An Ecologic and Taphonomic Analysis of Submarine Cave Communities: Salt River Canyon, St. Croix, U.S.V.I.

by

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ABSTRACT

Cryptic biotas comprise those organisms which encrust hard, sheltered habitats, which are known for restricted physical and biological disturbance. Despite the paleoecological and evolutionary significance of cryptic hard substrate biotopes such as reef cavities, relatively little is known of taphonomic processes in these settings. Recent cave-dwelling biotas of Salt River Canyon, St. Croix, U.S. V.I., have been investigated with respect to their ecological and taphonomic characteristics, in an attempt to clarify preservational processes active there.

Photographic censuses were compiled from cave substrates at four water depths, including 50 ft (13.2 m), 75 ft (22.9 m), 105 ft (32.0 m) and 125 ft (38.1 m). Analysis yields measures of substrate coverage, richness, and dominance diversity, and examples of competitive interactions on spatially limited substrates. Excluding corralline algae, total coverage is approximately 70%; including coralline algae, coverage exceeds 95%. Demosponges and colonial organisms cover the greatest proportion of available substrate, while solitary organisms such as corals, bivalves, brachiopods, and serpulid worms are restricted in areal extent. Demosponges expand greatly below 50 ft, and dominate deeper caves. As a result, most solitary organisms decline in proportional coverage with increased depth. At depths below 75 ft sclerosponges appear, and in addition to bryozoans, they are restricted to deeper portions of caves. Mean richness is 9.0 species per quadrat (37.5 cm^2), while dominance diversity is measured as .587 per quadrat.

Colonization appears to respond to distance from sources of environmental instability, (e.g., current activity, sedimentation, etc.). Substrate heterogeneity blurrs intracave patterns somewhat, and limits their resolution to three broad cave zones. Of these, the central cave appears most favorable to colonization. Greater water depth increases environmental stability and smooths intracave microenvironmental differences. Highest richness and diversity levels are found at 75 ft, and remain constant below that site.

Assessment of taphonomic loss due to nonpreservation required removal of unskeletonized organisms from their cave substrate, rephotographing, "cleared" transects, and calculation of "preservable" colonization levels. Significant amounts of taphonomic information loss are associated with modern cave communities, and may indicate high levels of taphonomic loss inherent to fossilized examples. Data reveal that 85.3% of organism coverage, 62.2% of richness, and 57.6% of dominance diversity in the original community are lost through nonpreservation of unskeletonized forms. If the skeletons of earlier stage organisms are included in preservable richness calculations, a reduced loss of 47.8% results, more closely approximating actual skeletonized organism richness observable in the fossil record. Taphonomic information loss increases with depth, due to increasing dominance of unpreservable demosponges in deeper caves. Preservable percent cover, richness and dominance diversity drop to their lowest levels at 125 ft reaching 14.7%, 37.8%, and 42.4% preservable, respectively.

Poor preservation through slow, infrequent burial and diagenetic destruction characterize cave biotopes. Moreover, the preservable component is a nonrandom subsample of cryptic biotas, dominated by pioneer, solitary, skeletonized taxa. Loss of detail in older skeletal remains beneath demosponges suggests that biocorrosion by later stage encrusters may act to "erase" the potential record of skeletonized forms, especially in stable environments. Thus, the fossil record of cave habitats is systematically biased toward heavily skeletonized members of early successional stages and is probably more incomplete in deeper, less physically disturbed environments.

Alternate forms of paleoecologic information in the form of skeletonized biotic interactions, trace fossils, and skeletal elements in cave floor sediments may ameliorate the record of cave-dwelling organisms to some extent.

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INTRODUCTION

Marine cryptic habitats are composed of well shaded to completely dark, semi-enclosed environments (Jackson et al., 1971). The dimensions of such environments range from cavities of a few square millimeters to tunnels or caves of several square meters. General characteristics of these cryptic environments include a self-supporting roof and wall, a relatively large void space, a floor, and if present, sediment on the floor. Various mechanisms may generate these habitats, including submergence of karst features, growth of porous skeletal organisms providing intra- and interskeletal porosities, storm deposition of rubble and submarine slumping of talus, or larger blocks. Biogenic boring, and other forms of long term erosion and undercutting may also produce such cavities. The inhabitants of cryptic environments are dominantly sessile encrusting invertebrates, variously known as cryptobionts (Jackson et al., 1971; Jackson, 1977, 1979b, 1981; and others), coelobionts (Kobluk, 1980; Kobluk and James, 1979), or as coelobites (Choi, 1982).

Recent research on the ecology of modern marine cryptic communities has concentrated on biotas encrusting the undersides of foliose corals or overhangs (Jackson and Winston, 1982) and on artificial substrate panels (Jackson, 1977; Russ, 1982). These small substrates provide particularly good study sites for the investigation of microenvironmental and community trends, competitive strategies and mechanisms, and food and spatial resource utilization (Sara, 1970; Jackson, 1977; Buss and Jackson, 1981; Jackson and Winston, 1982; Russ, 1982). Previous studies by Vacelet (1967b) and Vasseur (1974) have only qualitatively investigated the more general characteristics of the larger cave and tunnel environments. Time limits imposed by SCUBA diving have restricted in situ study of cryptic habitats. A massive, immovable nature has precluded extensive sampling of these environments. Consequently, the literature demonstrates that little is known of the distribution and abundance of cave-dwelling cryptobionts in modern reefs. This cave biotope is considered in the present study.

Though research to date has shed some light on the community ecology of modern cryptobionts, much less is known of their paleontologic record. A recent review of such literature has been presented by Kobluk (1980). Analogous hardground communities have been discussed in a similar review of Palmer (1982). Both works suggest an extensive record of coelobiontic communities extending back to the Early Cambrian. By virtue of their ubiquity, and frequently encrusting or endolithic nature, cryptic communities may afford unique opportunities for paleoecologic and evolutionary studies. In particular, the mode and tempo of Phanerozoic diversification and community changes may be studied in better detail, analyzing the cryptic biotope through time (Valentine, 1973; Raup, 1976). Data suggest that biolithic or diagenetic cryptic environments have been exploited since the earliest appearance of archeocyathid biostromes (Kobluk and James, 1979), and diagenetic hardgrounds (Brett and Liddell, 1978). These early cryptic communities contain most trophic groups found in modern analogs. If viewed in terms of community organization, the cryptic habitat may be characterized as one supporting progressive diversification without major community restructuring.

Valid paleoecological reconstructions necessitate an adequate understanding of preservation processes which may alter the competence of the fossilized cryptic community record. This is the concern of the science of taphonomy (Efremov, 1940; Lawrence, 1968). Preservation potential of certain Recent marine benthic communities have previously been studied by Johnson (1964, 1965), Lawrence (1968), Schopf (1978) and many others. Lasker (1976) has further quantified the effect of nonpreservation on faunal diversity measurement, and Stanton (1976) has called attention to the effect of non-preservation on trophic structure determination. However, no taphonomic studies of any kind have been made on the biotas inhabiting Recent cryptic environments -- biotas apparently quite analogous to those found in the fossil record.

The submarine caves of Salt River Canyon, U.S.V.I., provide an ideal site for the study of taphonomic characteristics associated with cryptic communities. Caves are plentiful there, and they may be studied over a considerable depth range. Further, normally restricted access to deep sites for extended periods of time is circumvented by the availability of the NULS-1 HYDROLAB system.

The intent of this study is to improve the validity of cryptic community paleoreconstruction. To that end, the present investigation is composed of three parts: (1) a critical assessment of the physical and biological environment, and its effects on cave community structure; (2) an assessment of the preservability of the indigenous cryptic biotas, and the level and direction of any selectivity in their preservation; and (3) the observation of any community-specific physical or biological activities which may undermine the preservation of cryptic biotas as a whole in the fossil record. With these data, perhaps the reconstruction of similar ancient environments will be of greater accuracy, and hence of greater value.

STUDY AREA

Salt River Submarine Canyon, St. Croix, U.S.V.I. was chosen as the site for the study of submarine cave-dwelling communities. Faile Marine Science Center (FMSC) is located at the head of Salt River Estuary, approximately 6 km northwest of Christiansted, St. Croix, maintaining shore-based support for the HYDROLAB Project (figure 1). Topography of Salt River Canyon has been described by Hubbard et al. (1981), and will be briefly summarized below The canyon heads into the shallow waters of White Horse barrier reef. It trends northnorthwest for 450 m with increasing slope, crossing the St. Croix insular shelf. At this point, the canyon axis plummets downward to depths of approximately 3500 m, where it is confluent with the termination of Christiansted Canyon, originating to the east.

Western and eastern margins of Salt River Canyon are quite dissimilar in morphology (Fig. 2). The eastern canyon margin is dominated by gently sloping sediment conduits, separated by small vertical rock outcrops. Some small caverns are located below such outcrops. This gently sloping morphology is probably due to the constant movement of calcareous sediment bedload by prevailing westward currents. Coral growth is somewhat inhibited here, due to heavy sedimentation. Similarly, the constant westward transportation of sediment may account for the steep slopes and the sediment-starved character of the western canyon margin.

The west wall is composed of huge, nearly vertical coral block promontories, separated by deeply incised reentrants. Bioeroded sediments flow through sediment chutes flooring these reentrants, and are ultimately conveyed to the canyon floor. In this way sediments bypass coral growth, and allow a lush fauna to develop. The corals Montastrea and Agaricia, as well as gorgonians, antipatharians, and sponges populate the west wall. Recessed within or below reefal promontories are large-scale submarine caves, protected from heavy sedimentation effects. The interior of the caves is elaborate, usually with an irregular roof extending inward to meet the sediment floor. Apertures are often covered by overhanging platy corals or sponges. The internal communities of the caves match or exceed the luxuriant growth found on the exposed reef; however, they are rarely seen. Submarine caves under study occur between 50 ft (15.2 m) and 130 ft (39.6 m) depths. Their large size permitted internal investigation and photographic sampling by SCUBA divers. Particular site locations are at 50 ft. (13.2 m), 75 ft. (22.9 m), 105 ft. (32.0 m), and 125 ft. (38.1 m) depths. The communities found within caves along this bathymetric gradient represent the focus of the present study (Fig. 2).

MATERIALS AND METHODS

In situ study of Salt River submarine caves required extensive underwater bottom time. To facilitate this, four SCUBA-equipped aquanauts manned the National Underwater Laboratory System-1 (NULS-1) HYDROLAB during mission #82-11 (5 August 1982 - 12 August 1982). HYDROLAB is run by the Manned Undersea Science and Technology Office (MUS&T) of the National Oceanographic and Atmospheric Administration (N.O.A.A.). It is located at a depth of 51 ft (15.5 m) at the mouth of Salt River Canyon, St. Croix, U.S.V.I. HYDROLAB Operations Manual may be consulted for further details.

The stationary 51 ft depth of the habitat enabled investigators to visit the caves between 50 ft (15.2 m) and 130 ft (39.6 m) depths, gathering data on five separate cave sites. In situ data retrieval required in excess of 188 man-hours, and was accomplished in the following manner.

Particular caves were located and marked at 50 ft (15.2 m), 75 ft (22.9 m), 105 ft (32.0 m), and 125 ft (38.1 m). Cave selection was made on the basis of adequate accessibility, sufficient internal dimensions, and bathymetric depth. Most caves contained a single aperture -- only the 105 ft site had an alternate aperture. Brightly colored 150 cm tailor tapes were used as transect gradient markers and attached to randomly selected apertural positions on the cave roofs. They were then extended inward, following roof contours as far as possible. An additional tape was attached end-to-end as needed, extending up to 280 cm into the cave. In all transects at 50 ft, 75 ft, and 125 ft sites the transect line ended at or near the sediment floor. Transects at the 105 ft site were laid on horizontal cave roofs; therefore these extend to only the central roof area, rather than approaching an alternate aperture.

General observations and notes on problematic taxa along the transect were recorded manually. Each transect was then photographed at 10 cm intervals using Ektachrome 64 film with a Nikonos III camera, macrolense, 1:3 framer, and an Oceanic 2001 strobe. Each frame records a 5.0 cm x 7.5 cm surficial quadrat, including the metric transect scale along the left edge (Fig. 3a). Some deviation from these dimensions in some cases may be due to camera angle, topographic irregularity, or spherical aberration at field perimeters. Camera settings were maintained constant (f.22, 1/16 sec, ∞) with only modification of strobe-surface distance. Schematic sketches of site gross morphology, dimensions, orientation, and sedimentation were made. In addition, wide angle (28 mm) photographs were taken inside and outside the cave.

The next stage required stiff brushes to clear soft unpreservable surficial biotas from previously photographed transects. This process is meant to simulate the destruction of unskeletonized organisms in the fossil record. Close-up photographs of remaining skeletonized forms were then made at positions identical to previous quadrat photographs (Fig. 3b). Before and after photo correspondence allows observation of the earlier skeletonized generations of organisms present below recent soft encrustation.

A Gossan Lunapro light meter was used at site SR125B to document within-cave changes in illumination relative to ambient light on the outer reef surface. Sediment samples were taken of distal cave and nearby chute sediments using a small piston syringe. This was performed at site IK50A to analyze depositional characteristics within cave environments. Samples were also taken of open sediment chutes to establish sedimentation differences which may exist between open and protected depositional sites.

Shore lab preparation and examination of all photographic and sediment samples followed at FMSC and the University of Rochester. Original and cleared transect photos were projected side-by-side to observe current and previous skeletonized and unskeletonized encrustations. Taxonomic lists were compiled for all distinctive taxa, as outlined later. In addition, preservable biotic interactions, boring activity, and other substrate-destructive processes were noted. Original transect photos were projected on tracing paper, and individual forms were outlined. Consistent four-fold magnification of the tracings minimized areal variations between quadrats. Areal coverage of distinct forms was then measured using a NUMONICS model 1224 electronic digitizer. The area which any distinctive taxa covered per quadrat was used as an importance factor, P_i, in the determination of the Shannon-Weiner dominance diversity index

$$H = -\Sigma P_i \log P_i$$

Percent coverage of individual taxa was also calculated from these areal measurements. In the case of many very small (i.e., solitary) organisms combined areal coverage was determined by a mean size approximation, multiplied by the number of individuals observed. Taxonomic richness was determined by simple counting of the different forms observed. Cleared transect photos were additionally observed, and earlier skeletonized faunal richness counts were made manually.

Percent cover, taxonomic richness and dominance diversity were calculated for the whole quadrat, as well as the unskeletonized (soft) and skeletonized (hard) subsets of the whole quadrat. This information was processed on an IBM 3032 computer. Transect, bathymetric site, and environmental means for all these parameters were also calculated.

Lab preparation of sediment samples follows procedures outlined by Ginsburg (1956). Wet-sieve technique was performed on samples at 1/2ϕ intervals from -1.0ϕ - pan (>4.5ϕ) to assess size frequency distribution and statistics. Qualitative observations on biogenic constituents were made on each size fraction using binocular and petrographic microscopes.

ECOLOGY: SALT RIVER SUBMARINE CAVES

PHYSICAL AND BIOLOGICAL ENVIRONMENT

Introduction

Cryptic coral reef environments include the undersurfaces of foliaceous corals, overhangs, and the walls of crevices and caves. They are generally well-shaded to completely dark, semi-enclosed areas within the reef structure (Jackson et al., 1971; Jackson, 1977). As such, the physical and biological parameters which shape the cryptic community can be expected to differ from those which shape the outer, exposed reefal community. The intimate relationships between physical and biological aspects of many ecological systems have been well documented (Odum, 1971). Less well known interactions between physical and biological parameters of the cave environment merit further investigation here.

All observations of Salt River caves were made during the week of August 5-12, 1982, during daylight hours, and, therefore, do not take seasonal, tidal, or nocturnal changes into account. A discussion of the principal caves studied follows. In addition, preliminary observations are included on the co-occurring cryptic community of coral plates when pertinent.

Structural Morphology

The west wall of Salt River Submarine Canyon is noted for its large scale promontories and re-entrants, commonly dissected by downward flowing sediment chutes. Such patterns are known as "spur and groove" structures. The promontories are composed of biologically and diagenetically cemented Holocene reef blocks, which have been accreting for at least the past 6000 years. Original hard substrate for deep forereef accretion may have been supplied by slumping within the canyon wall, followed by coral growth at depths within 7 to 10 ft (2.1 to 3.7 m) of present position (Hubbard et al., 1981). Similar reefal promontories have been found at comparable depths in North Jamaica (Goreau and Land, 1974). Early submarine lithification at depth has been recognized there, and probably contributes to the stability and prograding morphology of Salt River Canyon reefs as well. Progressive coalescence and outward growth has produced the interblock tunnels, crevices, and caves.

Salt River caves are analogous in structure to those found in the spur and groove zone of reefs of Tulear, S.W. Madagascar. That site has been the center of previous cave community studies by Vacelet (1967a) and Vasseur (1964, 1974, 1977).

The internal structure of Salt River caves is dictated by original slump block settling position, and the nature of subsequent coral growth prograding down the canyon wall. Therefore, the internal structure of each cave is unique. Figure 4a and b present generalized versions of the two general cave morphologies observed in this study. In most cases the area just above the aperture is overgrown by tubular sponges, including Verongia sp., and foliose corals, including Montastrea annularis, M. cavernosa, and Agaricia sp., thus shading even apertural areas of the caves somewhat. Cave apertures are generally between 2.5 and 3.5 m wide, and between 1.5 and 2.5 m high. These dimensions may simply pinch out internally at the distal roof/sediment floor interface (see Fig. 4a). However, variations on this simple profile are common. Cave dimensions may alternatively elaborate within the cave interior, in the form of roof "galleries." Such is the case at site IK105A, which also has more than one aperture (see Fig. 4 Fb). This phenomenon is observed at site IK105A only, and it may be responsible for internal environmental differences peculiar to this site. To limit incompatibility between single- and double-aperture cave data, transects taken in IK105A extend only to the midpoint between two such apertures.

The absolute internal length of caves, measured perpendicular to the aperture generally ranges from 1.5 - 4.5 m, though actual roof surface lengths may be greater. This is due to consistent observations of cave roof "roughness," or surficial convolutions of constructional or destructional origin.

Substrate

Most previously studied cryptic substrates (Jackson et al., 1971; Jackson, 1977; Vasseur, 1964, and others) are hard, and provide a limited spatial resource. Cuffey (1972) has observed that loose substrates do not support encrusting colonial cryptobionts of the type found here. The substrates of Salt River caves are characterized as massive, calcareous biolithites, largely overgrown by competing encrusting organisms.

The roof areas available for colonization range from about 2 to 16 square meters. This represents an overall cryptic substrate of significantly greater area than the more common and previously studied undersides of foliose corals. Jackson (1976) has demonstrated that during the early stages of substrate colonization (0 - 12 months) habitat area may be of fundamental importance to the development and maintainance of cryptic community structure and diversity. His observations of artificial cryptic substrates show that smaller surface areas allow quick surface monopolization by less competitive biotas. Conversely, large areas increase the chances of settlement and overgrowth by a superior competitor. Large cave substrates may therefore disallow early, rapid recruitment and space monopolization by weaker competitors. Smaller coral plate substrates may serve as refuges to less competitive cryptobionts; whereas large cave substrates may tend to support fewer inferior competitors.

Although the roof substrate is biotically dynamic, the skeletonized organisms involved are of only limited constructional ability. This results in the maintainance of a relatively constant two-dimensional substrate area within the caves. In this sense the cave substrate is static. This aspect of substrate growth therefore also differentiates the cryptic cave sites from the cryptic undersurfaces of foliose coral plates. Two-dimensional growth rates of approximately 6.3 mm/yr have been documented, specifically in Agaricia plates within this study area (Sadd, 1980). The divergent susceptibility to colonization between these two cryptic substrates may be of considerable importance to the final community structure. Jackson and Winston (1982) suggest that the continual opening of new substrate on coral plates may allow greater coexistence of superior encrusters with less competitive types. Their observations show less competitive biotas to encrust most often at the growing, immature plate edge; while static, mature plate centers are dominated by colonials and demosponges. Observations in Salt River caves suggest that cave substrates may be most comparable to the oldest central areas of coral plate undersurfaces -- both habitats are dimensionally static, and are dominated by competitively superior colonial ascidians and demosponges (Jackson, 1977; Russ, 1982). In particular, all solitary organisms and bryozoans appear to be less successful, and consequently less common on coral plate interiors as well as on similarly static cave substrates.

As mentioned above, substrate roughness in the form of furrows and convolutions tend to increase overall surface area. Surficial heterogeneities in the cave roofs may occur by processes of: (1) secondary encrusting framework growth, and (2) boring action of some endolithic organisms. General topographic heterogeneity increases away from the cave apertures, and may be related to enhanced biotic activity there. Previous studies in terrestrial caves (Poulson and Culver, 1969) and intertidal marine environments (Kohn, 1968) have shown habitat diversity to be increased by spatial heterogeneity. Original topographic heterogeneity within the cave roof may result in preferential biotic diversification in these irregular areas and promote further heterogeneity through a type of feedback loop (Hutchings, 1974). Such a phenomenon is apparently mediated through larval settling preferences for topographic irregularities.

Current Activity

Cryptic biotas are most often associated with habitats of little physical disturbance, and, therefore, are generally protected from extensive current activity. Attenuation of currents may be mediated by increasing water depth or distance into the caves. Cave habitats of Salt River provide a sheltered space, removed from large scale changes in current activity which may affect exposed coral reef zones. No fluorescent dye experiments have been performed within these caves, therefore no original quantitative data are available. However, the consistent observations of clear waters within caves, as well as the long residence time of diver-resuspended sediments (in excess of 3 hours) provide qualitative evidence of little current activity. No small current ripples were observed in cave floor sediments, although fine-grained sands would be expected to support such bed forms even in very low current regimes. Such bedforms are common on the canyon floor. Unpublished data of Koehl and Jackson show water movements to decrease within centimeters inward from coral plate edges. Much larger and more elaborate internal dimensions of cave environments (which are often fronted by coral plates) may create strong attenuation of current activity. Apertural zones are most obviously affected by currents due to their proximity to outer canyon water movements. Deeper cave zones may be expected to show decreased current activity. Complexities may be introduced by multiple apertures. It is suggested, for example, that greater flow may be present in site IK105A, due to two apertures being there. This would result in a shorter residence time of water within that particular cave.

Bathymetrically related current changes were unexplored by this study. However, divers did note that current induced "diver-instability" was present only at exposed 50 ft sites on the outer reef (tank change sites). It is suggested that deeper cryptic caves may experience a reduced level of current activity due to removal from the currents and waves associated with wave base. Lowered current activity has been documented with increased water depth in the similar forereef environment of North Jamaica (Hartman, 1973; Land and Moore, 1976).

Previous within-habitat colonization experiments using artificial cryptic substrates have linked small-scale current anomalies with larval settling behavior. Apparently, such anomalies are the result of current activity in small eddies which form around topographic irregularities. Such eddies may preferentially direct larvae to small prominences on hard substrates, which, as previously outlined, may provide them with some refuge from more competitive biotas. Encrusting bryozoans such as Steginoporella were observed to colonize relict bivalve shells cemented to the roof of some caves. As topographic irregularities appear to be concentrated in deeper portions of the cave, they may be of greatest significance in eddy production and subsequent preferred colonization there.

Sedimentation

All cryptic environments, by virtue of their sheltered morphology, afford some protection from the effects of direct sedimentation. Such physical stress would otherwise kill sediment-intolerant suspension feeding cryptic organisms (Jorgensen, 1966; Goreau, 1973; Reiswig, 1971, 1973). The caves examined in Salt River are positioned within promontories between sediment chutes, or are withdrawn below overhangs of such chutes. However, even within this generally protected sedimentary environment, some intra-cave variations in sedimentation effects are suggested. Within a given cave, apertural and distal zones are in closer proximity to spill-over and sediment floor turbidity effects, respectively. Apertural biotas are nearest to sands which accumulate on the upper surface of the cave lip, and periodically cascade over the cave aperture. Distal biotas are located closest to sediment floor sands and silts, the latter of which are easily resuspended by small sediment floor shifts through bioturbation. During examination, diver-resuspended fines rendered the cave extremely turbid (visibility less than 0.5 m) in excess of 3 hours. In some cases dead encrusting organisms were observed to be partially covered by fine sediments near the sediment/roof interface. Generally higher levels of sedimentation effects at distal and apertural cave zones may reduce the consistency or extent of colonization there. The cave sediments from site IK50A were analyzed to determine the source of the particles, as well as the depositional regime in which they were deposited. The results of a qualitative (presence/absence) constituent analysis are presented in Table 1. Constituent analysis shows cave sediments to be dominated by calcareous biogenic particles, many of which may be derived from organisms encrusting the cave walls. The majority of sand and larger sized particles may be derived from encrusting, cave-dwelling organisms. These include coralline algae, coral, bryozoan, and bivalve fragments. The examination of larger sediment sizes shows these delicate fragments to be angular and unabraded. This is suggestive of little transport and supports in situ deposition. Grain detachment from the hard roof substrate probably results from one of two processes. Detachment may be a result of loose skeletal articulation, such as in bivalves, or due to some form of bioerosion, such as in corals and coralline algae. Sediments also contain abundant fragile microfaunal associates of the attached fauna. These commonly include the microgastropods, and calcareous foraminifera. Fines which may more easily be washed in and settle out quietly are rich in gorgonian, tunicate, and demosponge spicules. Small size fractions are rich in clionid chips, produced through bioerosive mechanisms (Neumann, 1966; Rutzler and Reiger, 1973), active within the cave proper. All of these constituents were also found in samples from a sediment chute, located a few meters north of IK50A.

The net transport direction of cave floor sediments appears to be out of the caves rather than inward. This is indicated by an aperturally sloping and broadening sediment "apron," which begins distally and passes outward to supply sediment channels below the cave. The angle of inclination of each cave's sediment apron is highly variable. Dip is probably controlled by original cave block orientation, canyon wall angle, textural characteristics of the sediment, and the extent of infaunal burrowing activity within the sediments. Outward transport of sediments is mediated by creep, slump, or other substrate failure, preventing the sediments from significantly building up and occluding the aperture.

Grain size analyses of cave floor sediments as well as those of an external sediment chute at equivalent depth are presented in figures 5a and b. Grain size determinations may define environmentally related differences in transport and depositional mechanisms between any two depositional settings (Ginsburg, 1956). Grain size is controlled partly by source of supply and partly by transport mechanism. Though mean grain size within the cave and the sediment chute are in the fine sand range and nearly equal, an easily observed difference in sorting mechanism and extent is noted. The sediment chute sample is mechanically transported and deposited by sliding and saltation (Hubbard et al., 1981) while cave sediments appear most often to be deposited in situ. This results in noticeably low levels of wear on cave floor sediments. Though particles in both localities may be of the same origin, they are thereafter subjected to vastly different sorting mechanisms. Sediments within the cave are moderately to poorly sorted, while sediments within the chute are moderately to well-sorted; both distributions are mesokurtic. This suggests that chute sediments are more thoroughly sorted mechanically than cave sediments. Additionally, grain size distribution is bimodal for cave sediments, while chute sediments are unimodally distributed. The production of two discrete size classes, and less thorough sorting of cave sediments is probably due to the in situ availability of multi-sized skeletal components, produced through random bioerosion and detachment, and rapid deposition without current reworking. The unimodal distribution of chute sediments is probably produced by mechanical transport and deposition mechanisms acting on the same original constituents, similar to those of the cave sediments. Cave sediments differ most significantly from outer chute sediments in skewness. Cave samples are skewed toward the fines (+)0.180, and sediment chute samples are skewed toward the coarse fraction (-)0.216. Positive skewness suggests a significant reduction of current winnowing of fines within the cave environment, allowing their greater-than-normal representation. Conversely, the more energetic regime of the open sediment chute tends to retard the accumulation of fine grain sizes. Extremely clear waters within the cave environments further support quiet biologically mediated deposition therein, with little or no resuspension of the very fine floor sediments. This quiet accumulation scenario may on occasion be punctuated by rare, episodic sedimentation events, though none were observed during this short study period.

Bathymetric changes in cave floor sediment characteristics have not been explored by this study, though none were easily discernable over the small bathymetric gradient of 50 to 125 ft. Seasonally high canyon current velocities may increase cave turbidity, as well as trigger increased cave apron slumping. Tidal or wave-produced currents were observed by divers only at exposed 50 ft depths, and there at low levels. Such daily effects are not expected to significantly perturb within cave sedimentation processes.

Light Levels

Low light levels are characteristic of all cryptic environments by definition. Several physical parameters such as cave structure, outer surface overgrowth, compass orientation of apertures, and bathymetric depth may affect light intensity of any particular cave. Following the terminology of Garrett et al. (1971), all caves here are characterized as "gloomy to dark" in ambient light levels. Seasonal and daily changes in water clarity may vary the amount of light incident upon any cave site. During winter months, visibility has been observed to drop to less than 6 ft in the canyon proper due to the increase in suspended load (Rasmussen, 1980). Such high turbidity is presumed to substantially lower the amount of surface light reaching cave apertures.

