



SEPM Society for Sedimentary Geology

4111 S Darlington
Suite 100
Tulsa, Oklahoma 74135
USA

Phone: 918-610-3361
Fax: 918-621-1685
www.sepm.org

This PDF Content is made available by SEPM—Society for Sedimentary Geology for non-commercial use. This file does contain security features to prevent changing, copying items or printing the document.

Additional restrictions and information can be found below.

Connect to other SEPM publications below.

- www.sepm.org to learn more about the Society, membership, conferences and other publications
- www.sepm.org/bookstore/storehome.htm for purchase other SEPM Book Publications.
- www.sepmonline.org to access both Book and Journals online.

Copyright not claimed on content prepared by wholly by U.S. government employees within scope of their employment.

Individual scientists are granted permission, without fees or further requests to SEPM, to use a single figure, a single table, and/or a brief paragraph of text in subsequent works.

To make unlimited copies of items in SEPM publications for noncommercial use in classrooms to further education and science without fees please contact SEPM.

This file may not be posted to any other Web site.

SEPM provides this and other forums for the presentation for the of diverse opinions and positions by scientists globally. Ideas in this publications do not necessarily reflect the official position of the Society.

Coral Mounds on the West Florida Slope: Unanswered Questions Regarding the Development of Deep-Water Banks

CATHRYN R. NEWTON, HENRY T. MULLINS, and ANNE F. GARDULSKI

Department of Geology, Heroy Geology Laboratory, Syracuse University, Syracuse, NY 13244-1070

ALBERT C. HINE

Department of Marine Science, University of South Florida, St. Petersburg, FL 33701

GEORGE R. DIX

Department of Geology, Heroy Geology Laboratory, Syracuse University, Syracuse, NY 13244-1070

PALAIOS, 1987, V. 2, p. 359–367

Although some groups, such as the Mollusca and ahermatypic corals, do occur at great depths, they are too rare in the fossil record to be of value to the marine geologist.

—James Kennett, 1982, p. 537–538.

*Late Pleistocene deep-water coral mounds of 10–15 m relief occur in a 20 km linear zone parallel to the 500 m isobath along the West Florida carbonate-ramp slope. These relict mounds were constructed by the densely calcified, ahermatypic framework builder, *Lophelia prolifera*, and provided habitats for a host of associated invertebrates, including epizoans, epifaunal commensal organisms, nestlers and crevice dwellers, and macroendoliths. Scleractinian diversity and taxonomic composition are congruent with those of other *Lophelia* buildups in the North Atlantic, particularly buildups in the eastern Atlantic. The scleractinians also retain primary mineralogic, isotopic, and trace-element geochemical signatures, indicating relatively little diagenetic alteration, despite "dead" (>40,000 years b.p.) radiocarbon ages.*

The small but rapidly expanding global data base on deep-water coral mounds has magnified two key questions concerning the ecologic and environmental controls on mound nucleation, growth, and death. First, what are the principal ecologic controls on dominance within communities of deep-water framework builders? Second, why are there so many relict and so few living deep-water mounds in the modern ocean? Ecological and paleoecological investigation of these questions would elucidate much about the dynamics of deep-water mound growth.

INTRODUCTION

Recent years have witnessed an increasing number of reports of deep-water (>200 m) coral banks. These numerous

accounts attest that these deep, ahermatypic mounds are not biological oddities. Rather, they can be considered characteristic of regions at intermediate depths (200–1200 m) where local hard substrates are available for colonization by frame-building ahermatypes. These conditions are met in an extremely wide array of modern-day habitats including Chilean and Norwegian fjords, the western European and northwest African continental margins, the Blake Plateau, the Straits of Florida, the northern slope of Little Bahama Bank, the Mississippi Delta, and a sub-Antarctic seamount (Dons, 1944; Le Danois, 1948; Teichert, 1958; Moore and Bullis, 1960; Stetson et al., 1962; Neumann et al., 1977; Cairns, 1979; Popenoe et al., 1979; Cairns and Stanley, 1981; Mullins et al., 1981). The ecologic factor shared by these diverse sites is the presence of moderate to vigorous currents, which secondarily enhance the availability of rock pavements or submarine hardgrounds for colonization.

We present here the first report of areally extensive coral banks at depths of 500 m on the carbonate-ramp slope of the eastern Gulf of Mexico (Fig. 1). This paper defines the ecological and taxonomic composition of the scleractinian fauna and associated invertebrates, documents the mineralogic and geochemical signatures of the corals, and characterizes the age of the framework builders. In addition, we review the known occurrences of deep-water mounds in light of two ecological questions that may provide a stimulating agenda for future research on deep-water coral banks in the modern ocean.

STUDY AREA AND DISTRIBUTION OF THE MOUNDS

The West Florida slope is a distally-steepened carbonate ramp with an average dip of 1–2°. This subdued dip increases locally to 5–12° at seaward-dipping erosional scarps and regionally at the precipitous, high-relief West Florida Escarpment. From an oceanographic and ecologic perspective, the most

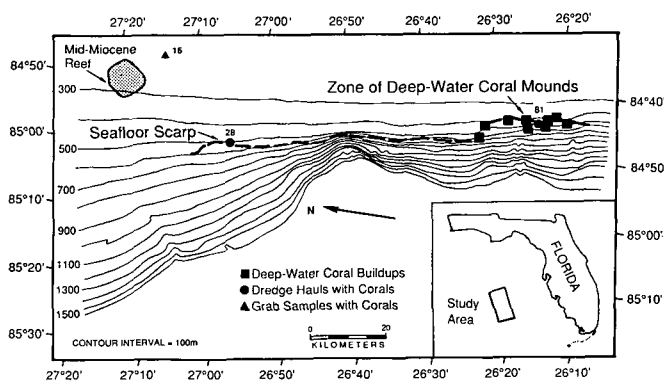


FIGURE 1—Location of West Florida coral banks, illustrating their association with an extensive, seaward-facing erosional scarp. (Note: the very steep Florida Escarpment lies far beyond the western margin of the maps included here.)

