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Front Cover: Close-up view of a patch-reef coral head in Grahams Harbor, north of Dump Reef. As shown here, Caribbean shallow-water reefs have declined since the mid-1980s and are now largely overgrown by fleshy green macroalgae and a variety of encrusting organisms. See Curran et al., "Shallow-water reefs in transition," this volume, p. 13. Photograph by Ron Lewis.

Back Cover: Dr. A. Conrad Neumann, University of North Carolina, Chapel Hill, NC, Keynote Speaker for the 11th Symposium and author of "Cement loading: A carbonate retrospective," this volume, p. xii. Photograph by Mark Boardman.

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BIOZONATION ON DEEP-WATER CARBONATE MOUNDS AND ASSOCIATED HARDGROUNDS ALONG THE WESTERN MARGIN OF LITTLE BAHAMA BANK, WITH NOTES ON THE CAICOS PLATFORM ISLAND SLOPE

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ABSTRACT

Carbonate mounds found in a broad band from about 325 to 700 m along the western margin of Little Bahama Bank exhibit consistent faunal zonations characterized by assemblages of attached, suspension-feeding macroinvertebrates dominated by sponges, octocorals, crinoids and stylasterid and scleractinian corals. Biozonation on hard substrates appears chiefly dependent on depth (and associated parameters, e.g., temperature) and current flow. Mounds in 325-435 m with up to 30 m vertical relief reveal dense assemblages on gentler upcurrent slopes and flanks, and an almost complete lack of macrofauna on steep downcurrent slopes. Macrofauna include stalked crinoids on upcurrent slopes and crest, octocorals on flanks, and branching ahermatypic corals and basketstars at and near the crest. Within-group taxonomic composition often varies between slopes and crest, and between up- and downslope flanks. In 540-580 m on the southwestern bank margin, mounds with up to 40 m vertical relief support a dense lithistid sponge and ophiacanthid ophiuroid assemblage; limited local biozonation here may be associated with a weaker flow regime. The pronounced zonation reported for lithoherms and adjacent hardgrounds to the north in 500-700 m (Neumann et al. 1977, Messing et al. 1990) is reviewed. The Caicos Platform island slope supports many of the same macroepibenthic taxa found at similar depths elsewhere in the Bahamas and northern Caribbean. However, because this habitat is a low energy environment relative to those west of Little Bahama Bank under the direct influence of the Florida Current, densities of sessile and sedentary suspension-feeding organisms are substantially lower.

INTRODUCTION

The deep western margin of Little Bahama Bank (LBB) exhibits a wide range of substrates including unconsolidated sediments, flat and sloping hardgrounds, vertical escarpments, and a variety of topographic features ranging from small-scale rubble to enormous mounds and ridges up to 50 m in vertical relief. The latter occur along the bank margin in a broad band from about 325 to 700 m depth. Malloy and Hurley (1970) mapped a swathe of these features north of 26°50'N chiefly in 600-730 m (with one area between 27°10' and 27°20'N penetrating as shallow as 360 m) as up- and downslope ridges and valleys. Subsequent geological investigations (Neumann et al. 1977, Mullins and Neumann 1979) identified the deeper of these features as lithified, elongated, biohermal buildups (lithoherms) oriented parallel to the bank margin. Mullins and Neumann (1979) extended the lithoherm facies in a narrow band around the southwestern margin of the bank as far east as Freeport. However, more recent submersible dives indicate that those features at least south of West End, Grand Bahama I. differ substantially from the lithoherms to the north (Llewellyn and Messing 1993, Messing 1997 & unpublished).