Within-cave variations in light intensity are presented for site SR125B in Table 2. As site SR125B represents one of the deepest cave sites studied, bathymetric attenuation of surface light intensity reaching the aperture may be most pronounced here. Data taken on 9 August 1982 at 09:00 hours using a Gossen Lunapro light meter show a progressive linear decrease in available light with distance into this single aperture cave. Within-cave variations in light intensity may be of great importance to the directed settlement of cryptofaunal larvae. Data of Ryland (1960) and Ryland and Stebbing (1971) indicate that lower surfaces are normally preferred by certain characteristic epizoic larvae, including those of serpulids, bryozoans, and boring bivalves. This preference is further augmented by a time-governed change from generally positive to negative phototactism through the larval stage. The observed reduction in light intensity with distance into the cave, paired with the photonegative settling of most cryptic biotas, may result in preferential faunal recruitment in the darker cave zones. On the basis of settling behavior, greater percent coverage and species richness may be predicted for darker cave zones, while lowest species richness is expected near the less shaded aperture. Garrett (1969) observed biotic distributions in Bermudan patch reef cavities of comparable size to those of Salt River; he suggested decreasing plant (producer), and increasing animal (consumer) densities are related to lowered light intensity inward. Though observed in Bermudan reef cavities, no such light governed trophic group distribution is observable here. In Salt River caves, no within-cave gradients in the distribution of producers and consumers were observed, and patterns of such coverage are probably dictated by other factors.

Nutrients and Oxygen

No data are available on nutrient and oxygen levels within the submarine caves examined here. Though no significant differences in nutrient or oxygen levels have been documented over the examined bathymetric or within-cave gradients, variations within these resources may be both present and significant. Previously, within-cave levels of suspended organic particulates and dissolved oxygen have been implied to decrease with distance into caves (Garrett, 1969). Though no quantitative data were presented therein to substantiate this trend, Garrett suggested that a nutrient and oxygen gradient resulted from autotroph concentration near the aperture, and heterotroph concentration distally. This colonization trend is not apparent in Salt

River submarine caves, and cannot be employed in defense of any nutrient or oxygen gradient here. If we consider an external supply of nutrients and oxygen, we may infer that both parameters decrease with distance into the cave based on reduced current activity there. Such a trend is suggested by Koehl and Jackson (unpubl. data), and Buss and Jackson (1981). Deeper cave sites in Salt River may also be characterized by depleted levels of nutrients and oxygen. Such a phenomenon could partially control changes in species richness and biomass at any point within the cave.

Suspended food concentrations have been observed to decrease with increasing bathymetric depth in analogous reefal environments of Jamaica (Reiswig, 1971, 1972). Recent studies of Brock and Smith (1982) and Choi (1982) suggest that cryptic hard bottom communities such as those living within caves may be quite sensitive to, and closely regulated by, limited food resource availability. Thus, both bathymetric as well as within-cave cryptobiont distributions may to some extent be governed by competition for food.

Predation

Jackson (1977) and others have stated that cryptic biotas are subject to very low levels of predation. This has been attributed to toxic chemicals and mineralized sclerites found in demosponge and ascidian tissues (Randall and Hartman, 1968; Bakus and Green, 1974), as well as the sheltered nature of the cryptic habitat. No direct examples of macropredation by grazing gastropods, echinoids, or parrot fish were witnessed on cave biotas during this study. The work of Bardach

(1961) and observations of this study suggest that parrotfish restrict grazing activity to the outermost apertural zones of the cave prominence, and become most active at night. However, no indirect evidence of predation in the form of grazing scars was observed inside the caves during daylight hours. Sediment constituent analysis shows large quantities of microgastropod tests, as well as less common echinoid fragments to be present within the cave floor sediments. The microgastropods are unidentified, and cannot be assumed to actively graze on cave roof biotas. However, even if they did, it is highly unlikely that their diminutive size would allow their control over biotic distribution within the cryptic community. It is possible that the limits of photographic resolution prevented their observation on the cave roof, though a more likely meiofaunal habitat is suggested for these gastropods. Thus, overall predation by grazing activity is suggested to be very low within the caves, and of doubtful importance to community structure.

Summary: Physical and Biological Stress Patterns

In summary, the cryptic environment of Salt River Canyon is one characterized by extreme stability. Predation or signs of predation (tooth marks, drill marks, bare zooids, etc.) were not observed, and physical disturbance on a significant scale at least greatly attenuated when compared with open reef surfaces. Apparently the protection afforded by the overhanging lip of the cave aperture, and the internal extent of the cryptic surface is enough to maintain a state of quiet, biological control over cryptic community structure. In the absence of periodic, external environmental perturbation (i.e., predation, sedimentation, currents), physical control is highly unlikely (Dayton, 1971). Observations of other workers suggest these to be common cryptic environment attributes (Jackson and Buss, 1975; Buss and Jackson, 1979).

Bathymetrically related increases in environmental stability in tropical environments are widely known and generally accepted (Hartman, 1973, and others). In reefal environments, increasing depth removes any biotope from the fluctuations associated with turbulent wave base. Such fluctuations include those of nutrients, oxygen, and sedimentation. Lower, more stable levels of food and oxygen resources may be found with greater bathymetric depth.

Intracave gradients in the above parameters are less well known. Sensitivity of cryptic biotas to fluctuating nutrients, oxygen, turbidity, and sedimentation may result in less than optimal colonization sites within the cave environment. Substrate selective larvae may be expected to colonize to more topographically irregular and darker cave zones, while also being directed by intracave physical differences. Several generalizations may be made with respect to intra-cave variations in environmental stress: (1) sedimentation effects are highest at the apertural and distal zones, (2) current activity, light intensity, and predation are highest at the apertural zone, and (3) nutrients and oxygen are probably most available, though most variable near the aperture. As the distribution of dominantly filter-feeding cryptic biotas is a function of larval substrate selectivity, the combined evidence of this and previous studies suggests that the distal cave zone should be less favorable for larval recruitment. This suggestion is made on the basis of obviously elevated sedimentation, and possibly depleted nutrient and oxygen levels there. Longer residence times of distal cave waters may prolong the detrimental effects of periodic turbidity events, and *in situ* nutrient depletion (Buss and Jackson, 1982). The apertural zone may also be preferentially stressed by elevated sedimentation, though its effects can be expected to be of shorter duration there. Higher predation, current activity, and light levels, and a generally more variable microenvironment may render the aperture less suitable for consistent colonization. In general then, the central cave zone is probably the zone most suitable for colonization. It is most distant from the disruptive effects of sedimentation and predation. It is also probably more stable in nutrient and oxygen levels than the apertural cave, and less depleted than the distal cave. Its central position results in significant attenuation of light levels, making it preferable to settlement by sciadophillic larvae.

CRYPTIC COMMUNITY STRUCTURE

Community Members

Introduction

Photographs taken of encrusting biotas permit quantitative estimates of areal coverage, morphospecies richness, and diversity for the cryptic surfaces of Salt River submarine caves. In order to consider the structure of the whole cave community with respect to these indices, it is valuable to outline the competitive dominance patterns which occur within - and between - phyla. Photographic methods of this study cannot reliably document competitive interactions within phyla, and are restricted to qualitative comments on inter-phyletic dominance patterns. Information on the mechanisms and patterns of within-phyla competitive interactions, which often require microscopic resolution, is drawn from previous work of other authors.

The intent of the following section is to document the cryptic taxa present, with a consideration of their autecology, areal abundance, and contribution to the cave's geologic structure. The various groups are presented in order of increasing complexity, with additional emphasis on areal abundance. Areal coverage is inherently skewed toward colonial organisms simply due to the nature of their indeterminate growth form. In order to give a more equitable representation of solitary organisms present, a qualitative measure of each taxon's frequency of occurence is included, listed as abundant, common, or rare. Additional information on skeletal contribution to cave floor sediments through life habitat or post-mortem disarticulation is also presented, and may be augmented by Milliman (1974). Lastly, the photographic faunal census data exclude endolithic micro- and macroboring organisms which do not show bodily evidence of their identity at the substrate surface. Therefore organisms such as boring bivalves and endolithic algae, though obviously present, have not been entered in quantitative community measures. The reader is referred to Table 3 for absolute areal coverages of any taxa on particular transects, and averaged over bathymetric sites. Figure 6 describes the bathymetric trends of organism distribution, including whole environment mean coverages.

Coralline Algae

Corallinaceae of the class Rhodophyceae are qualitatively abundant in the Salt River caves and account for approximately 29.8 ± 16.9% of all encrusting organisms present. Though coralline algae are grouped as "open space" in this study, two morphotypes have been differentiated on the basis of purple and red pigmentation. The most abundant types of coralline algae on St. Croix are Lithothamnion, Lithophyllum, Porolithon, and Neogoniolithon. A lack of taxonomic resolution suggests that the cryptic types observed here be generally grouped as the "lithothamnioids" of Goreau (1963).

Past work has shown that under conditions of heavy wave action coralline algae are capable of forming emergent "algal ridges." In such physically controlled environments, a lack of predation through grazing fish and molluscs apparently allows unrestricted "opportunistic" growth approaching 6 mm/yr (Adey, 1974). These elevated growth rates are not normally found within coral dominated reefs. However, the importance of coralline algae as coral reef frame builders and cementers has long been established (Gardiner, 1931; Stoddart, 1969). In protected cryptic habitats such as Salt River caves, lithothamnioids fill the multiple roles of secondary framework cementers, and binders and suppliers of loose sediments (Ginsburg et al., 1973; Vasseur, 1977). A lack of grazing predators suggests that the abundance and distribution of cryptic lithothamnioids must be controlled by some other environmental parameter. As the calcification rate of coralline algae is apparently insignificantly affected by light intensity or photosynthesis (Goreau, 1963), competitive ability is probably not related to within-cave or bathymetrically attenuated light levels. No linear decrease in areal coverage is associated with distance into caves or water depth. Goreau (1963) does report adverse conditions such as excessive sedimentation result in decreased calcification rates.

Lithothamnioids appear ubiquitously at nearly all cave sites. A lack of purple or red coralline algal pigmentation is noted only in IK105A. Here a problematic reddish-orange pigmentation is noted on all "open space." It is unknown whether such pigmentation is due to staining of truly open relict substrate, or to actual biotic cover by a previously unseen coralline algal form. Apparently "bleached," poorly pigmented examples of coralline algae were noted in all distal cave zones. Such bleached specimens may also account for the problematic open space of IK105A. It is suggested that the excessive sedimentation distally and within IK105A may be responsible for depauperate coralline algal cover there. Such areas, and infrequent areas of white, unstained space will be grouped with the coralline algae in Table 3 and Fig. 6.

Lithothamnioids appear to be easily overgrown or colonized by all other solitary or colonial organisms. In addition, they themselves colonize almost all hard substrate spaces which are unoccupied by other organisms, including those of hard solitary exoskeletons. Previous studies show coralline algae to form competitively "passive" substrate (Jackson, 1977, 1981), despite the probable use of allelochemical toxins in certain types (Buss, 1976). Our observations suggest that areal coverage of cryptic lithothamnioids is a simple function of the extent of alternate biotic overgrowth. Therefore, in percent cover, richness, and diversity measurements of actively competing organisms, coralline algae will not figure into calculations. They will instead be grouped with "open space." It should be noted then, that if coralline algae were included as normal interactive biota, the level of total areal substrate coverage would be approximately 99% overall. This is characteristic of almost all Recent cryptic environments (Jackson, 1977). Limited coactions of lithothamnioids and other biotas may be observed in the overgrowth of some solitary and colonial corals by coralline algae. However, it is probable that the coral polyp was dead prior to encrustation. In another case, an encrusting bryozoan (WMB) is apparently "absorbing" coralline pigmentation, but is seemingly not adversely affected by this interaction. This phenomenon appears diagnostic of the unidentified cheilostome designated WMB, and deserves further attention.

The passive nature of lithothamnioid encrustation may be further documented by studies of actively growing coral plate communities. In coral plate studies, Jackson and Winston (1982) report that coralline algae are severely restricted in their spatial distribution. Lithothamnioids were observed to encrust only the exoskeletons of solitary organisms, and also growing plate margins. In other words, they preferentially encrust enlarging substrates -- a competitive refugium mentioned earlier. The actively growing microenvironment of the plate edge is absent within cave environments. Therefore, the caves may show restricted distribution of coralline algae, especially in the well-overgrown central cave zone. Data show intracave coralline algal substrate to be common at less "covered" and somewhat less diverse apertural and distal zones. Bathymetric trends show coralline algal areal coverage to decrease markedly between 50 and 75 ft depths, then slowly decline thereafter (see Fig. 7a - g). This is in contrast to the noted areal expansion of algae in turbulent zones of Boyd et al. (1973) and Adey (1974). Perhaps this is due to the greater stability and consequent overgrowth associated with greater bathymetric depth. All evidence characterizes cryptic lithothamnioids as early successional substrate colonizers, opportunistic in distribution, and poorly competitive with other cryptobionts.

Green Algae

Fleshy, filamentous green algae and erect, white calcareous green algae of the class Chlorophyceae constitute approximately 6.87 ± 3.23% of observed cave substrates, and constitute the remaining cryptic flora which occupy surficial space. They are abundant, and occur directly over hard substrates, or epibiontically with coralline algae and demosponges. Erect calcareous algal types notably include Halimeda sp. and others which remain unidentified. Green algae have previously been classified as a weak, unimportant occupiers of cryptic space (Jackson, 1977), though their presence may limit coralline algal cover to some extent (Steneck, 1983). A generally low level of ambient light is thought to restrict photosynthetic green algal levels here which would otherwise be luxuriant in an environment of notably low grazing activity. Green algae are not considered dominant competitors on this cryptic substrate, and do not appear to restrict the distribution of cryptofaunas. Green algal cover tends to be concentrated in the more well-lit apertural and central cave zones (Table 4a - g). Distal cave zones are often without green algal cover, or maintain it at a notably low level. Great intracave fluctuations in areal coverage are thought to be controlled by the density of nearby overgrowing sponges and colonial organisms, and the extent to which these organisms tolerate epiphytes. No significant association was observed between areal cover and bathymetric depth over this interval, which was entirely within the photic zone.

Jackson (1981) and Jackson and Winston (1982) have also noted green algae to preferentially occupy periferal, growing margins of coral plates. This may be indicative of a poorly competitive, opportunistic life mode, similar to coralline algae. Green algae clearly exhibit the added colonization advantage of epibiosis with living demosponges and colonial ascidians. Cleared transects also show evidence of green algal cover below many demosponges, suggesting the possibility of commensalism.

Foraminifera

The red colonial encrusting foraminiferan Homotrema rubens has been identified, and accounts for approximately 0.07% of all available substrate. Its most common morphology is globose, as are the specimens observed here. It is abundant in all caves, though its presence varies greatly among different transects. Its limited areal growth and frequent overgrowth result in a very small percent cover. Homotrema is found extensively on cleared transects, and is in a limited way a ubiquitous secondary framebuilder, but more obviously it is a source of biogenic sediment.

Homotrema must act as an early substrate colonizer, as it cannot settle on demosponges or bryozoans (Colin, 1978). Overall low levels of competitive success as witnessed by common overgrowth characterize Homotrema as the weakest of the colonial organisms considered here. Any bathymetric or within-cave trends are unclear, and are suggested to be a simple function of the extent to which other organisms have colonized any particular site.

Demosponges

Demospongia, the largest class of the Porifera, are the most areally abundant faunal element within the caves. They occupy 43.5 ± 10.5% of the available cave substrate. Differentiation of various biological species is difficult, owing to the impracticality of taking in situ spicule samples, and the overall chaotic nature of demosponge taxonomy. Many species are similar in appearance, and individual forms are variable within the cryptic biotope (Pang, 1973; Fry, 1979). Morphospecies designated here are based on shape, color, texture, and effect on human epidermis. Areal dominance of encrusting demosponges suggests their importance to food and spatial resource competition, and overall diversity levels within the caves. Demosponges are considered to be the dominant filter-feeding cryptobionts and have been shown to limit the distribution of less efficient members of this trophic group in many cryptic environments (Buss and Jackson, 1981; Jackson and Winston, 1982; Russ, 1982). Some food resource competition has been identified between co-occuring populations of demosponges and bryozoans (Winston, 1977).

As active filter feeders, demosponge distribution is strongly limited by the delicate balance of the suspended sediment load (Reiswig, 1971). Vertical stratification of various sponge types above the substrate may result in limited spatial partitioning. This phenomenon has been demonstrated elsewhere in demosponge populations (Sara, 1970). Vertical strata include boring, hypobiotic, basal, and epibiotic levels -- all of which are observed here. However, highly interactive, anastomosing networks of basal demosponges demonstrate high levels of spatial competition. Examples of fusion, fission, partial mortality, and epibiosis are common (Rutzler, 1970; Stebbing, 1973). The complications of assessing age and life histories of these modular, dynamic organisms have been discussed by Hughes and Jackson (1980) and Winston (1981). Winston (1981) suggests the term "genet" for genetic individuals and stresses their high potential longevity in stable ancient environments such as these caves.

Bathymetrically associated environmental parameters seem to control demosponge distribution to some extent. A two-fold areal expansion of demosponges occurs between 50 ft and 75 ft. (Fig. 6). Increased depth has previously been characterized by nutrient depletion in similar reefal environments on the Jamaican North Slope (Hartman and Goreau, 1970). It is not unreasonable to suggest that, in St. Croix, both nutrient depletion and decreased current activity are also experienced at deeper reef zones. Filter feeding studies (Reiswig, 1971) and examination of cryptobiontic competition for food resources (Buss and Jackson, 1981; Jackson and Winston, 1982) suggest that demosponges are the most efficient cryptobiontic filter feeders, capable of exploiting such nutrient depleted environments. Such data may explain their observed areal dominance at greater depths. Previous literature shows demosponges to consistently dominate stable, quiet, deep zones of modern reefs (Lang, 1974; Hartman, 1973, 1977), suggesting their continued dominance beyond the bathymetric limits of this study.

Within individual caves, demosponge distributions show most consistently high areal coverage to be associated with central zones. As previously suggested, such zones would seem most stable by means of their distance from apertural and distal sources of physical disturbance. Apertural and distal zones display lower densities and diversities of demosponges, often as patches of a single type. Such phenomena result in anomalously low diversity quadrats in these zones. Previous coral plate studies have similarly demonstrated demosponge dominance in more stable, nongrowing inner regions of the coral plate substrate as well (Jackson and Buss, 1975; Jackson, 1981; Jackson and Winston, 1982). Inner plate zones maintain lower levels of current activity, and presumably less current-suspended nutrients. Based on within-cave observations, as well as data of Jackson (1977) and Russ (1982), it is suggested that demosponges be characterized as strong, later successional stage, cryptic community members. Their distribution and dominance is apparently related to their superior ability to exploit stable, low disturbance substrates, by virtue of efficient, active filter feeding, and efficient spatial competitive mechanisms.

The boring activities of some demosponges have long been noted (Otter, 1937; Yonge, 1963; Goreau and Hartman, 1963; and Neumann, 1966). Recent studies may have isolated an additional constructional role as well. Observations of Wulff and Buss (1979) suggest demosponges may act as short term binders of unconsolidated, or poorly cemented reef frame material prior to lithification. Scoffin and Garrett (1974) classify sponges as filling the roles of (1) coral growth inhibitor through space occupation and overgrowth, (2) framework destroyer and sediment producer through bioerosion, and (3) sediment producer through spicule production and disarticulation. Cryptic demosponges observed here fill all of the above roles, including those defined by Cuffey (1974) and Wulff and Buss (1979). Additionally, some demosponges may be corroding relict overgrown substrates, as is described in a later section.

Particular genera identified here include nonborers _Agellus_, _Chondrilla_, _Mycale_, and _Ulosa_, and boring forms _Cliona_ and _Siphodictyon_. Siliceous spicules derived from encrusting demosponges are common in cave floor sediments.

Sclerosponges

Two genera of Sclerospongiae account for 4.49% of the available cave substrates. _Ceratoporella nicholsoni_ and _Stromatospongia vermicola_ are found at 105 ft and 125 ft depths, respectively. They are qualitatively rare, and occur quite irregularly over the entire study area. Sclerosponges have only recently been identified in the caverns of Caribbean reefs (Hartman and Goreau, 1970). These authors suggest that modern sclerosponges are living analogs to fossil sclerosponges of the Mesozoic, as well as being phylogenetically related to Paleozoic stromatoporoids and chaetetid "tabulates" (Hartman and Goreau, 1972).

Modern sclerosponges are composed of a hard skeleton of aragonite, silica spicules, and organic fibers -- living tissue occupies a thin external veneer. Deeper caves appear to be stabilized, and in some cases roof columns are primarily constructed by sclerosponges. At greater depths, sclerosponges effectively "outlast" hermatypic corals in the role of primary framebuilders, as they do not rely on photosynthetic algal symbionts in the process of calcification.

Sclerosponges observed here show both intracave and bathymetrically related abundance patterns. Within any cave, sclerosponges appear in high density, low diversity patches in the most distal zones. Likewise, sclerosponges appear only at greater bathymetric depths in excess of 75 ft. Such deep, cavernicolous distribution agrees well with observations of Hartman and Goreau (1970) in similar environments of Jamaica, and suggests no bathymetrically related nutrient limitation of sclerosponge distribution. Unpublished observations of C. Moore and H.G. Multer in St. Croix at depths greater than 280 ft show Ceratoporella to be the dominant frame-building organism there (Milliman, 1974). The expansion of sclerosponges out of the caverns and into primary constructional roles at depths greater than 280 ft is correlated with greatly attenuated levels of hermatypic coral encrustation there. Within the depths of this study, caves with extensive sclerosponge growth were notably depauperate in ahermatypic coral growth also. These observations suggest that sclerosponges become superior food and/or spatial resource competitors in the deeper forereef open zones, as well as in more shallow caverns.

Ecologic observations of caverns in southern France and Madagascar by Vacelet (1967b) led that author to characterize modern sclerosponges as poorly competitive, "relict" faunas of ancient origin, now barely holding on in a "competitive refugia." Within-cave observations herein support this view. Sclerosponges are exploiting less diverse distal cave zones, and only at depths which limit other skeletonized faunas. Though sclerosponges have been shown to avoid heavy sedimentation in open areas (Lang, 1974), distal cave zones apparently are habitable nevertheless. Sclerosponge masses are occasionally half-buried in cave floor sediments, as well as "dusted" by re-suspended fines in these zones. In contrast with these general observations and those of Vacelet (1967b), Jamaican study sites yielded much more diverse sclerosponge assemblages in greater density (Hartman and Goreau, 1970). These indications of a healthy, expanding sclerosponge community were thought to characterize a successfully colonizing biota.

Though particular sites may vary in sclerosponge colonization, most authors agree that Recent cryptic communities of sclerosponges (and often co-occuring brachiopods) are probably descendants of an ancient, previously more common community. The sclerosponge-brachiopod community apparently invaded cryptic areas only after the rise of superior hermatypic corals in the Middle Jurassic (Jackson et al., 1971).

Observations made here characterize sclerosponge distribution as somewhat opportunistic, and less competitive. Within particular caves, they occupy the less diverse, somewhat physically stressed distal zones. Apparently sclerosponges are positioned within caves to avoid direct competition with other organisms. They only appear at greater bathymetric depths, where they progressively expand toward the cave aperture. They are not restricted to caverns at greater depths.

Cnidarians

Members of the order Scleractinia which are observed here are all ahermatypic forms, and constitute 2.75 ± 2.48% of the cave substrates. They are common in most caves, though conspicuously absent at site IK105A. This observation, in addition to the apparent lack of normal coralline algal growth there, again characterizes the IK105A site as somewhat anomalous.

Corals include three solitary genera, _Astrangia_, _Phyllangia_, and _Tubastrea_, and one colonial species, _Madracis_ _pharensis_. A single specimen of the anemone-like order Zoanthidea is identified as _Parazoanthus_ _swiftii_. Generally restricted areal coverage, as well as predominantly solitary growth form, preclude corals from consideration as more than secondary framebuilders. Their areal extent decreases markedly with depth, resulting in a structural contribution which similarly decreases. At depths greater than 75 ft, corals were found to be most commonly overgrown by demosponges. Corals also contribute large quantities of sediment upon bioerosion or other disarticulation of their skeleto

Solitary corals are most common in central cave zones, usually surrounded by demosponges, tunicates, and coralline algae. These potential overgrowers tend to use the upright coral exoskeleton as secondary substrate. Buss (1979) and Jackson (1977, 1979a) have demonstrated the distinct competitive disadvantages associated with solitary body construction in a biotope of co-occuring colonials. Indeterminant modular growth of demosponges over living solitary coral polyps is observed in all caves containing living corals. At all caves, cleared transects show relict biocorroded corals below demosponges (Fig. 10a and b). Corallites of Tubastrea are usually clumped into groups, implying some aggregative defensive behavior against such overgrowth (Jackson, 1977).

The within-cave or bathymetric distribution of corals cannot be directly related to light intensity, as all are ahermatypes, lacking zooxanthellae. Though poorly understood, the role of zooplankton in nutrition is apparently greater in these forms (Colin, 1978). Perhaps higher competition with demosponges for reduced nutrients and currents associated with increased depth may restrict suspension feeding corals somewhat (Hartman and Goreau, 1970; Reiswig, 1971). Unrestricted growth of demosponges is observed to increase with water depth, and may be responsible for a parallel decrease in areal coverage of corals. Within-cave preference of solitary corals for central areas may be associated with food resource abundance, lack of sedimentation, or enhanced stability there. The co-occurence of corals and demosponges in some high diversity central cave zones suggest that they possess a competitive mechanism other than upward growth to allow their continued presence. It is probable that corals possess allelochemical toxins which enable them to participate in a competitive network of encrusting organisms (Buss, 1976; Jackson and Buss, 1975). Mesenterial filaments may also defend living corals from incipient overgrowth (Lang, 1973).

Cryptic corals are probably best characterized as a stable, biologically accomodated group. Though early recruitment and solitary body form suggests that corals are opportunistic pioneers (Jackson, 1977), their continued presence in later successional stages of diverse stable cave zones attests to at least some competitive ability.

Cnidarians of the order Stylasterina account for 0.01% of the cave surface, with highly variable between-transect abundance. Stylaster roseus has been identified; it is an erect, pinkish white hydrozoan with a small basal attachment site. It is rare in this study area. The colony itself forms an erect, dendritic, plane surface, used to catch zooplankton within the water column. It is often found in highly diverse, crowded quadrats. Perhaps its erect construction allows it to exploit food resources out of reach of low-lying encrusters. Due to its delicate erect posture and limited size and extent, it contributes insignificantly as a secondary framebuilder. S. roseus is only observed in diverse central cave zones. No instances of incipient overgrowth by other colonial organisms or demosponges were noted. Apparently competitive defense mechanisms in the form of abundant dactylozooids are most effective.

Bryozoans

Cheilostome bryozoans of several morphotypes account for 2.30 ± 1.31% of the available cave substrates, and are rare. In contrast, other authors have found them to be quite abundant cryptically (Jackson, 1977). Identifiable cheilostome genera include Cleidochasma, Steginoporella, and Stylopoma. One unidentified erect bryozoan genus was observed as extremely rare. All encrusting forms are acting as minor secondary framebuilders and veneerers, and also contribute to cave floor sediments.

Data of Schopf (1974) and Cuffey (pers. comm., 1982) suggest that a very diverse assemblage of encrusting cheilostomes exists on the St. Croix shelf. Further, Jackson and Winston (1982) report abundant cryptic bryozoans encrusting the undersides of living coral plates. Coral plates collected near Salt River Canyon show a consistently rich bryozoan assemblage. Jackson (1981) and Jackson and Winston (1982) suggest that bryozoans opportunistically locate on growing periferal plate margins as a reflection of their poor competitive ability with respect to demosponges. Examples of this pattern are found on additional coral plates. Predictably, in stable, nongrowing cave environments, bryozoans are considerably less common than on growing coral plate substrates. The lack of newly opened substrate, as well as the abundance of demosponges present within caves seems to prohibit substantial bryozoan recruitment. Buss and Jackson (1981) suggest that this exclusion may be due to limited food resources as well as spatial competitive exclusion. Their results show that in dense communities where sponges are present, limited food resources usually results in reduction of the competitive success of bryozoans.

The above factors result in a generally depauperate level of living bryozoan encrustation, especially in central cave zones. Though inferior to that of demosponges, the competitive ability of bryozoa is noted to exceed all solitary cryptobionts (Jackson, 1981; Jackson and Winston, 1982; Russ, 1982). Within-cave bryozoan distributions are skewed toward distal cave recesses, away from central zones (Table 4a - g). Bryozoans, like sclerosponges, may be competitively excluded from demosponge-dominated central zones, and therefore occupy the less optimal microenvironment of the distal cave by default. Thus, this zone is again suggested to serve as a form of competitive refugium, for bryozoans as well as sclerosponges. Bryozoans and sclerosponges together form low diversity, high density patches distally. Such characteristics are consistent with predictions for communities located in more physically controlled microenvironments (Stearns, 1976).

