding community as they rolled or slid down the steep slope. The underlying substratum in this belt is recognizable as *Porites compressa* that has been filled in between its branches by sediments and consolidated, probably by *H. breviclavium*.

TENAREA TESSELLATUM-HYDROLITHON BREVICLAVIUM COMMUNITY: Seaward of the *Porites compressa-Hydrolithon breviclavium* community at depths below 28 m, the calcareous, pavementlike bottom slope increases abruptly and drops to depths beyond the limits of visibility from a "safe depth" for diving. There are scattered fragments of rubble in this area, and a species of "black coral" is present. *Tenarea tessellatum* (Fig. 3) is primary, surpassing *H. breviclavium* in cover, density, and frequency.

Maile Stations

At Maile, as at Waikiki, *Hydrolithon breviclavium* comprises the bulk of the encrusting community (Fig. 2), with *H. reinboldii* ranking second in area covered. *Tenarea tessellatum* and *H. breviclavium* (Fig. 4) become more abundant with depth, but *H. reinboldii* decreases with increasing depth. The major frondose algae are *Amansia*, *Symploca*, *Herposiphonia*, *Dictyota*, *Dictyosphaeria*, *Caulerpa*, and *Schizothrix*, which form a sparse turf. Small thalli of *Peyssonellia* occur in nearly every quadrat as do three species of sponges, whereas bryozoa are present in cracks or beneath rocks. Grazing by fishes and sea urchins on the frondose algal cover was observed to be extensive.

DISCUSSION

The two deepwater areas studied (Figs. 2, 3, and 4) are similar in the kinds of organisms present and in their order of importance. *Hydrolithon breviclavium* is primary at Maile (24.6-percent cover) as well as at Waikiki (37.2-percent cover). At Maile, *H. reinboldii* ranks second in relative importance (Fig. 2); on the other hand, at Waikiki (Fig. 2) *Tenarea tessellatum* and corals are so abundant at the deeper stations that they surpass *H. reinboldii* in total cover. Corals and *T. tessellatum* (Fig. 2) rank third and fourth, respectively, as important builders in the Maile deep area. At Waikiki, when density and frequency are considered with the cover values (Fig. 2), corals are second in importance followed by *H. reinboldii* and *T. tessellatum*. Total coralline cover is 11.4 percent greater at Waikiki than at Maile. The crustose coralline algae (38.3-percent mean cover) overshadow all other calcareous organisms in terms of standing stock and appear to have more influence biologically than other reef builders in the habitats studied.

Although the mean cover (38.3 percent) of deepwater crustose corallines compares closely with that of the fringing reef forms (38.9 percent), only *Hydrolithon reinboldii* is common to both habitats (Littler, in press). With three exceptions, there are no sharply defined patterns of zonation in the areas studied. Instead, there is a general trend whereby the fringing-reef forms gradually decrease in abundance with increasing depth (Figs. 3 and 4), while *H. breviclavium* and *Tenarea tessellatum* increase with depth. The three rather sharply defined deepwater zones described in detail earlier are: the

Sporolithon erythraeum-Dictyopteris community that occurs at 8 to 12 m depths; the *Hydrolithon breviclavium* aggregate community, at about 21 m; and the *Porites compressa-Hydrolithon breviclavium* community, at about 23 meters. These represent the first records of crustose coralline community structure from tropical waters deeper than 2 to 3 meters.

The interaction between the *Porites compressa-Hydrolithon breviclavium* community and the *H. breviclavium* aggregate community appears to be important in controlling or determining the depth profile. The band of *P. compressa* (Fig. 3) acts as a dam and prevents large amounts of living aggregates of *H. breviclavium* from being moved downward. Therefore, an area of relatively high standing stock is created and thalli are concentrated into a zone (substantially increasing the bulk) where consolidation occurs. This is shown by the underlying reef structure, which is dead *P. compressa* with both consolidated and unconsolidated reef materials filling the spaces between its branches.

These observations suggest an interesting speculation concerning reef-building processes in the Hawaiian Islands. *Porites compressa* as well as other corals occurs in abundance close to shore to depths of about 30 m in the geologically young (with the exception of new lava flows) and low mineral-nutrient areas around the islands of Hawaii (e.g., Kealakekua Bay and Honaunau Bay) and Maui (e.g., Kamaole). In view of the above, early reef development in these kinds of places might result largely from corals and other reef or land materials that become trapped by the highly branched *P. compressa*. As these coral bottoms build toward the surface and the habitat becomes nutrient enriched (from land runoff after biological succession has occurred), the corals probably would become gradually filled-in and replaced by crustose corallines in the shallower, shoreward portions of the reefs. By this process, a region of low fertilizer salts, shallow enough for *P. compressa* growth, might be driven seaward until it persists as a zone similar to that sampled at station 6 (23 m deep) off Waikiki. Evidence for the above speculation is provided by comparing the high percentage (Pollock 1928) of *P. compressa* (as finger coral) in the raised fossil reefs of Oahu Island to the predominance (except for low nutrient waters) of crustose corallines in living reefs (Littler, in press) of Oahu.

With regard to the *Hydrolithon breviclavium* aggregate community, the only other similar circumstance was mentioned (Adey 1968) in reference to semiexposed bays and fjords in the northwestern North Atlantic where species of *Lithothamnium* are broken free from shallow ledges and continue to grow as they are carried deeper. In some areas this process results in the formation of a thick but narrow zone below the area of ledges and boulders just inshore.

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