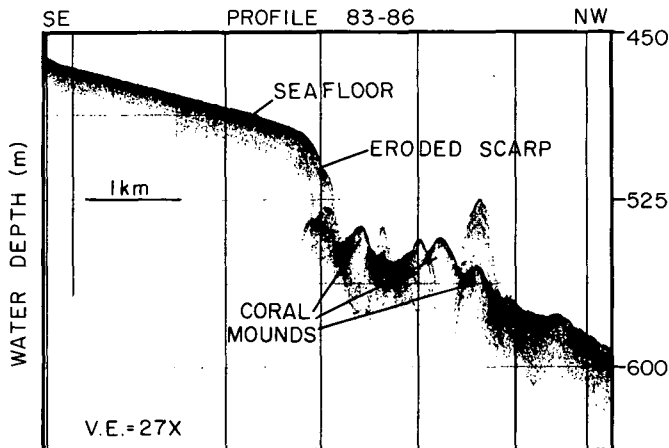


FIGURE 2—3.5 kHz Precision Depth Recorder profile across mound area, showing erosional scarp and scleractinian mounds of 10–15 m relief.

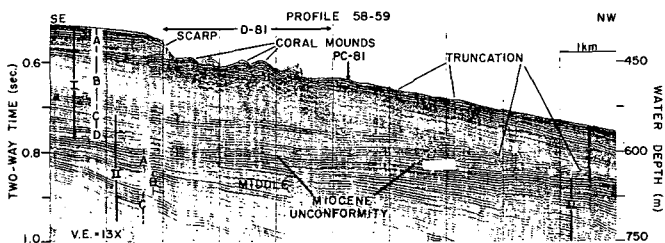


FIGURE 3—Single-channel, analog, 5 in³ air-gun seismic-reflection profile illustrating development of deep-water mounds on outcrops of seismic sequence IB (Pliocene), capped by a Pleistocene gravelly sand and hardground unit. Note also the erosional scarp and locations of piston cores and rock dredges. (Note: the white area to the upper right of "Miocene unconformity" occurred in preparation of diagram.)

salient feature of the margin is the eastern Gulf of Mexico Loop Current, a vigorous, north- and south-flowing current that migrates laterally through time. This lateral migration occurs not only as a long-term process but also seasonally, producing pronounced variation in temperature at shallow to intermediate depths (Leipper et al., 1972).

The zone of coral-mound development extends along the 500 m isobath for more than 20 km adjacent to a sea-floor scarp (Fig. 1). Individual mounds are 10–15 m high (Fig. 2) and rest on seismically defined, Pliocene outcrops capped by gravelly carbonate sand of Pleistocene age (the latter sampled in piston core 81 [Unit IB; Fig. 3, from Mullins et al., submitted]). The coral occurrences also coincide with the seaward edge of an area of extensive erosional pavements that were probably produced by intensification of the Loop Current during glacial intervals (Fig. 4, Mullins et al., submitted). *In situ* measurements of bottom temperature are not available for the mound areas; however, Nowlin (1972) presented data indicating winter temperatures of 7–8°C at the 500 m isobath for stations nearby in the eastern Gulf.

METHODS

The zone of coral mounds was initially recognized on depth records and high-resolution seismic-reflection profiles during cruise CH-1-84 of the *R/V Cape Hatteras* in January, 1984. Coral samples from the mounds were recovered in rock dredges on cruise CH-4-85 in February, 1985 (sample site 81; Fig. 1). Sparse corals were also recovered from non-mound areas in dredge and grab samples from sites 16 and 28 (Fig. 1).

Taxonomic identification and ecological interpretation of the scleractinians and associated invertebrates were carried out by Newton. Identifications of the ahermatypes were verified by Stephen Cairns of the Smithsonian Institution.

Mineralogical and geochemical analyses focused on characteristics of the most abundant ahermatypic scleractinian in the study area, *Lophelia prolifera*. The specimens selected range from very well preserved to bored and encrusted. All samples were cleaned ultrasonically to remove debris. Mineralogical determinations were based on standard X-ray diffraction techniques, using Milliman's (1974) peak-area method and corrected for aragonite percentages using the method of Boardman (1978). Sr Analysis of selected *Lophelia* specimens was conducted using a Direct-Current Plasma Emission Spectrometer at Syracuse University. R.K. Matthews of Brown University provided oxygen and carbon isotopic data from *Lophelia* subsamples. Radiocarbon dates are from the University of Texas Radiocarbon Lab.

PREVIOUS WORK

Relatively little is known about the ecology of the slope biota in the eastern Gulf of Mexico, although several valuable regional surveys have been conducted. The most extensive compilation is that of Collard and D'Asaro (1973), who present data for all benthic invertebrates in the eastern Gulf. The compilation of ahermatypic Scleractinia for the entire Gulf of Mexico (Cairns, 1978) also contributes to our study. Another study by Blake and Doyle (1983) on the West Florida slope emphasized infaunal rather than epifaunal organisms.

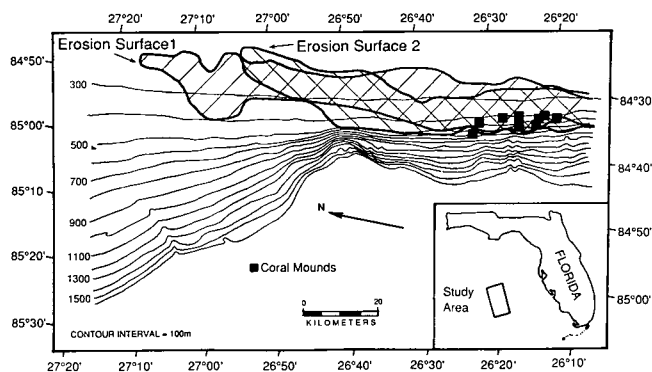


FIGURE 4—Zone of deep-water coral mounds in relation to zone of erosional surfaces as defined by seismic stratigraphic analyses (Mullins and others, submitted). Note that mounds occur in areas of overlap of the two erosional surfaces; these areas are inferred to represent locations of preferentially more intense scour.