Ascidians

Chordates of the class Ascidiacea occupy approximately 8.41 ± 5.06% of available cave substrates, and are considered qualitatively common. Colonial forms are observed most often, and are differentiated on the basis of color and transparency. Solitary ascidians are likewise differentiated, though these are notably less common. Photographic differentiation of ascidians from demosponges was based on the somewhat arbitrary qualities of a more shiny, slimy surface texture, and siphon presence. Therefore, a lack of taxonomic precision characterizes this group more than any other.

Colonial ascidians apparently follow the same distributional pattern as the more abundant demosponge populations. No obvious dominance relationship is observed between demosponge and ascidian populations on the basis of edge interactions. Rough equivalence in any proposed competitive hierarchy is probably most accurate (Russ, 1982). They do not appear to be limited to any within-cave zone. Colonial ascidians increase somewhat with depth, though not to the level of the demosponges. They are apparently unrestricted by bathymetrically related decreases in light, nutrient, or current levels. They are observed to easily overgrow solitary cryptobionts, though their relative competitive ability with respect to other colonials such as bryozoans is unknown. Based on their distributional similarities with demosponges, and their advantageous colonial overgrowth abilities, colonial ascidians are considered to be members of later successional stages.

Constructional or destructional roles of cryptic ascidians remain undocumented. They may be most accurately portrayed as relatively unimportant substrate veneerers, probably effecting little net change on cave structure. Ascidians are known to produce very fine aragonite spicules (Milliman, 1974), many of which were found to be of the Pyuridae type in floor sediment analyses.

Serpulids, Sabellids, Bivalves, and Brachiopods

Serpulid and sabellid worms, cementing bivalves, and articulate brachiopods combine to represent almost all solitary organisms considered here, with the exception of solitary ascidians. They account for less than 0.90% of all encrusted substrate observed. Their individual abundances are presented in Table 3. The obvious inequity of substrate partitioning between colonial and solitary organisms is of significance to later discussion pertaining to preservation potential of cryptofaunas. Serpulids, bivalves, and brachiopods act as substrate encrusting, secondary framebuilders of extremely limited extent. In addition, the breakdown of their hard, calcareous exoskeletons contributes to cavity floor sediments. In contrast, sabellid worms actively destroy the cave substrate through boring, thus contributing some bioeroded material to the cave floor. They secrete a non-calcareous mucous tube, which does not significantly add to cave sediments upon death.

Several serpulid morphotypes can be distinguished on the basis of size, coiling, color, and external structural ornamentation. The genus Spirorbis is positively identified, though Spirobranchus and Filograna are suspected to be present also. As serpulid apertures are nearly always present within any quadrat, they are designated as abundant. Most apertures are deflected upward away from the substrate, and the remaining portion of the tube is normally totally encrusted by other organisms. Only in quadrats with lower percent coverages are entire serpulid tubes obvious. A possibly symbiotic relationship between serpulid worms and the sclerosponge Stromatospongia vermicola observed by Hartman and Goreau (1970) has been observed here as well.

Sabellids are represented by one unidentified morphotype, having an erect, white, mucous tube. They are designated as common, appearing at all sites except IR105A. They are rarely found as single individuals, being more commonly clumped in groups of three to five. In only one specimen was a sabellid worm tube apparently being overgrown by an unidentified demosponge. Their apertures are normally 2-3 cm away from the substrate, and thus these worms appear to demonstrate food and spatial resource micropartitioning with lower-lying encrusters.

Bivalves are relatively common here. Two attachment types are observed: single valve cementation as seen in *Ostrea* and *Chama*, and commissural attachment as seen in ?*Isognomon*. Few living examples of cemented *Ostrea* or *Chama* are observed, though their exposed cemented valves appear ubiquitously on cleared transects. In most cases, they are partially overgrown by coralline algae, demosponges, or ascidians. Living examples of ?*Isognomon* are common only at 50 and 75 ft sites, and are less commonly observed to be in danger of overgrowth than cemented forms. ?*Isognomon* is most often found in clumped spatfalls of 2-3 individuals. As this form does not cement itself to the substrate, it is not observed on cleared transects. Within-cave distributional fluctuations of bivalves are apparently random, though they are more frequently observed away from apertural and distal zones.

Salt River caves are sustaining very small populations of reefal articulate brachiopods. Rare examples of the diminutive pink brachiopod *Frenulina* have been positively identified (C. Thayer, pers. comm., 1983) on only (4) quadrats at two sites (SR75B, IK105A). Apparent spatfalls are indicated by clumped distributions of 5-10 uniformly-sized individuals. Although all specimens are quite small, no brachiopods are in the process of being overgrown. This may imply that chemical or other defensive mechanisms are active in this genus. In addition, no relict shells are visible on cleared transects. No obvious distributional trends are suggested due to the limited number of specimens. They do however contribute to particularly diverse quadrat assemblages.

Stanley (1974) reviewed the diminished role of Recent reefal brachiopods and related their evolutionary decline to increased predation beginning in the late Mesozoic. Data also suggest that small individual size may be linked to their present cryptic habitat restriction. Grant (1971) has witnessed populations of cryptic Frenulina in similar environments of Eniwetok Atoll, Marshall Islands. However he notes much greater densities than were observed here. In Salt River, articulate brachiopods are of very limited constructional significance. These forms are assumed to detach and fall to the cave floor upon death. They, therefore, may fill a minor role in sediment production.

The low areal coverage of solitary organisms in the cryptic environment is a function of the determinate limits of their exoskeletal growth. This characteristic, in turn, may account for their status as the weakest competitors (Jackson, 1977, 1981; Russ, 1982, and others). Studies of artificial and living plates show solitary organisms are early substrate pioneers, by virtue of rapid explosive recruitment, and fast initial growth. They are observed most often at less competitive coral plate margins (Jackson and Winston, 1982). They are subsequently overgrown by colonial organisms and demosponges, and are treated as essentially secondary substrate. Only solitary corals seem to offer any resistance to overgrowth by colonials and demosponges. Masses of serpulids, as well as many bivalves, are exposed upon transect clearing processes, occasionally overgrown by bryozoans and demosponges successively. Apparentlv most solitary organisms have only limited defensive mechanisms in escape through size, and aggregative clustering (Jackson, 1977) (see predation section). Little allelochemical activity is known to exist within these forms, though biochemical defense in the form of punctae may characterize the brachiopods. Thus in the competition for food and space, solitaries appear to be at a distinct disadvantage compared to colonials and sponges, especially in nonexpanding cave environments. Serpulids, sabellids, bivalves, and brachiopods are all in least abundance at the 125 ft site. This may be related to dominant demosponge coverage, and the inability of settling larvae to colonize living colonial or demosponge tissue. The net result is construction of a two-group competitive hierarchy, wherein solitaries are subordinate to colonials (Russ, 1982).

Summary: Organism Distribution Patterns

In summary, though the cryptic habitat may provide a refugium from external physical stress and predation, its stable nature creates high levels of within-habitat competition. Though some micropartitioning of limited spatial and food resources through vertical stratification may exist, most of the fauna live on a near-surface (<1 cm) horizon. The preferential colonization of specific bathymetric and within-cave zones by particular faunas is environmentally controlled, and mediated through preferential larval settling patterns. Initial recruitment by solitary organisms is suggested by previous work, and supportive evidence of original and cleared transects herein. Solitary organism coverage is restricted by determinate growth patterns, and food capture mechanisms inferior to demosponges. Colonial organisms and demosponges rapidly colonize the exoskeletons of solitary organisms, particularly those other than corals. Physically undisturbed indeterminate growth commences, producing surficial patterns in a mosaic which we observe here. Reduced physical disturbance is characteristic of greater depths, and seems to favor increasing demosponge coverage, as well as the invasion of sclerosponges (Fig. 6). This development is controlled by nonrandom dominance relationships between colonial-colonial, solitary-solitary, or colonial-solitary organisms which may be based on specialized competitive mechanisms (Jackson, 1977; Russ, 1982; and others).

By combining the quantitative calculations of this and previous work, some broad generalizations may prove valid in the submarine cave biotope: (1) demosponges tend to dominate spatially all cave substrates, and (2) demosponges and colonial organisms together dominate all solitary forms. The dominance relationships above may be paired with microenvironmental trends to establish general spatial distribution relationships as follows: (1) the most stable cryptic substrates (deep caves and inner coral plates) support demosponges, which limit the abundance of less competitive colonial faunas (bryozoans) and solitaries (corals, serpulids, bivalves, etc.); (2) actively growing primary and secondary substrates in the form of coral plate margins, and growing solitary exoskeletons (e.g., encrusting bivalves), provide sites for the recruitment of less competitive colonial organisms and solitaries; and (3) distal cave zones provide a measure of refugia for colonization by less competitive, generally restricted organisms (sclerosponges, bryozoans, and solitary encrusters).

Community Colonization Indices

Introduction

The preceding description of organism distribution and abundance is based on areal cover data presented in Table 4 a - g. These data may be quantitatively transformed into numerical community colonization indices as shown in Figure 7 a - g. Such indices include biotic areal coverage (% C), morphospecies richness (S), and dominance diversity (H'). As the distribution of organisms in the cave environments is ultimately attributable to original larval settling preferences, numerical measures based on biotic distributions should reflect organism response to environmental differences. The above indices have been compared at various positions along cave transects (Fig. 7 a - g), and mean values are compared at (4) bathymetric depths (Fig. 8). A discussion of each is presented below.

Areal Coverage

The cryptic environment as a whole has been characterized as particularly stable and amenable to high levels of encrustation (Jackson, 1977). Sheltered, geologically old submarine caves in Salt River Canyon may be among the most stable and equable of cryptic substrates. Sources of large scale physical stress are all but absent here. In light of this, particularly luxuriant substrate encrustation is common. Including coralline algae as biotic coverage, Salt River's cave environment shows nearly complete substrate utilization, in excess of 95%. If coralline algae are excluded, the mean areal coverage is 69.9 ± 17.3%. As the emphasis of this study is on the ecology and subsequent taphonomy of the more interactive biotas, substrate-providing coralline algae are not considered in the following quantitative measures.

Fifty foot transects produce a total mean biotic cover of 42.9%. Within-cave values oscillate markedly. The only consistent sequence of percent cover levels appear to occur centrally at both 50 ft transects. However, a generally fluctuating pattern is noted as characteristic here. Anomalously high or low coverage levels occur most notably at the apertural and distal cave zones. These are a direct result of often monospecific demosponge patches, or "blooms" which occur there, and may cover an entire quadrat. Such wide fluctuations near the aperture may be the result of external environmental disturbances, which are suppressed with distance into the cave. Distal fluctuations may result from sedimentation or nutrient effects probable in that zone.

Seventy-five foot transects produce a mean biotic cover substantially higher than 50 ft sites, of 80.2%. Here coverage never dips below 26.4%, and shows fewer anomalously low levels. Nearly total encrustation on a quadrat is occasionally the result of single species patches, which at this depth include both demosponges and encrusting bryozoans. However, high percent cover is usually the product of encrustation by a variety of organisms. Percent cover oscillation within the cave is of smaller magnitude than that witnessed at 50 ft. Paired with generally high diversity levels, this is suggestive of greater levels of stability. Perhaps at this depth, the environmental differences between apertural and central cave positions are not as pronounced as at 50 ft sites, and result in reduced within-cave percent cover gradients. Hypothesized near-floor sedimentation effects do not result in distal percent cover anomalies here.

At 105 ft, approximately 80.5% coverage exists - very much comparable in magnitude to 75 ft levels, and significantly above that of 50 ft. Here coverage again appears more consistently stable from the apertural through the central zones than at 50 ft depths. Most frequent high magnitude fluctuations appear distally, and are a product of either bare substrate, or of large patches of sclerosponges and bryozoans. A similarly high level of consistent coverage is present throughout the single 125 ft transect, which shows 82.6% coverage overall.

To summarize, two trends seem obvious. First, bathymetrically related increases in environmental stability seem to result in higher overall percent cover at greater depth. A significant jump in percent cover occurs between 50 and 75 ft. Once beyond the 75 ft peak, biotic coverage appears to remain uniformly high. Associated with this is the observation of decreased oscillations within the elevated coverate witnessed at greater depths. Secondly, deeper caves may show decreased within-cave microenvironment gradients between aperture and center, due to their increased environmental stability. Moreover, at greater water depths any within-cave coverage fluctuations ·are usually restricted to the distal cave zone. At the deepest site (125 ft), even distal fluctuation is absent. At any given depth, greatest consistency in percent cover remains characteristic of the central cave zones.

Richness

Morphospecies richness (S) is indicated by the number of different taxa living within a particular community. It includes no account of their relative abundance or spatial dominance. As protected cave communities are likely to be extremely old, the assessment of richness is probably representative of later successional stage cryptic community levels. The caves observed here produce a mean richness of 9.0 ± 1.4 morphospecies per quadrat. Cleared transects may have greater skeletonized faunal richness as this process exposes skeletal remains of early successional stage organisms. In the following discussion, only the surficial community richness will be presented, with emphasis on its stability as well as absolute numerical levels within given transects.

Mean richness of 50 ft caves is approximately 7.8 ± 0.9 morphospecies per quadrat. Cave apertures maintain lowest richness, while inner zones fluctuate mildly at slightly higher levels. No obvious association between position within any cave zone and richness is otherwise noted. The least diverse demosponge assemblage is observed at this depth, with a greater proportion of observed richness attributable to solitary biotas here than at deeper sites.

Seventy-five foot transects yield a mean richness of 10.3 ± 1.2 morphospecies per quadrat, representing a sizable increase over 50 ft levels, and the highest richness of all depths considered (Fig. 8). This anomalous increase is partly attributable to diversification of the demosponge population, partly to incidence of brachiopod habitation. Within-transect trends differ greatly between transects SR75B2 and SR75B3. The latter is quite constant throughout the cave, while the former shows more fluctuation. Both have fewest species near the aperture. Most stable, consistently high richness is found centrally, with the exception of a single quadrat in SR75B2.

One hundred and five foot transects yield a mean richness of 8.9 ± 1.2 morphospecies per quadrat -- a notable decline from the 75 ft maxima. Again, the two transects measured are quite different in richness distribution. This is largely a result of sclerosponge appearance in IK105A4, occupying entire quadrat fields. Generally high, stable richness is associated with the central to distal cave zones, with the exception of such quadrat monopolization phenomena. As in 75 ft transects, the apertural zone is characterized by somewhat lower richness. Again, the 125 ft. transect is quite similar in richness level and zonal characteristics to the 105 ft depth. Based on the single SR125A1 transect, within cave fluctuations appear to be suppressed, even near the aperture. A mean richness of 9.4 morphospecies per quadrat is observed at 125 ft. The central zone is stably high in biotic richness, while apertural and distal end points are less rich.

Dominance Diversity

Dominance diversity is similar to richness in that it measures the absolute number of morphospecies present. However dominance diversity is sensitive not only to the number of forms present, but also to the extent to which any form dominates the community. In this respect, it yields much more information on community structure than richness calculations. By using areal coverage in its calculation, dominance diversity specifically expresses the extent to which space is partitioned among taxa present. Due to its sensitivity to spatial partitioning, this index may produce very different dominance diversity values for quadrats of equal richness. Thus the dominance diversity and richness indices may fluctuate somewhat differently along cave transects. However, when richness and diversity means from each bathymetric depth are compared, these indices parallel each other closely (Fig. 8). Apparently small scale dichotomies between the two measures are damped out when considered at the level of overall bathymetric means. In this sense, less rigorous richness calculations may provide a good relative approximation of diversity at any depth. Within any cave transect, richness and dominance diversity also appear to parallel each other, though the relationship is less concordant. At particular cave sites, general patterns of richness fluctuation and stability are paralleled by those of dominance diversity, and need not be repeated here.

The mean dominance diversity of all caves produces a community average of 0.587 ± 0.05. Particular depths yield the following diversity indices: 50 ft. = 0.5522 ± 0.04, 75 ft. = 0.650 ± 0.02, 105 ft. = 0.562 ± 0.03, and 125 ft. = 0.586. Standard deviations suggest good between-transect concordance at particular depths. In summary, shallower water depths show most fluctuating levels of biotic richness or diversity, with the exception of the effects of sclerosponge monopolization in IK105A4 and SR125A1 quadrats, causing anomalously low diversity "punctuations." This is underscored by a similar decrease in the magnitude of such fluctuations with increased bathymetric depth. Transect diversity flows more "smoothly" at greater depth. Diversity and richness still remain lowest near the aperture, generally increasing into the caves. Again, this pattern is only disrupted by sclerosponge monopolization effects on quadrat diversity, and only at sites IK105A4 and SR125A1. Central zones tend to be most stable in richness and diversity, while apertural and distal zones fluctuate more widely. Intracave biotic gradients may result from varying sedimentation, light, or other current-related differences in the cave interior.

Summary: Colonization Patterns

Bathymetric as well as intracave environmental gradients have been presented. In considering bathymetric changes in biotic community indices, we note generally good correspondence between transects at equivalent depths. This suggests that bathymetrically controlled environmental parameters exert some control over these indices. Large increase in percent cover, and slight increase in richness and diversity probably derive from attenuated physical disturbances at greater depths, and may be affected additionally by generally decreasing nutrient and light levels. In general, the deeper cave sites reflect greater environmental stability, through a "smoothing out" of within-cave trends. As greater depths create conditions of less frequent storm disturbance, they are associated with stable, low levels of food resources. Such environments tend to produce finely tuned, biologically accomodated mature communities (Sanders, 1968; Rollins and Donahue, 1975; Stearns, 1976). Community complexity and inter-member networks would further augment community stability, through increased biotic linkages (MacArthur, 1955; Leigh, 1965). As the cryptic community is apparently controlled by largely biotic competitive mechanisms, it is assumed that outside physical perturbations more common in shallow waters would create more community instability. Bathymetrically associated stability and food resource levels result in diversification and dominance of deep cave faunas by a diversity of demosponges. In contrast, shallow caves support the greatest diversity and percent cover of less competitive solitary organisms. This situation may be the result of more frequent physical disturbance, as well as greater fluctuation in food and spatial resources. Such fluctuations would destabilize a cryptic community structure sensitive to such changes (Brock and Smith, 1982; Choi, 1982), and may act to prevent spatial monopolization by competitive dominants. However, such action cannot exert as much influence on community structure here as in the intertidal environment of Dayton (1971). Deeper caves maintain only slightly elevated richness and diversity levels due to demosponge diversification paired with the decline of solitary organisms. Caves at greater depths show intracave community index fluctuations to be considerably "dampened." Observed within-transect randomness in all indices is of a much lesser magnitude at >50 ft sites. This supports the contention of Bretsky and Lorenz (1970) who suggest that general parameters such as depth exert greater control over community diversity that do local substrate heterogeneities. It is noted, however, that substrate heterogeneities in the form of topographic irregularities will randomize community index measurements by a form of localized substrate "overprint."

Observations of within-cave community index trends have been enumerated. Previous sections have referred to three spatial zones within any given cave -- designated apertural, central, and distal relative to the cave opening. These transect locations also correspond to within-cave zones of varying environmental characteristics. Generally, central cave zones remain most stable in all physical respects, and are characteristically dominated by later successional biotas. Greatest fluctuations in current activity and nutrients are expected of apertural zones, while highest sedimentation effects occur in distal zones. The apertural and distal microenvironments of frequent physical disturbance may correspond to zones of fluctuating community indices, and less competitive biotic encrustation. Apertural zones show most strongly fluctuating community diversity and richness indices, as well as encrustation by less competitive organisms. Anomalously high or low percent cover is often found here, particularly at shallower depths.

As suggested above, a progressive biotic stabilization of the apertural zone is witnessed with increased apertural environmental stability afforded by greater bathymetric depth. At greatest depths, the apertural and central zones are of apparently equivalent stability (see Fig. 7a - g). At great depth only distal cave zones show high community index fluctuations, suggesting the continued effect of distal sedimentation, and sclerosponge monopolization there. Distal intracave environments of bathymetrically deep caves are apparently exploited by less competitive sclerosponges, bryozoans, and scattered solitary organisms. Distal quadrat fields filled with only one such specimen results in low diversity/high percent cover anomalies there.

Thus, the distribution of numerical community indices, as well as of particular biota types suggest some control of biotic distribution by physical cave processes. Increased levels of biological community control are seen to occur at greater depths, as well as consistently in central cave zones. In both these areas cryptobionts are most protected from the effects of unpredictable environmental perturbations.

TAPHONOMY: SALT RIVER SUBMARINE CAVES

INTRODUCTION

The term taphonomy, coined by Efremov (1940), encompasses pre- and postburial phenomena which may alter the paleontologists interpretation of the fossil record. Such phenomena necessitate precise study, so that the source and extent of such alteration may be considered in paleoreconstruction. Taphonomic study includes the subdiscipline of biostratinomy, exploring the pre- and synburial relationships between dead organisms and their external environment, and fossil diagenesis, which considers the postburial processes acting on organic remains.

In his review of the nature and structure of paleoecology, Lawrence (1971) stressed that valid interpretations of ancient community relationships require an accurate assessment of possible taphonomic bias. Two types of taphonomic events may alter our interpretation of the fossil record: (1) loss of information through transport from the original community site, and (2) loss of information through imperfect preservation. Depending on the amount of pre- and synburial alteration through selective transport and burial, any fossil assemblage may be designated as one of three types: (1) residual communities, (2) transported fossil assemblages, or (3) mixed faunal assemblages (Fagerstrom, 1964). Chemical diagenesis may then further alter this assemblage through preferential dissolution of certain hard parts, mineral recrystallization, replacement, and other processes. Johnson

(1960) delineated three models of fossil accumulation, including (1) *in situ* by rapid burial, (2) *in situ* by slow burial, and (3) transported by current action. Criteria were also presented to designate which model any given fossil assemblage may fit.

Past literature has supported an extensive information loss through nonpreservation. Particularly pessimistic estimates placed the percent preservability of reefal species at less than 2.5% (Newell, 1959), while Simpson (1960) stated that less than 10% of all once living species are represented as fossils. In a later summary of nine modern faunas, Johnson (1965) suggested that approximately 30% of all living species possess hard parts, and can be expected to become fossilized.

More recently, paleontologists have explored improved techniques in the identification and quantification of taphonomic information loss. Studies have demonstrated that taxonomic differences in life mode and body construction, as well as environmental differences in substrate, predation and energy may selectively destroy the record of certain organisms (Craig and Jones, 1966; Driscoll, 1970; Trewin and Welsh, 1972; and others). Further site-specific quantification of such bias is necessary to determine the extent to which any fossil assemblage represents an accurate sample of the once living community. To address this need, Macdonald (1976) outlined several studies of presently accumulating life and death assemblages in various modern environments and communities. His objective was to predict confidence limits for the accuracy and significance of paleocommunity reconstructions within these biotopes. In general, he reported good confidence in the determination of environmental setting, spatial and temporal distribution, and taxonomic composition in the fossil record. However, more quantitative community characteristics of diversity, equitability, and trophic structure were found to be much less reliably determined (Johnson, 1965; Schopf, 1978). Schopf (1978) investigated recently accumulating life assemblages of an intertidal fauna in Friday Harbor, Washington, and has stimulated further investigation into the effect of habitat, trophic level, and overall life mode on the preferential preservation of particular community components. He contends that the reconstruction of paleocommunity trophic structures is possible, using well preserved trophic levels as key building blocks to whole community reconstruction.

Though investigations of preservation potential, preferential community group loss, and taphonomic bias of community characteristics have proceeded for nearly half a century, few data have been produced on taphonomic aspects of Recent hard-substrate encrusting and cryptic communities. The lack of data probably relates to only recent investigations into modern cryptic environments, much less of ancient ones. Recent works of Jackson (1977), Bonem (1977), Kobluk (1980), Brett and Liddell (1978), and Palmer (1982) have recognized the cryptic communities as a persistent subset of hard substrate biotas through geologic time. Despite the paleoecological and evolutionary significance of ancient hard substrate cryptic communities, relatively little is known of the preservational processes active in modern analogs. As of now, no quantification of taphonomic processes specific to Recent cryptic communities has been produced. The following observations on Recent submarine cave communities of Salt River Canyon, St. Croix, may direct attention to the potential for taphonomic information loss in this community type. General processes of mechanical, chemical, and biological alteration of the original community will be discussed, followed by a critical assessment of potential information loss, and means by which original community characteristics might be reconstructed.

TAPHONOMIC PROCESSES

Mechanical, biological, and chemical processes which actively alter all original communities are active to varying degrees in the submarine cave environment. By virtue of their particularly stable, protected environment, and a biotically dynamic nature, cryptic habitats of Salt River Canyon may be characterized as distinct microenvironments within the overall reefal biotope. Previous sections have shown that organism distribution and diversity maintainance within the cryptic environment is quite dissimilar from that of the more well understood open reef zones. Likewise, general reefal preservation models may not accurately portray within-cave fossilization processes. Particular alteration processes of taphonomic significance may be more or less intense here than in the exposed reefal zones, and, therefore, must be investigated separately. Ultimate burial of cryptic surfaces must also be considered, as it directly affects the fossilization potential of the cryptic biotope.

Mechanical Alteration

Mechanical alteration includes wave and current disarticulation and transport, and belongs within the category of biostratinomy. Unpublished data of Koehl and Jackson suggest current velocity attenuation over short distances within most cryptic environments. Observations here, and recent studies of other submarine cave environments suggest generally low levels of current fluctuation to be characteristic of this environment type (Garrett et al., 1970; Scoffin, 1972b). The encrusting bioadhesive or infaunal nature of most cryptic biotas make them inherently resistant to normal processes of mechanical removal. In an environment of demonstrably low current activity, such mechanical alteration would seem especially rare. Close in situ inspection of encrusting skeletonized faunas reveals no evidence of active current disarticulation, scour, or faceting. The presence of delicate, small cross-sectional diameter bryozoans of erect habit generally indicates low current regimes, although some debate still exists as to the reliability of this paleocurrent indicator (Schopf, 1969, 1980). Sediment floor analyses and bedforms also suggest little current activity sufficient to dislodge and transport most biotas (see paleoenvironment section). In summary, the endolithic or bioadhesive nature of the organism substrate interface reduces the liklihood of current transport. However, the delicate morphology of erect encrusters, and overall sediment floor characteristics are supportive of a lack of significant current activity present. Consequently mechanical transport and breakage are presumably of minor importance to cryptic community alteration.

Chemical and Biological Alteration

Normal chemical destruction of cryptobionts upon death can occur on two levels: (1) early decay and disintegration of soft tissues and skeletal components, and (2) later chemical solution of skeletal components.

Early Diagenesis

Early biochemical alteration occurs in the cryptic environment in three forms: (1) biochemical dissolution of soft parts, (2) bioerosion of hard parts associated with burrowing organisms, including boring bivalves and sponges, and (3) biocorrosion possibly associated with encrusting demosponges.

Dissolution

In any well-oxygenated benthic environment, benthic scavengers and bacterial infestation act quickly and efficiently to remove all traces of dead tissues. Thus, biochemical, or organic dissolution of nonskeletal soft tissue is almost universally observed following necrolysis. In tropical reef environments, a general scarcity of available nutrients makes this process particularly efficient and swift. Only under conditions of rapid burial in biologically sterile sediments do marine fossils with soft tissue preservation seem to occur (Raup and Stanley, 1978). All evidence presented herein suggests that the cryptic environment is tightly constrained by limited food resource availability (Hartman and Goreau, 1970; Buss and Jackson, 1981) as well as other density-dependent parameters. This condition suggests that rapid deterioration and loss of dead soft tissue is most common. The death of soft-bodied organisms such as demosponges and ascidians will be followed shortly by decay and taphonomic loss.

Bioerosion

The term bioerosion has been applied to the process of removal of consolidated skeletal or lithic substrate by the direct action of organisms (Neumann, 1966). Reefs and carbonate coastlines have been found particularly susceptable to destruction by such boring activity (Otter, 1937; Ginsburg, 1953). Warme (1975) has described the most common bioeroding marine organisms known through geologic time, including fungi, algae, sponges, sipunculids, polychaetes, gastropods, bivalves, and echinoids. Borings in recent coral reef environments compare well with ancient examples. Very analogous borings have been observed in Middle Ordovician hardgrounds (Palmer and Palmer, 1977; Brett and Liddell, 1978). Actual clionid sponge borings are observed to be extremely common in less ancient Middle Jurassic reefs (Fursich, 1979). Therefore, since at least the Jurassic, borers very similar to those of this study have existed. Boring organisms have figured prominently in the destructional processes affecting preservation of biologic reefs (Warme, 1977).

Most borers penetrate for their protection, but in the process they sculpt and bioerode exposed substrates. This process simultaneously creates increased surface area for further cryptofaunal encrustation, and sedimentary particles for ultimate cavity infilling (Goreau and Hartman, 1963; Warme, 1977). Data of Warme and Marshall (1969) suggest that biologically mediated mechanical and chemical erosion may penetrate carbonate substrates in excess of 10 cm, whereas chemical erosion alone rarely penetrates more than one centimeter. The processes of mechanical, chemical, and biological erosion act in concert. Deep burrowers allow chemical erosion to penetrate to greater substrate depths. In addition, extensive boring of cryptic substrates may allow for microenvironments of high pCO_3 - such biotic effects might create anomalous dissolution patterns in very restricted, small cavities (Garrett, 1969).

