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Compositional and Taphonomic Variations in Modern Crinoid-Rich Sediments from the Deep-Water Margin of a Carbonate Bank

Ghislaine Llewellyn
Harvard University

Charles G. Messing
Nova Southeastern University, messingc@nova.edu
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Compositional and Taphonomic Variations in Modern Crinoid-Rich Sediments from the Deep-Water Margin of a Carbonate Bank

GHISLAINE LLEWELLYN

Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA 02138

CHARLES G. MESSING

Nova Oceanographic Center, 8000 North Ocean Drive, Dania, FL 33004

Multivariate analyses of the coarse-grained fraction (>2 mm) of sediments accumulating in deep water (419–434 m) along the western margin of the Little Bahama Bank reveal identifiable, small-scale compositional and taphonomic variations among local subhabitats (ridge crest, slope, foreslope, base of slope, pavements and scour pit) separated by meters to tens of meters. Bulk composition varies between planktic- (crest and slope) and lithic-dominated (pavements, scour pit) sediments. Local macrobenthic skeletal components also vary significantly among subhabitats, but are commonly dominated by echinoid and crinoid material; crinoid columnals contribute 9–52% of the coarse skeletal component of 17 sediment samples considered. Distributional and taphonomic analyses (abrasion, encrustation, breakage) indicate that columnals produced in dense ridge-crest assemblages of Chladocrinus decorus are transported down and accumulate along an adjacent slope. Sediments from hardgrounds supporting scattered living assemblages show columnals with the highest levels of abrasion, implying prolonged local reworking. Elevated contributions of Endoxocrinus parrae columnals to the few subhabitats where this species dominates the living assemblage suggest limited lateral transport in the absence of steep gradients. High levels of biological encrustation in areas of thin sediment cover suggest control by length of exposure of grains at the sediment-water interface. Lack of any correlation between frequency of broken columnals in samples and any observed sedimentary or environmental parameters suggests the action of predators or scavengers in this deep-water setting.

Small-scale variations in sediment composition, benthic skeletal assemblages, and taphonomic characteristics are not unique to shallow-water settings, but can also be identified in deep-water carbonate bank-margin sediments. Such changes are largely a response to differences in benthic flow regime associated with small-scale topographic irregularities and may provide an important diagnostic tool for the interpretation of fossil assemblages.

INTRODUCTION

Subfossil skeletal remains of benthic marine invertebrates are widely used to diagnose taphonomic signatures and reveal changes in community structure over a variety of spatial and temporal scales. Such work provides important information about the transition between living communities and fossil assemblages (Cummins et al., 1986; Henderson and Frey, 1986; Fürsich and Flessa, 1987; Kidwell, 1988; Miller, 1988, 1989; Davies et al., 1989; Parsons, 1989; Staff and Powell, 1990a; Miller et al., 1992). Similar studies using fossil material contribute to the reconstruction of ancient communities and vastly improve our understanding of paleoenvironments (Brett and Baird, 1986; Norris, 1986; Speyer and Brett, 1986, 1988; Parsons et al., 1988; Meyer et al., 1989; Kidwell and Behrensmeyer, 1988). Although exceptions exist [e.g., Mullins et al., (1981) on the recognition of deep-water fossil coral bioherms], the great majority of this literature treats material from shallow-water environments.

Stalked crinoids were important components of shallow marine environments during much of the Paleozoic and Mesozoic and have successfully been used as taphonomic indicators in ancient crinoid-rich limestones (Blyth Cain, 1968; Ruhrmann, 1971a, b; Meyer et al., 1989, Meyer, 1990; Donovan, 1991; Baumiller and Ausich, 1992). As a result of the Mesozoic marine revolution, however (Vermeij, 1977), stalked crinoids moved into deep water, leaving shallow marine habitats to unstalked comatulid crinoids which

have since diversified substantially (Meyer and Macurda, 1977). Stalked crinoids have remained important components of a variety of deep-water habitats (Roux, 1980; Conan et al., 1981; Messing, 1985; Messing et al., 1990), but because they are relatively inaccessible, most studies of modern crinoidal skeletal material have concentrated on shallow-water comatulids. Although these unstalked crinoids are sometimes extremely abundant and have successfully been used in biostratinomic and taphonomic studies (Meyer, 1971; Liddell, 1975; Lewis and Peebles, 1988, 1989), they make only minor contributions to local sediments (Meyer and Meyer, 1986; Lewis et al., 1990).

Limited taphonomic and compositional information on modern stalked crinoid skeletal material does exist. In two sediment samples collected via submersible in the northwestern Bahamas, Messing (1985) notes that (chiefly stalked) crinoid ossicles contribute 11.6% by grain count (7.8% by weight) to a gravelly sand from lithoherm rubble (550 m) where living crinoids are few in number, and 8.8% by weight of a chiefly foraminifer/thecosome sand adjacent to a pavement with scattered isocrinids (300–400 m). Ameziane-Cominardi and Roux (1987) discuss bacterial and fungal biocorrosion of a variety of stalked crinoid ossicles recovered from cores taken off New Caledonia (735–1285 m). Although crinoid ossicles make up fewer than 10% of bioclasts, they distinguish autochthonous and allochthonous components. Ameziane-Cominardi's (1991) study of substantial numbers of ossicles also taken from New Caledonian cores includes morphological and distributional analyses, a comparison of expected and actual proportions of different skeletal components, and a discussion of hydrodynamic and biocorrosional processes as possible taphonomic agents. No direct comparisons are made between sediments and local living communities, however, and the relative contributions of crinoidal and other sedimentary components are not discussed.

This paper provides the first detailed compositional and taphonomic account of a modern, deep-water, carbonate sediment rich in stalked crinoid material. It also provides the first correlation of a living stalked crinoid assemblage with penecontemporaneous crinoidal sediment where columnals alone contribute a mean of 23% by grain count to the coarse fraction (>2 mm) of benthic bioclasts. As in shallow-water environments, both composition and taphonomic character of accumulating sediments reflect local topographic and habitat variations, permitting recognition of environmental distinctions and taphofacies characteristics in a relatively homogeneous, deep-water, carbonate environment. Criteria are proposed for recognizing similar environments in the fossil record. A deep-water model for the formation of coarse-grained, crinoid-rich limestones is also discussed.

This study grew out of trawling surveys (Meyer et al., 1978) and submersible observations (Neumann et al., 1977; Messing, 1985; Messing et al., 1990) that revealed dense assemblages of stalked crinoids in 300–600 m in the northeastern Straits of Florida under the influence of the Florida Current. In February 1991, the authors established a study site at about 430 m depth on the southwestern margin of
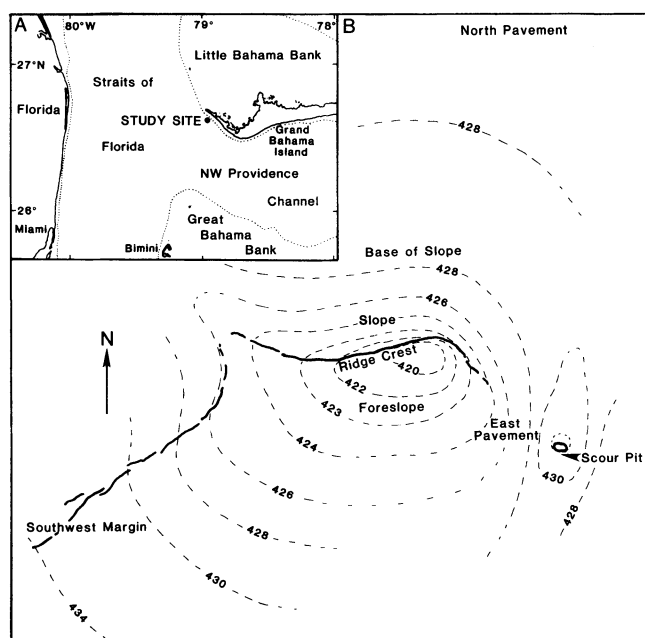

FIGURE 1—Map of study area. A—Geographic location of study site. B—Detailed map of study site. Dashed lines are isobaths in meters estimated from individual depth measurements taken during submersible dives. Area covered is approximately 100 m across.

the Little Bahama Bank in an area characterized by locally dense (to 12 individuals m^{-2}) populations of the isocrinids *Endoxocrinus parrae* (Gervais) and *Chladocrinus* (formerly *Neocrinus*) *decorus* (Carpenter). The results reported herein are part of a larger project investigating stalked crinoid biology and ecology, as well as taphonomy, and the possible use of modern stalked crinoids as analogues for fossil forms.

PHYSICAL SETTING

The study area is located on the southwestern slope of the Little Bahama Bank, 7.41 km south of Settlement Point and 4.55 km off the beach at the western end of Grand Bahama Island (26°38′ N lat., 78°59′ W long.; Fig. 1A). The substrate consists of extensive, gently sloping, submarine-cemented, carbonate pavements (hardgrounds), interspersed with areas covered by unconsolidated sediment, chiefly pelagic foram/thecosome material. Moderate-relief (to about 8 m) topographic irregularities include locally steeper slopes, ridges, escarpments and boulders. Larger features, perhaps to 30 m high, were detected in pre-dive sonar transects, but were not observed from the submersible. Regional studies indicate that unconsolidated sediments are subjected to winnowing and redistribution by contour currents (Mullins et al., 1980), and are largely underlain by carbonate pavements (Wilbur, 1976). Comprehensive descriptions of regional geology, depositional environments and sedimentation in the northern Bahamas can be found in Neumann (1974), Neumann

TABLE 1—Summary of subhabitat characteristics (see also Figure 1B).

Ridge crest (CRS)	Eastern portion of northern edge of hardground; 419–420 m (about 8 m above surrounding pavements); rippled, medium- to coarse-grained, well-sorted sand along the crest edge; remaining area barren of sediment; dense living crinoids almost exclusively *Chladocrinus decorus*.
Foreslope (FSL)	Gently sloping, smooth hardground immediately south of ridge crest; 420–423 m; thin sediment veneer; scattered crinoids including numerous *Endoxocrinus parrae*.
Slope (SLP)	North flank of ridge crest; 421–428 m; thick sediment cover (>5 cm); sample 2 taken from midslope area (424 m), sample 3 taken from closer to slope base, sample 4 from upper slope (423 m); virtually no crinoids.
Base of slope (BSL)	Pitted hardground at base of north slope; 429 m; sediment accumulation variable, thicker in pits; coarse thecosome lag visible; scattered crinoids.
Southwest margin (SWM)	Gently sloping northern edge of hardground at west-southwestern end of study area (continuous with ridge crest); 434 m; thin sediment veneer on hardground, thicker sediment north of visible edge of pavement; scattered crinoids.
East pavement (EPV)	Broken hardground southeast of ridge crest and west of scour pit; 428–431 m; thin sediment veneer with deeper pockets; scattered crinoids.
North pavement (NPV)	Pitted hardgrounds north of slope base; 429 m; thicker sediment than on East Pavement site; scattered crinoids.
Scour pit (SCP)	Crescentic depression at foot of a large boulder southeast of ridge crest; 431 m; much rubble and coarse-grained material apparently from break-up of adjacent hardground; dense *E. parrae*.

et al. (1977), Mullins and Neumann (1979), Mullins et al. (1980, 1981) and Hine and Mullins (1983).