Under the influence of the Florida Current, which parallels the bank margin, all of these features support diverse and often dense assemblages dominated by macroepibenthic suspension-feeding invertebrates, chiefly sponges, octocorals (alcyonarians), stylasterid (hydrozoan) and scleractinian corals, unstalked (comatulid) and stalked crinoids and ophiuroids. Submersible surveys reveal a succession of assemblages with increasing depth, as expected: the restricted bathymetric distributions of organisms typical of marine systems that are dependent upon depth and associated parameters such as temperature. However, on smaller scales within faunal depth zones, organism distributions often depend upon variations in water movement associated with local topography. Increased densities of deep-sea sessile and sedentary macroinvertebrates exposed to stronger bottom flow are well known (e.g., Genin et al. 1986 1992, Roux et al. 1991). Similarly, Boehlert & Genin (1987) note that organism densities on deep seamounts are often greater on knobs and pinnacles and on the upper parts of rocks. However, the bank-margin features discussed here also exhibit distinct biozonation in response to topographically mediated variations in current flow. Messing et al. (1990) reported on such biozonation in detail for the lithoherms. Their findings are briefly reviewed below with an updated taxonomy of resident organisms.

Observations were made during a series of submersible dives aboard DSV *Alvin*, RV *Johnson Sea-Link I & II* and PC-1802 between 1979 and 1998. Sponsoring agencies included the National Science Foundation, Smithsonian Institution, Harbor Branch Oceanographic Institute, and the former SeaPharm, Inc., Research Submersibles, Ltd. and the Deep Ocean Society.

RESULTS

Southwestern Margin, Little Bahama Bank

Features in 325-435 m

The shallowest major features that exhibit consistent biozonation are lithified mounds with relatively gentle southern and southwestern slopes, and much steeper or vertical northern faces. Highest elevations appear in the northeast, closest to the bank margin. Overall vertical relief reaches ~25 m. Surfaces are smooth with a thin (<2-cm) sediment veneer that is deeper in widely scattered irregular pits or depressions, but virtually absent on the crests. On one mound (402-427 m), which has been examined in greater detail than others, most of the south-facing slope supports a vast, almost monospecific meadow of the stalked crinoid, *Endoxocrinus muelleri* (formerly *E. parrae*, see David 1999) (Family Isocrinidae) that generally increases in density from 1-4 individuals m^{-2} on the lower and middle slope to maximum local densities of 12-13 m^{-2} just below the crest (Figure 1). Taller, more slender *Neocrinus decorus* (formerly *Chladocrinus decorus*, see Roux et al. 2002) (Isocrinidae) occurs as scattered individuals on the upper slopes and replaces *E. muelleri* at the crest. Other attached taxa here include widely scattered small sponges and white ellisellid octocoral whips (perhaps also some antipatharians: *Cirrhipathes* sp). Abundant colonies of an undescribed species of the octocoral, *Paracalyptrophora* (Primnoidae), grow on the western slopes. Each forms a double fan that neatly cages a squat lobster (Anomura:Chirostylidae) (Figure 2).

Figure 1. Southern upper slope of a large mound, SW margin of LLB, with numerous E. muelleri, *depth 420 m. Arrows indicate* N. decorus. *Crinoid crowns are concave upcurrent into flow from SE. Photo diameter (foreground) ~2 m.*

Figure 2. Western slope of same mound, with numerous Paracalyptrophora *sp.; depth 409 m. Photo diameter ~1.5 m.*

Higher on the NW slope, in addition to *E. muelleri* and a few *N. decorus*, are numerous small yellow and purple octocoral fans (Plexauridae: Stenogorgiinae) (formerly Paramuriceidae), large flabellate colonies of the ahermatypic scleractinian, *Madrepora carolina* (Oculinidae), comatulids, small sponges and stylasterids, and a few solitary corals. In contrast, the steep eastern margin supports a population of another primnoid, *Plumarella* sp. The steep, often vertical, northern slope faces downcurrent and is relatively barren of macrofauna. Flow recorded during dives is generally from the SE, parallel to the bank margin, with occasional reversals from the NW, perhaps associated with current meanders or eddies (Leaman & Molinari 1987). Velocities recorded 1.5 m above the bottom usually vary between 0 and 25 cm sec^{-1}, although episodes exceeding 100 cm sec^{-1} have been observed.

Along the steep eastern flank of another mound briefly visited (350-325 m), densities of *E. muelleri*, comatulids and *Madrepora carolina* increase upslope from ~335 to 325 m. The basket star, *Astracme mucronata*, occurs chiefly at higher elevations (Figure 3) and, again, *N. decorus* only appears near the crest.