All cave substrates observed in this study were found to be heavily bored. Most common borers included lithophagid bivalves, sabellid polychaetes, and clionid sponges. As photographic data only allowed quantification of macroscopic and surficial organism bioerosion, few data are presented on microborer and infaunal bivalve infestation.

Previous investigations of microbial infestation of dead substrates in St. Croix suggest that microboring is active within Salt River caves (Perkins and Tsentas, 1976). Microborings are known to increase the efficiency with which the larger macroboring biotas colonize hard substrates (Golubic et al., 1975). It was noted that lithophagid-like burrows are abundant at all sites, particularly in the central and distal areas of all transects. Whether these cavities are now occupied by living lithophagids is undetermined; however, the destructive effect of such action is unquestioned.

Transect photos and sediment samples were closely examined for evidence of sponge bioerosion. Cleared quadrats commonly show distinctive patchy concentrations of boring sponges deep within cave substrates. Most borings were probably the work of members of the family Clionidae. The limitations of photographic resolution probably lead to gross underestimation of the abundance of Cliona as noted in Table 4 a - g. It has been shown that at least two additional families of "burrowing" sponges (Fam. Adociidae and Fam. Spirastrellidae) are active in this region. The adociid Siphonodictyon has been observed within Salt River sites as living specimens as well as diagnostic deep excavations (Warme, 1975).

Sedimentary evidence for clionid boring in particular is presented in Table 1, a floor sediment constituent list of site IK50A. The floor sediments are rich in clionid chips, which comprise much of the abundant fine silt and mud-sized fractions. Site IK50A maintains the lowest areal coverage of demosponges, and may represent a site of minimal bioerosive activity. Such chips are easily identifiable with the light microscope, and their morphology appears identical to the C. lampa chips of Rutzler and Rieger (1973, p. 150, fig. 4). Large quantities of sediment of clionid boring origin may contribute greatly to sediment production in this environment, as well as others (Neumann, 1966; Rützler and Rieger, 1973; Futterer, 1974). In addition to micro-chip evidence, many sand-sized and larger floor sediment constituents were observed to have characteristic clionid boring traces.

Clionid sponges were observed to attack preferentially the nonliving, tissue-free portions of living solitary corals such as Tubastrea. Solitary corals have frequently been documented as highly susceptible to boring sponge infestation, owing to a large proportion of tissue-free surface area relative to colonial corals (Goreau and Hartman, 1963; Scoffin, 1972b; Bak, 1976). Indeed, clionid infestation was not observed on specimens of colonial Madracis. In addition, solitary coral (e.g., Phyllangia(?)) fragments sampled from cave floor sediments showed extensive evidence of clionid boring. Preferential attack and disarticulation of solitary corallites relative to colonial forms may ultimately result in a reduced in situ record of their presence in fossilized reefs. The hard skeletal substrate "islands" supplied to reefal talus through bioerosive weakening may serve a "facilitative taphonomic" role as outlined by Kidwell and Jablonski (in press). The constant supply of bioeroded material to forereef talus effectively promotes the outward progradation of the reef into deeper waters (Goreau and Land, 1974).

Due to the lack of taxonomic precision in the identification of clionids, absolute abundance and bioerosive activity calculations are impossible here. However, an admittedly crude estimation of demosponge boring activity can be made if demosponge areal cover is used as an indication of the relative abundance of boring types (Fig. 6) Demosponge areal coverage increases markedly at >50 ft depths, with a maximum peak of 54.1% at 75 ft sites. Increased substrate bioerosion is therefore predicted to be generally higher at greater depths. Such predictions are supported by demosponge observations in Jamaica at greater depths by Hartman (1973, 1977). Mean percent cover of 43.5% in Salt River Caves implies high levels of demosponge bioerosion in this environment. Demosponge density varies markedly over each transect, from 0 - 100% coverage per quadrat. No preferentially enhanced activity at any particular cave zone is inferred. Improved taxonomic resolution and observations at greater depths may more precisely assess demosponge bioerosive activity, and consequent substrate destruction.

Biocorrosion

Biocorrosion has not been previously documented in the literature, and represents a corrosive/erosive process, seemingly associated with demosponge overgrowth. It is here defined as the surficial structural dissolution of calcareous substrates beneath demosponges. The removal of soft tissue enabled observation of numerous biocorroded surfaces on quadrats in all cave sites (see Fig. 10 a and b). The most prominent result of biocorrosion is a loss of fine septal detail on solitary corallites which have been overgrown by demosponges. This is a qualitative observation only; the possibility of prior microboring or boring sponge degradation of the "biocorroded" skeletons cannot be ruled out. What is apparent, is that areas now covered by non-boring demosponges are apparently corroded to some preferential degree, relative to uncovered areas. The actual mechanism of substrate degradation is presently unknown, but may be destructive bioadhesion at the demosponge/substrate interface. An alternate possiblity is that rapid demosponge overgrowth of dead or weakened corallites precludes the cementing effects of coralline algal overgrowth. This would result in the uncemented structures being more susceptable to normal dissolution or microboring processes. However, it is somewhat unlikely that endoliths would thrive beneath a thick cover of encrusting demosponge. Varying degrees of biocorrosion have been observed (Fig. 9).

Three observations may distinguish this phenomenon from previously described bioerosion: (1) it is not preferential to dead substrate, as demosponges actively overgrow living hard biotas; (2) it is not associated with boring demosponges; and (3) its effects seem only surficial.

In previous sections, the dominance of demosponges in the cave environment has been documented. Competitive attributes of colonial faunas, and especially demosponges, results in their later successional stage encrustation over earlier pioneer biotas (Jackson, 1977; Jackson and Winston, 1982; Russ, 1982). Therefore, biocorrosive effects of demosponges are suggested to be at a particularly high level within the mature cave environment.

As described earlier, within-transect demosponge abundances are generally random, though central areas are most consistently covered. All zones are probably equally susceptable to demosponge biocorrosion. Greater differences are found when bathymetrically associated demosponge abundances are considered. As demosponge density increases greatly from 50 ft to 75 ft, the most obvious biocorrosion effects may be witnessed at greater depths. Observations at greater depth by Hartman (1973, 1977) again support continued increases in such "biotic erasure" with water depth.

Ancient benthic communities encrusting hard substrates are believed to have supported similarly abundant demosponge populations, largely on the basis of trace fossils and preserved spicules. A review by Palmer (1982) suggests diverse demosponge assemblages may have been established on hardgrounds as early as the Middle Ordovician. This suggests in turn, that similar ancient environments may all have suffered some loss in fine structural detail due to early biochemical processes, specifically biocorrosive and bioerosive effects. Indeed, similarly corroded fossils (e.g., crinoid holdfasts with "smoothed" surfaces) have been reported on ancient hardgrounds (Brett and Liddell, 1978). Data presented here further suggest that the extent of such biotic erasure may be positively correlated with bathymetric depth. Therefore accurate assessment of taphonomic information loss through demosponge encrustation should take relative depth and stability into consideration as relevant factors.

Burial

The dynamic processes of reef destruction by growth inhibition and boring have been outlined by Zankl and Schroeder (1972) and Scoffin and Garrett (1974). Constructive or destructive actions of organisms within the cryptic biotope have been designated in the description of cryptobionts (see ecology section). Though reefal biotas may be well documented and their functional roles understood, their patterns of distribution and activity are complex. Constructional and destructional processes are largely a function of abundance and activity rates, which are presumably dictated by ambient environmental parameters such as light, nutrients, stability, etc. The competing processes of reef construction and destruction play critical roles in determining the final preserved reef structure (Scoffin, 1972a). As final burial represents a crucial step in the preservation of ancient cryptic communities, it becomes important to consider the sedimentary processes which are actively filling Salt River caves.

Overall Salt River Canyon sedimentation characteristics have been described by Hubbard et al. (1981). Of greater interest are the sedimentary characteristics of the within-cave environment, as discussed previously (Fig. 5 and Table 1). These data suggest that in situ sedimentary particles dominate sedimentary floor constituents, with evidence of minor inward transport. Net movement of cave sediments appears to be outward. Diagramatic cross sections in Figs. 4a,b show the cave sediment apron at all sites. Fine sediments derived from the cave walls are supplied to outer sediment chutes, for transport down-canyon. It is clear from productivity estimates of similar recent reefs (Land, 1974) and reef age determinations of Hubbard et al. (1981) that these caves would have been infilled had not net transport been outward. The caves are characterized by slow, quiet biological infilling processes (Swinchatt, 1965), though ultimately controlled by gravitational slump of sediments out of the aperture. Generally low canyon current velocities of ≤5 cm/sec, with seasonal maxima of approximately 50 cm/sec (Hubbard et al., 1981) make catastrophic burial through storm activity extremely unlikely.

It is, therefore, suggested that the sediments in the Salt River caves are examples of recently accumulating "condensed facies" (Fürsich, 1978). As such, their preserved communities tend to be highly time-averaged samples, rather than instantaneous "snapshots." In addition, mature cryptic biotas encrust most successfully in areas most removed from sedimentation effects. This is a general characteristic of Salt River cave environments, though certain variations in sedimentation patterns within cave microenvironments have been suggested. Fewer organisms survive at distal and apertural cave zones, while most diverse assemblages appear centrally. In the central zones, cave dwelling biotas are buried extremely gradually, probably over many thousands of years. Scoffin (1972b) has observed that similarly slow burial of patch reefs may preferentially preserve only sediment-tolerant latecomers to that reef biotope. Likewise, the slow increase in sediment buildup in Salt River caves probably results in the preservation of only the last surviving organisms, those associated with high physical stress. Thus, in the absence of quick burial, the previous mature, biologically accomodated cryptic community is "hidden" by the later physically controlled, highly sediment-tolerant community.

These cases of slow cave community burial are in direct contrast to the normally rapid burial processes observed for co-occuring coral plate cryptofaunas. The oldest attachment sites of foliaceous coral plates are known to be extremely susceptable to bioerosion. This highly vulnerable connection to the reef proper is preferentially attacked by boring organisms, making the plate structure more susceptible to breakage by storm activity (Scoffin, 1972b; Mah and Stearn, 1983). Winter storm surges active in Salt River Canyon could effect an annual clearing of the weakest plate structures, resulting in their transport and ultimate burial in deeper, finer sediments. Quick burial would stop most biochemical destruction processes which would otherwise alter the attached cryptic community. This scenario results in the burial of relatively unaltered assemblages of normal plate communities, and would result in their preferential preservation.

Late Chemical Alteration of Hard Parts

Skeletonized organisms represent the vast percentage of potential fossils here, as in other biotopes (Bambach, 1977; Muller, 1979). Even with reduced susceptibility to early biochemical destruction, hard skeletal components are generally preserved only under conditions of rapid burial and limited exposure on the substrate surface. The preservation of cryptobiontic body fossils depends to a large extent on the original composition of skeletal components and the post-depositional diagenetic environment (Matthews, 1974). Many authors have attempted to construct a hierarchical sequence of relative skeletal composition solubility (Chave, 1964; Milliman, 1974; and others). Although some conflicting opinions exist as to the precise ordering of stabilization and precipitation phenomena in normal marine waters, most authors agree that high magnesian calcites (10-15 mole % $MgCO_3$) and aragonite are most soluble, while low magnesian calcites (<10 mole % $MgCO_3$) are least soluble (Milliman, 1974).

Land (1967) and Matthews (1974) address the questions of preservability of skeletal carbonates, and reef associated processes of diagenesis, respectively. In particular, Land (1967) notes generally enhanced reaction rates of skeletal aragonite and Mg- calcites, as well as phylum-specific reactivities of skeletal material. Matthews (1974) has suggested that an organism's life processes may effect early diagenetic destruction of the substrate which it occupies. Moreover, the same author notes the characteristically poor preservation of reefal limestones through later diagenesis. High porosity and permeability associated with cavernous, bored reefal substrates would allow easy percolation of corrosive waters upon late diagenetic exposure to the marine phreatic or vadose zones. The dissolution of high-Mg calcitic and aragonitic cryptobionts may ultimately promote dolomitization. Diagenetic dissolution and dolomitization are characteristic of many well known Paleozoic reef complexes (Newell et al., 1953), and have also been observed in subaerially exposed Miocene reefs of St. Croix and Jamaica (W.D. Liddell, pers. comm., 1982). The emergence of aragonite as a major skeletal building block did not occur until the middle Triassic. Skeletal aragonite and magnesian calcite dominate skeletal components in modern cryptofaunas. In view of this, more extensive diagenetic information loss through skeletal dissolution may be expected for at least post-Paleozoic cryptic communities. However, the effects of time-dependent late diagenetic alteration make net potential skeletal preservation of ancient cryptic communities a complex problem.

Summary

In summary, evidence suggests rapid early dissolution of all soft tissue upon death of any cryptobiont. As many of the dominant cryptic space occupiers are unskeletonized, this may critically changė apparent colonization in fossil examples. Later, long term, diagenetic alteration may be preceeded by the active processes of bioerosion and biocorrosion identified in Salt River caves. Both bioerosion and biocorrosion may be bathymetrically skewed forms of early biogenic alteration. Bioerosion's extensive role in the maintainance, destruction, and ultimate burial of the cave environment has been emphasized here. Biocorrosion may promote surficial erasure of skeletal structures. Bathymetrically associated increase in sponge bioerosion and biocorrosion may be of particular importance to cryptofaunal taphonomy.

Burial processes associated with the cave environment are slow. They will tend to produce infrequent time-averaged assemblages of the skeletonized component of original communities. Rapid burial of coral plates may result in a more abundant and precise record of skeletonized cryptic community members. Such divergent burial processes may be of taphonomic consequence. Lastly, the vulnerable mineralogy of post-Paleozoic cryptobionts, paired with the highly active reefal diagenetic environment, imply that even skeletonized structure may be easily destroyed through time.

TAPHONOMIC EFFECTS

In the previous section, processes of taphonomic information loss have been described with respect to their activity and distribution within the submarine cave environment. Non-random alteration processes have been observed to preferentially destroy the record of certain community members, particularly those with little skeletal structure, or more exposed exoskeletal surface area. Chemical or mechanical processes are thought to have been equally active in cave environments throughout geologic time. In addition, previous paleontologic investigations have described apparently conservative taxonomic evolution rates in stable environments through geologic time (Bretsky, 1969; Bretsky and Lorenz, 1970). Based on indirect evidence supplied by ancient and recent trace fossils and sediment floor constituents, it is not unreasonable to suggest that most biologic processes now active in the cave environment have been active in ancient cryptic sites. Examples of well preserved cryptic communities in the fossil record demonstrate great similarity with modern counterparts. Most workers now contend that particular community members may have changed very little from the lower Paleozoic to the Recent (Brett and Liddell, 1978; Kobluk, 1980; Palmer, 1982; and others). However, the absolute abundance of boring organisms such as clionid sponges may have been at reduced levels prior to the Mesozoic (Palmer, 1982). Generally then, processes of cryptic community alteration can be qualitatively extrapolated back to Paleozoic cave dwelling biotas. In the following sections, the effect of these processes on quantitative and qualitative measures of ancient coelobiontic community structure is assessed.

Areal Coverage Alteration

In describing the ecology of the recent cave community, percent coverage, richness, and dominance diversity were used as indices of community density, diversity, and thus overall maturity. Percent cover may be equated to the extent of substrate utilization and spatial competition present in the cave community. In further discussion, all "hard" skeletonized organisms will be assumed to be preservable -- though this may be a tenuous assumption (Schopf, 1978), it seems necessary. Due to the generally high areal percent coverage of "soft" nonskeletal organisms on the cave roofs, overall loss through biochemical decay and scavengers is expected to be great. Figures 7 a - g and figure 8 present percent cover of total and hard organisms within the individual transects, and averaged at four bathymetric depths, respectively. It is noted that skeletonized coverage contributes very little to total organism coverage, and, moreover, that it seems to fluctuate independently. Within-transect information loss through nonpreservation is therefore generally very high. Therefore no obvious gradient in information loss is observed on the quadrat level with respect to distance into each cave. Only at 105 and 125 ft sites, where large skeletonized sclerosponges occur, does hard coverage approximate total coverage. Other high fluctuations may be due to small-scale sampling intervals and quadrat sizes, and the randomizing overprint of topographic irregularity.

In general central, stable, transect positions rarely display open space, and characteristically support consistently higher coverage of soft biota such as demosponges. Transect end points most often maintain larger quantities of skeletonized solitary organisms and sclerosponges. In central zones we may expect a greater measure of information loss through nonpreservation of abundant soft biotas. Anomalously dense patches of soft or hard organisms predominate at less stable apertural and distal portions of each cave. This phenomenon will remain unrecognized in a fossilized community transect, if such patches are of unskeletonized biotas.

Within transects small scale heterogeneities in percent cover information loss are smoothed when whole transect means are averaged at different water depths. Figure 7 a - g gives mean information loss data of each transect, while figure 8 shows this same statistic averaged at each depth. Good correspondence in mean percent loss between different cave transects at equivalent depths seem to indicate some bathymetric control over this statistic. The mean percentage of areal cover information loss over all depths is 85.3%; only 14.7% of original community areal coverage may be "apparent" or observable in the fossil record over this depth range (see Fig. 9).

Hard organism proportional coverage increases only slowly with depth, even if one considers the contributions of large areal extent sclerosponges at 105 and 125 ft. (It should be recalled here that the above calculations exclude coralline algal cover from the skeletonized category -- instead it is considered to be passive open space.) Areal coverage of soft-bodied organisms doubles between 50 and 75 ft sites; then seems to remain generally stable at this high level down to 125 ft depths. The combination of slight skeletonized organism increase, and large soft organism expansion results in a slight net decrease in the percentage of preservably colonized area between 50 and 125 ft. Particular depth values for percent preservable of the original cave areal cover are as follows: 50 ft. = 17.6%, 75ft. = 11.2%, 105 ft. = 15.3%, and 125 ft. = 17.4%. It is noted, however, that without the appearance of deep-dwelling sclerosponges, percent loss of areal cover information would be much greater.

The taphonomic consequences of an increasing soft:hard areal ratio between shallow and deep sites would be increased proportions of apparently unoccupied space on the preserved ancient substrate. Whether this space was in fact unoccupied in life or actually covered by nonpreservable organisms is a difficult question to answer. In the absence of other sources of information on soft biota presence, Palmer and Palmer (1982) regarded such apparently open hard substrate as truly uncolonized area, but based on modern data, it is highly unlikely that there was much unoccupied space. Some forms of alternate paleoecological evidence for soft biota presence are observed, even in Recent Salt River caves covered mainly by soft organisms. Such kinds of alternate evidence as found in recent Salt River substrates are presented and discussed in a later section.

Richness Alteration

Species richness has commonly been considered the most valid measure of community diversity in paleoreconstruction (Johnson, 1965; Macdonald, 1976; and others). Richness determination requires only partial preservation of any community member's skeleton, trace fossil, or other indirect evidence of its presence (Dodd and Stanton, 1981).

Patterns of skeletonized organism richness seem inconsistently related to patterns of total richness on the fine quadrat scale (Fig. 7 a - g). Only a rough shadowing effect is noted, though this too is inconsistant. This may to be a product of small-scale substrate heterogeneity and sampling size, and the extent to which the broad categories of "soft" and "hard" organisms respond to microtopographic irregularities. The fine scale complexity of the hard to total richness relationship prevents the use of hard richness as a reliable indicator of once present total richness on the quadrat level. As soft organism richness and percent cover appear to be generally higher and more stabile in central zones, the central cave may yield the highest levels of information loss. However, more central zones generally maintain higher richness of skeletonized biotas (particularly corals) as well, and therefore central richness may be preservable in the fossil record.

An environmental mean of preservable richness of 3.40 species per quadrat is observed; this compares with an actual mean richness value of 9.0. Thus, a mean loss of 62.2% of original community richness per quadrat, or an apparent richness per quadrat only 37.8% that of the original community results. Total community richness exhibits some evidence of a slight overall increase with depth, from 7.8 to 9.4 species per quadrat. A notable richness peak is observed at 75 ft, corresponding to an increase in both soft and hard organism richness there. Table 3 shows bathymetric means of preservable richness to be generally stable from 50 - 125 ft, while those of soft biota show a net increase over the same interval. In concert with data on percent cover change, we observe increased significance in the underestimation of taxonomic groups with increasing depth. This is simply due to the observed increase in soft organism richness between 50 and 125 ft. Although sampling at greater depths is required to establish this as a significant trend, these data are supported by studies at greater depths in structurally and environmentally similar environments of the Jamaican north slope (Hartman, 1973, 1977; Goreau and Hartman, 1963; Goreau and Land, 1974; Land and Moore, 1976; Lang, 1974). All of these workers observed increasing areal coverage, as well as diversification of soft demosponges in the forereef at 245 ft and deeper. In contrast, most commonly observed skeletonized taxa (e.g., corals and serpulids) decrease in areal abundance with bathymetric depth. Rare, but preservable sclerosponges are found to become more common at depth, as is discussed earlier. Precise bathymetric levels of preservable original community richness per quadrat are as follows: 50 ft. = 39.4%, 75 ft. = 36.6, 105 ft. = 37.7%, and 125 ft. = 33.0%. This suggests that an increased loss of overall richness preservation is characteristic of greater depths.

To more realistically assess overall community richness loss, individual transects cleared of nonpreservable soft tissues were observed. By including the overgrown skeletons of previous successional stage hard organisms, this sample more closely approaches that of the actual whole community skeletonized organism richness (see Fig. 9). Whereas richness characteristics of skeletonized _originally_ visible organisms produced only 37.8% preservability values, use of _cleared_ richness increases the preservable organism levels to 52.2%. In paleoecological investigations, it is this sample which would actually be measured as an indication of species richness in the original skeletonized community. The increase in preservable richness underscores the condensed nature of encrusting assemblages.

Dominance Diversity Alteration

Past paleoecological studies demonstrate that reconstruction of original community diversity is extremely susceptible to error due to poor preservation of nonskeletal organisms (Lawrence, 1968; Bambach, 1977; Macdonald, 1976; Dodd and Stanton, 1981). However, an assessment of its usefulness in reconstruction of ancient cryptic communities in particular is of great importance.

Figures 7 a - g and 8 present data on diversity levels within transects and averaged for each water depth. Again, microtopographical irregularities are suspected to blurr diversity trends. No correlation was observed between preservable and total diversity at the quadrat level. Soft-bodied organisms may totally dominate some quadrat samples, which therefore have very low levels of preservable diversity. Diversities are consistently high in central cave zones. We may again generalize that high diversity of soft-bodied organisms in central areas may lead to consistently high nonpreservation, and consequently high diversity information loss. Nevertheless, these central zones are also characterized by higher, more stable diversities of skeletonized biotas than transect end points. Thus, preservable diversity of paleontological interest should be higher centrally, despite the high degree of information loss due to unskeletonized organisms there. Lower preservable diversities found aperturally and distally may allow correct interpretation of these zones as of characteristically lower overall diversity. Erratic, generally lower diversity end points will be seen to grade into more stable, higher diversity central zones on the basis of preserved, skeletonized biotas alone.

When all samples of skeletonized organism diversity are considered, a mean preservable diversity of 0.249 per quadrat is observed over the entire environment. This corresponds to a mean loss of 57.6% of original community diversity information per quadrat; or an apparent diversity level only 42.4% that of the original community. Figure 8 illustrates bathymetric trends of nonpreservable, preservable, and whole community diversities. Diversity levels of nonpreservable organisms tend to increase with depth, though somewhat gradually. In contrast, hard diversity generally decreases gradually with depth, from a high at 75 ft. Whole community diversity is relatively stable over the 50 - 105 ft range as a result of these competing trends, though a slight bathymetric increase is shown. Thus, total dominance diversity trends are observed to parallel roughly those of richness over the same bathymetric gradient. While a few more morphospecies are added with greater water depth, levels of spatial partitioning remain generally constant. However, specific skeletonized organism diversity trends, when compared to total organism trends, again suggest an increasing information loss with depth. This loss is due to nonpreservation of soft organisms which diversify between 105 and 125 ft. At 105 ft, hard diversity declines. Details of this phenomenon show that the nonpreservable/preservable diversity change at this point is mainly due to demosponge diversification, and decline of corals. Prior to the sponge diversification at 105 ft, both preservable richness and diversity vary similarly with nonpreservable richness and diversity (see Fig. 8). Only beyond 105 ft does the diversification of unskeletonized organisms increase markedly, and exceed the rate of skeletonized organisms decline in diversity. Individual bathymetric levels of dominance diversity preservability are as follows: 50 ft. = 44.2%, 75 ft. = 45.1%, 105 ft. = 40.2%, and 125 ft. = 38.1%. This suggests elevated levels of whole community diversity information loss with increasing bathymetric depth, probably at an accelerating rate. This extrapolation is consistent with observations of Hartman (1973, 1977) and Lang (1974) in Jamaica.

Summary

The relatively low proportion of skeletonized cryptic organisms, slow burial processes, and continual early and late diagenetic destruction suggest that cave-dwelling biotas should have a particularly poor fossil record. Great alteration of apparent percent coverage, richness, and dominance diversity as a result of non-preservation of unskeletonized organisms is expected. Small-scale variations in the proportion of hard- and soft-bodied organisms appear to be of no great significance in paleocommunity studies, especially on topographically heterogeneous surfaces. Perhaps more general and larger-scale variations are discernable in fossil examples, if they are considered along a probable environmental gradient. In any given cave, highest levels of taphonomic information loss seem characteristic of central cave zones, which support consistently dense and diverse assemblages of unskeletonized organisms.

When transect means for caves at four depths are averaged, indices of percent cover, richness, and dominance diversity based on hard organisms only are underestimated in the amount of 85.3%, 62.2%, and 57.6% respectively. Complementary percent preservability estimates are portrayed by figure 9. In the absence of alternate information on soft organism presence, these indices are susceptable to selective forms of bathymetrically associated taphonomic bias. In the case of richness and dominance diversity, progressive taphonomic information loss is seen to accompany increasing water depth, especially beyond 105 ft levels. At greater depths most commonly observed skeletonized taxa become scarce. Only skeletonized sclerosponges increase at depth. Even with sclerosponge presence, this expansion of preservable organisms is overshadowed by rapid diversification of soft organisms. The use of cleared transects to estimate paleontologically observable hard organism richness results in predictably lower information loss. As many skeletonized organisms are well cemented, this may be a more realistic estimate of observable original skeletal richness. It is, however, a time-averaged sample.

The bathymetric increase in the abundance of large sclerosponges maintains preservable areal coverage information at greatest depths at levels approximately equivalent to those at the more shallow 50 ft depth. In their absence, a larger bathymetrically related information loss would result. This is be seen at 75 ft sites, where soft diversification occurs prior to sclerosponge appearance (Fig. 9). At that point, preservable information on areal coverage is at its lowest level.

ALTERNATE SOURCES OF PALEOECOLOGICAL INFORMATION

Data presented in previous sections point to the high degree of taphonomic bias which is likely to be present in the reconstruction of submarine cave paleocommunities. In order to remove some degree of taphonomic overprint in fossilized benthic communities, Lawrence (1968) suggested the use of "redundant evidence." Such evidence considers alternate forms of preservable data which can indicate the original presence of otherwise unpreservable organisms. Evidence of this sort has been used extensively, and with good results in many paleocommunity reconstructions (Warme, 1975; Scott, 1978; and others).

Preservable redundant evidence of soft organism presence is presently accumulating in three forms in the observed cave biotope. These include preservable biotic edge interactions, trace fossils, and sedimentary skeletal components.

Biotic Interactions

Jackson (1977, 1979, 1981) has observed examples of preservable biotic interactions between skeletonized encrusting organisms and nonskeletonized or poorly skeletonized fauna. The interface between nonskeletal and skeletal forms may yield preservable evidence of both original soft biota presence, and the nature of the interaction itself. While observing competitive interactions of bryozoans and other cryptobionts, Jackson (1981) notes three particular morphological responses of bryozoans to the threat of overgrowth, all of which are preservable: (1) redirection of zooarial growth, including recurving, (2) formation of nongrowing edges, and (3) building of specialized barriers to prevent overgrowth, including upturned edges and "giant" buds (Jackson, 1979b). Atrophication and necrolysis of overgrown edges would result in preservably "stunted" zooecia. Such evidence may allow significant statements concerning contemporary soft organisms, as well as the relative importance of spatial competition in the original cryptic community.