The study site spans an area approximately 100 m (east/west) by 150 m (north/south) centered on a sediment-veneered, low-relief pavement that slopes downward in all directions from its northeastern apex (419–420 m) to 434 m in the southwest and west (and deeper beyond the area studied), and to 429–431 m to the north, east and southeast (Fig. 1B). The eastern portion of the norther margin of this hardground forms a distinct ridge with a rounded northeastern corner and a steep sediment-covered slope to the north. Removal of sediment between successive dive operations has exposed a near vertical scarp up to 0.5 m high in some places along the pavement margin. The ridge/pavement margin slopes down to the west and becomes even with the sediment. Approximately 30 m southeast of the pavement/ridge apex, lies a large boulder (approximately 2 m across and 1.5 m high). A crescentic scour pit runs around its southern half while its northern flank slopes into a flattened shoulder—apparently a lithified sediment shadow. Pavement east and southeast of the boulder exhibits considerable erosion into loose slabs and rubble.

Current flow at the study site is generally northbound and under the influence of the Florida Current. However, during the course of this study important variations in velocity and direction were observed, perhaps due to tidal influences. Velocities (measured approximately 2 m above the substrate) typically range from less than 5 to about 25 cm sec⁻¹, but, during initial operations in February 1991, unexpected strong flow from the north bent crinoids over and produced a narrow band of active asymmetric linear ripples on the ridge crest. This flow, probably intensified by local topography, reached perhaps 50 cm sec⁻¹ within a meter of the substrate. Time-lapse camera exposures (Messing and Llewellyn, unpubl.) reveal a complete current reversal within 48 hr of the initial observations. Dislocation of deployed equipment between successive dive series suggests that much stronger currents may exist intermittently. Such flow variations probably contribute to variations in sediment composition described below.

METHODS

Sediment samples were collected in February, August and November 1991 using a suction device mounted on the submersible *Johnson-Sea Link* (Harbor Branch Oceanographic Institute, Fort Pierce, Florida). Relatively thin sediment layers underlain by cemented pavements precluded coring. Substantial amounts of fine material were lost during the collection process although large enough volumes (sometimes several liters) of sediment were usually retained for analyses. Sampling was precluded on some ridge crest and foreslope areas because of insufficient sediment cover. For the following analyses, subhabitats are distinguished on the basis of location, depth, topography, substrate and macroepibenthos visible from the submersible, and are described in Table 1.

Samples were fixed in 70% ethanol immediately upon surfacing (to preserve any living organisms), and split, dried and sieved through a standard 2 mm mesh screen in the laboratory. For compositional analyses, all grains >2 mm and recognizable as bioclasts are identified at least to major taxonomic and ecologic (for example, planktic vs. benthic) group, with non-biogenic clasts treated as lithic

TABLE 2—Abrasion scale for crinoid columnals.

Abra-sion scale	Diagnostic features
1	Virtually pristine: very minor abrasion
2	Minor abrasion of crenelations and edges
3	Crenelations reduced in height: abrasion of edges
4	Crenelations indistinct: extensive edge rounding
5	Crenelations completely removed: edges rounded

grains. Samples must include an adequate coarse-grained fraction (at least 50 grains) and a precise location within the study area. A total of sixteen samples meet both of these criteria and are included in subsequent tests. The only exception is a single sample of fine-grained, actively rippled sand from the ridge crest (sample 1a) that contains too few non-crinoid grains >2 mm to permit inclusion in compositional analyses. It does, however, have sufficient crinoid grains and is included in the taphonomic study described below.

We use principal components analysis and cluster analysis to examine relationships among sub-habitats, gross sediment composition (planktic/benthic/lithic) and benthic skeletal assemblages (css: Statistica, Complete Statistical System, 1986–1991 Statsoft, Inc.). Cluster analysis organizes data into clusters according to degree of similarity; principal components analysis creates new axes that best explain variation within the dataset. These techniques have been successfully used with a variety of biological, paleontological and sedimentological data sets (Reyment, 1963; Wilkinson and Cheshire, 1989; Meyer et al., 1989; Miller, 1988; Valentine and Peddicord, 1967; Colby and Boardman, 1989; Doyle and Feldhausen, 1981). In our analyses, samples are percent-transformed to account for differences in sample size. In analyses of gross sediment composition, only variables present in at least 75% of samples are included in order to produce a reduced data set containing only the more common variables. All taxonomic categories are included in analyses of benthic skeletal assemblages. Cluster analysis uses the Unweighted Pair-Group Method with Arithmetic Averaging (UPGMA; Imbrie and Van Andel, 1964; Harbaugh and Merriam, 1968; Sneath and Sokal, 1973) with an average Euclidean distance similarity measure and single linkage joining algorithm (see, for example, Martin and Wright, 1988). Principal components analysis uses an average Euclidean distance measure with a raw varimax rotation on the appropriate number of factors (Scree test: Cattell, 1966) of the correlation matrix.

In this paper, analysis of taphonomic alteration treats abrasion, biological encrustation and breakage of stalked crinoid columnals. Abrasion refers to the amount of degradation of articular facet sculpturing and rounding of ossicle edges measured on an arbitrary scale of 1 to 5 (Table 2). Figure 2 illustrates an example of each level of abrasion
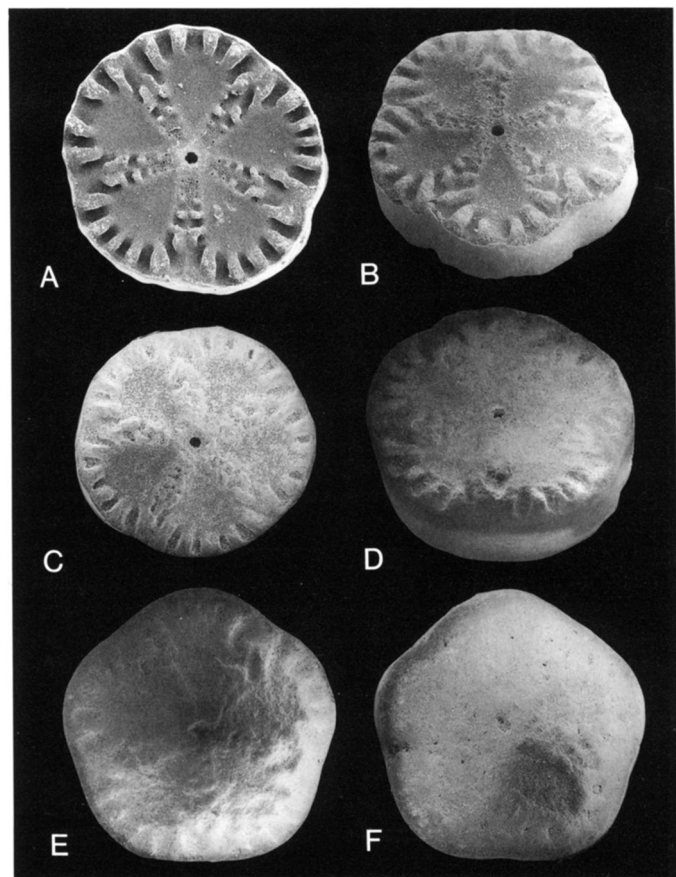
FIGURE 2—Scanning electron micrographs (SEMs) of columnals from *Chladocrinus decorus* illustrating range of abrasion values. A—Pristine; taken from a preserved specimen (all organic tissue removed), ×22.7. B—Virtually pristine, ranked 1 on abrasion scale. Broken surface on front margin results from disarticulation of two partially fused columnals, not produced by abrasion, ×19.8. C—Ranked 2 on abrasion scale, slight abrasion of crenelations, ×19.9. D—Ranked 3 on abrasion scale, moderate abrasion of both crenelations and margin, ×22.0. E—Ranked 4 on abrasion scale, extensive abrasion of both columnal face and margin, ×18.8. F—Ranked 5 on abrasion scale, extremely abraded columnal, surface features barely visible, ×19.7.

for *Chladocrinus decorus* with an ossicle dissociated from a living specimen for comparison. Between-sample comparisons (described below) use mean values derived from all grains measured in a sample. Biological encrustation refers to any deposit on a columnal produced by another organism (that is, not including mineral cements); taphonomic breakage includes any damage to a columnal surface not obviously produced by abrasive wear (Fig. 3). Encrustation and breakage are assessed on a presence/absence basis per grain and expressed as the percentage of grains exhibiting any encrustation or breakage per sample.

Ossicle color also exhibits considerable variation. Fresh columnals are pure white whereas many apparently older, typically more abraded ossicles display a range of discoloration from yellow through beige to various shades of brown, with occasional iron oxide staining. Color may also
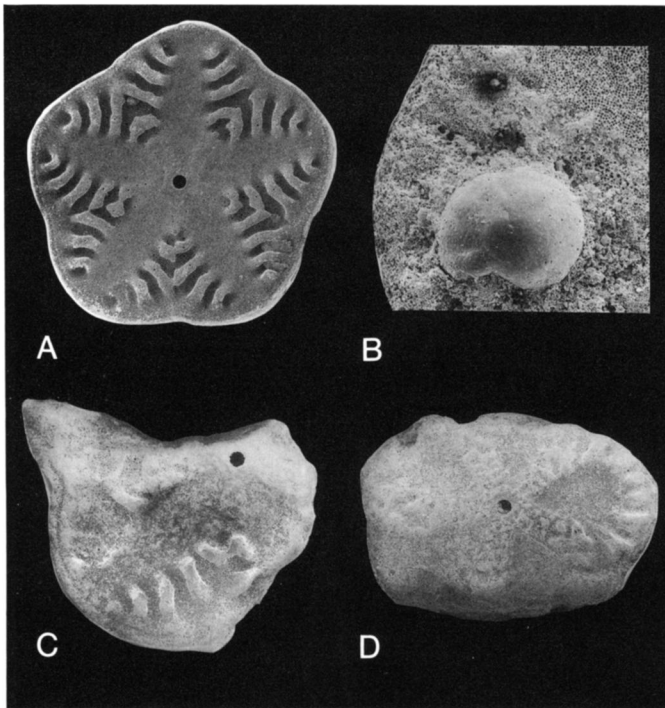
FIGURE 3—SEM of A—pristine *Endoxocrinus parrae* columnal from a preserved specimen (all organic tissue removed), ×16.0. B—*Chladocrinus decorus* encrusted by benthic foraminiferan. C—*Endoxocrinus parrae* columnal showing breakage, ×21.0. D—*Chladocrinus decorus* columnal showing taphonomic breakage, ×18.4

vary on a single ossicle. These variations have proven difficult to quantify objectively and are, therefore, not included in taphonomic analyses.