RESULTS

Scleractinian Taxonomic Composition and Ecology

The mound biotas show a strong dominance by the ahermatype *Lophelia prolifera* (Pallas), which occurs as massively calcified colonies (the “*brachycephala*” form of earlier workers) and also as more delicately branched specimens (the “*gracilis*” form) (Fig. 5). Associated with *Lophelia*, but greatly subordinate in abundance, are the colonial *Madrepora oculata*, the solitary, epithecate *Bathypsammia*, and a very small, indeterminate caryophyllid coral.

All scleractinians recovered from the mounds were dead. A host of mound-associated invertebrates was also recovered from the buildups; among these, most were also dead, represented only by skeletal remains. The freshness of skeletal material varies greatly, from pristine to highly bored and altered.

Epizoans

Atop and within the large *Lophelia* colonies are a variety of small epizoans. These include sponges, serpulids (two forms), annelids represented by agglutinated tubes, octocorals, and encrusting bryozoans. The agglutinated worm tubes are visually striking: they commonly use tests of *Globigerinoides ruber* and other foraminiferal species. The small, solitary caryophyllid coral mentioned above is also an epizoan on *Lophelia*.

Epifaunal Commensal Organisms

Conspicuous, cylindrical voids within colonies of *Madrepora oculata* reflect commensalism and intergrowth with polychaete worms. Cairns (1979) has previously commented on the frequent association between the cosmopolitan scleractinian *M. oculata* and the polychaete (*Eunice* sp.), but evidently the precise ecological interactions are not known.

Nestlers and Crevice Dwellers

Terebratulid brachiopods frequently occupy small crevices with *Lophelia* colonies and are the most abundant nestlers

retrieved in dredge samples (Fig. 6). Dimensions of the brachiopods (2.5–3 cm across) are large in comparison to the relatively narrow crevices they inhabit, suggesting that the voids limit brachiopod growth.

The terebratulids apparently colonize these small crevices at a small body size, then grow until restricted by the minimum diameter of the void. In this sense, the brachiopods bear ecological resemblance to suspension-feeding macroendoliths on the mounds.

Other, less abundant nestlers include corals such as *Bathypsammia*, a solitary epithecate scleractinian that requires basal attachment to a substrate throughout ontogeny (Stetson et al., 1962). Small arcid bivalves ($\bar{L} = 1.5$ cm) and an indeterminate gastropod ($\bar{H} = 8.1$ cm) are also inferred to have formed part of the interstitial fauna. In summary, these nestlers and crevice inhabitants compose a small but numerically (and ecologically) significant component of the mound biota.

Macroendoliths

Colonies of *Lophelia prolifera* preserve diverse patterns of secondary biogenic porosity resulting from excavation by macroendoliths. Large-scale borings formed by lithophagid (?) bivalves occur on massively constructed colonies. Smaller borings are typical of both “*gracilis*” and “*brachycephala*” morphs; these include traces of polychaetes (similar to *Polydora*), clionid sponges, and bryozoans. A particularly striking aspect of borehole distribution in *Lophelia* is the high frequency of stereome-specific tunneling; as Figure 7 illustrates, borers commonly excavate tunnels within the outer, massive stereomal aragonite, but do not penetrate the septal areas of the corallum.

Mineralogy and Geochemistry

Scleractinian Mineralogy

Coral specimens representing a spectrum of preservational textures, from extremely fresh in appearance to encrusted, bored, and Mn-oxide coated, were analyzed for carbonate mineralogy. Of six specimens, all but one are 100% aragonite. The lone exception was L-6, the most severely altered and encrusted specimen, which is 68% aragonite. Thus, all but the most highly corroded specimens have (thus far) retained their primary aragonitic mineralogy.

Scleractinian Geochemistry

Sr analyses of *Lophelia* reveal primary geochemical signatures in the range of 8747–9110 ppm (Table 1). This range is consistent with Sr determinations for modern scleractinians (6850–8407 ppm; Burke et al., 1982). The one specimen with significantly lower Sr levels is the poorly preserved L6, which yields values of 6680 ppm Sr. Although the Sr values for L6 are appreciably depleted relative to the West Florida data set, they are not extremely low by comparison with the overall range of modern scleractinians.

Isotopically, the *Lophelia* samples retain signals characteristic of deep-water ahermatypes; $\delta^{13}\text{C}$ values range from -2.28 to -6.33 and $\delta^{18}\text{O}$ ranges from 1.00 to 2.23 (relative to PDB). These results generally plot within the field for deep-water ahermatypes compiled by Mullins et al. (1981) based on data