Unfortunately, due to the relative scarcity of encrusting cheilostomes in Salt River caves, as well as the limits of photographic resolution, little macroscopic evidence of bryozoan competitive interactions is observed. Observation of the above zooarial modifications would require destructive sampling of cave substrates, and transferral of the samples to the surface for microscopic observation. Such sampling was beyond the scope of this project. Preservable bryozoan modifications were initially assumed to lie beneath the mature surface of cave biota. However, cleared transects show little significant increase in the abundance of bryozoan encrustation even at these earlier colonization stages. This could be the result of low original bryozoan coverage, subsequent biotic erasure (bioerosion or biocorrosion), or destructive clearing techniques which result in no preservable examples of bryozoan competitive interaction. Preservable edge interactions between corals and demosponges were observed upon soft tissue clearing procedures. Colonies of <u>Madracis</u> which bordered on demosponges were seen to produce upturned edges. In most cases this barrier proved to be of only minor deterrence to ultimate overgrowth by the demosponge. However, the evidence of this earlier event remains for inspection.

Abundant interactions of skeletonized serpulid worms with unskeletonized demosponges are preservable and widely observed in this environment. <u>Spirorbis</u> tubes, which normally spiral parallel to the substrate, abruptly deflect perpendicular to the surface in areas of high demosponge overgrowth. In many cases large numbers of <u>Spirorbis</u> apertures were observed to extend upward and "through" the overgrowing demosponge cover. This advantageous elevation of aperture away from the substrate has been previously documented by Hadfield et al. (1972), and Stebbing (1973). It represents the "escape in size" strategy of these solitary animals to avoid colonial overgrowth

(Jackson, 1977). This mechanism is also employed by the solitary corals Tubastrea and Phyllangia, which continuously elevate themselves away from incipient overgrowth. In addition, a marked tendency to clump feeding apertures in dense monospecific stands is observed in solitary corals here, and in many other solitary organisms elsewhere (Wilson, 1968). This phenomenon is termed "aggregation" by Jackson (1977), and is presumed to reduce the probability of successful settlement by larvae of other species, and also inhibit overgrowth by adjacent biota.

No evidence of predation in the form of grazing by echinoids, gastropods, or fish was found in any cave site. In some cases such activity would be expected to be preservable. No preservable evidence of predation in the form of grazing trails or scrapes is documented here. Though this may again be due to the limits of photographic resolution, macropredation is not suspected here.

Trace Fossils

Through the life processes of feeding or seeking shelter, some soft-bodied organisms may leave evidence of their presence in the form of preservable trace fossils. The great value of trace fossils in the reconstruction of ancient communities and environments has been recognized, and literature on the subject has expanded rapidly in the past two decades (Crimes and Harper, 1970, 1977; Hantzschel, 1975; Seilacher, 1978; Frey, 1975). The recognition of taxonomically and environmentally specific trace fossil types is particularly useful in the reconstruction of ancient cryptic communities, as the majority of cave dwellers may have been unskeletonized. Borings produced by endolithic organisms may give excellent indications of both their presence and relative importance to the original cryptic communities (Warme, 1975). Many studies have come to rely heavily on the use of infaunal boring organism traces in the reconstruction of ancient hard substrate communities. Kobluk et al. (1978) and Palmer (1982) have demonstrated that the boring habit extends back to the Lower Cambrian. Further, it has played an active role in the maintainance and destruction of the reef habitat since at least Middle Triassic time (Otter, 1937; Warme, 1977). Studies of deep water cryptic environments of Jamaica and St. Croix have shown boring organisms to be particularly important to erosive and sedimentation processes in deep forereef zones (Goreau and Hartman, 1963; Hartman, 1973, 1977; Lang, 1974; Budd and Perkins, 1980). Similar activity is characteristic of some shallow water environments (Neumann, 1966; Warme, 1977). Information losses in deep environments may be partially ameliorated by extensive boring activity and consequent trace fossil production there. Such traces may yield information on depth, energy, and environmental stability characteristics (Budd and Perkins, 1980). The fine structure of the clionid/substrate interface has been determined to be taxonomically distinctive among various species of clionids by microscopic methods (Rutzler and Rieger, 1973). This discovery may allow refinement of clionid species taxonomy in ancient carbonate substrates such as cryptic habitats (Lawrence, 1969).

Sediment Constituents

The last form of alternate evidence of original soft biota presence is provided by the sedimentary infilling of cave floors. Constituent and textural analyses have been used extensively in modern carbonate sedimentology and are known to reflect many biological and mechanical parameters of the depositional environment (Ginsburg, 1956; Milliman, 1967). However, some authors have demonstrated the susceptibility of biogenic sedimentary components to breakdown through biological and mechanical means (Ham and Pray, 1962; Swinchatt, 1965). Due to unpredictable levels of skeletal breakdown in various environments, microscopic skeletal elements derived from largely soft-bodied forms such as sponges should not be used as precise indicators of original relative faunal abundance. Statements on trophic group distribution as well are highly susceptible to bias through differential mechanical transport and biologic attack, largely as a function of environmental energy (Chave, 1964; Swinchatt, 1965; Scott, 1978).

Previously discussed sedimentary characteristics of the cave environment (see sedimentation section) suggest that the great majority of cave floor sediments are autochthonous, with limited dilution by inward transport of outside sediments. Constituent analyses of cave floor biogenic sediments may give good indications of particular organisms which inhabited the cave environment, without reference to quantitative dominance patterns. Such analyses reveal the presence of large quantities of clionid chips as well as large skeletal fragments individually bored by Cliona. Clionid chips, as well as diagnostically bored autochthonous skeletal fragments may yield preservable evidence of the activity of past boring sponges (Lawrence, 1969; Futterer, 1974). However, the majority of cave dwelling demosponges are not boring types, and as such produce no diagnostic domichnia or bioeroded debris. Such nonboring demosponges may be identified on the basis of tetractine siliceous spicules. Such spicules are abundantly accumulating in cave floor sediments, but may not survive a post-depositional diagenetic environment characteristically undersaturated with respect to silica (Milliman, 1974). Clearly, then, quantitative abundance may not be measured with accuracy on the basis of such data. The presence of such forms alone represents a valuable bit of paleoecologic information. Another major soft-bodied faunal constituent with internal structural elements are the ascidians. The aragonitic sclerites of ascidians are easily identifiable and present cave floor sediments (Table 1). They may yield valuable evidence of ascidian presence if their aragonitic composition is not diagenetically destroyed.

In addition to the presence of skeletal elements of predominantly soft-bodied cryptofauna, epi- and/or meiofaunal associates are found within cave sediments. Large numbers of porcelaneous and hyaline benthic foraminifera, ostracodes, and microgastropods are identifiable and structurally intact. Such faunal associates, if preserved, may yield useful information for environmental reconstruction through specific environmental tolerances or possible stable isotope analysis.

Size-frequency characteristics of the cave floor sediments have been shown to reflect quiet biological production and breakdown processes. Positive skewness, fine sand angularity, and less extensive sorting reflect the low mechanical energy available to rework sediments in this protected environment. Such sedimentary characteristics of cavities contrast with sediment chute samples, and allow for better differentiation between the two subenvironments (see figures 5a and b).

Summary

Biotic interactions between skeletonized and unskeletonized biotas may be a valuable source of paleoecologic information on presence of unpreservable faunas, as well as the levels of community spatial competition. However, such preservable interactions may not always be common in environments which generally restrict the proliferation of skeletonized community members -- such as submarine caves. The more abundant colonial taxa may supply such information through the anomalous perturbation of their growing edge. Trace fossils serve a most important function of filling information gaps created by nonpreservation, and may specifically add to species richness data through unique trace fossil patterns. Sedimentary particles of previous structural function in unskeletonized organisms are abundant, and may provide similar information on nonboring sponges and ascidians. Such data must be used with caution, owing to selective biochemical breakdown processes which may be extensive in this low energy environment. Faunal associates as well as textural statistics may yield environmental information, suggesting the presence of certain unpreserved biotas with similar environmental tolerances. All such information is extremely valuable in an environment which may provide a body fossil record for only 38% of it original inhabitants.

PALEOECOLOGICAL AND EVOLUTIONARY PERSPECTIVES

LIFE HISTORY AND SUCCESSIONAL BIASES

The necessity of accurate taphonomic reconstruction in paleoecological investigations has been stressed in the previous discussion. This investigation of modern cryptic communities in Salt River submarine caves has important implications for paleoecology and evolutionary paleobiology. A consistently high level of soft organism encrustation in modern caves indicates that severe taphonomic information losses are present in the reconstruction of similar ancient communities. Data presented herein suggest that only 14.7% areal cover, 37.8% richness, and 42.4% dominance diversity are preservable, given the normal processes of soft part destruction. Such losses in widely used ecologic community parameters would drastically alter the interpretation of original paleocommunity structure and function.

Progressive information loss is suggested to follow increases in water depth, as unskeletonized organisms expand in coverage, richness, and diversity along the 50 - 125 ft gradient. Likewise, intracave distributions of unskeletonized organisms make central, sponge-dominated positions of poorest preservational integrity. These data suggest that bathymetric and intracave environmental changes are altering biotic distribution patterns; and in doing so, they alter the degree of taphonomic bias present. As environmental distribution of particular organisms is nonrandom, so are the taphonomic losses associated with the structure and preservability of those forms. Environmental gradients such as water depth and intracave distance should be considered important factors in accurate reconstruction of ancient cave-dwelling cryptic communities. Data presented herein suggest that the levels of preservable community percent cover, richness, and diversity may be misinterpreted due to commonly unskeletonized body construction. Lowered colonization and diversity levels may direct paleoreconstructions toward less diverse, and thus less mature levels. Lowered diversity and maturity of any community has often been associated with physically controlled environments -- clearly an incorrect conclusion in this case.

We may now address another source of skewed paleocommunity reconstruction -- selective preservation of particular life strategy types. Studies of modern cryptic environments of Jamaica (Jackson, 1977) have characterized cryptic hard substrate pioneers as predominantly solitary, skeletonized organisms. Cleared transects from Salt River caves were examined for evidence of such early, solitary spatial opportunists. Evidence in support of Jackson's contention is suggested by a lack of skeletonized colonial forms beneath more recent overgrowth stages. Early encrusters included a greater variety and abundance of solitary organisms (e.g., serpulid worms, corals, and encrusting bivalves), than that found on the original surface. This group of dominantly solitary substrate pioneers is a significant subset of the total skeletonized, and thus preservable biotas in the cave community. In contrast, with the exception of regionally present sclerosponges at depth, later stage, more successful encrusting biotas are primarily unskeletonized colonial ascidians and demosponges. Therefore an ancient cryptic community may be expected to suffer preferential losses of particular life strategy groups due to nonpreservation. The preferred preservation of solitary organisms is dictated by an overall high preservability of less mature, early successional stage community members. Paleoecological reconstructions on the basis of body fossils alone may be highly under-representative in terms of more mature later seral stages, composed dominantly of unskeletonized colonial organisms and demosponges. Thus we observe a systematic bias toward "pioneer" community members, and immature structure in the preservable cave record. This may cause investigators to underestimate the maturity and diversity of the cave community at the time of burial.

Previous studies (Rollins and Donahue, 1975; Stearns, 1976; Scott, 1976) have shown that the diversity and maturity of particular benthic communities reflect the stability of the environment in which they live. In this sense, if paleocommunity reconstructions are in some sense biased or askew, that error may perpetuate into an incorrect assessment of original paleoenvironment. Paleoecologists have transferred the ecologic nomenclature of "physically controlled" and "biologically accommodated" to the definition of paleocommunity types. To a large extent, these endmembers are distinguished by the types and abundances of particular community members, and the level of overall community diversity. Body plans and life histories of organisms present have also been associated with ambient environmental conditions.

The validity of applying ecologic principles to paleoecological studies of cryptic communities is strongly dependent on the preservational quality of the fossil assemblage in question. Preservation of cryptic organisms appears to be taxonomically and successionally biased; therefore, the interpreted community type is likely to be biased toward a particular end of the "physical or biological control" spectrum. Misinterpretations of original environmental characteristics (e.g., stable-mature, unstable-immature) or other trends may result. This study has demonstrated that increased environmental stability due to greater water depth results in demosponge areal expansion and diversification. This community trend, linked to an environmental trend, will remain unrecognized in the fossil record due to nonpreservation of demosponges. A systematic bias toward community immaturity may further mislead investigators to characterize the ancient cave biotope as one which is less stable -- even physically controlled (Scott, 1976). In reality, cave environments support diverse, biologically accommodated communities. In this case, however, much of the mature community structure is unpreservable. Previous documentation of slow burial rates suggests the "progressive necrolysis" of the stable, mature community structure. This phenomenon may produce a final, largely skeletonized (and thus preservable) surface which is not an accurate reflection of the usually stable, unstressed biotope character. In fact, it is an atypical sample of the cave biota as a whole, and not reflective of stable, preburial conditions. In this case the preservable organisms are again indicative of community immaturity, and physical control of community structure.

Additional data have been presented on differing burial phenomena associated with particular cryptic substrates. Coral plate communities, which support more diverse communities of skeletonized pioneer organisms may be quickly and frequently buried -- producing a good fossil record. In contrast, cave communities are restrictive to generally skeletonized substrate pioneers, and therefore maintain lower numbers of skeletonized biotas. Cave substrates are slowly and infrequently buried, and due to their association with very destructive later diagenetic environments, may be expected to produce a sparse and poorly preserved fossil record. Thus, highly mature cave environments preserved in the fossil record are notably rare, mainly due to characteristics of the biota, and poor burial and preservation characteristics. More likely specimens for discovery should be the less stable, less mature coral plate cryptofauna. The preferential preservation of coral plate cryptic substrates and the earlier stages of cryptobionts they support may enhance the overall interpretive bias toward early seral stages in the fossilized cryptic community record.

The generally enhanced record of solitary biotas may be balanced to some small extent by the susceptibility of solitary organisms to bioerosion. As noted, clionid sponges bore only into nonliving substrates. Due to the proportionally greater tissue-free area of solitary organisms, these organisms are expected to be infested preferentially. Resulting exoskeletal destruction may reduce the preserved record of solitary biotas somewhat. It is thought, however, that this selective destruction effect is less thorough than the preservation effect, usually destroying only structural resolution. In addition, other bioerosive sponges of the adociidid family show no preference for dead substrates, and would be expected to bore into living colonial skeletons indiscriminately.

In summary, cryptic communities can be expected to be selectively biased toward early, less mature community structure for three reasons:

1. Most early stage cryptobionts are solitary and preservable, while most members of later stages are unpreservable (e.g., colonial tunicates and demosponges).
2. Coral plates are preferentially preserved in the fossil record, and themselves maintain greater numbers of early substrate pioneers -- which are dominantly hard.
3. Cave substrates are preferentially destroyed in the fossil record; and even if preserved, will record only skeletonized forms -- which are dominantly pioneers.

MARINE REFUGIA AND SUBMARINE CAVES

The cave habitat may be considered a refugium for certain once extensive faunas, now found in only limited abundance (Vancelet, 1967b; Jackson et al., 1971). These forms include the sclèrosponges, which may be Recent relatives of Mesozoic stromatoporoids and chaetetid "corals." In addition, groups such as bryozoans, brachiopods, and crinoids, now only observed commonly in shallow cryptic or deep water environments, were once observed to occupy less restricted, exposed benthic environments (Stanley, 1974). Some of the cryptic "refugees" are observed to be nearly identical to ancient ancestors, or in fact "living fossils." Serpulid worms, such as <u>Spirorbis</u>, and the cyclostome bryozoans Berenicia and Stomatopora have remained little changed since the Middle Ordovician (Brett and Liddell, 1978). The evolutionary longevity of some cryptic community members recalls that of relict deep-sea faunas, such as coelacanth fish and the hemichordate Rhabdopleura. Apparently, competitive exclusion in certain shallow marine environments through geologic time has resulted in either the extinction or migration of less competitive forms (Sepkoski, 1981). Migration of primitive forms to cryptic and deep-sea environments has effectively reduced direct competition with evolving superior competitors. In both cases, the present environment is one of restrictive food resources, possibly limiting further expansion in these habitats (Sanders and Hessler, 1969; Hartman and Goreau, 1970). In the case of submarine cave communities, increased levels of spatial competition create additional conditions of low level environmental stress due to restricted spatial resources. Both environments are conducive to construction of biologically accommodated community structures, existing at environmental carrying capacity. Both environments are observed to offer refugia from drastic environmental perturbations.

Consideration of within-habitat cryptofaunal distributions in shallow submarine caves has allowed speculation on finer scale cave community attributes, and possibly their relation to similar attributes of the marine realm as a whole. Shallow (50 - 75 ft) caves are most influenced by near wave-base environmental irregularities. Thus, they yield the most visible within-cave environmental gradients, and resultant colonization gradients. In the earlier ecological review of faunal and numerical index distributions within caves, transects were subdivided into three zones -- apertural, central, and distal. These designations were defined on the basis of differences in microenvironmental stress, colonization by specific taxa, and colonization index attributes. The interrelationship between these parameters generally resulted in either parallel or overlapping distributions. To generalize a shallow cave's ecological attributes, the apertural and distal zones are characterized as most stressful, and tend to fluctuate most frequently. Faunal encrustation is erratic, and often of anomalously high density and low diversity, as a whole quadrat is monopolized by a single species. Currents, sediments, and predators may disturb the apertural zone, while sediment floor proximity and lower nutrient levels probably affect the distal zone. In these respects apertural and distal zones may be more physically controlled, compared to the central zone. The central cave zone is of consistently high diversity and density, and apparently least stressful. The episodic effects of current fluctuation, sedimentation, or predation are likely to be minimal here. Biological control of community structure probably characterizes this central zone.

The marine realm has been analogously subdivided on the basis of faunal and environmental gradients in both the Recent (Sanders, 1968) and the Paleozoic (LaPorte, 1969; Ziegler et al., 1968; Bretsky, 1969). These zones specifically include: (1) the predictably unstable intertidal, highly stressed and less diverse; (2) the unpredictably stable shallow subtidal, least stressed and most diverse; and (3) the predictably stable deep-marine, highly stressed and less diverse. These large-scale marine zones may be somewhat analogous to the within-cave zones with respect to distance from shallow/apertural sources of disturbance. Similar patterns may be the result of comparable environmental parameters of stress, stability, and predictability on both levels. Local heterogeneity effects blurr these patterns in both environments, but exert less control overall than broader environmental gradients (Bretsky and Lorenz, 1970). Understanding the processes at work on the smaller cave-scale may contribute to the understanding of the marine environment on a larger, whole-marine scale. Tracing the Phanerozoic evolution and distribution of cryptic communities as Jackson et al. (1971) suggest, may prove valuable and complementary to tracing the evolution and migrations of Phanerozoic marine communities (Valentine, 1973; Raup, 1976; Sepkoski, 1981).

CONCLUSIONS

1. Submarine caves, having elaborate, irregular internal morphologies, provide habitats of attenuated physical and biological disturbance. Such protection results in habitation by biologically accomodated cryptic communities, often comprised of organisms of ancient affinity (e.g. sclerosponges, brachiopods).
2. Central cave zones appear to be most favorable to colonization, as consistently high percent cover, richness, and dominance diversity are found there. Lower diversities typify apertural and distal zones This pattern is somewhat blurred by topographic irregularities in the substrate.
3. Low levels of current transport are associated with cave floor biogenic sediments, and with attached encrusting or endolithic cryptobionts. This results in a fossil assemblage predominantly in situ in nature.
4. As the majority of cryptic organisms indigenous to cave substrates are unskeletonized, general taphonomic information loss through nonpreservation is characteristically high. Losses approximate 85.3% of original areal coverage, 62.2% of original richness, and 57.6% of original dominance diversity.
5. Caves at greater depths are associated with increased environmental stability, and support the expansion of

demosponges and colonial organisms. As these forms are largely unskeletonized, the most significant levels of taphonomic information loss through nonpreservation occurs at greater depths.

6. Most cryptic substrate pioneers are solitary, skeletonized organisms, which are subsequently overgrown by unskeletonized demosponges and colonial organisms. Fossilized cryptic communities are therefore biased toward preservation of earlier successional stages of encrustation.
7. Cave environments support diverse assemblages of bioerosive and biocorrosive organisms. Their activity, paired with later slow burial, and diagenesis, acts to inhibit the preservation of normal cave community structure.
8. Alternate forms of potential paleoecological information are presently accumulating in caves in the form of skeletonized organism interactions and traces of activity. These preservable phenomena may permit recognition of original colonization patterns, competitive hierarchies or networks, and environmental stability in ancient cave biotopes.

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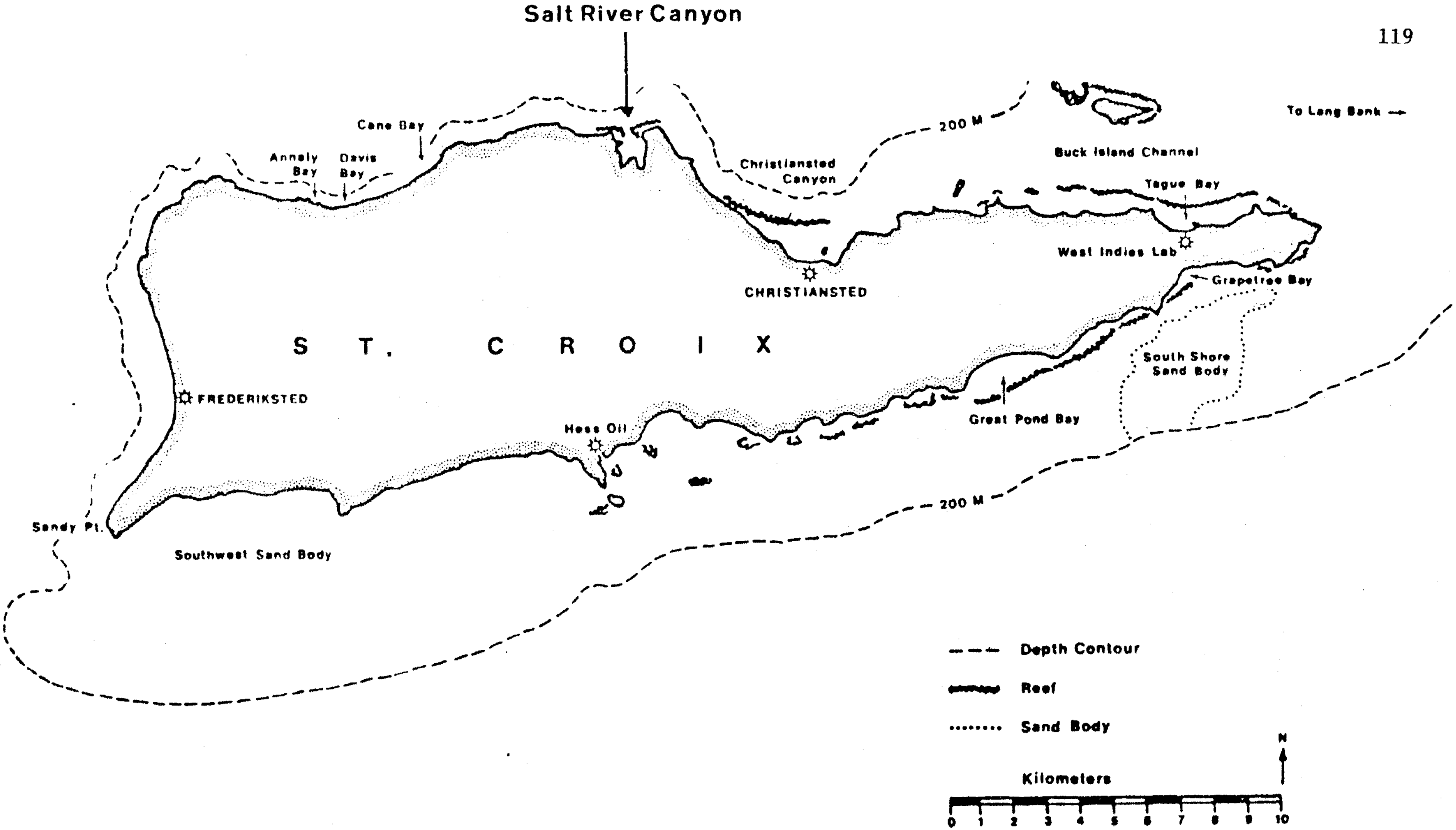


Figure 1. Map of St. Croix, U.S. V.I., showing key points in reference to Salt River Canyon study area. From Hubbard, et al. (1981).

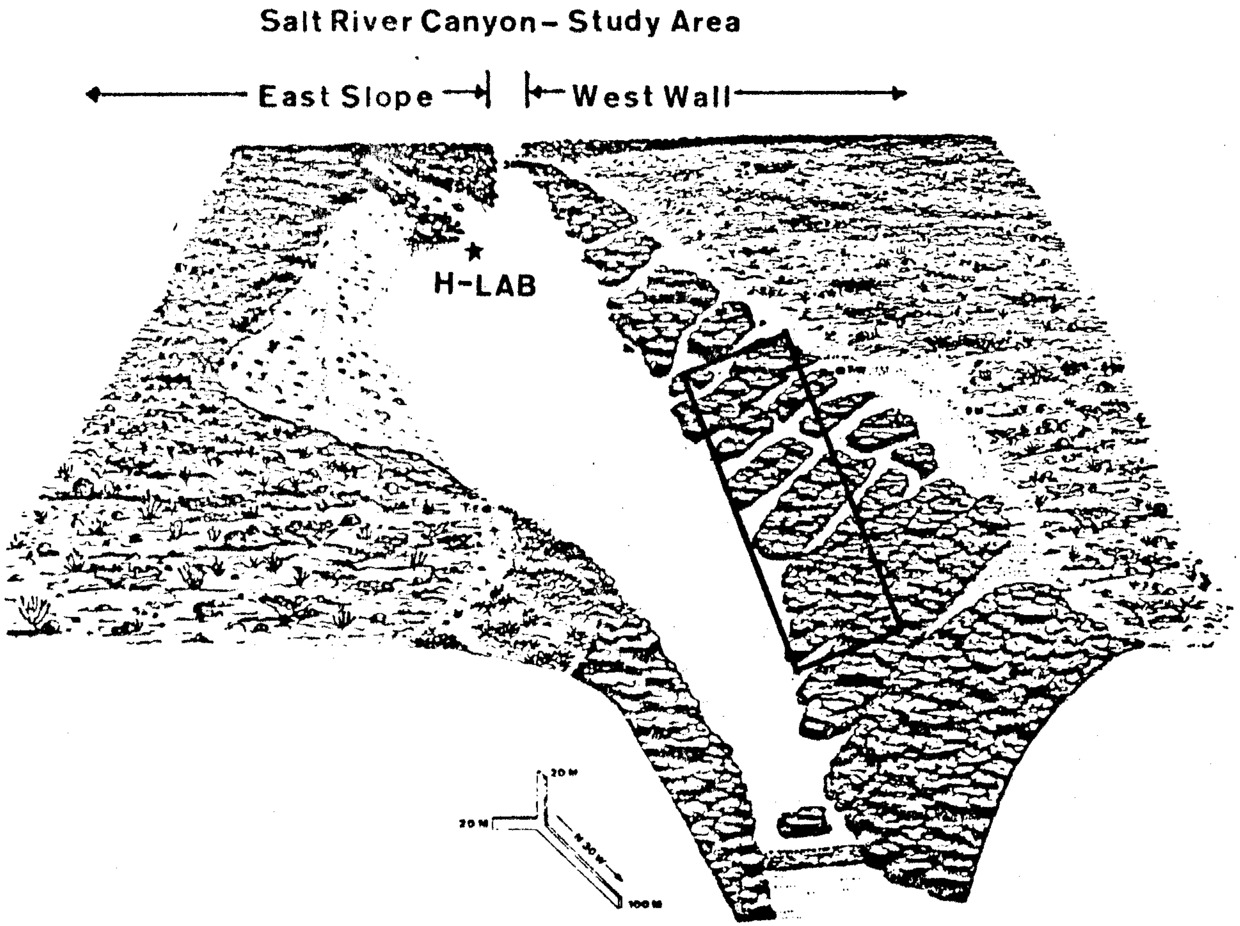


Figure 2. Salt River Canyon site locations and gross morphology. Boxed area indicates approximate locations of all observed caves, which occur beneath coral overhangs. From Hubbard, et al. (1981).