We analyze taphonomic characteristics using Multi- and Univariate Analyses of Variance (MANOVA and ANOVA). These techniques test the validity of groupings by comparing differences in means, and are widely used in analyses of biological and taphonomic data (for example, Wilkinson and Evans, 1989; Wilkinson and Cheshire, 1989; Davies et al., 1989; Staff and Powell, 1990b). Multi-Between-Groups ANOVA's and MANOVA's are used to determine if any significant interactions exists in the data set. Multi-way interactions revealed by these analyses are tested using Wilks' Lambda multivariate criteria. Three-way univariate ANOVA's are used to investigate specific effects of individual independent variables on dependent variables, testing individual interactions for significance with Newman-Keuls post hoc tests (Winer, 1971). Independent variables are habitat and sediment type; dependent variables are abrasion, breakage and encrustation. Sediment type is classified as thin (≤ 2 cm surface veneer, ≤ 5 cm in pockets), thick ($\gg 2$ cm surface layer) or rippled. For taphonomic analyses, several subhabitats are combined on the basis of geographic proximity and visual similarity, to obtain a more manageable design (following, for example, Meyer et al., 1990; Davies et al., 1989) and more statistically rigorous results. Slope and base of slope sam-

ples are combined as "Slope"; north and east pavement, scour-pit and southwest margin samples are combined as "Hardground." The foreslope sample has some aspects in common with both "Slope" and "Hardground" categories. It possesses a typical hardground aspect, supporting a typical hardground fauna yet is tilted up towards the ridge and is located only a few meters away from the crest. Analyses are therefore repeated including foreslope in both categories to detect any differences. The two ridge crest/ rippled sand samples are sufficiently distinct in taphonomic and sedimentary characteristics to merit their own category in both habitat and sediment classifications.

Differences in crenelation patterns on columnal articular faces permit easy distinction of the two local species. Figure 3A illustrates a columnal dissociated from a living *E. parrae* for comparison with the pristine *Chladocrinus decorus* shown in Figure 2A. *C. decorus* columnals are sufficiently abundant to be analyzed as a separate group, allowing comparison between taphonomic characteristics of a bulk columnal sample with those of a single species. Recovery of too few *Endoxocrinus parrae* columnals precluded a similar comparison.

The relationship between living and death assemblages of crinoids is examined by comparing 1) local population densities of living crinoids with abundances of crinoidal material in sediment samples, and 2) the relative contributions the two species make to local living populations and sediment samples. Densities and species composition of living crinoid assemblages are assessed from video taken in the vicinity of a sample; the abundance and composition of crinoidal material in the benthic skeletal component of sediment samples characterizes the death assemblages. A univariate ANOVA is used to analyze the relationship between living crinoid population density and abundance of crinoidal material in the sediment. Living crinoid density is the independent variable; samples are classified as dense (at least several individuals m^{-2}), scattered (one or a few individuals per several m^2) or none. Relative abundances of the two crinoid species in living populations and sediment from the different habitats are compared to investigate whether any correspondence exists between species composition in living and death assemblages.

RESULTS

Sediment Composition Analysis

Figure 1 illustrates the locations of subhabitats at the study site at which sediment samples were collected. Table 1 summarizes the general features of sampled subhabitats. Compositional analysis of >2 mm grains (Table 3) reveals three main sources of coarse sediment: 1) lithic grains; 2) tests of calcareous planktic/pelagic organisms (chiefly thecosome "pteropods"); and 3) calcareous skeletal material produced by benthic invertebrates. Crinoid and echinoid grains dominate the latter component, and are accompanied by clasts produced by alcyonarians, corals, gastropods, bivalves, benthic foraminiferans, decapod crustaceans and other minor components [stylasterids,

TABLE 3—Grain counts from sediment samples taken at 419–434 m on the southwestern slope of the Little Bahama Bank. Samples labeled according to sample number (No.), month of collection and subhabitat (Subh.). See Table 1 for subhabitat abbreviations. Grain composition abbreviations: PLG, planktic gastropod; PLF, planktic foraminiferan; CRI, crinoid; ECH, echinoid; OPH, ophiuroid; GST, benthic gastropod; BIV, bivalve; BNF, benthic foraminiferan; COR, coral; ALC, alcyonarian; STY, stylasterid; BCH, brachiopod; DEC, decapod crustacean; OST, ostracod; SPO, sponge; BRY, bryozoan; WOR, worm tube; LTH, lithic; UNI, unidentifiable; TOT, total. All sediment >2 mm.

No.	Month	Subh.	PLG	PLF	CRI	ECH	OPH	GST	BIV	BNF	COR	ALC	STY	BCH	DEC	OST	SPO	BRY	WOR	UNI	LTH	TOT
1	Aug	CRS	425	0	32	86	1	8	12	3	14	0	1	0	25	0	6	4	6	1	17	641
2	Aug	SLP	172	0	275	121	4	103	24	91	26	45	17	7	43	0	10	3	0	19	364	1324
3	Oct	SLP	378	0	134	94	1	33	13	13	4	6	2	4	44	0	27	0	3	0	36	792
4	Oct	SLP	244	0	123	109	4	28	20	2	0	2	3	3	29	0	7	0	2	3	22	601
5	Oct	FSL	205	1	75	124	2	44	18	10	22	46	12	13	24	4	44	4	5	0	141	794
6	Feb	BSL	38	0	18	20	0	16	0	13	7	7	1	1	6	2	3	2	0	0	41	175
7	Oct	BSL	258	0	112	183	7	39	33	5	8	20	0	3	64	7	29	0	3	6	99	876
8	Oct	SWM	161	0	124	134	2	54	23	14	3	18	3	10	32	3	6	0	4	15	252	858
9	Oct	SWM	126	0	63	114	0	42	26	22	0	9	1	7	14	2	5	1	1	1	196	630
10	Feb	EPV	280	0	62	47	0	47	20	22	7	40	0	2	27	6	17	6	0	17	397	997
11	Aug	EPV	443	0	51	112	6	65	15	71	16	96	7	12	60	0	11	1	1	11	1259	2237
12	Feb	NPV	234	0	25	34	0	24	3	24	1	16	1	2	9	3	3	1	6	0	374	760
13	Feb	NPV	645	0	121	105	0	88	13	71	11	77	0	16	79	7	7	4	0	48	1413	2705
14	Feb	NPV	146	0	37	47	0	20	8	30	2	24	0	1	19	8	3	0	0	1	222	568
15	Oct	NPV	158	0	116	44	0	33	9	69	8	1	3	8	33	11	14	3	2	1	449	962
16	Feb	SCP	747	0	49	53	0	59	6	179	14	139	5	6	14	6	1	0	0	55	3281	4614

brachiopods, sponges (siliceous), bryozoans, brachiopods, serpulid polychaetes and ostracods]. We find no coarse grains derived from shallow water. Dead sea grass (*Thalassia testudinum*) blades occasionally observed on the substrate indicate that off-bank transport may bring fine-grained material to the study site (Heath and Mullins, 1984; Hine et al., 1981), but the extent of such off-bank transport could not be assessed because much of the finer grain-size fractions was not recovered.

Abundances of the three main sediment categories (>2 mm) vary among subhabitats and are assessed using multivariate techniques. A Q-mode cluster analysis dendrogram distinguishes three major sample clusters (Fig. 4). Samples from individual subhabitats group together within clusters with only one exception. Examination of abundance data, ordered according to results of two-way cluster analysis (Q and R mode), reveals the relationship between constituent grains and cluster designations (Fig. 5). Relative abundances of planktic (thecosome) and lithic grains appear to control the three major groupings; benthic skeletal components are relatively unimportant. Cluster I includes the crest and two slope samples, with at least 40% planktic grains; Cluster III comprises north and east pavement (hardground) and scour pit samples, with at least 39% lithic grains; and Cluster II contains the foreslope, slope base, southwest margin and one slope samples, with intermediate abundances of planktic and lithic grains.

To test the validity of these groupings, a principal components analysis was performed on the same data set. The first two axes explain 75% and 20% of the variance, re-

spectively, and are used to carry out a varimax rotation. Consideration of eigenvalues for constituent grains shows that axis 1 is governed principally by abundance of lithic grains while axis 2 is controlled mainly by amount of thecosome (planktic) material. Sample distribution with respect to the first two rotated axes (Fig. 6) confirms the groupings produced by cluster analysis. Samples, labeled according to cluster analysis assignments, fall along a broad gradient from those rich in planktic (upper right of Fig. 6) to those rich in lithic grains (lower left). Group I, at top right, comprises the ridge crest and two slope samples; high in planktic and low in lithic grains. Group III, at lower left, consists of hardground and scour pit samples, all with abundant lithic, but few planktic grains. The scour pit sample (16), at the extreme lower left, contains the largest lithic component and smallest skeletal component. The remaining samples (Group II) occupy the central portion of the diagonal and display compositions intermediate between the other groups.

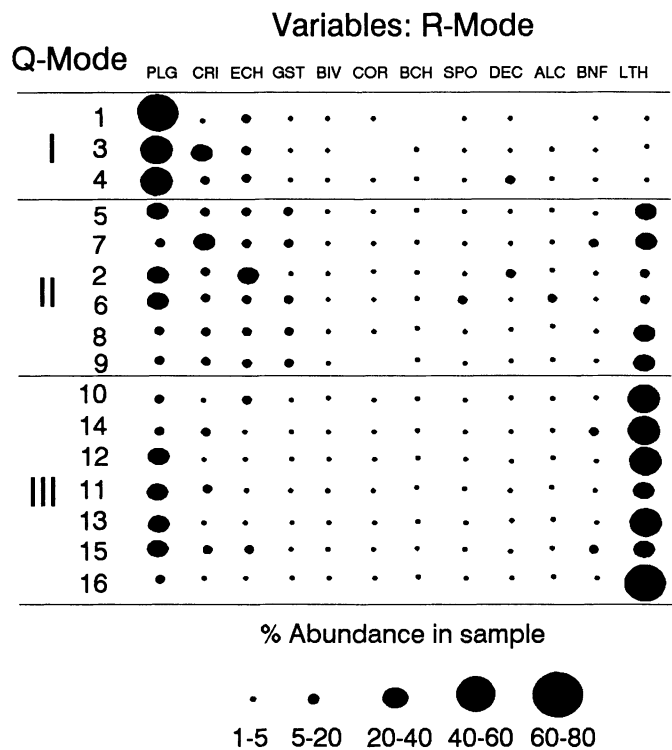### Benthic Skeletal Assemblage Analyses

Crinoid and echinoid clasts dominate the coarse (>2 mm) benthic skeletal component of most of the 16 sediment samples (Table 4). Crinoid ossicles (columnals) contribute 9.2 to 37.1% by grain count. Four samples are more than 30% crinoidal, five samples 20–29%, five samples 15–19% and two samples 8–10%. Echinoid material contributes 10.0 to 43.4% and consists chiefly of plate fragments of spatangoid echinoids. Secondary contributors include
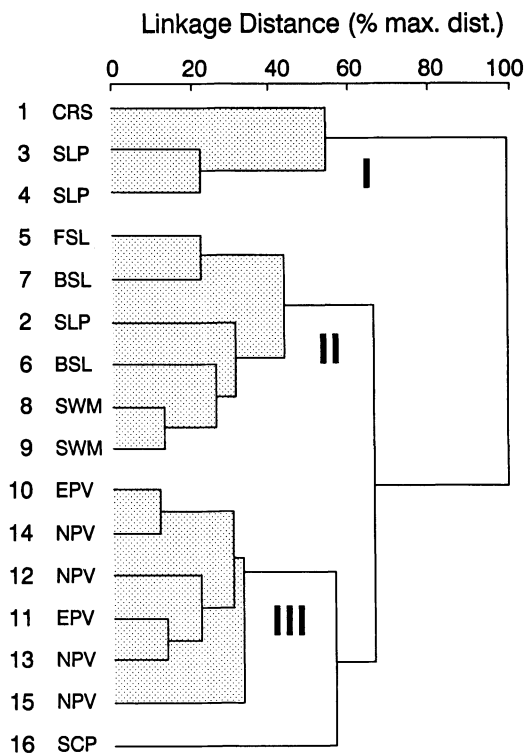
FIGURE 4—Dendrogram for Q-mode cluster analysis of sediment composition using reduced data set (unweighted pair-group method with arithmetic averaging; percent transformation of samples; average Euclidean distance measure; single linkage). Large letters indicate cluster designations discussed in text; numbers and labels designate samples and sampling environment.