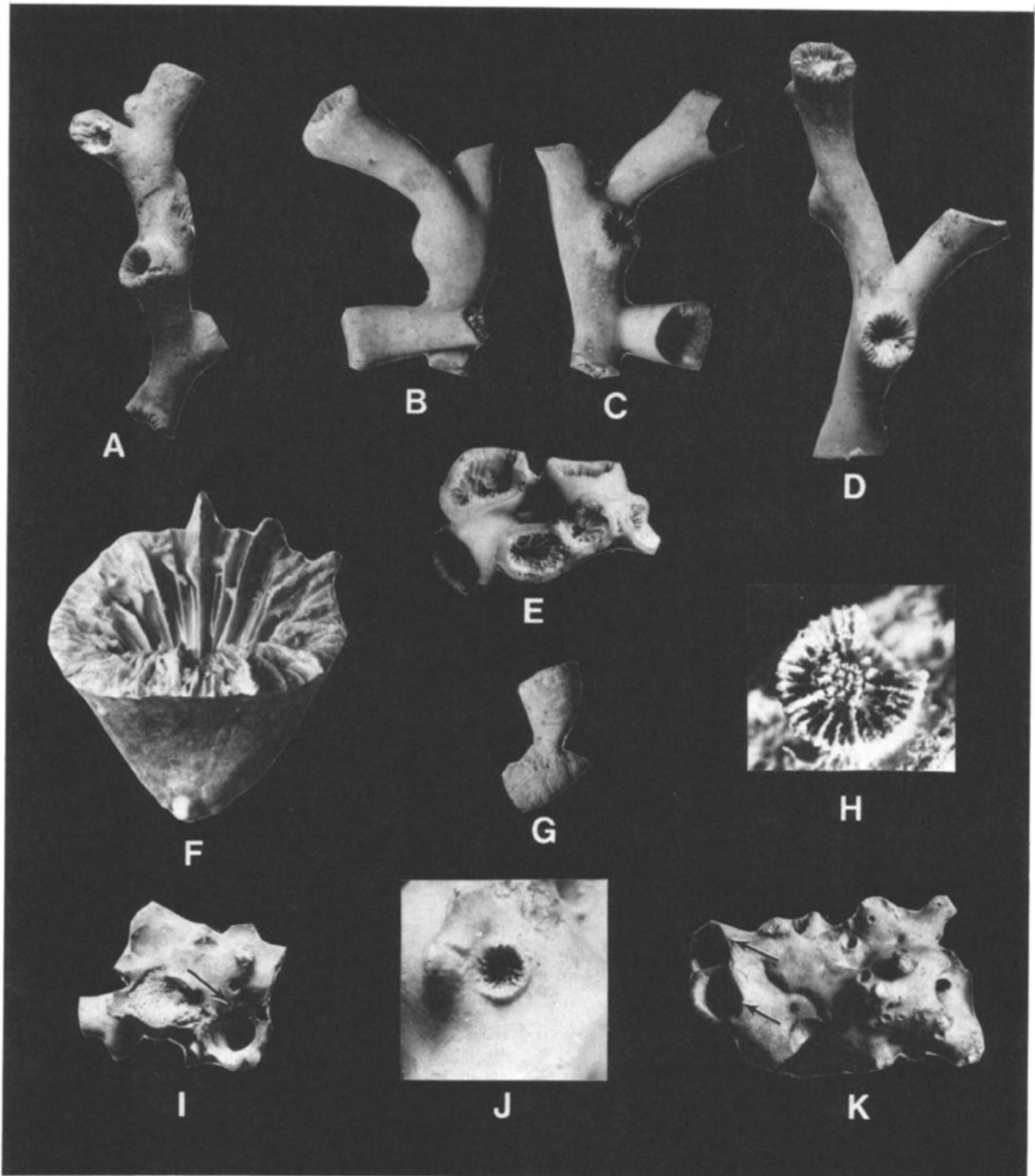


FIGURE 5—Deep-water, ahermatypic Scleractinia from the West Florida carbonate slope. **A-D)** *Lophelia prolifera* (delicately branched, "gracilis" morph) from sample site 81, x1; **B,C** represent opposing views of same specimen. **E)** *Lophelia prolifera* (more densely anastomosing, "brachycephala" morph), site 81, x1. **F)** solitary coral *Flabellum moseleyi*; specimen collected live in dredge sample 28, x1. **G)** *Bathypsammia* sp., two dead specimens from grab sample 16, x1.5. **H)** Indeterminate caryophylline attached to *Lophelia* colony in sample from station 81, x4.7. **I-K)** *Madrepora oculata*; **I,K**, colonies with cylindrical voids produced by intergrowth with polychaetes (arrows indicate voids), x1; **J**, enlargement of calical view, x3.



FIGURE 6—Terebratulid brachiopod in crevice within *Lophelia* debris, from sample site 81. Scale bar indicates 1 cm.

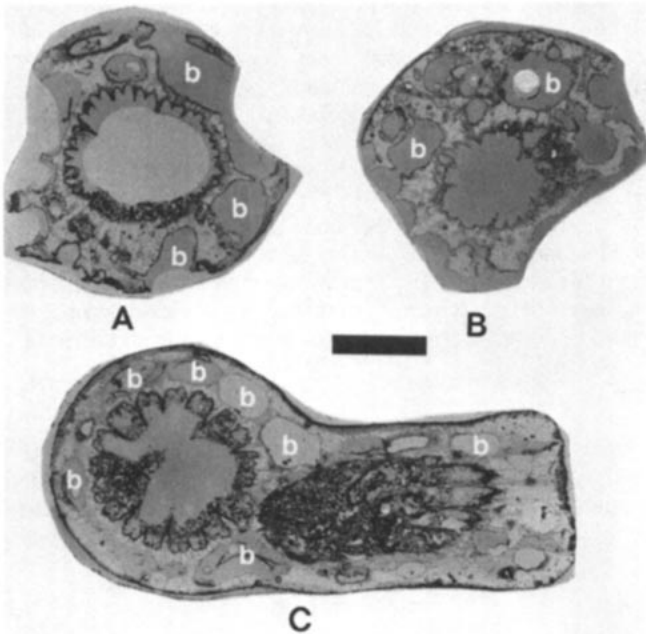


FIGURE 7—Transmitted-light photographs of thin sections of epoxy-impregnated *Lophelia* calices, illustrating high frequencies of macroborings in outer, stereomal parts of colonies. Some of the larger borings are indicated with a "b". **A-B**) sections oriented nearly perpendicular to *Lophelia* calices; **C**) section perpendicular to calice of lower corallite (left) and subparallel to calice of upper corallite (right). Scale bar represents 5 mm.

from Weber (1973) and unpublished results of A. C. Neumann and R. J. Wilber. Outlier points do exist, however, indicating that the lower range of the $\delta^{13}\text{C}$ field should be redefined

slightly; in Figure 8, the dashed line defines the field for deep and cold ahermatypes originally recognized by Mullins et al. (1981). Other isotopic results for *Lophelia* from Norwegian fjord and shelf localities (Mikkelsen et al., 1982) are generally consonant with the revised field in Figure 8 but are more variable. The variation in $\delta^{18}\text{O}$ values in the Norwegian samples may be in part a consequence of freshwater influx (Mikkelsen et al., 1982).