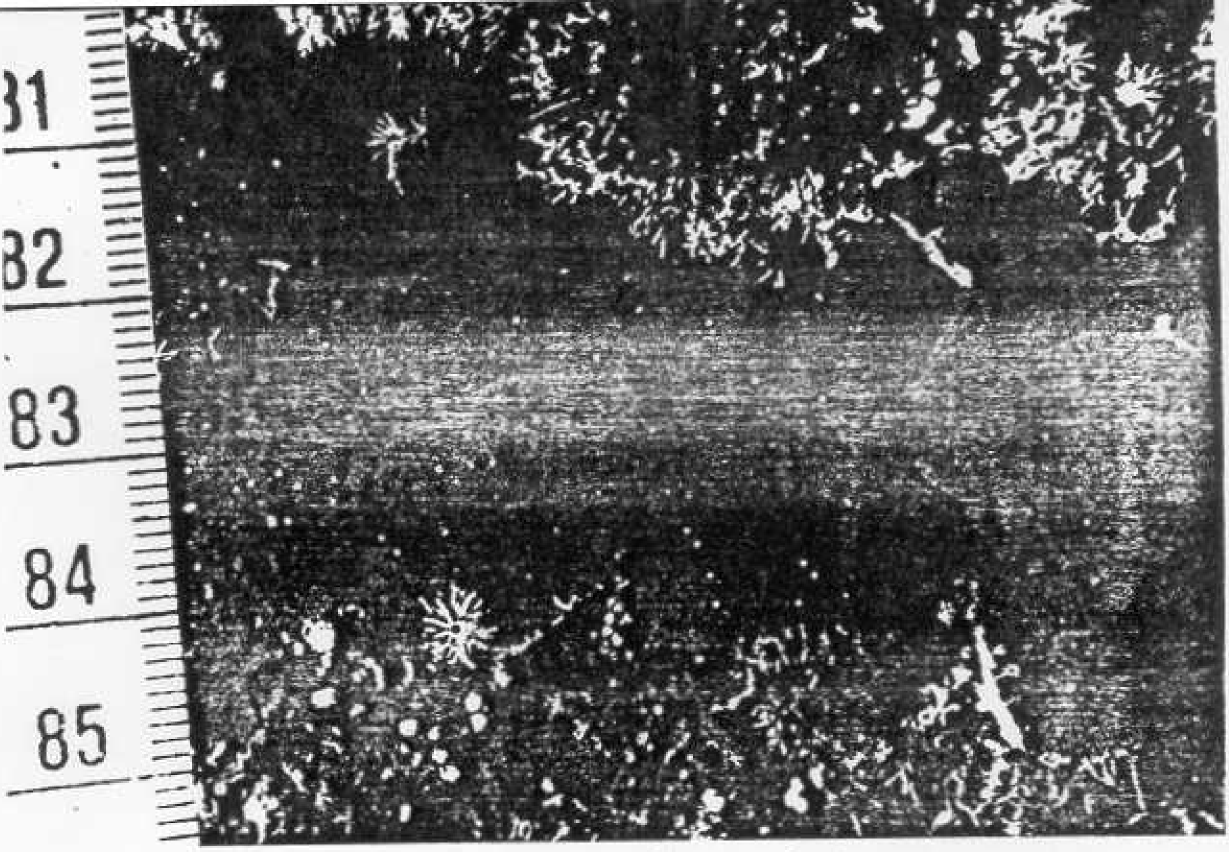


Figure 3a. Original quadrat photograph (SR50A1, #22) from which most all numerical data may be generated. A red demosponge (rs-2) encrusts coralline algal substrate. Erect filaments are calcareous green algae-ubiquitous in most quadrats. Scale is in centimeters, and corresponds to distance into the cave.

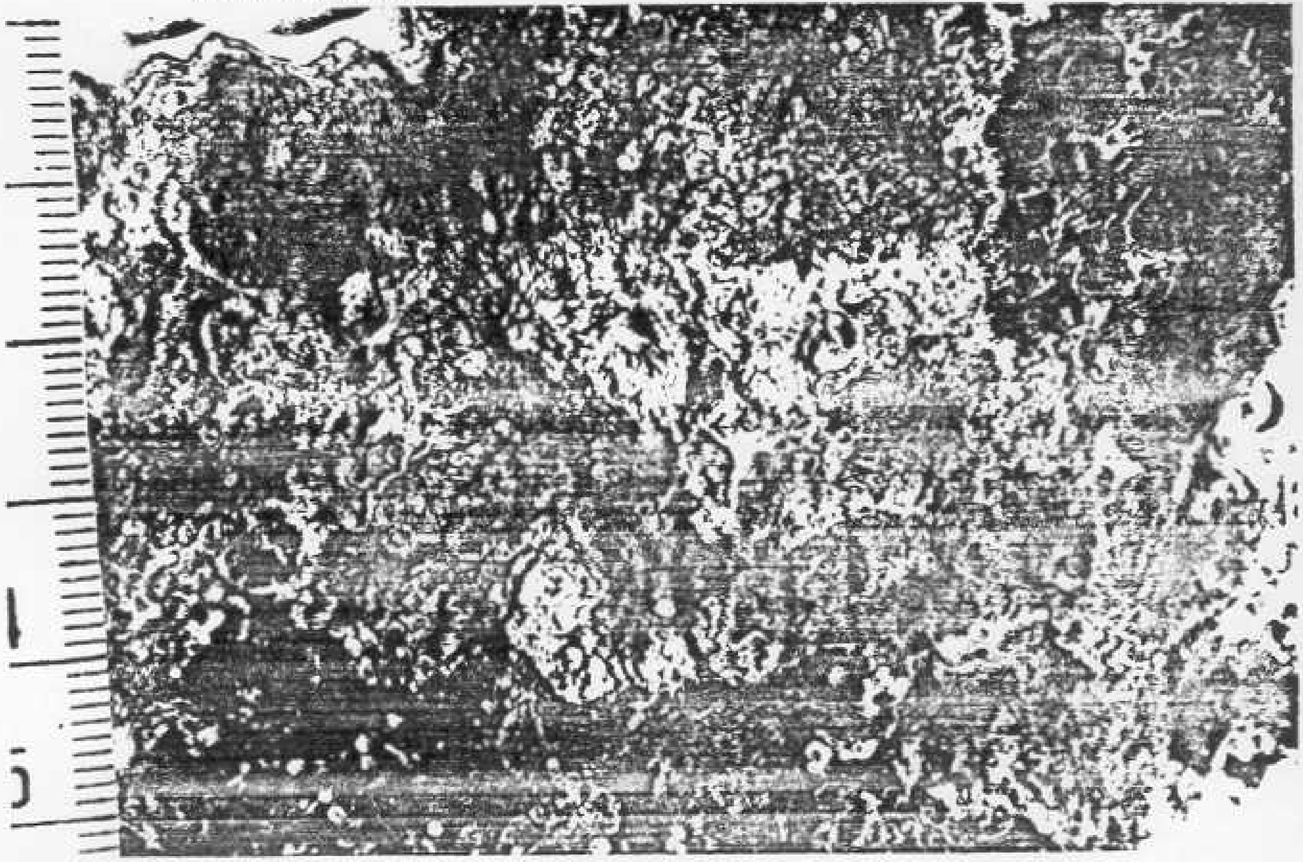


Figure 3b. Cleared quadrat photograph removed of all soft organism overgrowth to expose the preservable record of skeletonized organisms below. Earlier serpulid worms and solitary coral specimens are observed. Cleared richness data may be

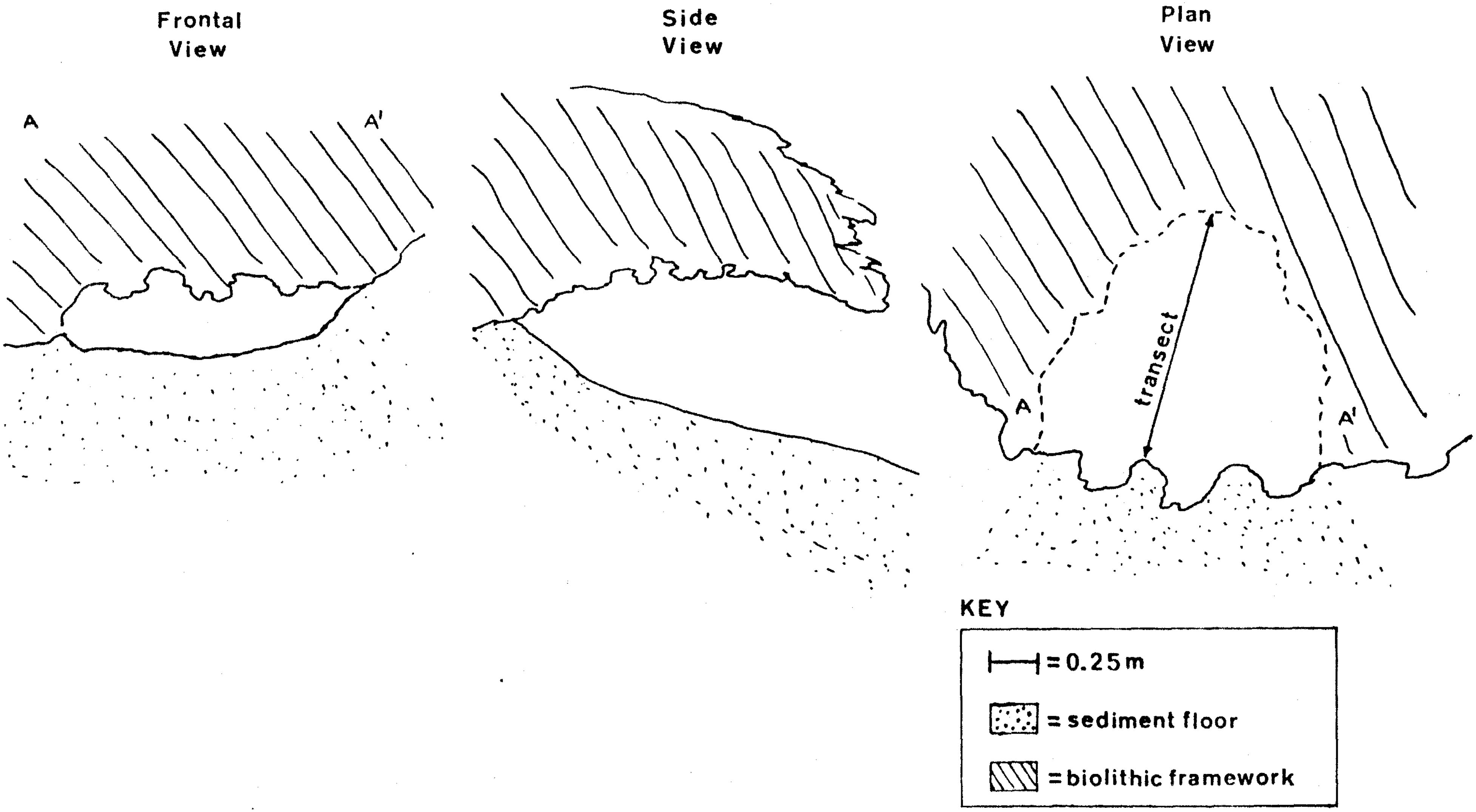


Figure 4a. Generalized diagram of single-aperture cave morphology, showing frontal, side, and plan views. Roof convolutions are most pronounced in central and distal cave zones. Note that distal transect zones approach the sediment/roof interface. Diagram approximates all sites but IK 105A.

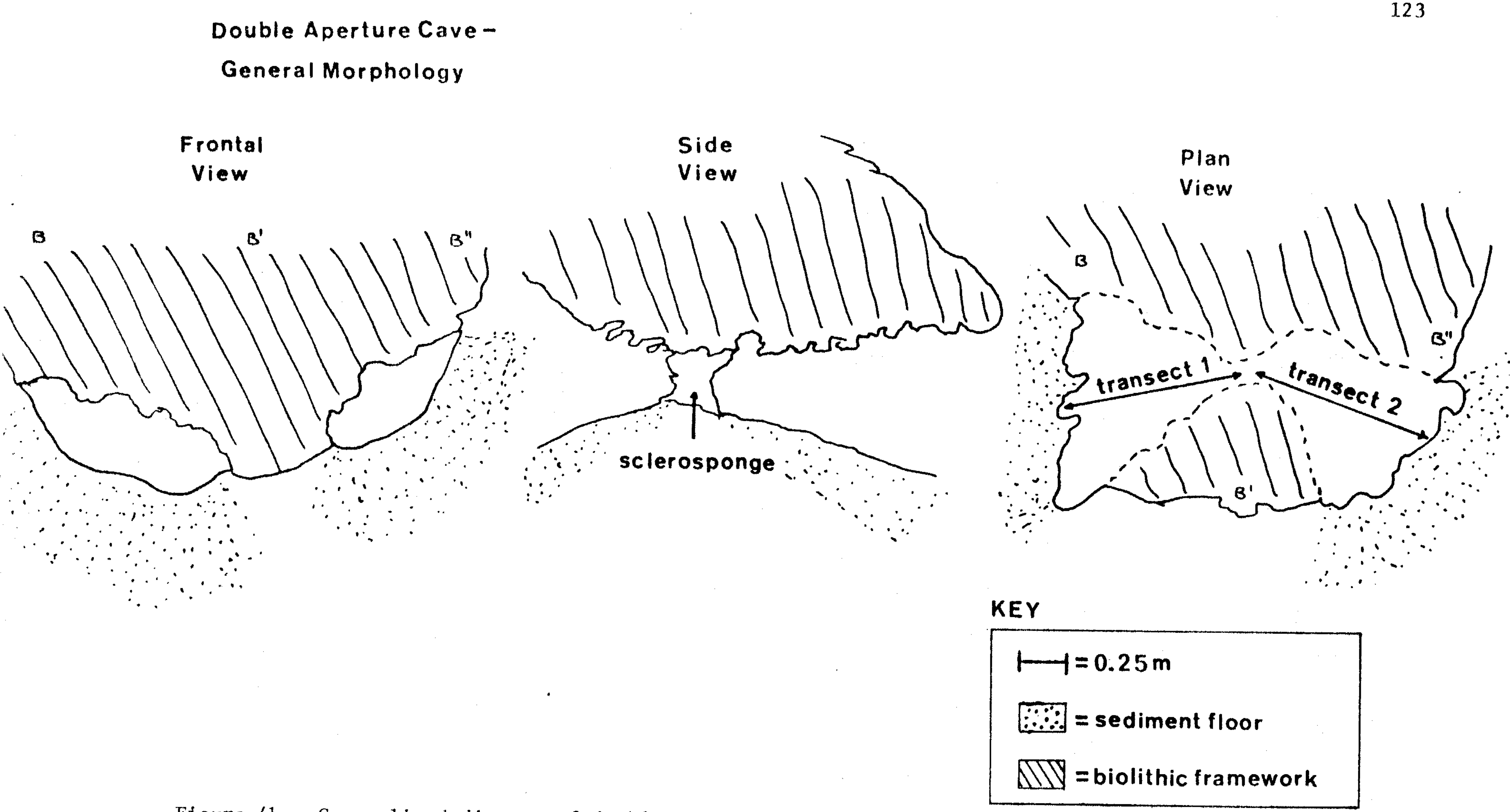


Figure 4b. Generalized diagram of double-aperture cave morphology typified by site IK105A only. Transects extend only to the most central parts of the cave roof, and again approach the sediment/roof interface distally. Excessive roof convolution was notable here, as were sclerosponge structural elements.

CONSTITUENT ANALYSIS: CAVE FLOOR SEDIMENTS, SITE IK 50A

Constituent types	Size Fraction (ϕ)											
	-1	-.5	0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Halimeda	ⓧ	ⓧ	x	x	x	x	x	x				
echinoid-test	x	x	x	x		x						
echinoid-spine	x	x	x	x	x	x	x	x	x	x		x
hydrozoan		x	x									
Homotrema	x	x	x	x	x	x	ⓧ	x	x	x	x	x
coral	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	x	x				
bryozoan- erect			x	x		x		x	x			
bryozoan-encrust.			x									
bivalve	x	x	x	x	x	x	x	x				
brachiopod												
serpulid			x	x	x	x	x	ⓧ	x	x		
cor. algae	x	x	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	x	x
foram.-porcel.		x	x	x	x	x	x					
foram.-hyaline			x	x	ⓧ	ⓧ	x	x	ⓧ	x		
microgastro.			x	x	x	x	x	x	x			
sponge-spicule			x	x	x	x	x	x	x	x	x	ⓧ
sponge-spongin	x		x									
octo. spic.			x		x	x	x	x	x			
ascidian spic.						x	x	x	x	ⓧ	ⓧ	x
ostracode					x	x	x	x	x	x		
barnacle			x									
crustacea				x								
unk. skel.	x	x	x	x	x	x	ⓧ	ⓧ	ⓧ	ⓧ	ⓧ	x
clionid chips											x	x
ooids												

Table 1. Cave floor sedimentary constituents present (x) at site IK50A are shown for particular size fractions. Circles (ⓧ) indicate most abundant constituent(s) in each size class, as measured qualitatively. Significant quantities of structural elements from poorly skeletonized organisms are present, as are abundant clionid chips and bored debris. Pellets may be absent due to preparation technique (Ginsburg, 1956). List modified from Milliman (1974).

GRAIN SIZE ANALYSIS: CAVE FLOOR SEDIMENTS SITE IK 50A

SIZE Ø	CLASS mm	WEIGHT(g)	%	CUMM. %
-1.0	2.00	0.3065	1.278	1.278
-0.5	1.41	0.7393	3.081	4.359
0	1.00	1.1640	4.852	9.211
0.5	.707	1.4820	6.177	15.39
1.0	.500	1.7320	7.261	22.65
1.5	.354	2.2350	9.316	31.97
2.0	.250	4.6800	19.510	51.48
2.5	.177	2.5102	10.460	61.94
3.0	.125	3.7780	15.751	77.69
3.5	.088	1.8611	7.757	85.45
4.0	.063	0.8850	3.689	89.14
4.5	.044	0.8983	3.744	92.88
>4.5	Pan	1.7112	7.132	100.00
TOTAL		23.992		

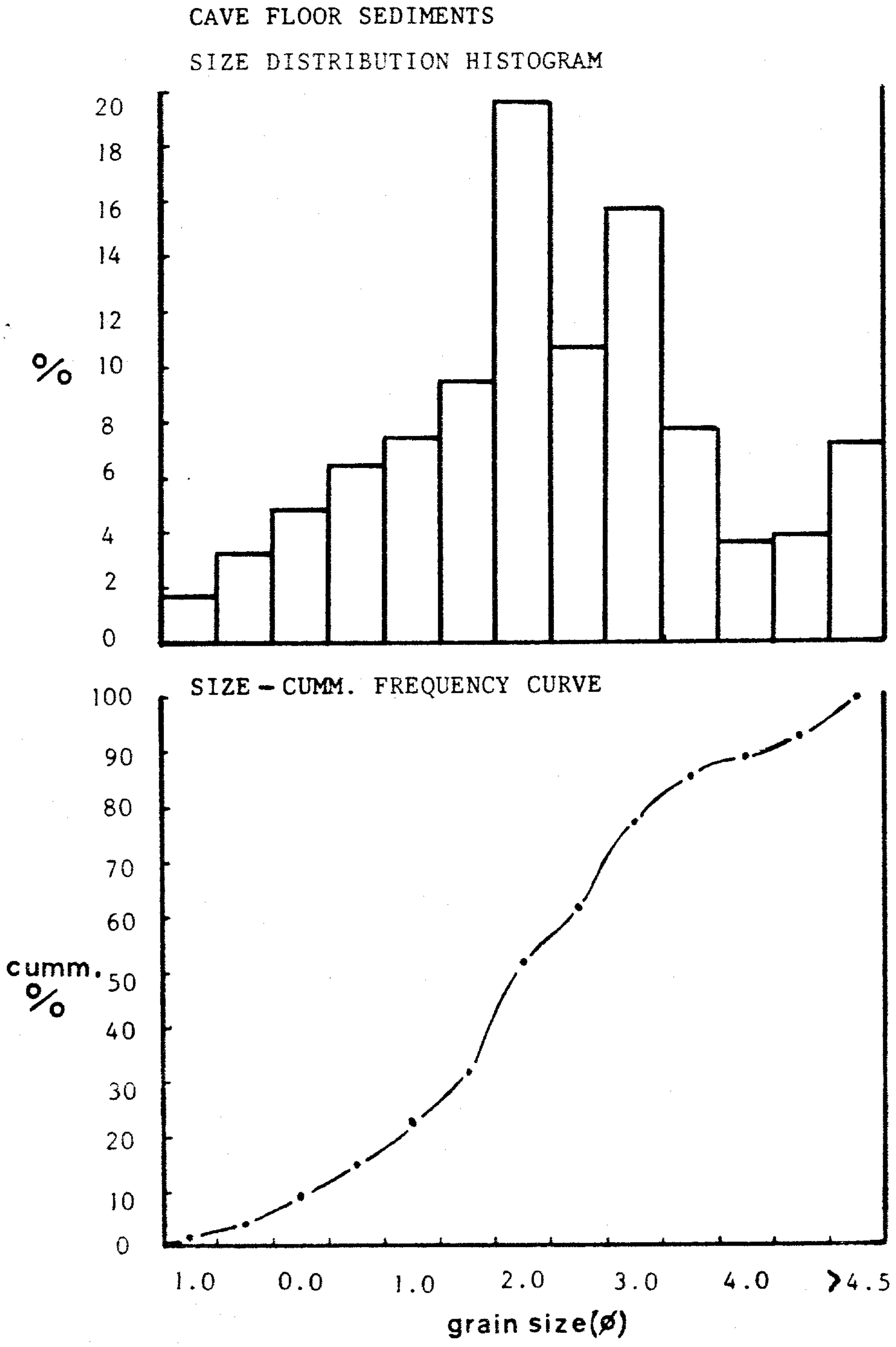
MØ = 1.97 Fine sand

SO = 1.49 mod - poor

SKØ = 0.180 slight (+)

K = 1.17 mesokurtic

Figure 5a. Cave floor grain size analyses include grain size statistics, histograms, and cummulative frequency curves (next page). Grain size statistics (Folk and Ward, 1957) indicate moderate-poor sorting and positive skewness within caves. The histogram for these sediments is bimodal. The cummulative frequency curve has multiple breaks in slope, suggesting complexity of sediment supply and transport mechanisms. Biologically mediated production and deposition mechanisms in a quiet environment are inferred.



CAVE FLOOR SEDIMENTS

SIZE DISTRIBUTION HISTOGRAM

SIZE – CUMM. FREQUENCY CURVE

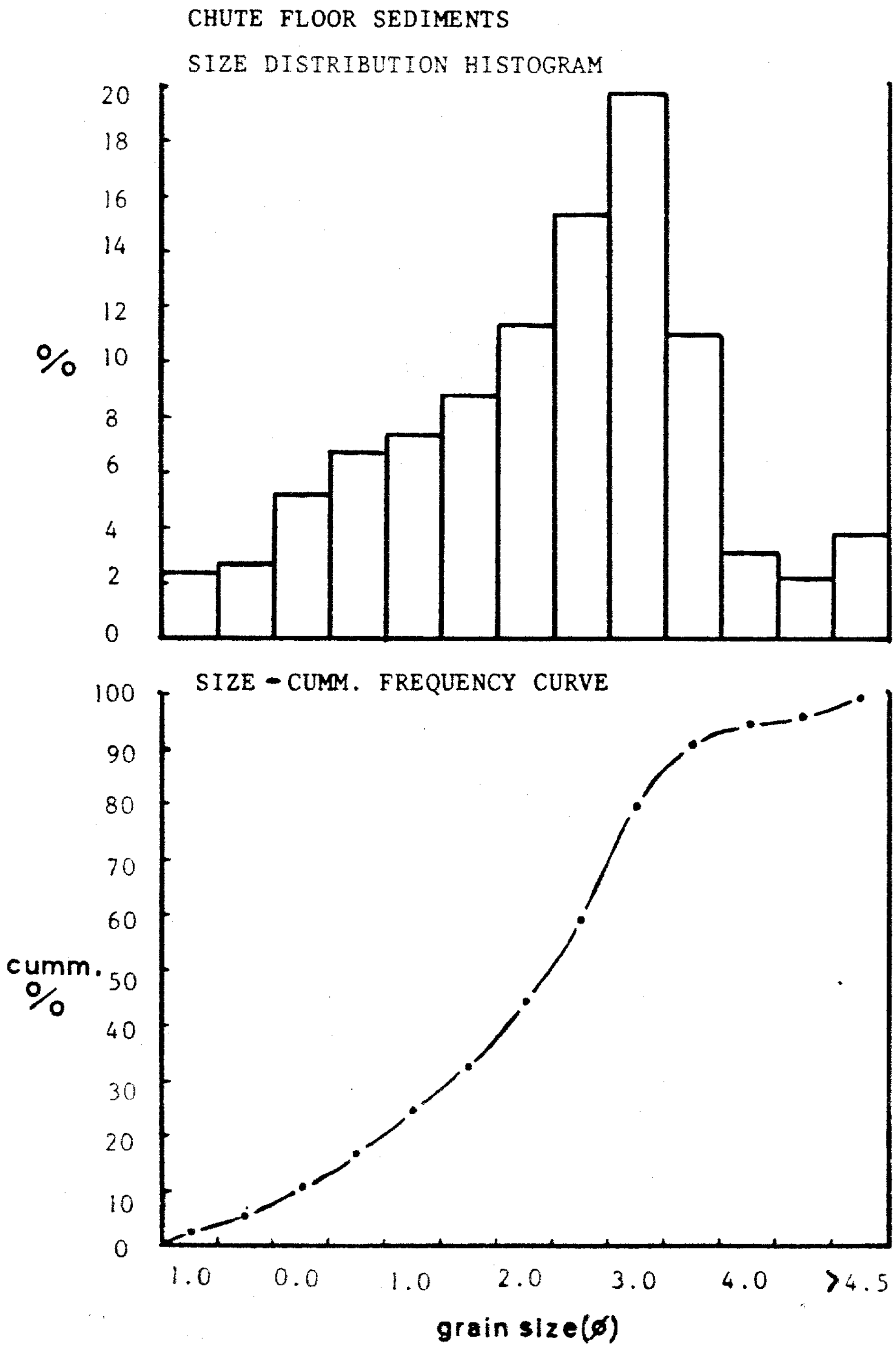
Fig. 5a (cont'd.)

GRAIN SIZE ANALYSIS: SEDIMENT CHUTE 5 m NORTH OF IK 50A

SIZE 0	CLASS mm	WEIGHT(g)	%	CUMM. %
-1.0	2.00	0.2657	2.3626	2.3626
-0.5	1.41	0.2923	2.5992	4.9618
0	1.00	0.5787	5.1458	10.108
0.5	.707	0.7624	6.7793	16.887
1.0	.500	0.8166	7.2613	24.148
1.5	.354	0.9825	8.7364	32.885
2.0	.250	1.2788	11.371	44.256
2.5	.177	1.8278	15.364	59.621
3.0	.125	2.2206	19.746	79.367
3.5	.088	1.2353	10.984	90.351
4.0	.063	0.3328	2.9593	93.310
4.5	.044	0.2295	2.0407	95.351
>4.5	Pan	0.4225	3.7569	99.108
	TOTAL	11.2455		

M0	= 1.96	Fine sand
SO	= 1.25	mod - well
SK0	= 0.216	slight (-)
K	= 1.10	mesokurtic

Figure 5b. Grain size analyses on sediments collected from a sediment chute, located 5 meters north of IK50A. Negative skewness and greater mechanical sorting suggests environmental differences between cave and open sediment environments (Folk and Ward, 1957). The histogram and cummulative frequency curve is unimodal, and less complex, respectively. Both indicate more thorough and continuous sorting in a higher energy regime than that of cave sediments.



CHUTE FLOOR SEDIMENTS

SIZE DISTRIBUTION HISTOGRAM

SIZE - CUMM. FREQUENCY CURVE

Fig. 5b (cont'd.)

INTRACAVE LIGHT ATTENUATION: SR 125B

	CAVE ZONE/DISTANCE FROM APERTURE		
Experimental Trial No.	Aperture/0 cm	Central/60 cm	Distal/120 cm
(1)	9.00	8.75	6.00
(2)	9.50	7.50	4.50
(3)	13.0	9.50	No Data
Mean	10.5	8.58	5.25

Table 2. Intracave light attenuation results from site SR125B measure light changes into that cave. Data was taken at 0900 hrs, 10 August 1982. Figures represent relative units of light intensity. A linear decrease in light correlates with distance into the cave, and may favor settlement by sciadophillic larvae.