FIGURE 5—Percent abundance diagram for sediment composition. Samples and variables grouped according to Q- and R-mode cluster analyses. Abbreviations as in Table 2.

gastropod shells and fragments (8.0–16.7%), benthic foraminiferans (0.6–33.7%), decapod crustacean fragments (2.6–13.2%) and alcyonarian fragments (0–26.2%). Benthic foraminiferans and alcyonarians dominate a single sample (scour pit). Alcyonarian fragments consist chiefly of slender cylindrical axis segments produced by the isidid *Lepidisis caryophyllia*. Other groups rarely contribute more than 7% to any given sample.

Multivariate analysis of the benthic skeletal component of sediment samples reveals additional variations associated with environmental setting. A Q-mode dendrogram of all major taxonomic groups (Fig. 7) produces two broad clusters and an outlying sample, labeled A, B, and C, respectively. Cluster A represents crest, slope, foreslope, base of slope and southwest margin subhabitats and one hardground sample (15). Cluster B contains all remaining hardground samples and one slope base sample. The outlier, cluster C, is the scour pit sample. These groupings are not as unequivocal as those obtained in analyses of bulk sediment (Fig. 4); samples from each subhabitat do not cluster together uniformly (for example, the two base of slope samples fall into separate clusters). In addition, the greater relative linkage distances between samples within clusters indicate that the degree of similarity among samples is

also lower than for bulk sediment. The R-mode dendrogram for benthic skeletal variables (Fig. 8) shows that crinoids and echinoids, the two most abundant coarse-grain types, are distributed largely independently of each other. They link at 80% of the maximum distance. The remaining taxonomic groups cluster together with a high degree of similarity relative to echinoid and crinoid components. Examination of linkage distances, however, reveals that degree of similarity is largely a function of relative abundance in samples. (Compare Fig. 8 with Table 4.) Crinoids and echinoids, the most abundant, are least similar. Decapod crustaceans, gastropods, benthic foraminiferans and alcyonarians, the next most abundant groups, exhibit intermediate linkage distances. Finally, the least abundant groups such as ophiuroids, stylasterids, bryozoans appear most similar.

A principal components analysis of the same data set confirms the pattern of two broad subhabitat clusters and an outlying sample seen in the cluster analysis. Inspection of eigenvalues shows that the first two axes explain 77% and 12% of the variation, respectively. The first axis is most highly correlated with abundance of echinoid and crinoid material; the second axis depends more on gastropod, benthic foraminiferan and alcyonarian fragments. A plot of the first two principal components (Fig. 9) distinguishes the following groups: group A at top right contains ridge crest, foreslope, southwest margin and most slope
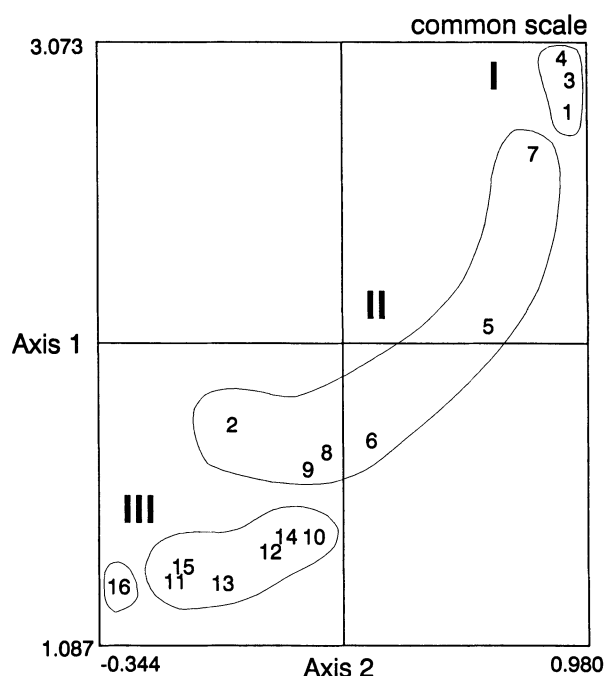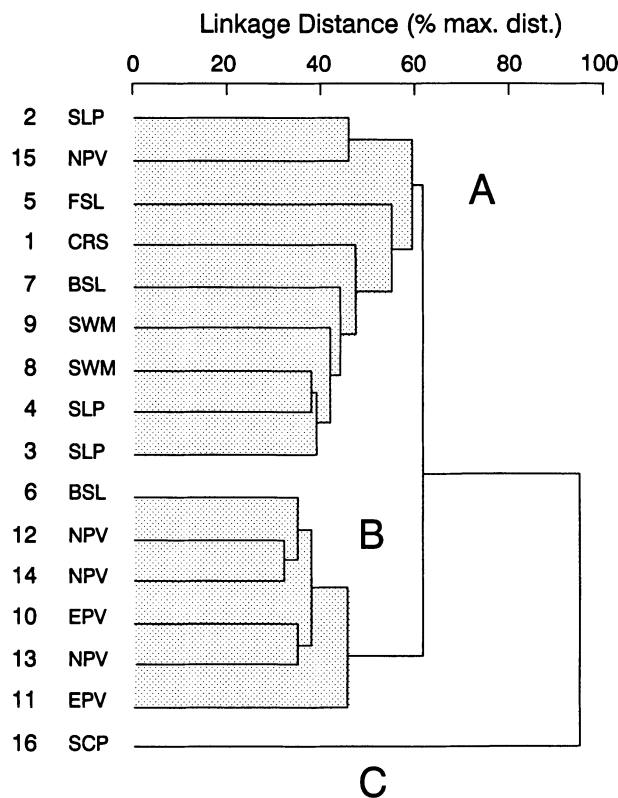
FIGURE 6—Plot of axes 1 and 2 for Principal Components Analysis of sediment samples using reduced data set (raw varimax rotation and normalized factor loadings computed from 3 factors of a correlation matrix). Large letters refer to group designations from cluster analysis; small numbers refer to sample numbers. See text for discussion of meaning of axes.

FIGURE 7—Dendrogram for Q-mode cluster analysis of benthic skeletal material (unweighted pair-group method with arithmetic averaging; percent transformation of samples; average Euclidean distance measure; single linkage). Large letters indicate cluster designations discussed in text; numbers and labels designate samples and sampling environment.

samples and is high in echinoid and crinoid, low in gastropod, alcyonarian and benthic foraminiferan clasts; group C at bottom left includes only the scour pit sample which is dominated by alcyonarian and benthic foraminiferan material; group B towards the center consists of most pavement samples and has a composition intermediate between the other two. Again, the groupings are not perfect, as the pavement group (B) also contains a slope and base of slope sample. Because the scour pit sample plotted so far from the rest of the data points, principal components analysis was repeated without this sample. The resulting plot (Fig. 10) shows the same two groups, but with the ridge crest sample isolated at a greater distance. In this analysis, the first two axes explain 81% and 8% of the total variation, respectively. Axis 1 is most highly correlated with crinoid grains, but also contains major components from gastropod, benthic foram, and alcyonarian material; axis 2 represents an echinoid axis. Plotting at lower left, the pavement group (plus a slope and base of slope sample) contains little crinoid and echinoid material. By contrast, echinoid material dominates the ridge crest sample at upper right.

Living and Death Assemblages

Density and species composition of living crinoid assemblages vary considerably throughout the study area (Table 5). Figure 11 illustrates two distinct assemblages: a dense stand of *Chladocrinus decorus* on the ridge crest (Fig. 11A)

and scattered *C. decorus* accompanied by isidid alcyonarians on a sediment-veneered pavement (Fig. 11B). The ridge crest and the isolated boulder adjacent to the scour pit exhibit the highest densities, but vary dramatically in species composition. Along the ridge crest, in a narrow band 1–2 m wide and about 30 m in length, the crinoid fauna is almost entirely *Chladocrinus decorus* and reaches densities of about 12 individuals m^{-2} with a mean of 4.8 m^{-2} (Fig. 11A). In contrast, thirty-nine *Endoxocrinus parrae* and one *C. decorus* cling to an area of about 0.5 by 2.0 m across the crest of the boulder adjacent to the scour pit. Much of the slope subhabitat is barren with a few scattered individuals at the base and just below the ridge crest. The slope appears to be shielded from northbound flow by the ridge crest and is likely subject to reduced and unfavorable water movement for colonization by crinoids. Thicker sediment here also limits the area of substrate suitable for attachment. All remaining areas: north and east pavements, southwest margin and foreslope, support a scattered crinoid fauna (Fig. 11B). Densities based on timed 30–160 m transects range from about 0.1 to 0.8 crinoids m^{-2} although two or three individuals of either or both species occasionally occur within a single square meter. Substantial barren stretches also occur. This scattered fau-