Age of the Buildups

Radiocarbon dates indicate an age of *Lophelia* beyond the temporal resolution of the ^{14}C technique. The best-preserved corals are in excess of 40,000 years, whereas a more poorly preserved sample (L-6) indicates an age of $27,660 \pm 1690$ years (probably indicating slight contamination; Table 1). The *Lophelia* framework is clearly pre-Holocene. Because the mounds nucleated on a Pliocene erosional surface capped by Pleistocene sand, we infer that they are Pleistocene in age.

Other Scleractinian Localities on the West Florida Slope

Scleractinian corals occur in surface samples at two additional sites within our study area, although these occurrences are not associated with coral banks. A living specimen of the large, solitary coral, *Flabellum moseleyi*, was retrieved in dredge samples from site 28 (Figs. 1, 5), at a water depth of 500 m, near the erosional scarp laterally associated with the coral banks. Two indeterminate coral specimens were also recovered in grab samples at site 16, from a depth of 240 m.

DISCUSSION

The West Florida coral mounds preserve a scleractinian diversity and taxonomic composition that compare favorably with other *Lophelia* buildups in the Atlantic Ocean and Gulf of Mexico. The scleractinian species richness (4 spp.) represents an intermediate diversity, viewed in the context of the range of 2–10 species previously reported from modern *Lophelia* buildups in the Norwegian fjords, western European and northwest African continental margins, Blake Plateau, Straits of Florida, and Mississippi Delta (Dons, 1944; Le Danois, 1948; Teichert, 1958; Moore and Bullis, 1960; Stetson et al., 1962; Neumann et al., 1977; Cairns and Stanley, 1981). The aggregate diversity of scleractinians from the West Florida mounds is slightly higher than that from the Mississippi Delta (2 spp.) and slightly lower than that reported from the Blake Plateau and Straits of Florida (10 and 7 species, respectively; Cairns and Stanley, 1981). These disparities should not be overemphasized, because in most cases *Lophelia* and perhaps one other species (e.g., *Enallopsammia*, *Madrepora*) predominate, with only minor occurrences of other scleractinian taxa. Thus, the aggregate diversity reported for most sites will be highly sensitive to the vagaries of remote sampling of the rarer forms.

Taxonomic composition of the West Florida scleractinians is consistent with the ahermatypic species lists for the Gulf of Mexico published by Cairns (1978), although some minor range extensions of species within the Gulf are indicated. *Bathypsammia* has been previously reported from the eastern Gulf, whereas *Lophelia* and *Madrepora* have been previously re-

TABLE 1—Geochemical and radiometric data for subsamples of *Lophelia*

SAMPLE	$\delta^{18}\text{O}$ (PDB)	$\delta^{13}\text{C}$ (PDB)	Sr(ppm)	^{14}C AGE (YRS.)	MINERALOGY	PRESERVATION
L1	1.15	-5.70		27,660 + 1690	100% aragonite	heavily bored
L2	1.35	-3.95		>40,000	100% aragonite	freshest specimen
L3	1.28	-5.53	8747		100% aragonite	bored
L4	1.66	-3.47		>40,000	100% aragonite	fresh
L5	1.00	-5.27			100% aragonite	fresh
L6	2.23	-2.62	6680		68% aragonite; 26% MgCO_3 ; 5% calcite	most heavily bored
L7	1.69	-4.28	8867		100% aragonite	heavily bored
L8	1.88	-6.33	9110		100% aragonite	relatively fresh
L9	2.18	-2.28	8794		100% aragonite	relatively fresh

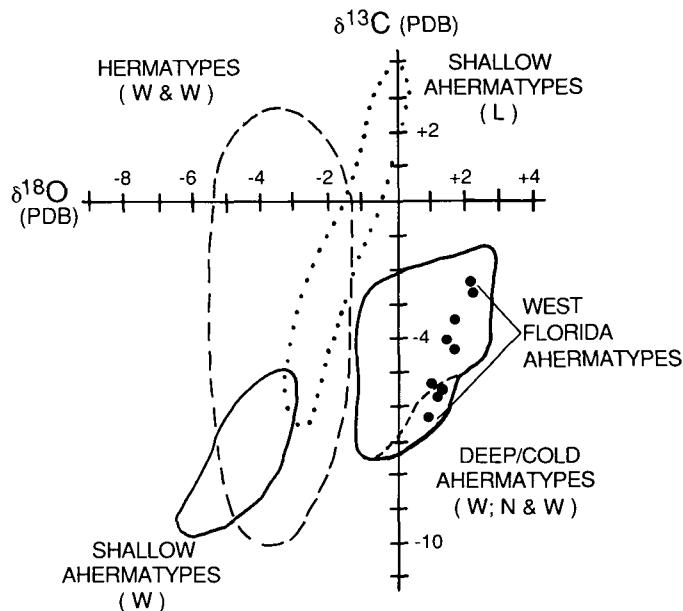


FIGURE 8—Isotopic compositions of West Florida corals (dots), relative to fields for hermatypes, shallow-water ahermatypes, and deep/cold ahermatypes, based upon data from Weber and Woodhead (1970), Weber (1973), Land et al. (1977), Neumann and Wilber (unpubl. data) and this report. The dashed line within the field of deep/cold ahermatypes indicates the boundaries of the field as initially reported by Mullins et al. (1981); the solid line includes data from this study.

corded only in the northern Gulf. Hence, a slight extension of geographic range is in order for these two colonial taxa.