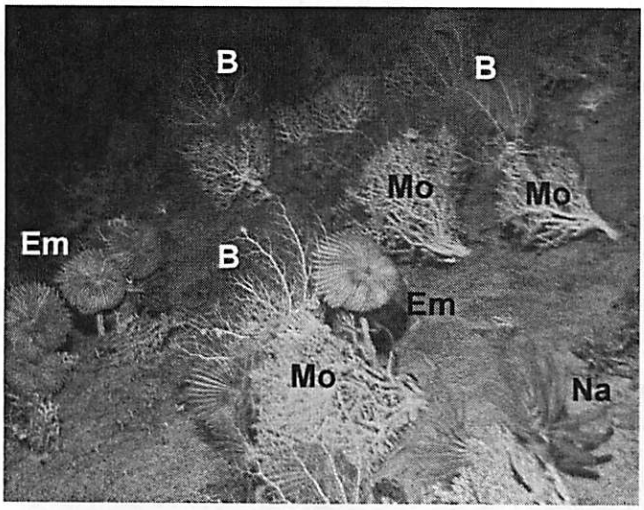

Figure 3. Eastern upper mound slope, SW margin of LLB; depth ~330 m. Stalked crinoid, Endoxocrinus muelleri *(Em), coral,* Madrepora carolina *(Mo), comatulid,* Neocomatella alata *(Na), basketstars,* Astracme mucronata *(B). Flow from left rear. Foreground photo diameter ~1 m. Photo by A. C. Neumann.*

On a lower topographic feature with a total vertical relief of ~14 m (420-434 m), a mixed assemblage of *E. muelleri* and *N. decorus* occurs on the gentle SSW slope and is replaced by a dense monospecific stand of *N. decorus* (up to ~18 m^{-2}) with a few stenogorgiine fans along the northern crest. *E. muelleri* usually occurs at least 2-3 m away from the northern edge of the crest. Unlike the previous, larger features, the northern margin is a sediment-covered slope, steeper than the SSW slopes, but less than 45°, with a near vertical scarp of about 0.5 m along its eastern end just below the crest (Llewellyn & Messing 1993).

The stalked crinoids also exhibit variations in posture and morphology; specimens on elevated substrates subject to topographically intensified flow have lower crown elevations and shorter stalks than those on flat hardgrounds (Messing & Llewellyn 1991).

Smaller topographic features in this area include small scarps, ledges, rises (possibly lithified sand waves), rubble associated with eroding hardgrounds, and a wide variety of irregular boulders (Figure 4), and benches, some of which may be slump blocks, but which sometimes appear to be part of surrounding hardgrounds (revealed where current scour has eliminated sediment veneers).


Figure 4. South face of isolated boulder, ~2m across, SW margin of LLB, depth 413 m. Large black arrows infer mean flow direction from orientation of stylasterid fans. Large white arrows indicate stylasterid fans oriented to flow into plane of photograph. Small arrows reflect momentary flow up and over boulder as indicated by orientation of E. muelleri *crowns.*

Both stalked crinoids occur here, although *E. muelleri* is most common, often occurring in dense clusters of up to ~40 individuals that span the upcurrent brow of boulders and benches. Delicate fan-shaped stylasterids (e.g., *Stylaster* spp.) are also often abundant here; colony orientations may generate detailed diagrams of mean flow around isolated boulders and ledges (Figure 4).

On flat hardgrounds in this area, scattered stalked crinoids of both species (>1 m^{-2}; *N. decorus* : *E. muelleri* ratio 4.5-10:1) are accompanied by scattered octocorals (tall pinnate *Callogorgia americana* and other primnoids, and *Keratoidisis flexibilis* [Isididae]), sponges, and smaller unidentified arborescent cnidarians (possibly hydrozoans, octocorals or antipatharians). On all substrates in this area, sessile invertebrates host a variety of epizoans that use their elevated perches for better access to suspended food: e.g., the comatulid crinoids, *Stylometra spinifera* (on *M. carolina* and the stalks of *N. decorus*) and *Neocomatella alata* (on *M. carolina*, stylasterids and sponges), and asteroschematid ophiuroids, e.g., *Asteroschema tenue* (on *Callogorgia americana* and other octocorals).