TABLE 4—Percentage abundances of benthic skeletal grains by major taxonomic group and station. Percentages omit consideration of unidentifiable grains. See Table 3 for explanation of abbreviations.
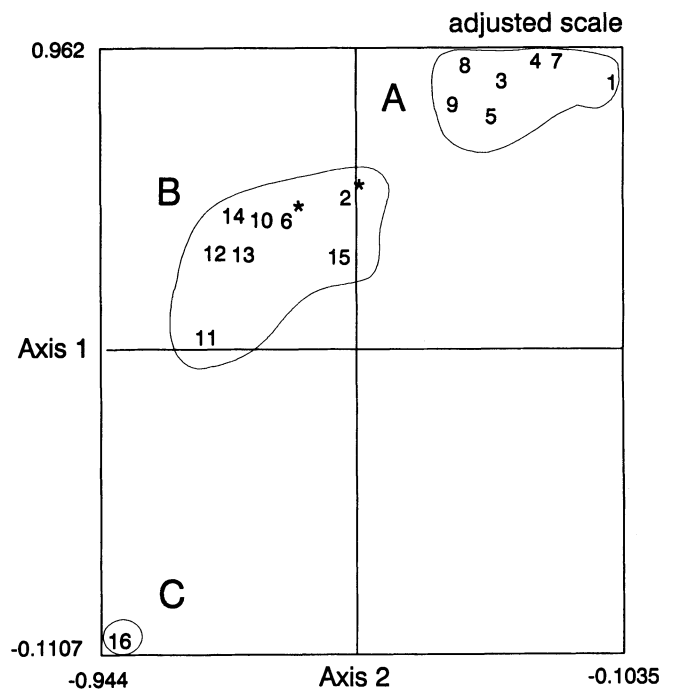
No.	CRI	ECH	OPH	GST	BIV	BNF	COR	ALC	STY	BCH	DEC	OST	SPO	BRY	WOR
1	16.2	43.4	0.5	4.0	6.0	1.5	7.1	0	0.5	0	12.6	0	3.0	2.0	3.0
2	35.8	15.7	0.5	13.4	3.1	11.8	3.4	5.9	2.2	0.9	5.6	0	1.3	0.4	0
3	35.5	24.9	0.3	8.7	3.4	3.4	1.1	1.6	0.5	1.1	11.6	0	7.1	0	0.8
4	37.1	32.8	1.2	8.4	6.0	0.6	0	0.6	0.9	0.9	8.7	0	2.1	0	0.6
5	16.8	27.7	0.5	9.8	4.0	2.2	4.9	10.3	2.7	2.9	5.8	0.9	9.8	0.9	1.1
6	18.8	20.8	0	16.7	0	13.5	7.3	7.3	1.0	1.0	6.3	2.1	3.1	2.1	0
7	21.8	35.7	1.4	7.6	6.4	1.0	1.6	3.9	0	0.6	12.5	1.4	5.7	0	0.6
8	28.8	31.2	0.5	12.6	5.4	3.3	0.7	4.2	0.7	2.3	7.4	0.7	1.4	0	0.9
9	20.5	37.1	0	13.7	8.5	7.2	0	2.9	0.3	1.1	4.6	0.7	1.6	0.3	0.3
10	20.5	15.5	0	15.5	6.6	7.3	2.3	13.2	0	0.7	8.9	2.0	5.6	2.0	0
11	9.7	21.4	1.2	12.4	2.9	13.6	3.1	18.3	1.3	2.3	11.5	0	2.1	0.2	0.2
12	16.5	22.4	0	15.8	2.0	15.8	0.7	10.5	0.7	1.3	5.9	2.0	2.0	0.7	4.0
13	20.2	17.5	0	14.7	2.2	11.9	1.8	12.8	0	2.7	13.2	1.2	1.2	0.7	0
14	18.6	23.6	0	10.1	4.0	15.1	1.0	12.1	0	0.5	9.6	4.0	1.5	0	0
15	32.8	12.4	0	9.3	2.5	19.5	2.3	0.3	0.9	2.3	9.3	3.1	4.0	0.9	0.6
16	9.2	10.0	0	11.1	1.1	33.7	2.6	26.2	0.9	1.1	2.6	1.1	0.2	0	0
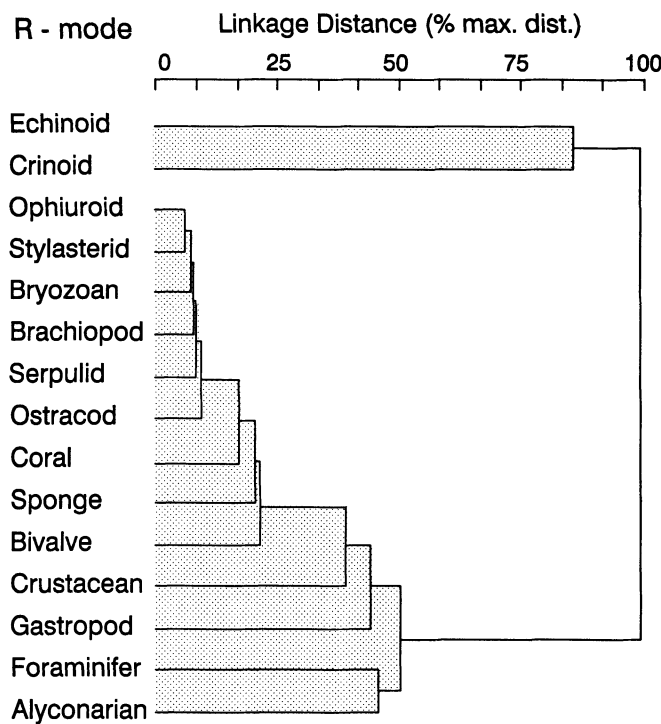
FIGURE 8—Dendrogram for R-mode cluster analysis of benthic skeletal material (unweighted pair-group method with arithmetic averaging; percent transformation of samples; average Euclidean distance measure; single linkage).

FIGURE 9—Plot of axes 1 and 2 for Principal Components Analysis of benthic skeletal material (raw varimax rotation and normalized factor loadings computed from 3 factors of a correlation matrix). Large letters refer to group designations from cluster analysis; small numbers refer to sample numbers. See text for definitions of axes. * = Anomalous sample position.

na is dominated by *C. decorus* with one exception: the foreslope subhabitat a few meters south of the ridge crest supports *E. parrae* in greater numbers than *C. decorus*.

Sources of crinoid mortality at the study site remain unknown. Although we observed no large crustaceans or durophagous fishes, several large nonpredatory (on crinoids) fishes occur at the study site (misty grouper *Epinephelus mystacus*, rough shark *Oxynotus caribbeus*, and
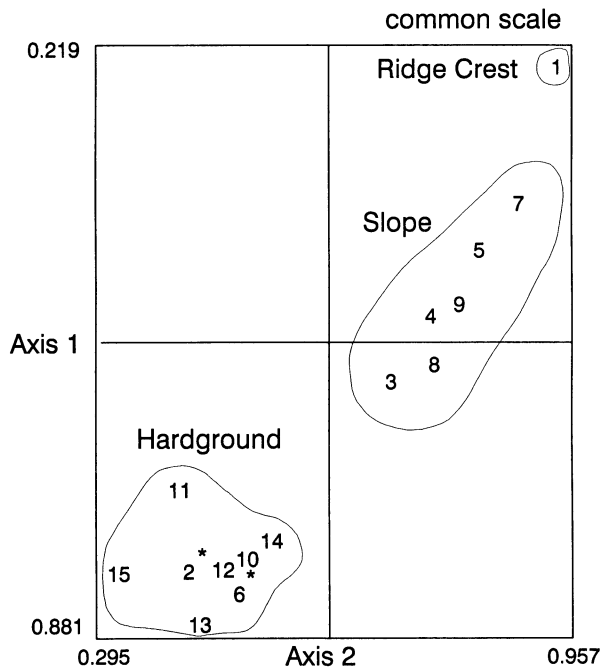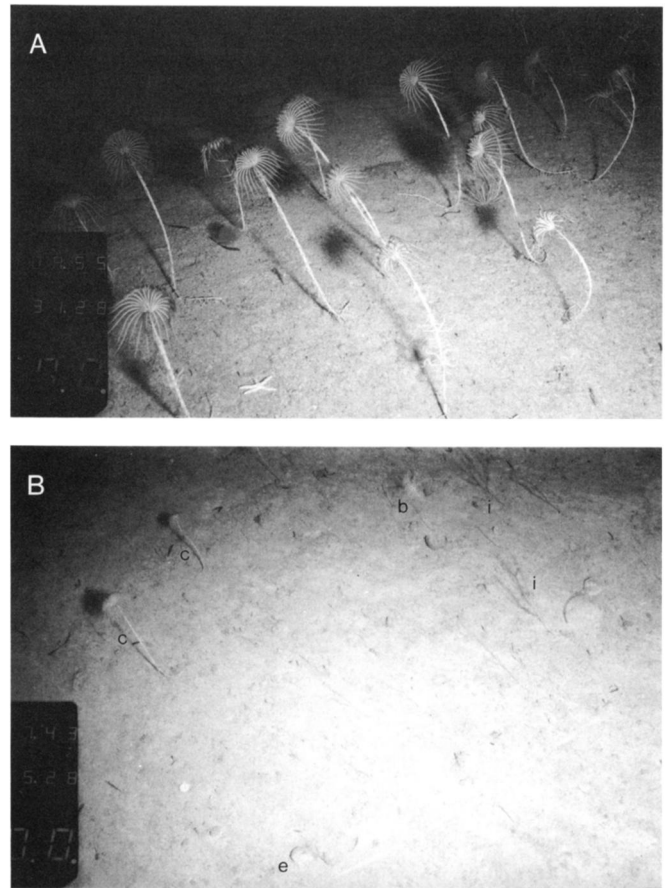
FIGURE 10—Plot of axes 1 and 2 for Principal Components Analysis of benthic skeletal material removing the scour pit sample (raw varimax rotation and normalized factor loadings computed from 2 factors of a correlation matrix). Large letters refer to group designations from cluster analysis; small numbers refer to sample numbers. See text for the definitions of axes. * = Anomalous sample position.

FIGURE 11—A. Dense stand of *Chladocrinus decorus* on the ridge crest with rippled sand in the background. Foreground is barren of sediment. Current from right foreground. Depth: 420 m. B. Typical hardground with scattered *C. decorus* (c), isidid alcyonarians (i), basketstars (b) and spatangoid echinoid test (e). Depth: 428 m. Straight line across lower right was made by submersible in moderately thick sediment veneer.

large unidentified carcharhinid sharks) that may disrupt or destroy crinoids incidentally, especially while chasing prey or avoiding larger predators. The large echinoid *Calocidaris micans* has been implicated in the disruption of isocrinid filtration fans elsewhere (Messing et al., 1988) and occurs at the study site. We observed a few crownless stalks in life position but no recently dead, intact specimens.

Crinoids at the study site also apparently contribute to sediments via autotomy of distal stalk segments. We observed several detached stalk segments consisting of one or a few noditaxes among dense *C. decorus* along the ridge crest. Sediment samples include some pluricolumnal grains although the majority of columnals occur as individual ossicles. *In situ* and laboratory experiments (unpublished data) indicate that noditaxes of both species may remain intact for at least several months.

Abundance and species composition of crinoid columnals in the sediment both vary throughout the study area (Table 3). Species composition, measured as the ratio of *C. decorus* to *E. parrae* columnals, ranges from 2.3 for the scour pit to 54.0 for a southwest margin sample (Table 5). The two ridge crest samples are interesting in that one (sample 1a; not included in compositional analyses) shows the greatest crinoidal contribution (52.0%) to the coarse benthic skeletal component of any sample, while the other has a relatively low proportion of crinoid material (16.2%). This may be a function of local patchiness, seasonal vari-

ation, or the small size of the sample with abundant crinoid material (sample 1a in the Taphonomy section below).