The ecological association of framework builders on the West Florida mounds deviates slightly from what one would expect for western Atlantic and Gulf of Mexico *Lophelia* buildups. Off West Florida, *Lophelia* occurs with *Madrepora oculata*, the latter present in only minor abundance. Cairns (1979) has

observed that such *Lophelia-Madrepora* associations typify eastern Atlantic deep-water mounds, in contrast to the *Lophelia-Enallopsammia* associations of most western Atlantic mounds. The only mounds previously reported from the Gulf of Mexico, on hardgrounds seaward of the Mississippi Delta, preserve only one colonial scleractinian—*Lophelia prolifera*. Thus, the taxonomic composition of the West Florida buildups differs subtly from that of western Atlantic and northern Gulf buildups.

A late Pleistocene age for the West Florida buildups is indicated by the off-scale ("dead") radiocarbon dates (Table 1) and the nucleation of the mounds on the upper surface of a Pliocene stratigraphic sequence capped by Pleistocene gravelly carbonate sand (Fig. 3). To date, only sparse living scleractinians have been recovered from the West Florida slope; no vigorous, extant *Lophelia* mounds are known from this area.

Research Questions

Two ecological enigmas emerge from our research on deep-water mounds and from an overview of the published literature. We discuss them briefly in hopes that they may catalyze future research on deep-water ahermatypic buildups.

What Controls the Distribution of Deep-Water Framework Builders?

Sufficient data now exist to define multiple ecological associations of deep-water framework builders. First, and by far most abundant, are mounds formed primarily by *Lophelia prolifera*, with secondary input from other colonial corals, chiefly *Madrepora oculata* and *Enallopsammia profunda*. As we have noted, this framework association is widespread in the Atlantic Ocean and Gulf of Mexico. The species richness of scleractinians within this association is generally low (range 2–10 spp.), although the framework of loosely branched *Lophelia* typically provides habitats for a wealth of associated species (up to 300 spp. reported from a group of thickets in the Norwegian fjords; Teichert, 1958). In some cases (e.g.,

Stetson et al., 1962), the order of dominance in the *Lophelia-Enallopsammia* association is reversed, with *Enallopsammia* the dominant form.

A second, and locally more diverse, deep-water coral association is that afforded by frameworks of the colonial scleractinian, *Solenosmilia variabilis*. Two widely separated areas of bank construction by *S. variabilis* have been reported: the carbonate slope north of Little Bahama Bank and a sub-Antarctic seamount (Mullins et al., 1981; Cairns and Stanley, 1981). The mounds north of Bahama Bank represent the highest scleractinian species richness (16 spp.) reported to date from any deep-water ahermatypic buildup. The mound-associated fauna contains a wide array of invertebrate taxa representing more than 14 benthic invertebrate types from seven phyla. The other *Solenosmilia* mound locality, a seamount at 55°S, yields 5 scleractinian species and contains mound-associated taxa from 32 groups representing 13 phyla (Cairns and Stanley, 1981).

Three other deep-water scleractinians are of local importance in constructing buildups. The colonial *Dendrophyllia cornigera* is the dominant species in some western European coral thickets with 3–4 ahermatypic species. Another minor ahermatypic framework builder is *Desmophyllum cristagalli*, a cosmopolitan species that forms thickets in the Chilean fjords; these Chilean mounds also have 3–4 ahermatypic species (Cairns and Stanley, 1981). The last framework builder of local importance is *Goniocorella dumosa*, the dominant species on a coral coppice 40 m in height on the Campbell Plateau off New Zealand (Squires, 1965); only two associated scleractinian species have been reported from this locality. Overall, very little is known of the diversities of coral-associated organisms or the ages of these three localized types of deep-water buildups.

What, then, are the primary controls on framework builders in these deep-water coral banks? *Temperature* has been widely cited as a first-order control in the distribution of deep-water corals, particularly of the genus *Lophelia*. Teichert (1958) and Cairns (1979) have documented a habitable thermal range of 3–12°C for *Lophelia* in the North Atlantic and surrounding margins. Excellent evidence for the upper limit of this thermal range can be seen in a natural experiment in Norwegian fjords, where late Holocene glacial rebound of fjords has raised *Lophelia* thickets to progressively shallower depths within the subtidal zone. Once at depths of 55–60 meters or less, elevated temperatures cause killoffs of *Lophelia*, so that only dead thickets exist within the low subtidal parts of the fjords (Teichert, 1958; Mikkelsen et al., 1982). All *Lophelia* buildups with well-documented temperature data fall within the range of 4.6–10.4°C (Cairns and Stanley, 1981), with maximal bank development in the 5–8°C range.

Still unresolved, however, is the issue of how temperature might control which framework builder dominates in a given mound; among *Lophelia*, *Solenosmilia*, *Desmophyllum*, and *Dendrophyllia*, one may occur in a dominant role with the others as only minor components. Alternatively, other factors such as *substrate type* and *current velocity* are critical factors in mound location (e.g., Strømngren, 1971) and may further determine which framework builder predominates. Another potentially crucial aspect of relative dominance patterns among

the framework builders is the possible effect of stochastic processes in *larval dispersal* of the deep-water ahermatypes, with the historical sequence of colonization the major determinant of dominance on a given mound. This list of possible controlling factors, although clearly not an exhaustive one, provides reasonable—and testable—hypotheses for looking at dominance in deep-water coral mounds.

We further predict that patterns of nutrient availability may also impose an important first-order control on geographic occurrences of deep-water coral mounds. Hallock (1985) and Hallock and Snyder (1986) have demonstrated a linkage between oligotrophic nutrient systems and the vitality of larger foraminifera and hermatypic corals. We suspect that even for deep-water, ahermatypic corals, oligotrophic systems will provide greater long-term resource stability than eutrophic environments; hence, we predict that most deep-water coral banks will occur in oligotrophic habitats and that such mounds will be absent or scarce in upwelling environments. The presently known distributions of deep-water coral banks support this contention, with maximum bank development in oligotrophic areas. Conversely, no deep coral mounds have been reported from coastal upwelling regions such as the Arabian, Peruvian, or California continental margins. More field and experimental evidence will be necessary to document fully the possible role of nutrient availability in controlling the distribution of ahermatypic framework builders.