ORGANISM COLONIZATION AND PRESERVATION DATA: SALT RIVER SUBMARINE CAVES

TRANSECT	ORGANISM COVERAGE (%)													% COVER			RICHNESS				DIVERSITY		
	DEMO.	ASCID.	GR.ALG.	SAB.	SCLERO.	CORAL	BRYO.	SERP.	BIVAL.	FORAM.	BRACH.	HYDRO.	COR. ALG. OPEN	TOT.	HARD	SOFT	TOT.	HARD ORG.	HARD CLEAR.	SOFT	TOT.	HARD	SOF
IK 50A 1	34.0	4.20	0.59	0.47	0.00	3.29	2.05	0.16	0.07	0.01	0.00	0.00	55.2	44.8	5.56	39.2	6.9	1.9	3.5	6.0	.514	.144	.44
SR 50A 1	26.2	1.27	4.09	0.32	0.00	7.12	0.61	1.12	0.21	0.11	0.00	0.05	57.6	40.9	9.29	31.9	8.7	4.4	5.0	4.3	.590	.343	.44
50' MEAN	30.1	2.74	2.34	0.40	0.00	5.21	1.33	0.64	0.14	0.06	0.00	0.03	56.4	42.9	7.43	35.6	7.8	3.2	4.3	4.6	.552	.244	.44
																	±0.9	±1.3	±0.8	±0.4	±0.04	±0.10	±0.0
SR 75 B 2	61.0	4.32	8.93	0.57	0.00	3.72	3.55	0.70	0.17	0.00	0.00	0.00	17.7	82.3	8.07	74.3	9.1	3.3	4.7	5.8	.634	.262	.53
SR 75 B 3	47.2	50	8.26	0.33	0.00	4.50	3.84	0.52	0.27	0.04	0.18	0.00	32.0	78.0	9.82	68.6	11.4	4.2	5.8	7.1	.665	.323	.56
75' MEAN	54.1	6.41	8.60	0.45	0.00	4.11	3.70	0.61	0.22	0.02	0.09	0.00	19.9	80.2	8.95	71.5	10.3	3.8	5.3	6.5	.650	.293	.55
																	±1.2	±0.5	±0.6	±0.7	±0.02	±0.03	±0.0
IK 105A 3	45.7	16.7	10.9	0.00	0.00	0.00	3.22	0.69	0.22	0.19	0.02	0.04	21.9	78.1	3.70	74.4	10.0	3.9	6.6	6.1	.594	.299	.50
IK 105A 4	40.3	12.2	8.76	0.00	20.5	0.00	0.26	0.62	0.00	0.12	0.00	0.00	17.1	82.9	21.5	61.4	7.7	2.8	3.2	4.9	.529	.152	.47
105 MEAN	43.0	14.5	9.83	0.00	10.3	0.00	1.74	0.66	0.11	0.16	0.01	0.02	19.5	80.5	12.6	67.9	8.9	3.4	4.9	5.5	.562	.226	.44
																	±1.2	±0.6	±1.7	±0.6	±0.03	±0.08	±0.0
R 125 A 1	50.0	11.7	6.57	0.09	10.9	0.60	2.56	0.31	0.00	0.00	0.00	0.00	17.2	82.6	14.4	68.2	9.4	3.1	4.3	6.3	.586	.223	.56
ENV. MEAN	43.5	8.41	6.87	0.21	4.49	2.75	2.30	0.59	0.13	0.07	0.03	0.01	29.8	69.9	10.2	59.7	9.0	3.4	4.7	5.6	.587	.249	.50
	±10.5	±5.06	±3.23	±0.21	±7.54	±2.48	±1.31	±0.29	±0.10	±0.07	±0.06	±0.02	±16.9	±17.3	±5.54	±15.9	±1.4	±0.8	±1.1	±0.9	±0.05	±0.74	±.04

Table 3. Organism colonization is presented for each taxon present as mean percent coverage. Colonization indices of percent cover, richness, and dominance diversity are calculated for total organisms, and skeletonized (hard) and unskeletonized (soft) components. Note all values are measured per standard 37.5 cm^2 quadrat. These calculations are based directly on data of Tables 4a-g.

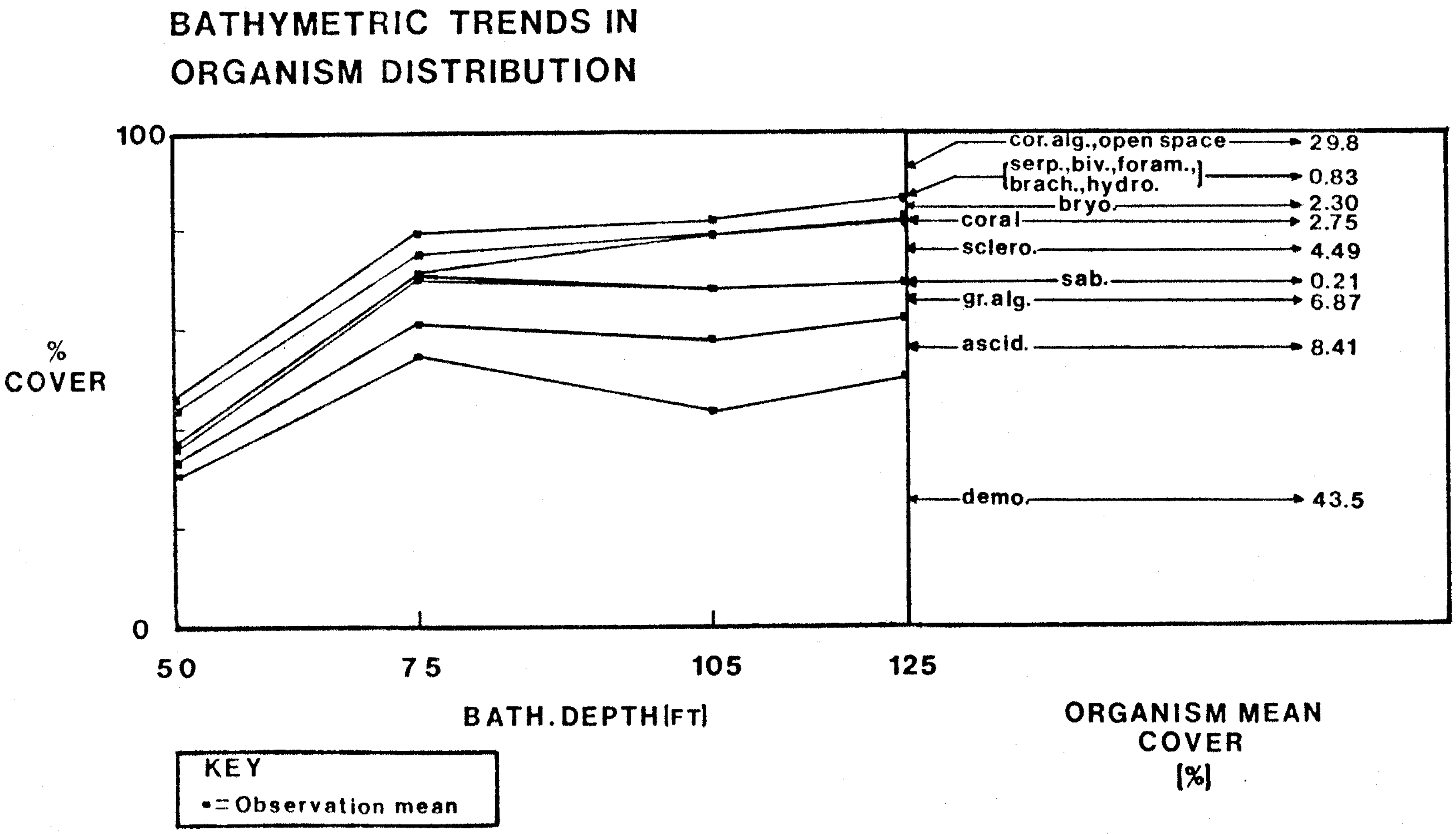


Figure 6. Bathymetric trends in organism distribution were measured between 50 and 125 ft depths. Note the areal dominance of unskeletonized organisms (lower section of list), and the relatively small area occupied by skeletonized forms (upper section of list). Demosponge abundance increases between 50 and 125 ft, severely limiting solitary organisms. Sclerosponges appear below 75 ft, and occupy distal cave zones with bryozoans.

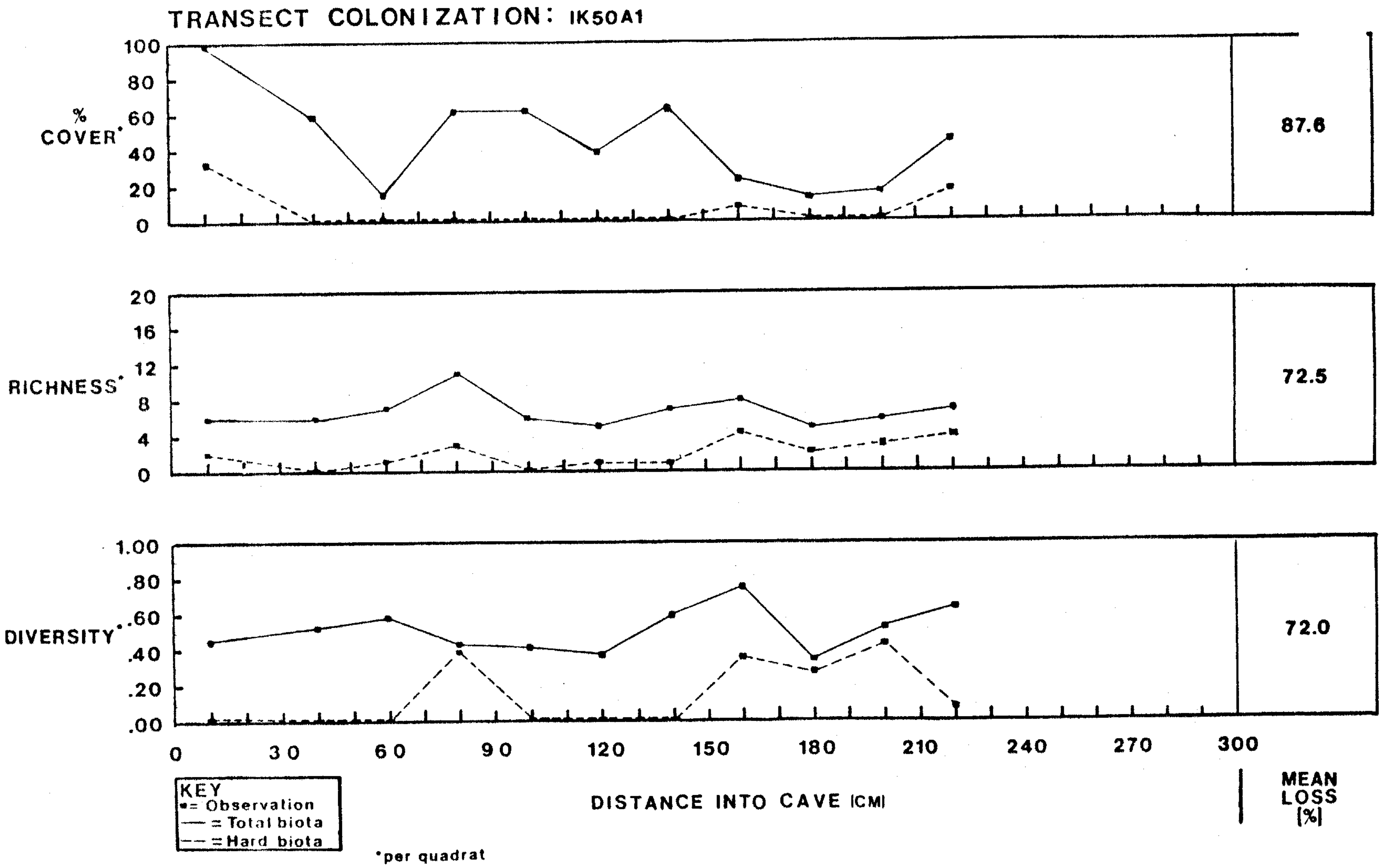
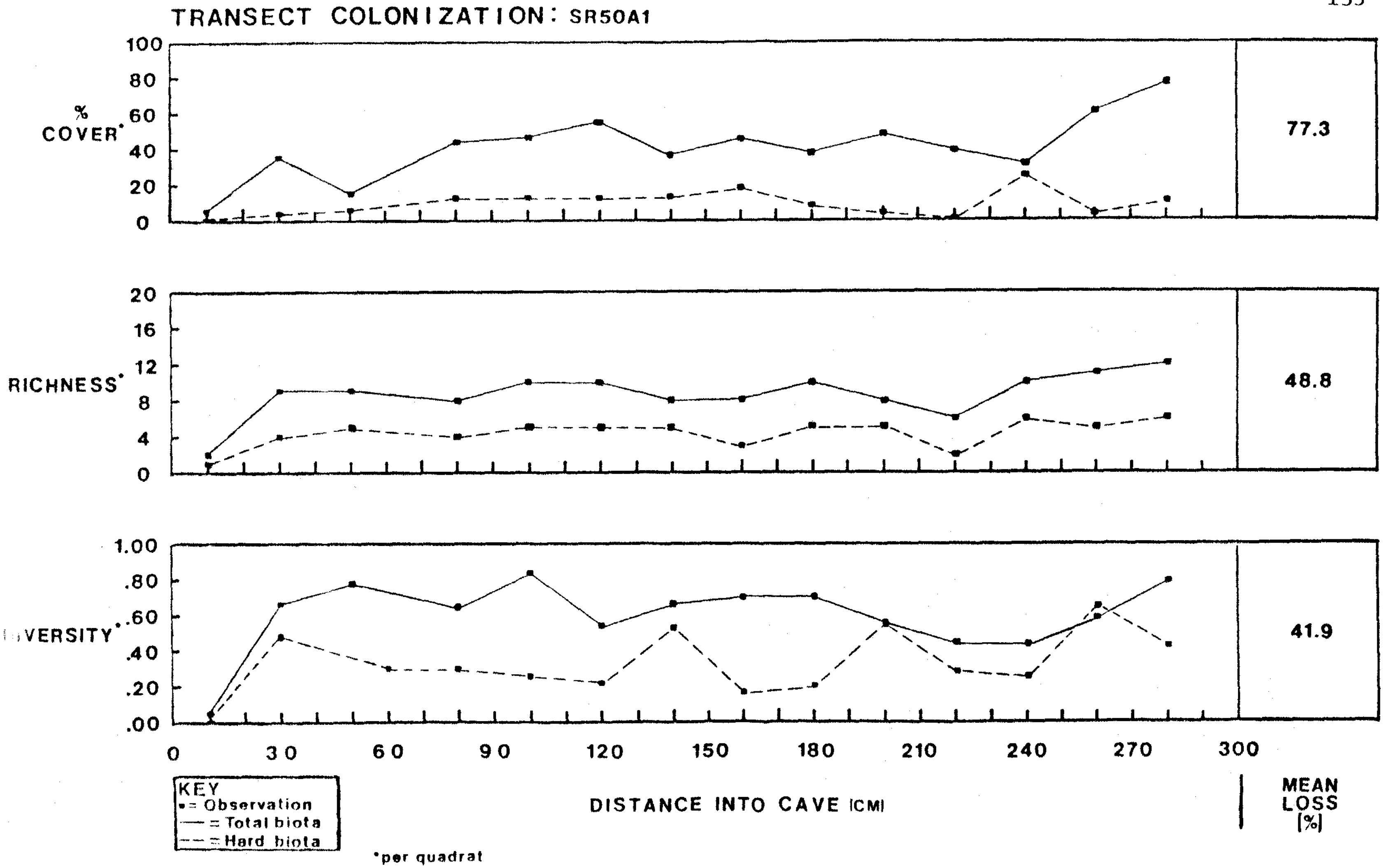
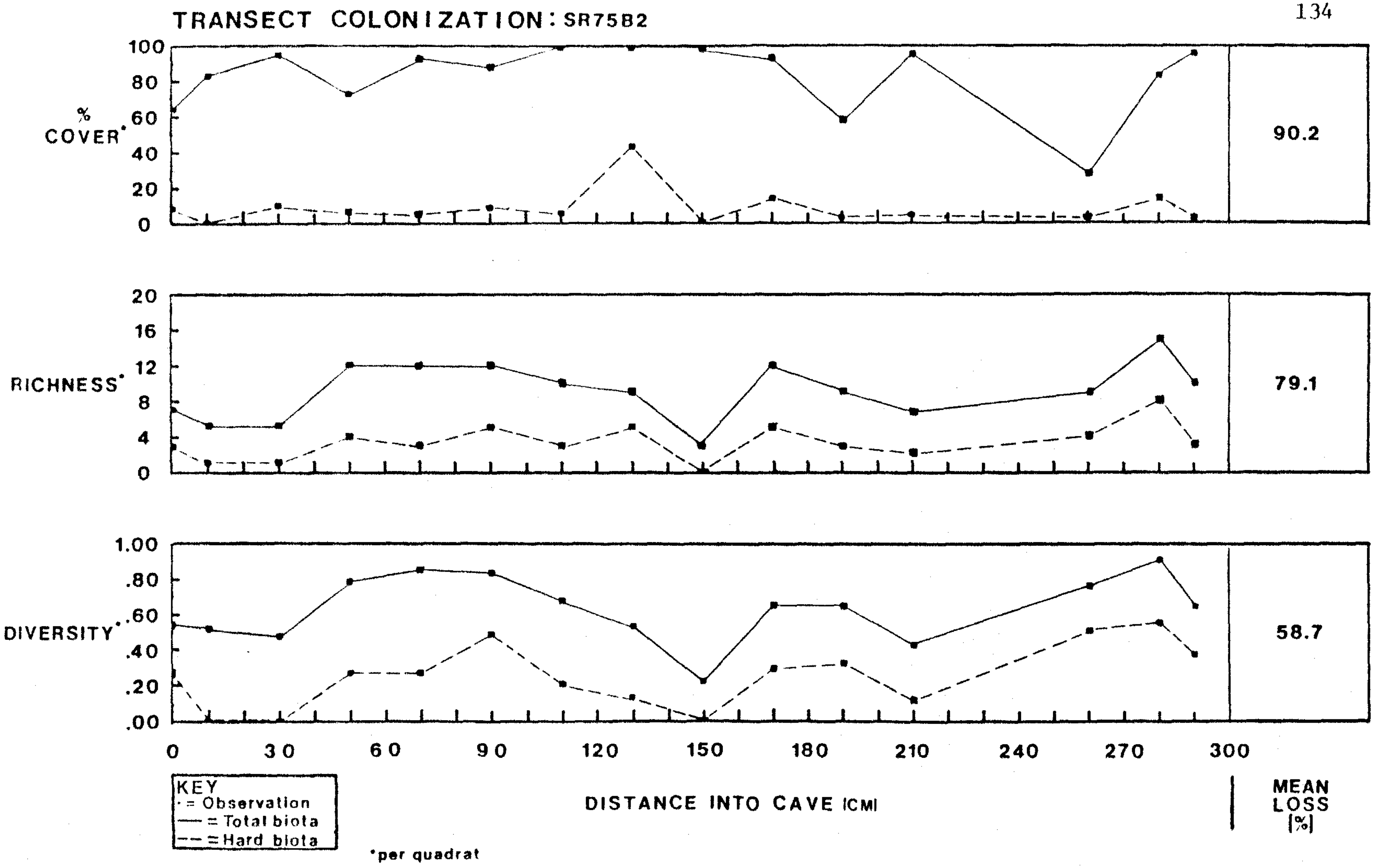


Figure 7. Transect colonization patterns are presented for all sites, considering percent cover, richness, and diversity of total and skeletonized (preservable) organisms. Nonpreservation of unskeletonized forms yields mean percent information loss values listed to the right.

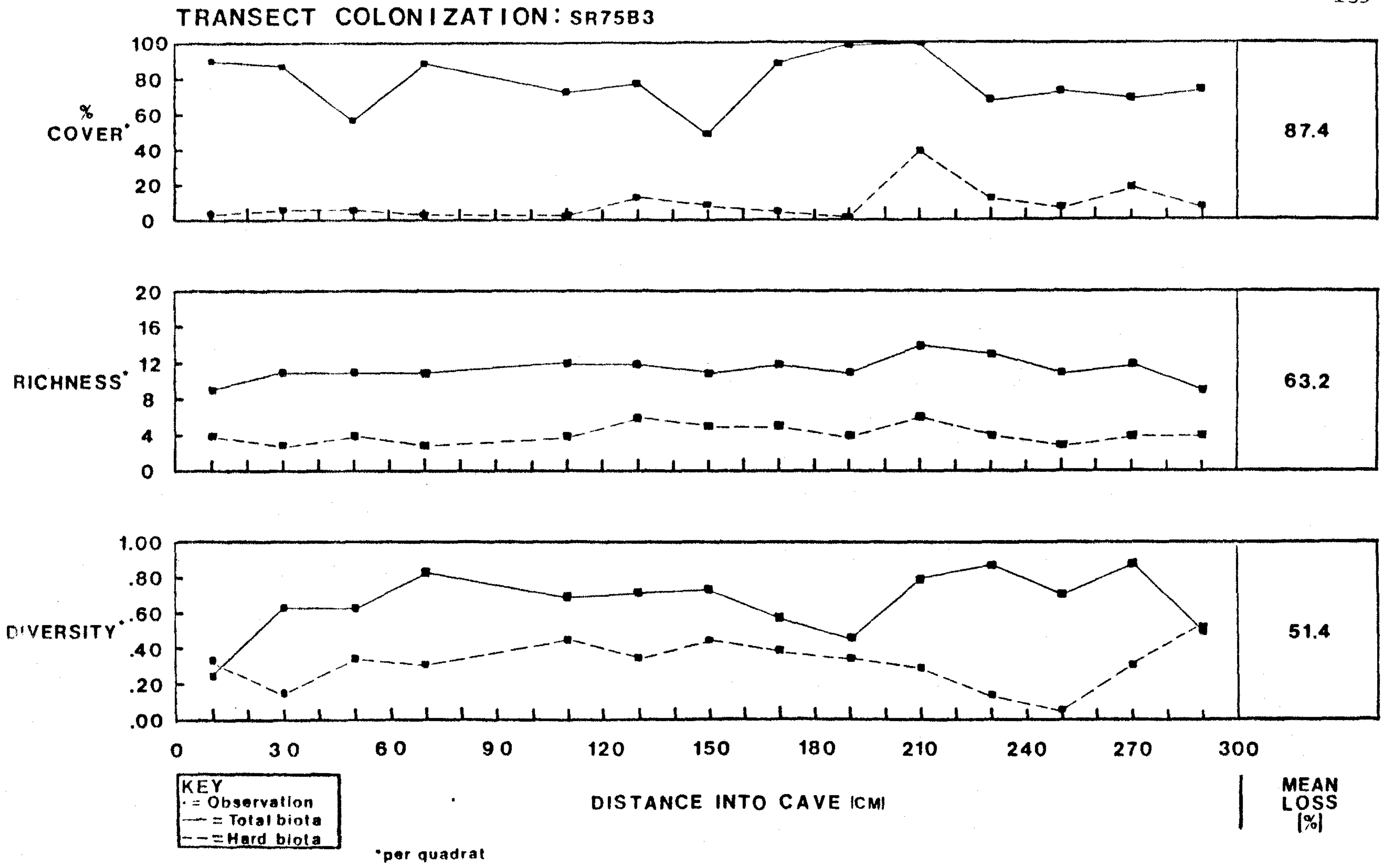
7a) IK50A1


TRANSECT COLONIZATION: SR50A1
% COVER*
100
80
60
40
20
0
77.3
RICHNESS*
20
16
12
8
4
0
48.8
VERSITY*
1.00
.80
.60
.40
.20
.00
41.9
0
30
60
90
120
150
180
210
240
270
300
DISTANCE INTO CAVE (CM)
MEAN LOSS (%)
KEY
■ = Observation
—— = Total biota
– – – = Hard biota
*per quadrat

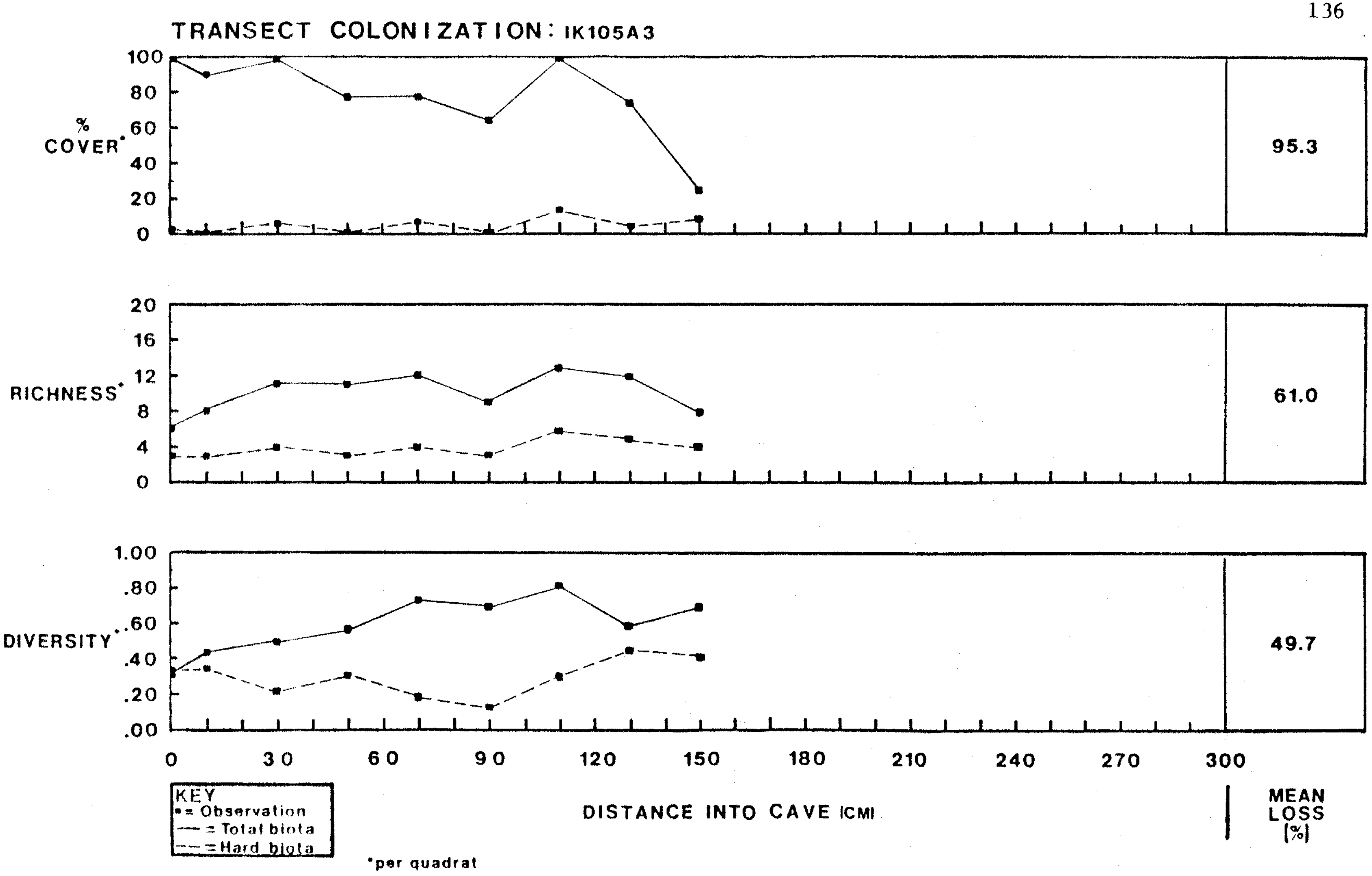
7b) SR50A1


TRANSECT COLONIZATION: SR75B2
% COVER*
100
80
60
40
20
0
90.2
RICHNESS*
20
16
12
8
4
0
79.1
DIVERSITY*
1.00
.80
.60
.40
.20
.00
58.7
0
30
60
90
120
150
180
210
240
270
300
DISTANCE INTO CAVE (CM)
MEAN LOSS (%)
KEY
• = Observation
— = Total biota
– – = Hard biota
*per quadrat

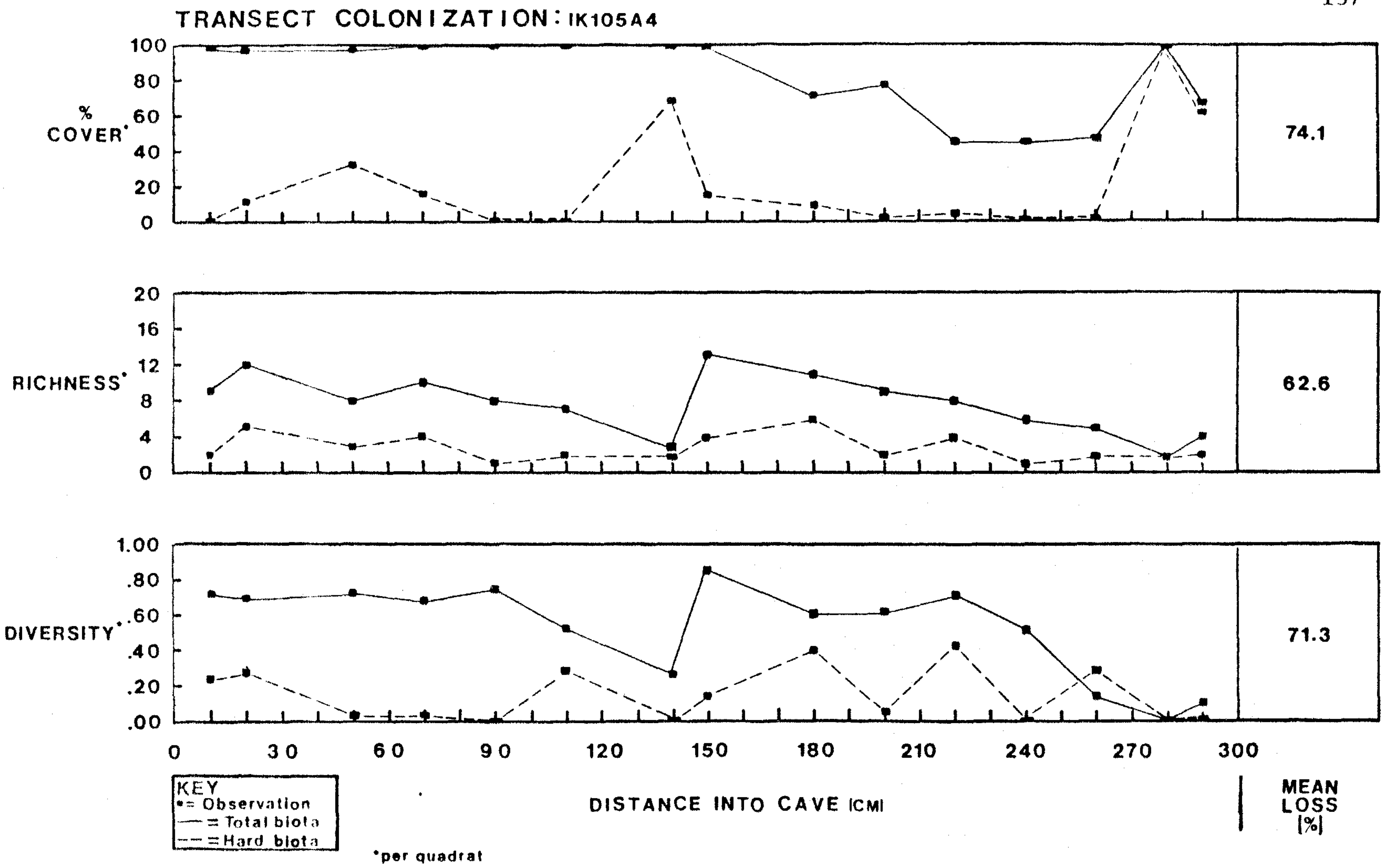
7c) SR75B2


TRANSECT COLONIZATION: SR75B3
% COVER*
100
80
60
40
20
0
87.4
RICHNESS*
20
16
12
8
4
0
63.2
DIVERSITY*
1.00
.80
.60
.40
.20
.00
51.4
0
30
60
90
120
150
180
210
240
270
300
KEY
• = Observation
— = Total biota
- - = Hard biota
DISTANCE INTO CAVE (CM)
MEAN LOSS (%)
*per quadrat