Slope samples exhibit a rough gradient in crinoidal contribution to sediment. Crinoid ossicles compose 18.8–21.8% of slope base samples, collected no closer than about 40 m to the dense stands on the ridge crest, and 35.5–37.1% of slope samples proper, collected 15–27 m from the crest. Species ratios for crest and slope range between 8.0 and 17.1. Pavement and southwest margin samples show a wide range of relative abundance values (9.7–32.8%) and species ratios (7.5–54.0). The foreslope sample has the second lowest species ratio (6.7) and a fairly low abundance of crinoid material while the scour pit sample exhibits the smallest crinoid component (9.2%) and the lowest species ratio (2.3). Both of these low ratios reflect the relatively high contribution of *E. parrae* to adjacent living assemblages.

No direct overall correspondence exists between density of living crinoids and the contribution of crinoid ossicles to the benthic skeletal component of adjacent sediments

TABLE 5—Summary of taphonomic data from crinoid columnals in >2 mm sediment samples. Subhabitat—See Table 1 for abbreviations. Sediment type—Character of surficial sediment: thick, >2 cm; thin, <2 cm; ripples, linear asymmetrical ripples. Local living crinoid assemblage—Population density of living crinoid assemblage: dense, $\gg 1$ m^{-2}; scatterd, ≤ 1 m^{-2}; none, no crinoids within immediate area. Mean abrasion—Mean level of abrasion for all columnals per sample. % Encrustation—Percentage of encrusted columnals per sample. % Breakage—Percentage of columnals displaying breakage. Species ratio—Ratio of *Chladocrinus decorus* to *Endoxocrinus parrae* columnals and pluricolumnals.

No.	Month	Subhabitat	Sediment type	Local living crinoid assemblage	% Crinoid contribution to benth. skel. sed.	Mean abrasion	% Encrustation	% Breakage	Species ratio (n:1)
1	Feb	CRS	Rippled	Dense	16.2	1.5	6.9	32.0	8.0
1a	Aug	CRS	Rippled	Dense	52.0	1.3	8.3	8.3	infinity
2	Aug	SLP	Thick	None	35.8	2.0	17.9	32.8	17.1
3	Oct	SLP	Thick	Scattered	35.5	2.7	17.8	26.3	15.5
4	Oct	SLP	Thick	None	37.1	2.5	8.8	25.8	7.5
5	Oct	FSL	Thin	Scattered	16.8	2.6	32.4	27.0	6.7
6	Feb	BSL	Thick	None	18.8	3.1	41.9	29.7	8.5
7	Oct	BSL	Thin	Scattered	21.8	2.8	33.5	18.1	10.3
8	Oct	SWM	Thin	Scattered	28.8	3.1	26.4	20.2	25.8
9	Oct	SWM	Thick	Scattered	20.5	3.1	20.3	23.7	54.0
10	Feb	EPV	Thin	Scattered	20.5	3.1	23.7	18.4	37.0
11	Aug	EPV	Thin	Scattered	9.7	2.7	41.9	29.7	18.5
12	Feb	NPV	Thin	Scattered	16.5	3.0	56.0	40.0	7.5
13	Feb	NPV	Thick	Scattered	20.2	2.8	34.8	31.3	11.5
14	Feb	NPV	Thin	Scattered	18.6	2.9	31.6	34.2	14.3
15	Oct	NPV	Thick	Scattered	32.8	2.6	15.7	16.9	36.0
16	Feb	SCP	Thin	Dense	9.2	2.8	41.1	27.1	2.3

(Table 5). Sediments from areas supporting dense living assemblages (>1 crinoid m^{-2}: ridge crest and scour pit boulder) display the complete range of crinoidal contributions (9.2–52.0%). In areas where living crinoids are scattered (<1 crinoid m^{-2}: pavements, foreslope, base of slope, SW margin), crinoid ossicles contribute 9.7 to 35.5%. The crinoidal contribution to sediments in areas lacking crinoids (slope and slope base) ranges from 18.8 to 37.1%. Much of this pattern can be explained with reference to local topographic and hydrodynamic factors (see Discussion).

Species ratios of living assemblages and columnals accumulating in sediment samples correspond to a greater degree. As mentioned above, the low species ratios (high *E. parrae* contributions) of foreslope and scour pit sediments reflect the relatively dense living *E. parrae* assemblages in those subhabitats. Species ratios from other subhabitats all favor *C. decorus* and reflect the general and often overwhelming dominance of that species in living assemblages.

Taphonomic Analyses

Taphonomic analyses are based on the same set of sediment samples as compositional analyses described above with an additional sample from the ridge crest subhabitat (sample 1a). Significant interactions exist between dependent taphonomic variables (abrasion, encrustation and breakage) and both independent variables (habitat and sediment type) (Multi-between-groups ANOVA; Table 6). Univariate ANOVA's performed on individual taphonomic variables reveal the specific nature of these interactions (Table 7).

Levels of abrasion differ significantly among all three grouped subhabitat categories (Table 7). Abrasion is minimal in ridge crest samples (range: 1.33–1.52, $\bar{x}$ = 1.42), intermediate in slope (including foreslope and slope base) samples (range: 2.01–2.83, $\bar{x}$ = 2.47), and most pronounced in material taken from hardgrounds (pavements, scour pit and southwest margin areas) (range: 2.61–3.14, $\bar{x}$ = 2.90). Mean frequency of biological encrustation is significantly lower in crest sediment than in hardground material. The percentage of damaged columnals (Fig. 3C, D) in samples does not differ significantly among any habitat categories (Table 7).

Both abrasion and encrustation vary significantly relative to sediment type, but in both cases this is a consequence of the effects of a single sample type. Abrasion is significantly lower in rippled sand samples compared with either thick or thin sediments, while frequency of biolog-

TABLE 6—Levels of significance for Multi-Between Groups ANOVA's to investigate interactions between abrasion, encrustation and breakage for habitat and sediment type.

Dependent variables	Sediment type		Habitat	
	Wilks' lambda	P level	Wilks' lambda	P level
Abrasion Encrustation Breakage }	0.14	0.0004	0.15	0.0006

TABLE 8—Mean values for taphonomic variables grouped according to habitat and sediment type categories.

		Mean abra- sion	% Encrus- tation	% Breakage
Sediment type	Rippled	1.4	7.6	20.2
	Thick	2.9	35.8	26.8
	Thin	2.5	22.5	26.6
Habitat	Crest	1.4	7.6	20.2
	Slope	2.5	25.4	26.6
	Hardground	2.9	32.4	26.8

TABLE 7—Levels of significance for 3-way univariate ANOVA tests for variations in taphonomic attributes: abrasion, breakage, encrustation, with habitat and sediment type. Habitat abbreviations: CR, crest; SL, slope (includes SLP and BSL subhabitats; HG, hardground (includes NPV, EPV, SWM and SCP subhabitats). See Table 1 for subhabitat abbreviations. Sediment type abbreviations: RI, ripples; TK, thick; TN, thin.

Indepen- dent variable	Dependent variable		
	Abrasion	Breakage	Encrus- tation
Habitat	F = 31.77 P = 0.000006 HG > SL > CR	F = 0.61 P = 0.56 HG = SL = CR	F = 3.53 P = 0.006 HG ∨ ⟍ CR = SL
Sediment type	F = 21.73 P = 0.00005 TK ∥ ⟍ TN > RI	F = 0.61 P = 0.56 RI = TN = TK	F = 6.84 P = 0.008 TK ⟋ ⟍ TN > RI

TABLE 9—Levels of significance for Multi-Way ANO- VA's (MANOVA's) to investigate interactions between environment and sediment type for dependent variables: abrasion, breakage, and encrustation. Analyses were carried out using two categories of environment (hardground and slope) and two categories of sediment type (thick and thin).

Dependent variable	F value	P level
Abrasion	0.02	0.88
Breakage	1.86	0.20
Encrustation	0.02	0.90

ical encrustation is significantly higher in thin sediments relative to either rippled or thick sediment areas (univariate ANOVA's; Table 7). Frequency of columnal breakage demonstrates no significant between-habitat results although areas of thick sediments show almost significantly less (P = 0.056) breakage than areas of thin sediment. Mean values for taphonomic characteristics by habitat and sediment are summarized in Table 8.

Univariate ANOVA's repeated using *Chladocrinus decorus* columnals alone show the same patterns of significance and non-significance reported above; these results are not shown. Analyses repeated with the foreslope sample included in the Hardground category (see Methods section) again show the same patterns of significance and

non-significance as those reported above, and the results are not illustrated.

The two ridge crest samples constitute both the crest habitat category and the rippled sand sediment category, resulting in a direct correspondence between habitat and sediment type for those samples. We used MANOVA's to investigate whether any other interactions exist between slope, hardground, thick or thin sediment categories (exclusive of crest/rippled samples), but none are significant (Table 9). MANOVA's were not conducted using all categories together because the resulting empty cells in the analysis would create artificially significant results.

DISCUSSION

Sediment Composition

Previous compositional analyses of modern deep-water sediments in the northern Bahamas (Stetson et al., 1962; Wilbur, 1976; Mullins and Neumann, 1979; Mullins et al., 1980) emphasize regional variations. The features described, such as winnowed sands, lithoherms and hardground horizons, provide major clues about general sedi-

mentary settings, but offer little information about small-scale variations in depositional environment. Multivariate statistical techniques, successfully used to distinguish sediments from moderate depths elsewhere (Doyle and Feldhausen, 1981), reveal that samples taken within 100 m of each other at the study site differ significantly in proportions of coarse-fraction (>2 mm) lithic and planktic grains. These variations reflect a combination of topographic and geomorphic controls acting throughout the area, and are clearly displayed in results of cluster analysis (Fig. 4), two-way abundance plot (Fig. 5), and principal components analysis (Fig. 6). Lithic grains occur in greatest abundance in areas where lithified pavements show some evidence of breaking up (for example, scour pit and pitted pavements). On the ridge crest, slope and base of slope subhabitats, the hardground either appears more consolidated or is buried under thicker sediment. Here, sediment samples are dominated by planktic and/or benthic skeletal material. Local topography intensifies flow over elevated areas such as the ridge crest, and reduces flow in areas shielded from currents by upstream elevations (scour pit, slope, base of slope). In the former area, intensified flow generates high densities of suspension-feeders such as crinoids with relatively greater skeletal production. The latter act as sinks for the accumulation of both planktic tests and bedload-transported benthic skeletal grains.

Planktic grains in the >2 mm fraction are almost exclusively aragonitic tests of pelagic gastropods—thecosomatous "pteropods" and heteropods—that have settled out of the water column (Pilskaln et al., 1987; Berger, 1978). These thin-walled shells are particularly susceptible to winnowing and redistribution (Berger, 1978), but are not affected by dissolution at study site depths. High concentrations of thecosome tests form conspicuous dark lags in troughs of ripples on the ridge crest and at the base of the slope, indicating lateral transport by bottom currents followed by preferential deposition in protected downcurrent areas or pockets within an otherwise high-energy setting.