In conclusion, basic ecological questions regarding dominance in deep-water ahermatypic buildups remain unanswered, even in the face of multiple, testable hypotheses.

Why So Many Dead Coral Mounds?

Living specimens of frame-building ahermatypes—*Lophelia*, *Solenosmilia*, *Desmophyllum*, and *Dendrophyllia*—have been recovered from many sites. Yet, pervasive among recent discoveries of deep-water mounds is an extremely high frequency of relict buildups; this frequency is especially high in the Atlantic Ocean and Gulf of Mexico. The Pleistocene West Florida banks reported here are typical of this class of extinct coral banks, now exposed in depositional relief in the modern ocean. Other examples include mounds north of Little Bahama Bank and many of the lithoherms in the Straits of Florida. Most of the corals on banks of the Blake Plateau are also dead (Stetson et al., 1962). Viewed from a paleoecological perspective, these relict coral banks offer potentially valuable insight into the paleoclimatic context of moundbuilding and the post-mortem taphonomic processes of deep-water buildups.

Two types of explanations can be offered for the high frequency of extinct buildups. A “dynamic equilibrium” explanation for the anomalously large volumes of deep corals derives from genetic models for deep-water mound accretion developed by Squires (1964) and amplified by Mullins et al. (1981). The thicket → coppice → bank transition proposed in these models involves upward and outward coral growth, to a bank phase with considerable vertical relief. In this mature phase, the mantle of living coral is negligible relative to the large volume of dead coral debris. This model offers an interpretation for coral buildups in which living framework builders are present but not volumetrically abundant. However, it fails to account for mounds in which *all* corals recovered are dead, as

in the West Florida, northern Little Bahama Bank, and many lithoherm examples.

Paleoclimatic models provide an alternative explanation for the high frequency of relict mounds. The key to interpretation will be accurate radiometric dating of the youngest (generally the best-preserved) elements of the framework biota; such studies will be most informative when linked with documentation using side-scan sonar, underwater photography, and mapping of the mounds via submersibles.

Preliminary evidence from several relict mounds suggests diachroneity in the mortality of deep-water buildups in the Florida-Bahama region. The West Florida corals yield "dead" ($> 40,000$ years) radiocarbon dates even for the freshest aragonitic specimens, suggesting mound extinction prior to the latest glacial maximum, with a maximum age unconstrained within the mid- to late Pleistocene. In comparison, radiocarbon dates from a pilot *Lophelia* sample in the Straits of Florida indicate an approximate age of $28,170 \pm 500$ years (Neumann et al., 1977), and whole-rock radiocarbon dates of coral rudstone-floatstone from the lithoherms are $26,620 \pm 500$ years (Wilber and Neumann, unpub. data). Youngest of all the relict deep-water mounds are those north of Little Bahama Bank, where the best-preserved specimens yield radiocarbon dates of 860 ± 50 and 940 ± 40 years (Mullins et al., 1981). Thus, as those samples suggest, mound extinctions cannot be viewed as a single, geologically recent event; they may reflect a series of iterative climatic or paleoceanographic events (e.g., glacial cycles).

Both the paleoclimatic and "dynamic equilibrium" models presented above are generally consistent with the sparse data now available. Further testing of these and other hypotheses will clearly be necessary to answer the question of why there are so many extinct deep-water mounds.

CONCLUSIONS

Areally extensive, ahermatypic coral buildups of Pleistocene age occur on the West Florida carbonate ramp slope at depths of 500 m. These deep-water coral banks formed through framework building by the cosmopolitan ahermatypic, *Lophelia prolifera*, and incorporate a host of associated invertebrates including epizoans, epifaunal commensal organisms, nestlers and crevice dwellers, and macroendoliths. The banks compare favorably in scleractinian species richness (4 spp.) and taxonomic composition with other *Lophelia* buildups in the Atlantic Ocean. Scleractinians from these mounds still preserve primary mineralogical, isotopic, and trace-element geochemical signatures, despite their relative antiquity as indicated by "dead" radiocarbon dates.

In contradiction to the statement by James Kennett (see introductory quotation), banks formed by ahermatypic corals are widespread at intermediate depths in the modern ocean and are likely to be increasingly recognized in the Mesozoic-Cenozoic fossil record. The expanded view of deep-water coral buildups afforded by recent discoveries in the Florida-Bahamas region, Chile, and the sub-Antarctic region (Neumann et al., 1977; Cairns and Stanley, 1981; Mullins et al., 1981; this report) has magnified two basic ecological questions regarding the origin and demise of these structures: What are the

primary controls on distribution of the framework builders? Why are there so many dead coral mounds? Finding the ecological and paleoecological solutions to these questions can provide a stimulating agenda for research on deep-water coral banks.

ACKNOWLEDGMENTS

This research was supported by NSF grants OCE-8308168 and OCE-8517622 to H.T. Mullins. We thank R.K. Matthews of Brown University for assistance in the isotopic analyses and S.D. Cairns of the Smithsonian Institution for verifying identifications of the ahermatypic Scleractinia. We also thank Alan Allwardt for his editorial assistance.