Features in 540-580 m

Rubble, boulders, outcrops, benches, menhirs and mounds support dense assemblages of sponges, chiefly lithistids, e.g., *Discodermia* sp. and *Corallistes* sp., accompanied by numerous ophiacanthid ophiuroids (e.g., *Ophiotreta lineolata*), stalked crinoids, small stylasterids and octocorals (Figures 5 and 6).

Figure 5. Base of a large irregular block with numerous lithistid sponges, SW margin of LLB, 572 m. Ophiacanthid ophiuroid visible at upper right. Photo diameter ~1.3 m.

These features have irregular, apparently bioeroded surfaces and occur in clusters or are separated by expanses of unconsolidated, bioturbated sediment or irregular, rubbly or flat hardgrounds with fewer sessile organisms. Surface morphology of these features is unlike that of the lithoherms found at similar depths to the north (Neumann et al. 1977, Messing et al. 1990), although a few crescentic embayments and thick crusts overhanging apparently less lithified material were observed.

The largest feature observed is a mound of ~40 m overall vertical relief that rises as a steep whaleback ridge from the southwest with a sheer vertical northern wall. Biozonation is not immediately obvious on any of these features (although densities are sometimes greater along edges), but possible differential distribution of sponge species has not been investigated. However, short-stalked *Endoxocrinus carolinae* is restricted to sides, edges and corners of boulders and other features, an apparent response to flow modified by local topography. Similarly, stylasterids, small octocorals and ophiuroids sometimes line up along edges of blocks and ledges. By contrast, taller

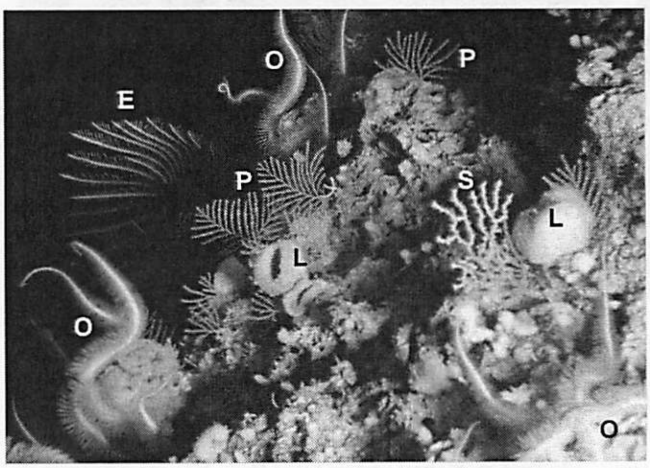

Figure 6. Close-up of another large irregular block, SW margin of LLB, 572 m. Lithistid sponges (L), Endoxocrinus sp. *(E), ophiacanthid ophiuroids (O), primnoid octocorals (probably* Plumarella *sp.)(P), probable stenogorgiine octocoral (S). Photo diameter ~28 cm.*

Endoxocrinus prionodes (formerly included in *E. parrae*) occurs chiefly on flat substrates. Initial current measurements suggest a weaker flow regime than over the shallower mounds or lithoherms (below).

Western Margin, Little Bahama Bank

Lithoherms, 550-700 m

Because Messing et al. (1990) described the biozonation of lithoherms in detail, comments here are chiefly restricted to updating the taxonomy of resident organisms. Reed (2002) briefly compared lithoherms with deep-water coral mounds found to the north on the Blake Plateau (see also Stetson et al. 1962, Mullins et al. 1981, Paull et al. 2000).

Messing et al. (1990) described three lithoherm biozones. In the upcurrent Coral Zone, found only on larger lithoherms, the dominant scleractinian coral is now referred to as *Lophelia pertusa* (formerly *L. prolifera*), a species that occurs as far north as Norway. Downcurrent of the Coral Zone along the ridge crest, the Zoanthid Zone is dominated by large flabellate colonies of the colonial anemone, *Gerardia* sp., which reach ~1.0 m tall and 1.5 m across. Unlike most zoanthids, which are encrusting, *Gerardia* sp. is arborescent and produces a dense protein axis similar to that of gorgonian octocorals. Druffel et al. (1995) report $\Delta^{14}C$ data suggesting an age of 1800 ± 300 years for specimens collected in 620 m.