Benthic Skeletal Assemblages

Most studies documenting the spatial fidelity of life and death assemblages concentrate on macrobenthic skeletal material from shallow-water settings (Johnson, 1965; Warme, 1969; Peterson, 1976; Ekdale, 1977; Bosence, 1979, 1989; Staff et al., 1986; Henderson and Frey, 1986; Carthew and Bosence, 1986; Staff and Powell, 1988, 1990a, b; Miller, 1988). That little information is available on deep-sea settings is not surprising. Pelagic sediments dominate and skeletonized macrobenthos decrease in diversity, relative abundance, and level of mineralization with increasing depth. Substantial contributions to deep-water sediments by skeletonized macrobenthos can only be expected above the $CaCO_3$ compensation depth or where currents impinge on the bottom and permit noncalcareous suspension-feeders such as sponges and antipatharians to survive in numbers.

At this study site, moderate depths and temperatures (12–16° C), substantial current flow and a carbonate environment support a diverse, highly skeletonized macrobenthic assemblage. Benthic skeletal material from the >2 mm size fraction of sediment samples includes clasts produced by crinoids, ophiuroids, alcyonarians, corals, stylasterids, brachiopods, bivalves, bryozoans and sponges (all chiefly suspension-feeders), echinoids (chiefly irregular, deposit-feeding taxa), gastropods and crustaceans (most likely predators/scavengers), and benthic foraminiferans.

Although not the subject of this paper, it is worth noting that assessment of noncrinoid living assemblages via submersible does not accurately reflect the death assemblage. Visual observations emphasize large, chiefly suspension-feeding taxa (for example, crinoids, alcyonarians, sponges) and underestimate small sessile and vagile forms (for example, brachiopods, many gastropods and crustaceans). By contrast, analysis of only the coarse sediment fraction certainly underestimates the contribution of sponges to local communities due to their chiefly smaller spicules.

Multivariate analyses demonstrate that crinoids and echinoids, the two most abundant grain types, behave very differently, clustering at 80% of the maximum linkage distance (Fig. 8). Both groups also exhibit wide variations in relative abundance among samples. The increasing degree of similarity between many other benthic skeletal components chiefly reflects their overall decreasing relative abundances rather than their concordance of distribution. Thus, groups that contribute uniformly little to sediments (that is, ophiuroids, stylasterids, bryozoans, brachiopods, serpulid worms, ostracods) exhibit the greatest similarities (Fig. 8).

Q-Mode Cluster analysis (Fig. 7) and principal components plots (Figs. 9, 10) illustrate how variations in echinoid, crinoid and other aspects of the benthic skeletal assemblages can distinguish samples from different subhabitats. Crinoid grains contribute the greatest relative amounts to slope samples, most likely due to downhill transport from dense living aggregations on the ridge crest. The low proportion of crinoid material in the single ridge crest sample used in the compositional analysis may be due to rapid down-slope transport of crinoid grains or, perhaps, an artifact of limited sampling.

Echinoid grains are proportionally most abundant in the crest and southwest margin samples and in one slope and base of slope sample, and are generally less important in pavement samples. Most grains are derived from irregular urchins that are typical of areas of deeper sediment. Echinoid grain distribution provides evidence that sediments are subject to substantial lateral transport in this area. Their abundance on the ridge crest suggests that tests or fragments may be moved uphill with intense, intermittent southbound flow as we observed in February 1991, and then deposited there when the current reverses and weakens (Messing and Llewellyn, in prep.).

Scour pit material is unique in being particularly low in both echinoid and crinoid and high in alcyonarian and benthic foraminiferan grains. The minimal contribution of crinoid material may be explained, despite the presence

of about 40 *Endoxocrinus parrae* on the boulder imme- diately above the sample site, by the fact that *E. parrae* has fewer columnals per crinoid than *Chladocrinus de- corus* which dominates in most other areas. *E. parrae* also tends to contribute a greater proportion of its stalk seg- ments as pluricolumnals than *C. decorus* (personal obser- vation). Alcyonarian grains are more important here than in any other sample perhaps because the dominant form is a slender cylindrical axis segment produced by the abun- dant isidid, *Lepidisis caryophyllia,* that may roll along the bottom and collect in depressions. Alternatively, this spe- cies, abundant elsewhere in the study area, may have grown here previously.

Additional evidence for substantial lateral transport of sediment exists in the discrepancies in clustering of sed- iment samples from the same subhabitats. Samples that do not cluster with others from the same subhabitat were uniformly collected at different times. Thus, for example, slope sample 2 which falls into Cluster II (bulk sediment Q-mode dendrogram and principal components analysis) was taken in August 1991 while slope samples 3 and 4 which group closely together in Cluster I were both col- lected in October 1991 (Figs. 4, 6). Variations in bottom current velocity and direction with time and locality prob- ably contribute to these within-subhabitat discrepancies. The possibility exists, however, that significant differences occur on finer spatial scales within visually indistinguish- able subhabitats. A greater number of synoptic samples taken within subhabitats, as well as time-series of samples from precisely identified sites, are needed to thoroughly understand variations in sediment composition in this area.

Living and Death Assemblages

As mentioned in the results section above, no overall direct correspondence exists between the density of living crinoids and the contribution of crinoid ossicles to the benthic skeletal component of adjacent sediments. Lim- ited patterns of correspondence do occur, however, and local geomorphology explains some discrepancies between crinoidal abundance in sediment samples and densities of autochthonous living crinoids, but sources of variation are not completely understood.

The ridge crest is an area of high crinoid density where crinoid columnals are being actively added to the sedi- ment. Still photographs and videotape taken along the crest show several detached pluricolumnals with intact cirri on the substrate. Rather than remaining on the crest, however, columnals apparently move downslope, either by gravitational settling or active transport via northbound flow, accumulating in roughly decreasing relative abun- dance with increasing distance from the ridge crest source. Living crinoids are virtually absent from the slope, most probably because thick accumulations of sediment largely eliminate hard substrate anchoring sites and because the area is shielded from adequate flow by the usually upcur- rent ridge crest.

Pavement and southwest margin samples show a wide range of crinoidal contributions to the sediment although

living assemblages are typically scattered (<1 individual m^{-2}). Oji (1989) estimates that the stalk of the Pacific isocrinid *Metacrinus rotundus* grows between 30 and 60 cm y^{-1}. If such growth rates apply to local species, the possibility exists that the composition and density of living assemblages, and the autotomized columnal contribution to the sediment, could change markedly over relatively short periods of time. Such variations in the absence of extensive lateral sorting could produce very different lo- calized, time-averaged sediments.

The scour pit possesses the lowest proportion of crinoid skeletal material of any sample despite the dense popu- lation of *E. parrae* on the adjacent boulder. This sample site lies in a depression relative to surrounding hard- grounds and may thus act as a sink for grains that dilute the crinoid component. As an example, the single scour pit sample is uniquely rich in cylindrical isidid alcyonarian axis fragments that are perhaps more easily transported along the bottom than discoidal crinoid columnals. Alter- natively, *E. parrae* probably contributes columnals to the sediment at a much slower rate than *C. decorus*. Stalks of the former consist on average of little more than a third as many columnals as the latter. *E. parrae* also produces proportionally more pluricolumnal sediment grains than *C. decorus,* further reducing its contribution by grain count. The high proportion of *E. parrae* grains in this sample relative to others (species ratio of *C. decorus* : *E. parrae* = 2.3:1) certainly reflects the abundance of adjacent living *E. parrae.* That *C. decorus* grains still account for the majority of crinoidal clasts, however, may be due either to the scour pit acting as a sink as mentioned above, or to time-averaging from a period when living *C. decorus* dom- inated the adjacent boulder, or both.

In areas dominated by *C. decorus* (ridge crest, pave- ments, southwest margin), both the overall crinoidal con- tribution to and the ratio of *C. decorus* to *E. parrae* ossicles in local sediments vary widely although species ratios all favor *C. decorus.* However, in the two areas where *E. par- rae* dominates the living fauna (foreslope and scour pit), it (*E. parrae*) contributes proportionately more to the sed- iment than elsewhere (species ratios of 6.7 and 2.3, re- spectively). This suggests that widespread lateral mixing of sediments is not an important process here and that sediments may reflect at least some aspects of small-scale faunal differences. Alternatively, *E. parrae* grains are so rare compared to those of *C. decorus* that dramatically different ratios may be a result of minor variations in local abundance of *E. parrae* grains.

Taphonomy

Diagnostic taphonomic signatures of benthic skeletal material distinguish a wide variety of shallow-water en- vironments (see reviews by Kidwell and Bosence, 1991 and Donovan, 1991). Despite the range and variety of descrip- tions of modern taphofacies, however, little information exists on the taphonomic condition of deep-water benthic skeletal material. With respect to stalked crinoids, Ame- ziane-Cominard and Roux (1987) describe intensive, os-

tensibly microbial biocorrosion of ossicles recovered from cores taken in 785–1285 m off New Caledonia. They suggest that microbial degradation of organic material within the stereom increases ossicle fragility and permits rounding without hydraulic abrasion. Ameziane-Cominardi (1991) discusses taphonomic modifications of the same and additional material from the same area: connected ossicles are exceptional; discoloration and degrees of abrasion vary from none to strong; and sediments are enriched in columnal and brachials, and depleted in cirrals and pinnulars, relative to expected values derived from dissociated whole specimens. Both of these studies are limited, however, because the data were extracted from core samples; no comparisons could be made between local living and death assemblages.

In the current study, a comparative taphonomic examination using ossicle abrasion, encrustation and breakage offers an effective means of distinguishing samples on a fine spatial scale (meters to tens of meters), as well as providing information on biotic interactions and post-mortem histories of deep-water crinoidal material. Columnals appear to be excellent indicators of taphonomic change, revealing significant variations in levels of abrasion and encrustation for the habitats under consideration.

Columnal abrasion at the study site increases progressively and significantly from rippled-sand, ridge crest samples through slope to hardground samples. The former exhibit the least abrasion whether counted as "crest samples" in analysis by habitat, or "rippled samples" in analyses by sediment type. Downslope migration of columnals from dense, ridge crest, living assemblages explains increased abrasion between ridge crest and slope (Hoskin et al., 1986; Boss and Liddell, 1987), but does not account for increased abrasion in hardground samples where columnals are ostensibly being produced *in situ*. Increased abrasion of columnals on hardground may result from *in situ* reworking, small-scale lateral transport, or greater time of exposure at the sediment-water interface (Chave, 1964; Driscoll, 1967, 1970; Driscoll and Weltin, 1973; Watson and Flessa, 1979; Hoskin et al., 1983; Cutler, 1987; Fürsich and Flessa, 1987; Meldahl, 1987). No significant differences in abrasion exist between thick and thin sediment samples, however, as might be expected if duration of exposure at the sediment surface were a factor contributing to abrasion. Durations of exposure and transport required to produce the various degrees of observed abrasion remain unknown. Local rates of sedimentation, and hardground cementation and erosion are similarly unknown. We, therefore, do not know at present the extent of time-averaging that these sediments represent. While the "fresh" columnals that dominate the ridge crest certainly represent a less time-averaged sediment than the hardground sediments, the possibility exists that particularly degraded columnals may be reworked from eroding pavements which would vastly expand the period over which the sediment is time-averaged.