REFERENCES

- BLAKE, N.J., and DOYLE, L.J., 1983, Infaunal-sediment relationships at the shelf-slope break, in STANLEY, D.J., and MOORE, G.T., eds., *The Shelfbreak: Critical Interface on Continental Margins*: Society of Economic Paleontologists and Mineralogists Special Publication 33, p. 381-389.
- BOARDMAN, M.R., 1978, Holocene Deposition in Northwest Providence Channel, Bahamas [unpub. Ph.D. dissert.]: Chapel Hill, University of North Carolina, 155 p.
- BURKE, W.H., DENISON, R.E., HETHERINGTON, E.A., KOEPNIK, R.B., NELSON, H.F., and OTTO, J.B., 1982, Variation of seawater $^{87}\text{Sr}/^{86}\text{Sr}$ throughout Phanerozoic time: *Geology*, v. 10, p. 516-519.
- CAIRNS, S., 1978, A checklist of the ahermatypic Scleractinia of the Gulf of Mexico, with the description of a new species: *Gulf Research Reports*, v. 6, p. 9-15.
- CAIRNS, S., 1979, The deep-water Scleractinia of the Caribbean Sea and adjacent waters: Studies on the Fauna of Curaçao and Other Caribbean Islands, v. 56, p. 1-341.
- CAIRNS, S., and STANLEY, G.D., 1981, Ahermatypic coral banks: Living and fossil counterparts: Proceedings of the Fourth International Coral Reef Symposium, v. 1, p. 611-618.
- COLLARD, S.B., and D'ASARO, C.N., 1973, Benthic invertebrates of the eastern Gulf of Mexico, in JONES, J.I., RING, R.E., RINKEL, M.O., and SMITH, R.E., eds., *A Summary of Knowledge of the Eastern Gulf of Mexico*: St. Petersburg, State University of Florida Institute of Oceanography, p. IIG1-27.
- DONS, C., 1944, Norges korallrev: Norske Videnskabers Selskab, Trondheim, Forhandling, v. 16A, p. 37-82.
- HALLOCK, P., 1985, Why are larger Foraminifera large?: *Paleobiology*, v. 11, p. 195-208.
- HALLOCK, P., and SNYDER, S.W., 1986, Nutrient control of biogenic sedimentation in low-latitude, shallow-water environments [abstr.]: Society of Economic Paleontologists and Mineralogists Midyear Meeting, v. 3, p. 49.
- KENNETT, J., 1982, *Marine Geology*: Englewood Cliffs, New Jersey, Prentice-Hall, 813 p.
- LAND, L.S., LANG, J.C., and BARNES, D.J., 1977, On the stable carbon and oxygen isotopic composition of West Indian (Jamaican) scleractinian reef coral skeletons: *Marine Biology*, v. 33, p. 221-233.
- LE DANOIS, E., 1948, *Les Profondeurs de la Mer*: Paris, Payot, 303 p.
- LEIPPER, D.F., COCHRANE, J.D., and HEWITT, J.F., 1972, A detached eddy and subsequent changes (1965), in CAPURRO, L.R.A., and REID, J.L., eds., *Contributions on the Physical Oceanography of the Gulf of Mexico*: Texas A & M Oceanographic Studies, v. 2, p. 107-117.
- MIKKELSEN, N., ERLKENKUSER, H., KILLINGLEY, J.S., and BERGER, W.H., 1982, Norwegian corals: radiocarbon and stable isotopes in *Lophelia pertusa*: *Boreas*, v. 11, p. 163-171.
- MILLIMAN, J.D., 1974, *Marine Carbonates*: New York, Springer-Verlag, 375 p.
- MOORE, D.R., and BULLIS, H.R., 1960, A deep-water coral reef in the Gulf of Mexico: *Bulletin of Marine Science*, v. 10, p. 125-128.

- MULLINS, H.T., NEWTON, C.R., HEATH, K., and VANBUREN, H.M., 1981, Modern deep-water coral mounds north of Little Bahama Bank: Criteria for recognition of deep-water coral bioherms in the rock record: *Journal of Sedimentary Petrology*, v. 51, p. 999–1013.
- MULLINS, H.T., GARDULSKI, A.F., HINE, A.C., MELILLO, A.J., WISE, S.W., and APPLGATE, J., submitted, Three-dimensional sedimentary framework of the carbonate slope of Central West Florida: A sequential seismic stratigraphic perspective of a modern scenario: *Geological Society of America Bulletin*.
- NEUMANN, A.C., KOFOED, J.W., and KELLER, G.H., 1977, Lithoherms in the Straits of Florida: *Geology*, v. 5, p. 4–10.
- NOWLIN, W.D., 1972, Winter circulation patterns and property distributions, in CAPURRO, L.R.A., and REID, J.L., eds., *Contributions on the Physical Oceanography of the Gulf of Mexico: Texas A & M Oceanographic Studies*, v. 2, p. 3–51.
- POPENOE, P., COWARD, E.L., VAZZANA, M.E., and BALL, M.M., 1979, A high resolution seismic survey of the Florida-Hatteras shelf and slope and the Blake Plateau and Escarpment: *Geological Society of America, Abstracts with Programs*, v. 11, p. 209.
- SQUIRES, D.F., 1964, Fossil coral thickets in Wairarapa, New Zealand: *Journal of Paleontology*, v. 38, p. 904–915.
- SQUIRES, D.F., 1965, Deep-water coral structure on the Campbell Plateau, New Zealand: *Deep-Sea Research*, v. 12, p. 785–788.
- STETSON, T.R., SQUIRES, D.F., and PRATT, R.M., 1962, Coral banks occurring in deep water on the Blake Plateau: *American Museum of Natural History Novitates* no. 2114, 39 p.
- STRØMGREN, T., Vertical and horizontal distribution of *Lophelia pertusa* (Linné) in Trondheimsfjorden on the west coast of Norway: *Kongelige Norske Videnskabers Selskab, Skrifter*, v. 6, p. 1–9.
- TEICHERT, C., 1958, Cold- and deep-water coral banks: *American Association of Petroleum Geologists Bulletin*, v. 42, p. 1064–1082.
- WEBER, J.N., 1973, Deep-sea ahermatypic scleractinian corals: isotopic composition of the skeleton: *Deep-Sea Research*, v. 20, p. 901–909.
- WEBER, J.N., and WOODHEAD, P.M.J., 1970, Carbon and oxygen isotope fractionation in the skeletal carbonate of reef-building corals: *Chemical Geology*, v. 6, p. 93–117.



Systems . . . are in the sciences what the passions are in the human mind: they may be the source of great errors, but they are also the cause of great exertions . . . objects apparently minute acquire an interest and importance; views are suggested which often lead to real acquisitions; facts are analyzed which would have remained isolated; and relations traced which would not have been observed.

—John Murray