Lithoherm flanks and downcurrent crests constitute the Crinoid/Alcyonarian (or Octocoral) Zone. The most abundant stalked crinoid here, formerly identified as ?*Diplocrinus maclearanus*, is now treated as a probable new species of *Endoxocrinus* (David 1998) (Figure 7).

E. prionodes (reported as *E. parrae* in Messing et al. 1990) is also found here and, less commonly, on intervening flat hardgrounds and low outcrops, as at the deep site on the southwest bank margin described above. *Democrinus* sp., which occurs in this zone, on hardgrounds and on unconsolidated sediment, is almost certainly *D. rawsoni* (Bathycrinidae) (Figure 6). Although it typically bears a root-like radix at the base of the stalk for anchoring in sediment, some specimens expand the radix as a holdfast suitable for hard substrates. Sponges chiefly found on hardgrounds and low outcrops and formerly identified only to genus or family include fan-shaped *Phakellia ventilabrum* (Axinellidae) and amphitheater-like *Pachastrella monilifera* (Pachastrellidae). *Isocrinus blakei* (Isocrinidae), which attaches to bits of rubble or shell or isolated hard substrates on chiefly unconsolidated bottoms, is now treated as *Neocrinus blakei* (Roux et al. 2002).

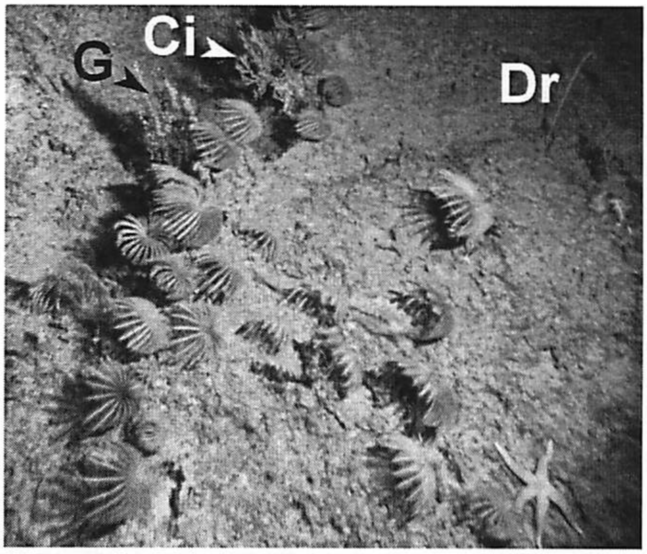

Figure 7. Lithoherm Crinoid/Alcyonarian Zone with numerous Endoxocrinus *n. sp.,* Democrinus rawsoni *(Dr), the primnoid octocoral,* Candidella imbricata *(Ci) and a small colony of the zoanthid,* Gerardia *sp. (G); depth ~600 m. Photo by A. C. Neumann.*

Caicos Platform Island Slope

On 9-13 March 1985, a series of four submersible dives were made using the Perry Systems PC-1802 off the northwestern margin of the Caicos Platform at Providenciales I. A brief summary of observations was included in Wanless et al. (1989). The following description is restricted to features below the vertical deep forereef escarpment.