It is also worth noting that this study extends the range of environments in which abrasion must be recognized as an important taphonomic agent. Kidwell and Bosence

(1991, Fig. 10) limit abrasion to environments above storm weather wave base. Although they refer to predominantly molluscan assemblages and we have analyzed only crinoids in detail, we have found substantial abrasive degradation in skeletal grains from all major taxonomic groups.

Unlike shallow-water environments in which many different benthic taxa encrust shells partially to completely (Ware, 1975; Jackson, 1977; Balson and Taylor, 1982; Bishop, 1988; Taylor et al., 1989), encrustation at the study site is chiefly limited to isolated serpulid worm tubes and benthic foraminiferans. Many host columnals are abraded, with encrusting organisms usually on articular faces, indicating that settlement usually occurs after disarticulation.

Frequency of encrustation is significantly greater in samples taken from thin sediment veneers than from either rippled (ridge crest) or thick sediment samples. When analyzed by habitat, rippled sands from the ridge crest exhibit significantly less encrustation than hardground samples. The extent and frequency of encrustation is usually taken to indicate duration of exposure on the sea floor (Driscoll, 1970; Kidwell and Bosence, 1991). It follows, then, that columnals taken from thin sediments have been exposed longest at the sediment-water interface, while columnals from the ridge crest have been exposed least. That ridge crest samples also demonstrate the least abrasion is additional evidence that material here is relatively "fresh," having suffered little exposure to either abrasive or encrusting taphonomic agents. The ridge crest with its dense living assemblage of *C. decorus* is presumably a crinoidal sediment production site, but rather than remaining on the crest, columnals are transported downhill and accumulate on the slope.

Unlike degrees of abrasion and frequency of encrustation, the frequency of damaged or broken columnals in samples shows no significant overall or specific relationship with either habitat or sediment characteristics. One analysis approaches significance (P = 0.056), suggesting that thin sediments may contain more damaged columnals than thick sediments. The lack of correlation between frequency of breakage and habitat implies a causal agent acting independently of environment. The nature of the damage— irregular grooves, pits and fractures—rules out abrasion. The most likely explanation for such damage is a biological agent such as a predator or scavenger that causes deliberate or incidental biogenic fragmentation. Several researchers have observed crownless isocrinid stalks in upright life position still attached to the substrate by cirri, and typically lacking the most proximal portion (Conan et al., 1981; Fujita et al., 1987; pers. obs.), additional evidence for predators or, at least, some important agent of disturbance. Such crownless stalks can survive in this condition for at least several months (Amemiya and Oji, 1992; pers. obs.).

Meyer et al. (1984) and Meyer (1985) record predation on modern, shallow-water comatulid populations, while several authors use regenerated arms as indirect evidence of sublethal attacks in populations of both ancient and modern shallow-water crinoids (Mladenov, 1983; Meyer

and Ausich, 1983; Arendt, 1985; Meyer, 1985; Schneider, 1988). Predation pressure has apparently been an important factor in stalked crinoid evolution and distribution, and is widely held at least partly responsible for the Mesozoic retreat of stalked crinoids to deep water (Vermeij, 1977; Meyer and Macurda, 1977; Lane, 1984; Signor and Brett, 1984; Meyer, 1985; Aronson, 1991). Nevertheless, although predation intensity may be lower than in shallow water habitats, the appearance of upright crownless stalks and broken columnals in 430 m strongly suggests that modern deep-water stalked crinoids are not exempt from potentially lethal disturbance. The precise nature of such disturbance events (that is, whether related to predation or incidental collisions with large fish) remains unknown. Alternatively, upright crownless stalks may represent recently dead individuals subject to differential post-mortem disarticulation rates between crown and stalk, regardless of cause of death.

Post-mortem modification by scavengers or deposit feeders is widely recognized in shallow-water shelly deposits and may also explain columnal breakage (Schäfer, 1972; Meldahl and Flessa, 1990; Kidwell and Bosence, 1991; Tshudy et al., 1989; Walker, 1988; Gregory et al., 1979; Bertness and Cunningham, 1981; Alexander, 1986). Scavengers act mainly at the sediment-water interface. Reduced (although not quite significant: 0.056) breakage of columnals from thick sediments relative to those from thin sediments suggests that scavengers may play a role in post-mortem degradation of columnals.

MODEL AND APPLICATIONS

Modern deep-water skeletal sediments rich in stalked crinoid material offer potential opportunities for better understanding of fossil assemblages. Although deep-water environments are traditionally thought of as low-energy relative to shallow-water settings, particular configurations of benthic current activity and regional geomorphology, such as the deep-water contour currents along the western margin of the Little Bahama Bank (Neumann and Ball, 1970; Leaman et al., 1987; Messing et al., 1990), can produce relatively coarse-grained sediments and benthic communities dominated by suspension feeders (but see Thistle et al., 1985 for a different environmental response to deep near-bottom currents). These crinoid-rich deposits also display small-scale variations in taphonomic and compositional character more commonly associated with shallow-water environments. If such environments were represented in an ancient marine sequence, subtle diagnostic criteria would be the only way of confirming their deep-water origin.

Mullins et al. (1981) describe criteria by which ancient deep-water coral mounds may be distinguished from shallow-water coral complexes in the rock record. Because they conducted their study in a high-energy, bank-margin, carbonate environment north of the Little Bahama Bank similar in many ways to the current study site, their criteria are worth noting as they apply to the recognition of deep-water, coarse-grained, crinoid-rich paleoenvironments. It

is also important to repeat that "no one criterion alone is diagnostic, but rather a combination of criteria should be used whenever possible" (Mullins et al., 1981, p. 1008).

1) The presence of algae or other organisms identifiable as photosynthetic is the most obvious indicator of a shallow-water environment, although particularly steep bank-margin slopes permit transport of shallow-water skeletal material below the euphotic zone. The latter case may be distinguished by recognition of bedforms attributable to slumping, talus deposits and grain flows (Mullins and Neumann, 1979). A lack of such organisms does not guarantee that material was deposited in deep water, but the possibility of a deep-water origin should be considered with reference to other criteria.

2) Skeletal grains of planktic/pelagic origin are rare in modern shallow-water carbonate deposits whereas they typically dominate deep-water carbonate sediments. Planktic gastropod shells (thecosome and heteropod) contribute 13–66% of the >2 mm fraction of sediment samples examined in the current study. A qualitative examination indicates that planktic foraminiferans contribute substantially to finer fractions.

3) Vertical and lateral facies transitions should differ considerably between shallow- and deep-water crinoidal deposits. Along the margins of the Bahama Banks, the winnowed sands of the study area grade into obvious basinal deposits characterized by pelagic oozes and turbidities. Debris and grain flow deposits are absent. In the other direction, "peri-platform sand facies" (Mullins and Neumann, 1979) still retain a substantial pelagic component. By contrast, Oji (1985) recognizes an isocrinid assemblage in the Miyako Group (Upper Aptian of Japan) as shallow-water via a transition from the crinoid-containing siltstone to fossil beachrock.

4) Although numerous potential biases exist (see, for example, Schopf, 1980), stable oxygen isotope ratios offer a possible means of distinguishing at least warm versus cool paleoenvironments. The mean temperature in the study site area is about 15–16° C (Leaman et al., 1987). This figure is unusually high for this depth because isotherms exhibit strong geostrophic tilting across the Straits of Florida. Similar temperatures occur in 100 m along the Florida slope. Isotope analyses that suggest similar or lower paleotemperatures in otherwise tropical settings may indicate a deeper-water environment.

The lack of recognition of ancient deep-water crinoid-rich deposits may reflect either their actual sparseness or their misinterpretation in the literature due to lack of an appropriate recent example. This study provides a carbonate bank-margin model for the production of relatively coarse-grained, crinoid-rich sediments that may permit reinterpretation of some ancient crinoid-rich limestones. Ruhrmann (1971a), for example, explains the occurrence of Devonian offshore crinoid-rich calcarenites by invoking uphill transport of crinoid material onto a seaward shoal (p. 244–245). Using the model proposed in this paper, increased flow along the bank margin crates a locally higher-energy regime with associated winnowed crinoid-rich sediments without resort to extensive and unlikely upslope

transport. Similarly, an increased flow regime rather than a lowered sea level may explain the development of coarse crinoid facies on the flanks of a Waulsortian mud mound complex otherwise recognized as relatively deep water (220–280 m; Bridges and Chapman, 1988).

Small-scale variations in taphonomic and compositional character produced, for example, by the downslope movement of crinoid ossicles from dense ridge crest populations, may provide a model for understanding similarly scaled relationships between flanking crinoidal sediment accumulations and living assemblages on a variety of ancient mounds including Waulsortian (Wilson, 1975) and smaller Ft. Payne (Osagean) buildups (Meyer et a., 1989; D.L. Meyer, personal communication, December, 1992). Further examination of the paleontological literature may provide more examples of ancient deep-water, crinoid-rich limestones.

CONCLUSIONS

1) Coarse-grained, crinoid-rich sediments are found on the southwestern margin of the Little Bahama Bank in water depths of 419–434 m. Extensive flat, hardground pavements characterize much of the study area, with low relief ridges and isolated boulders affording occasional topographic elevation.

2) The three main sources of coarse sediment are: a) lithic grains derived from break-up of pre-existing hardground; b) tests of planktic/pelagic organisms; and c) benthic skeletal material produced *in situ* by echinoids, crinoids, gorgonians, corals, gastropods, bivalves, benthic foraminiferans, and other minor components. Crinoidal skeletal material shows considerable fidelity with respect to living assemblages, and both sediment composition and benthic skeletal material demonstrate small-scale variations corresponding to differences in local environment. Gross sediment composition varies mainly in proportions of lithic and planktic grains present in samples, while benthic skeletal assemblages vary mainly in proportions and abundance of echinoid and crinoid material, which together account for over 45% of total coarse (>2 cm) benthic skeletal grains.

3) A comparative taphonomic analysis, carried out using crinoid columnals, reveals small-scale variations in taphonomic characteristics related to differences in local environment. Abrasion levels demonstrate significant increases from ridge crest to slope and hardground habitat groups, reflecting down-slope transportation and reworking. Encrustation is greatest in areas of thin sediment, apparently reflecting length of exposure at the sediment/water interface. Breakage frequency does not correlate with any observed physical variables and is presumed to represent the action of predators and/or scavengers in the area.

4) Regional bank-margin contour currents in the study area contribute to the production of relatively coarse sediments and favor benthic communities dominated by suspension-feeders, especially where flow exposes hard substrates. Variations in benthic current regime, notably the augmented flow over small-scale topographic irregularities, explain much of the variation observed in living crinoid assemblages, and at least some of the compositional and taphonomic variations found in the >2 mm sediment analyses.

5) This environment provides a high-energy, deep-water, basin-margin model for the formation of coarse-grained, crinoid-rich sediments. Criteria for the recognition of such an environment in ancient crinoid-rich limestones include lack of photosynthetic organisms such as algae, abundance of planktic/pelagic components, and lateral facies relationships.

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