At ~175 m, the vertical wall of the deep forereef escarpment begins to slope away from the vertical. Although the slope is still about 70° in 183 m, much more of the surface is covered with sediment. Lens-shaped, slightly overhanging embayments are abundant; widely scattered attached organisms include sponges, small octocorals and antipatharian whips (*Cirrhipathes* sp.). The slope gradually becomes shallower (~60° by 250 m) and sediment accumulation becomes greater with increasing depth. By 190-200 m, the cemented slope is less irregular and more rubble has accumulated; embayments protected from sediment accumulation are fewer; occasional large promontories (possibly slump blocks) appear, with sediment and smaller slump blocks banked up on their upslope sides; rare sessile macrofauna includes colonies of the branching ahermatypic coral, *Madracis myriaster* (Stylophoridae), the stalked crinoid, *Cenocrinus asterius* (Isocrinidae) and the octocoral fan, *Nicella guadalupensis* (Ellisellidae), some of which may exceed 0.5 m across. By ~240 m, attached organisms are more abundant, especially on projecting crests and sides of blocks and promontories, and include *M. myriaster*; the solitary corals, *Desmophyllum cristagalli* and *Javania cailletti*; the octocorals, *Nicella* spp. and *Callogorgia americana*; *Cirrhipathes* sp., and the crinoids, *C. asterius, Comactinia meridionalis hartlaubi*, *Endoxocrinus muelleri*, *Democrinus rawsoni* and *Neocrinus decorus*. By 240 m, the slope is 45-50°; elongated, sediment-veneered pavements, 2-4 m across and oriented with the slope, begin to appear (Figure 8).

These pavements are raised above intervening expanses of sediment 3-5 m across, but lie at the same slope angle and are present to the greatest depth reached on these dives (400 m). Pavement margins are often irregularly eroded and overhanging, sometimes fenestrated. Occasionally, multiple exposed layers record successive episodes of sub-sea cementation (Figure 8). Accompanying rubble is often in the form of flattened slabs: probably pieces of broken pavement. Between ~250 and 290 m, at least two vertical scarps or steep irregular slopes from 0.5 to several meters high cut across at least a few adjacent pavements. In one case, a pavement extends beyond a scarp as a deeply eroded overhang (Figure 9). On one dive, at least three ridges, apparently of unconsolidated sediment, oriented with the slope and ~2-3 m high, were observed, with irregular eroded pavements in the troughs between them.

Figure 8. Caicos Platform island slope; lithified elevated pavement surrounded by deeper unconsolidated sediment, 305 m depth, with an unidentified ophiuroid clinging to the octocoral, Callogorgia americana, *and the comatulid,* Comactinia meridionalis hartlaubi *(black arrow). White arrows indicate two successive layers of cementation. Photo diameter ~2m.*

Figure 9. Caicos Platform island slope; lithified pavement projecting beyond vertical scarp (visible at left) as deeply eroded overhang, 275 m depth. Photo diameter ~1.5 m.

Promontories, knobs and small and large slump blocks, veneered with sediment and with sediment banked up on their upslope sides, occur to at least 350 m. It is not always clear if a projecting mass is a slump block or an irregular projection of the island slope itself. In some cases, the surface texture of the large blocks resembles cake frosting, while in others, the surface is deeply eroded, coarsely fenestrated and labyrinthine. Projecting and overhanging surfaces may support numerous sessile suspension-feeding organisms as noted previously. Additional attached organisms that appear by ~260 m include the barnacle-like crinoid, *Holopus rangii* (Holopodidae), and the dandelion-like octocoral, *Nidalia occidentalis* (Nidaliidae). Mobile benthic organisms include the echinoids, *Paleopneustes cristatus* (Paleopneustidae), *Araeosoma belli* (Echinothuridae) and *Calocidaris micans* (Cidaridae). Baumiller et al. (2001) discovered that the latter preys on the stalks of isocrinid crinoids and suggested that such predation may have contributed to the evolution of shedding of terminal stalk segments and concomitant increased mobility in members of this crinoid family. By ~350 m, the angle of slope decreases to ~30° and sediment accumulation increases.

This area of the Caicos Platform margin appears to be a low energy habitat removed from the direct influence of any major current. Although sessile and sedentary suspension-feeding macroepibenthic invertebrates may be common and even crowded on promontories and other topographic irregularities that project well beyond the surrounding island slope, densities are in general substantially less than in the northeastern Straits of Florida, where the Florida Current impinges upon the sea floor. Similarly low densities with occasional concentrations on projecting topography also occur on the western island slope of Grand Cayman Island (Messing, unpublished) and the north slope of Jamaica (Lang 1974, Moore et al. 1976).

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