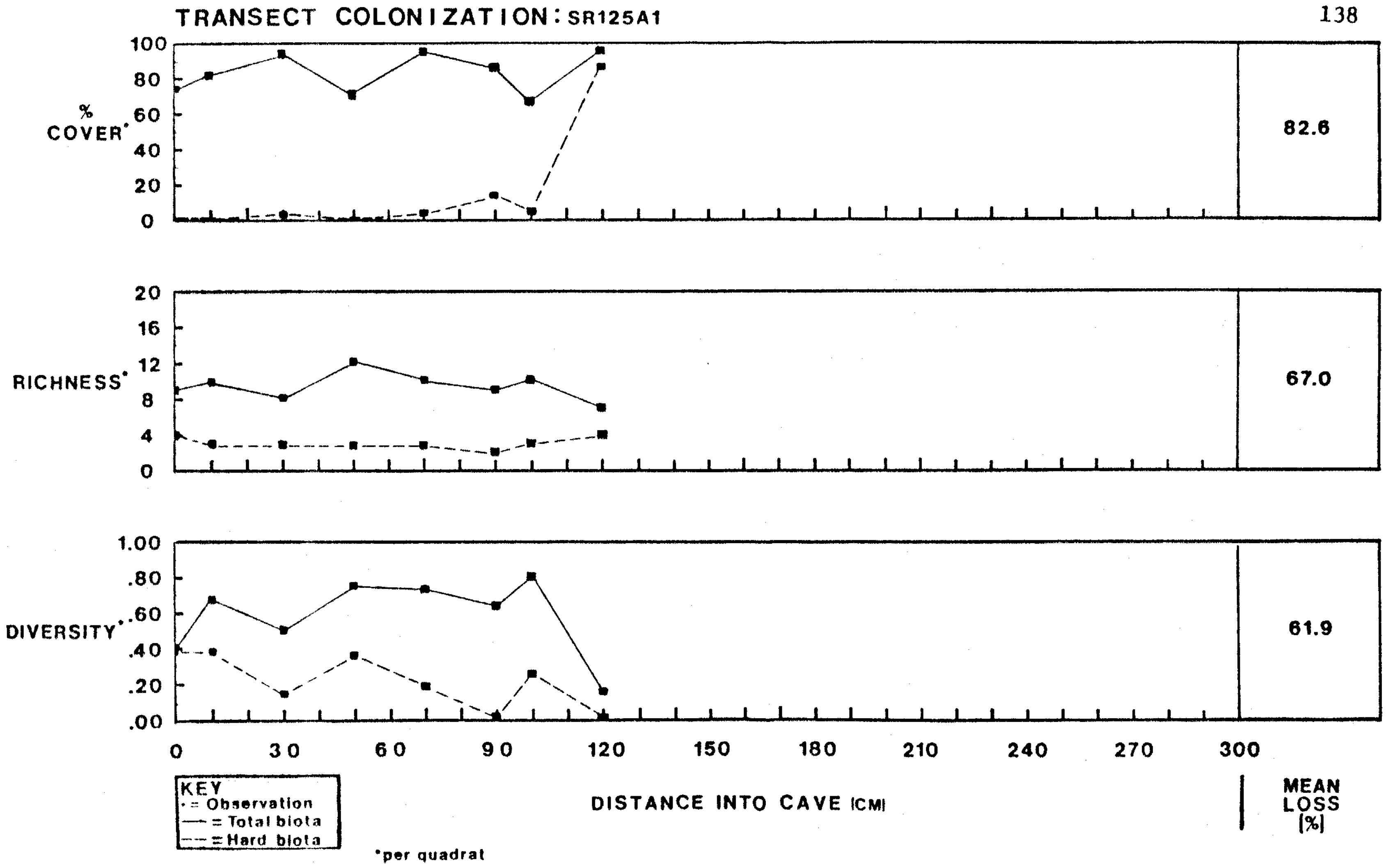
7d) SR75B3


TRANSECT COLONIZATION: IK105A3
% COVER*
100
80
60
40
20
0
95.3
RICHNESS*
20
16
12
8
4
0
61.0
DIVERSITY**
1.00
.80
.60
.40
.20
.00
49.7
0
30
60
90
120
150
180
210
240
270
300
DISTANCE INTO CAVE (CM)
MEAN LOSS (%)
KEY
■ = Observation
— = Total biota
--- = Hard biota
*per quadrat

7e) IK105A3


TRANSECT COLONIZATION: IK105A4
%
COVER*
100
80
60
40
20
0
74.1
RICHNESS*
20
16
12
8
4
0
62.6
DIVERSITY*
1.00
.80
.60
.40
.20
.00
71.3
0
30
60
90
120
150
180
210
240
270
300
DISTANCE INTO CAVE (CM)
MEAN LOSS (%)
KEY
■ = Observation
—— = Total biota
- - - = Hard biota
*per quadrat

7f) IK105A4


TRANSECT COLONIZATION: SR125A1
%
COVER*
100
80
60
40
20
0
82.6
RICHNESS*
20
16
12
8
4
0
67.0
DIVERSITY**
1.00
.80
.60
.40
.20
.00
61.9
0
30
60
90
120
150
180
210
240
270
300
DISTANCE INTO CAVE (CM)
MEAN
LOSS
(%)
KEY
• = Observation
—— = Total biota
– – = Hard biota
*per quadrat

(g) SR125A1

ORGANISM		DISTANCE INTO CAVE(cm.)										
		10.0	40.0	60.0	80.0	100.0	120.0	140.0	160.0	180.0	200.0	220.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.22	0.0
	RS-2	0.0	13.80	0.0	5.58	0.0	0.0	10.00	2.40	0.0	0.0	0.0
	WS-1	0.0	1.03	0.49	0.26	0.0	3.60	0.0	1.75	0.0	0.87	0.0
	WTS-1	0.0	0.0	0.0	0.0	1.51	0.0	0.0	0.0	0.0	0.0	0.0
	WDS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	DS-1	0.0	0.0	2.93	0.81	0.0	0.0	0.0	0.0	0.0	0.0	3.89
	BDS-1	0.0	1.36	0.47	0.0	0.0	0.0	3.30	0.0	3.15	2.76	1.10
	FPS	24.40	1.52	0.0	19.30	18.90	0.0	0.0	0.0	1.38	0.0	0.0
	GS	0.0	4.56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHON	0.0	0.0	1.61	1.10	0.0	8.14	9.72	0.0	0.0	0.0	0.0
	CLI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.40	0.0	0.0	0.0
	ULD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	5.13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	DCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PCCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.35
	WCCT	0.0	0.0	0.0	0.32	0.60	0.0	0.62	0.27	0.0	0.0	0.62
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	2.78	0.0	0.0	0.0	0.27
	LCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RBCT	0.0	0.0	0.0	0.0	2.99	0.0	0.0	0.0	0.0	0.0	0.0
	BCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.37	0.0	0.25	0.24	0.68	0.30	0.22	0.0	0.07	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	0.12	0.71	0.07	0.07	0.38	0.60	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	15.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PHYL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.12
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.36	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.14	0.0	0.0	0.0
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STYLO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.08
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.01	0.0	0.0	0.01	0.0	0.0	0.0	0.01	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.13	0.0	0.16	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.06	0.0	0.0	0.05	0.0	0.04	0.0	0.0	0.04	0.08	0.0
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.0	0.0	0.12	0.05	0.0	0.0	0.06	0.0	0.07	0.06	0.09
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	0.0	15.40	35.60	0.0	7.51	9.11	15.30	17.80	30.90	0.0	0.0
	PCA	0.0	0.41	0.0	18.20	13.10	11.60	0.43	14.60	0.0	29.60	18.70
OPEN SPACE		0.0	0.28	0.0	0.0	0.0	0.92	0.0	0.0	0.0	3.06	3.53
TOTAL AREAS:		46.1	39.1	41.7	[illegible]	42.2	33.3	42.4	41.9	35.5	[illegible]	40.8

Table 4. Original areal coverage data measured the space occupied by each morphospecies in cm^2. Total quadrat areas vary according to the amount of "unlit space" in original photographs. All subsequent numerical calculations are based on these results.

DISTANCE INTO CAVE(cm)

ORGANISM		10.0	30.0	50.0	80.0	100.0	120.0	140.0	160.0	180.0	200.0	220.0	240.0	260.0	280.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RS-2	0.0	0.0	0.0	4.10	0.20	0.0	7.70	5.70	0.0	3.48	10.00	0.0	14.80	0.0
	MS-1	0.0	3.43	0.60	0.0	0.0	0.0	0.0	0.80	2.57	6.48	0.0	0.44	1.15	1.35
	MTS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MCS-1	0.0	0.0	0.0	0.0	1.70	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.50	3.00
	YS-2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OS-1	0.0	0.0	0.10	7.00	0.0	0.0	0.90	0.0	6.21	0.0	1.26	0.40	0.0	10.20
	BOS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.64	0.0	0.0	2.37	0.0	3.68	6.57
	FPS	0.0	0.0	0.0	0.0	6.40	12.60	0.0	0.0	0.0	10.20	0.0	0.0	0.0	0.0
	GS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	0.0	0.0	0.10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHON	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.60	0.0	0.0	2.40	0.10	0.0	0.0	0.05	0.0	0.0	0.0	0.0	0.0
	ULO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	0.0	0.30	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.41
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.49	0.0	0.0	0.0	0.0	0.0
	PCCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.11	0.0	0.0
	MCT	0.0	0.0	0.0	0.0	1.73	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WCCT	0.0	0.0	0.0	0.0	0.0	1.10	0.0	0.0	0.69	0.0	0.0	0.0	0.0	0.0
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.09	0.0	0.0	0.0	0.0	0.0	0.0
	LCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RBCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BLUE	BCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.0	0.0	0.0	0.11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.69	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	1.90	4.79	1.40	0.62	0.0	3.00	1.30	0.69	1.12	0.0	0.75	0.45	0.58	4.75
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.10	0.0	1.32
	PHYL	0.0	0.0	1.00	3.40	3.80	4.40	2.40	6.34	3.03	0.80	0.12	0.20	0.28	0.04
	TUB	0.0	0.70	0.72	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	MAB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.30	0.0	2.29
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WE	0.0	0.0	0.0	0.0	0.0	0.0	0.40	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIOD	0.0	0.0	0.0	0.0	0.21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STYLO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.25	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.0	0.0	0.21	0.0	0.10	0.0	0.0	0.0	0.0	0.20	0.0	0.0	0.07	0.03
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.14	0.12
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.20	0.0	0.30	0.0	0.15	0.12	0.0	0.26	0.08	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	A	0.0	0.10	0.0	0.10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.12	0.0	0.0
	B	0.05	0.20	0.05	0.0	0.01	0.10	2.10	0.20	0.06	0.27	0.0	0.15	0.0	0.0
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.0	0.0	0.02	0.51	0.40	0.20	0.45	0.52	0.11	0.12	0.20	0.56	0.10	0.05
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	0.0	0.0	23.70	14.00	16.70	10.50	5.00	15.30	16.40	0.0	18.90	25.80	2.25	0.0
	PCA	33.70	20.20	7.20	5.30	2.70	7.50	21.80	6.06	9.01	19.90	4.32	0.13	13.10	9.51
OPEN SPACE		0.0	0.09	0.0	0.0	0.0	0.0	0.50	0.0	0.0	0.0	0.09	0.0	0.31	0.0
TOTAL AREAS:			31.3	36.0	37.1	34.3	39.8		39.3	40.0	41.5	38.0	37.8		40.5

4b) SR 50A1

SR75B2

ORGANISM		DISTANCE INTO CAVE(cm.)														
		0.0	10.0	30.0	50.0	70.0	90.0	110.0	130.0	150.0	170.0	190.0	210.0	260.0	280.0	290.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.47
	RS-2	0.0	12.30	22.10	11.00	3.65	10.40	0.0	16.30	29.80	19.20	9.06	4.66	2.33	2.27	0.0
	WS-1	0.90	0.82	0.0	2.60	9.53	3.20	12.40	4.44	0.0	1.12	1.30	0.22	1.45	8.70	0.67
	WTS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WOS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.69	0.0	0.0	0.0	0.35	0.0	0.0	0.34	0.0	0.0	2.77	0.89	0.0
	YS-2	0.0	0.0	0.0	0.0	0.71	0.0	0.0	0.0	0.0	0.0	6.07	4.92	0.0	0.0	0.0
	CS-1	0.0	0.0	4.41	0.0	0.0	0.0	10.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.65
	BOS-1	0.0	0.0	0.0	1.61	3.11	8.52	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.63	0.0
	FPS-1	0.0	0.0	0.0	0.0	1.73	4.59	0.0	0.0	0.0	0.0	4.16	28.20	0.31	0.84	14.10
	GS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.34
	AGELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHON	0.0	0.0	0.0	4.19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.73	0.0	0.0	0.0	0.0	0.0	0.0
	ULO	3.58	8.85	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	0.0	0.0	0.0	0.0	0.0	0.0	2.60	0.0	0.0	7.92	0.0	0.0	0.0	0.0	16.80
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.27	0.0	0.0	0.10	0.0	0.0	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GST	0.0	0.0	0.0	0.0	0.0	0.0	0.34	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	FCCT	0.0	0.0	0.0	0.26	0.58	1.05	0.0	0.0	0.0	0.20	0.0	0.0	0.0	0.0	0.0
	WCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WCCT	0.0	0.0	0.0	0.0	8.27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.35	0.0
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.70	0.0	0.0	0.0	0.0
	LCT	1.21	0.0	0.0	0.56	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RBCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BCT	0.0	0.0	0.0	0.0	1.61	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.0	0.0	0.0	1.24	0.0	1.62	0.33	0.0	0.0	0.12	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	10.90	9.91	4.25	2.61	1.30	1.73	6.30	0.55	0.19	3.37	0.0	0.43	2.35	4.15	3.01
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.90	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.20	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.90	0.0	0.0	0.0	1.95	0.0
	PHYL	2.02	0.0	3.35	1.99	1.47	1.90	1.70	0.36	0.0	0.75	0.0	0.0	0.14	0.0	0.24
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.00	0.0	0.0	0.0	1.49	0.0	0.0	0.0
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.29	0.0
	STYLO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.84	0.0	0.0	0.0	2.47	0.0
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.0	0.0	0.12	0.0	0.16	0.0	0.14	0.0	0.0	0.58	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.07	0.0	0.0	0.13	0.15	0.16	0.25	0.02	0.0	0.04	0.14	0.0	0.56	0.08	0.03
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.09	0.0	0.0
	SPIR	0.56	0.03	0.0	0.09	0.20	0.18	0.04	0.07	0.0	0.10	0.05	0.12	0.34	0.20	0.27
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	2.90	0.0	0.0	5.61	2.43	0.0	0.0	0.0	0.0	0.70	5.51	0.0	0.0	0.0	0.0
	PCA	9.50	6.89	1.58	5.05	0.0	5.30	0.0	0.50	0.54	3.20	11.30	1.71	6.85	6.41	0.0
OPEN SPACE		2.15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.00	0.0	2.10
TOTAL AREAS:		35.8	26.9	34.9	37.5	36.0	40.1	34.3	38.2	37.3	41.7	39.0	41.7	39.2	37.5	44.7

4c) SR75B2

ORGANISM		DISTANCE INTO CAVE(cm.)													
		10.0	30.0	50.0	70.0	110.0	130.0	150.0	170.0	190.0	210.0	230.0	250.0	270.0	290.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	10.40	0.0	0.16	0.0	0.0	1.01	0.0	0.0	0.0	0.0
	RS-2	32.20	15.80	13.40	5.20	0.0	0.0	0.0	2.01	25.50	0.0	2.09	14.10	7.87	22.[illegible]
	WS-1	0.0	0.74	0.90	2.76	5.14	0.36	0.0	3.19	1.94	1.97	9.46	4.09	1.65	1.24
	WTS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WOS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.65	0.12	0.55	0.0	0.0	5.27	0.0	0.0	0.0	0.0	0.0	0.0
	YS-2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.98	0.0	0.0
	OS-1	0.0	2.28	0.0	0.0	0.0	0.0	3.51	0.0	0.0	11.80	1.09	0.0	0.0	0.0
	BOS-1	0.0	0.0	0.0	9.49	2.77	0.0	0.0	0.0	0.0	0.48	2.32	0.0	0.0	1.12
	FPS	0.0	0.0	0.0	2.42	0.0	0.0	1.47	23.50	0.64	0.0	1.02	0.0	6.32	0.0
	GS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.28	0.0	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.54	1.25	0.0	0.0	0.0	0.0	0.0
	CHUN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.25	0.0	0.0	0.29	0.0	1.54	0.0	0.0	0.0	0.0	0.50	0.0	0.0
	ULO	0.0	10.30	0.0	0.0	3.15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	0.0	0.0	0.0	0.0	0.0	4.68	0.0	0.0	0.0	0.79	1.44	0.77	0.0	0.0
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PCCT	0.0	0.22	0.0	0.0	0.0	1.03	0.0	0.0	0.0	0.0	0.0	0.0	2.42	0.0
	WCT	2.01	0.0	0.0	2.63	0.0	0.0	0.27	0.0	0.0	0.0	0.0	0.0	2.43	0.0
	WCCT	0.23	0.0	1.98	2.13	0.46	11.00	0.0	0.0	0.0	2.54	2.45	1.87	0.78	4.46
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LCT	0.0	0.0	0.22	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	FBCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.30	0.56	0.30	0.0	0.13	0.05	0.0	0.07	0.06	0.04	0.05	0.20	0.06	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	0.94	2.10	2.96	2.51	0.0	4.72	7.60	0.48	9.21	5.81	5.06	1.27	1.81	0.41
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.95	2.83	2.85	0.74
	PHYL	0.90	2.00	0.48	0.62	0.42	3.19	1.60	1.40	0.50	2.39	0.0	0.0	0.0	0.0
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	UN. HON	0.27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.62	1.40
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.47	0.0	0.0	0.0	0.55	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STYLO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.60	0.0	0.0	0.0	0.0
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.19	0.0	0.0	0.0	0.0	0.0	0.0
	STEG	0.0	0.0	1.67	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.0	0.0	0.0	0.0	0.03	0.06	0.03	0.0	0.03	0.03	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STROM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.36	0.0	0.08	0.70
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OSTR	0.0	0.0	0.0	0.0	0.0	0.0	1.39	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.16	0.0	0.0	0.0	0.0	0.0	0.0
	3	0.25	0.15	0.06	0.16	0.24	0.04	0.05	0.07	0.08	0.23	0.07	0.04	0.0	0.0
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.03	0.04	0.11	0.06	0.08	0.29	0.20	0.09	0.05	0.05	0.03	0.05	0.10	0.13
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	0.0	0.0	0.96	0.0	0.0	0.57	0.0	0.0	0.0	0.0	0.22	0.0	0.0	0.0
	PCA	4.13	5.05	15.40	3.40	6.94	7.25	18.30	5.02	0.76	0.47	14.10	9.00	8.74	4.3[illegible]
OPEN SPACE		0.0	0.0	0.63	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.79	5.37	7.24
TOTAL AREAS:		41.1	39.[illegible]	39.8	30.5	72.5	34.4	36.2	43.[illegible]	40.3	40.7	44.7	39.5	46.1	43.[illegible]

IK105A3

ORGANISM		DISTANCE INTO CAVE(cm.)								
		0.0	10.0	30.0	50.0	70.0	90.0	110.0	130.0	150.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.50
	RS-2	0.0	0.0	0.0	0.0	7.74	0.0	1.55	0.0	0.0
	WS-1	5.59	0.0	2.94	1.01	1.61	0.0	3.05	7.48	1.48
	WTS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WDS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.0	0.0	5.16	0.0	0.0	0.0	0.0
	YS-2	0.0	0.70	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	DS-1	0.0	0.59	1.08	0.16	0.15	0.0	0.0	0.0	0.0
	BDS-1	0.0	0.0	0.36	1.58	0.54	0.0	7.03	0.0	0.0
	FPS	0.89	0.0	0.0	0.0	0.0	4.09	5.92	0.0	0.0
	GS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHON	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.0	0.0	2.77	0.0	7.82	0.0	0.34	0.0
	ULD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	24.20	19.10	27.00	0.0	0.0	0.0	2.31	0.0	0.44
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.37	3.99	0.22	0.42	0.72	0.0	0.42	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	0.0	0.0	0.30	0.0	0.0	0.0	0.0	0.0	0.0
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PCCT	0.0	0.0	0.15	1.19	0.18	0.0	1.50	0.21	0.0
	WCT	0.0	0.0	0.0	3.77	0.0	0.80	0.0	0.0	0.0
	WCCT	0.0	0.0	0.0	19.00	0.0	3.86	0.0	1.21	4.60
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RBCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.80	0.0
	BCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	0.0	11.90	0.95	0.0	4.35	2.66	15.40	1.61	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PHYL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WME	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.35	0.0	0.47	0.10	0.49	0.12	0.14	0.61
	STYLO	0.0	0.0	0.0	0.0	1.57	0.0	4.35	0.20	2.51
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.0
	STEG	0.0	0.0	1.72	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.45	0.04	0.03	0.0	0.0	0.02	0.01	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.03	0.09	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	UNK.	0.0	0.0	0.0	0.0	0.0	0.0	0.85	0.0	0.0
SERPULID	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.30
	B	0.20	0.0	0.10	0.06	0.04	0.0	0.10	0.0	0.0
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.0	0.0	0.12	0.09	0.06	0.02	0.08	0.35	0.24
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	0.0	0.0	0.0	1.07	0.0	0.0	0.0	0.0	0.0
	PCA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
OPEN SPACE		0.0	4.00	0.0	9.20	6.71	11.50	0.0	10.10	33.80
TOTAL AREAS:		31.4	37.1	38.7	39.6	28.7	[illegible]	42.3	37.6	44.5

4e) IK105A3

IK105A4

ORGANISM		DISTANCE INTO CAVE(cm)														
		10.0	30.0	50.0	70.0	90.0	110.0	140.0	150.0	180.0	200.0	220.0	240.0	260.0	280.0	290.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RS-2	0.0	0.0	0.0	0.0	0.0	0.0	8.20	9.08	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WS-1	2.10	0.0	2.53	0.0	7.57	1.23	0.0	0.51	14.60	10.40	3.80	10.70	0.71	0.0	0.0
	WTS-1	0.0	0.0	0.0	0.0	1.34	0.0	0.0	0.51	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WDS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.0	0.0	0.0	15.30	0.0	0.0	0.0	0.0	2.34	0.0	0.36	0.0	0.0
	YS-2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	DS-1	0.0	0.0	0.0	0.0	7.26	0.0	0.0	1.62	0.0	6.00	0.0	0.0	0.0	0.0	0.0
	BDS-1	5.40	0.36	0.0	0.0	0.0	0.0	0.0	1.10	0.0	0.0	0.0	2.22	0.0	0.0	0.63
	FPS	1.32	0.75	1.61	5.35	2.46	15.80	0.0	0.0	0.0	0.0	0.0	0.78	0.0	0.0	0.0
	GS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.69	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHON	0.0	1.23	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.0	0.0	5.00	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0	0.0	0.0	0.0
	ULO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	BSS-1	14.40	15.20	5.53	1.55	2.89	0.0	0.0	4.13	1.08	3.08	0.0	1.17	0.0	0.0	0.0
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.30	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	1.74	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	FCCT	0.0	0.25	0.0	0.0	0.24	0.0	0.0	0.0	0.0	0.17	0.0	0.0	0.0	0.0	0.0
	WCT	3.09	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.59	0.0	0.0	0.0	0.0	0.0	0.0
	WCCT	0.0	3.74	6.47	15.10	0.0	2.95	0.0	2.95	2.48	0.0	1.39	2.21	16.50	0.0	0.71
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	ABCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.25	0.0	0.0	0.0	0.0	0.0
	BCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	8.20	5.07	1.90	2.24	4.60	2.08	0.0	9.09	2.25	0.52	4.47	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PHYL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YSP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.22	0.39	0.0	0.0	0.0	0.0
	STYLO	0.0	0.20	0.0	0.0	0.0	0.0	0.0	0.0	0.39	0.0	0.0	0.0	0.0	0.0	0.0
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.01	0.02	0.08	0.04	0.09	0.0	0.0	0.18	0.02	0.01	0.03	0.0	0.0	0.02	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	2.63	9.39	3.30	0.0	0.0	17.80	5.13	2.37	0.0	0.0	0.0	0.0	36.60	21.70
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRACHIOPOD	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	0.40	0.0	0.03	0.0	0.04	0.0	0.04	0.24	0.0	0.20	0.12	0.18	0.0	0.04
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.03	0.02	0.04	0.03	0.0	0.0	0.03	0.21	0.11	0.0	0.98	0.0	0.15	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	RCA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PCA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
OPEN SPACE		0.0	0.69	0.64	1.28	0.0	0.0	0.0	0.0	10.10	7.00	16.80	20.90	20.10	0.0	11.50
TOTAL AREAS		37.3	30.6	29.2	36.0	[illegible]	39.4	26.0	35.9	24.5	30.7	[illegible]	38.2	33.0	36.6	24.6

4f) IK105A4

SR125A1

ORGANISM		DISTANCE INTO CAVE(cm.)							
		0.0	10.0	30.0	50.0	70.0	90.0	100.0	120.0
DEMOSPONGE	RS-1	0.0	0.0	0.0	0.0	0.0	2.16	2.17	0.0
	RS-2	14.60	12.00	22.10	2.64	15.00	0.0	0.0	0.0
	WS-1	0.29	0.0	0.0	0.50	5.35	2.24	0.0	0.0
	WTS-1	0.0	0.0	0.24	0.0	0.0	0.0	0.0	0.0
	WCS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LS-1	0.0	3.05	0.0	0.0	0.0	0.0	0.0	0.0
	YS-1	0.0	0.0	0.0	0.0	2.36	0.0	0.0	0.0
	YS-2	16.00	8.65	0.0	0.0	0.0	0.0	0.0	0.0
	OS-1	0.0	0.0	0.0	0.22	1.18	0.0	0.0	0.0
	BCS-1	0.0	0.21	0.0	9.59	0.0	1.60	7.44	1.44
	FPS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GS-1	0.0	0.0	0.0	0.42	0.0	0.0	0.0	0.0
	AGELL	0.0	0.0	0.0	2.23	0.0	17.90	0.0	0.0
	CHON	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLI	0.0	0.0	0.0	0.0	0.0	0.0	0.89	0.0
	ULO	0.0	0.0	7.64	0.0	0.0	0.0	0.0	0.0
	PS-1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TUNICATE	CST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WST	0.0	0.0	0.0	0.0	0.0	0.22	0.0	0.0
	YST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	GCT	0.0	2.90	8.72	0.0	0.0	0.0	0.0	0.0
	OCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	PCCT	0.0	0.0	0.0	0.0	0.21	0.56	0.55	0.0
	WCT	0.0	0.0	0.0	0.49	0.0	0.0	5.23	0.84
	WCCT	0.0	0.0	0.0	3.79	9.39	0.0	2.07	0.0
	YCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LCT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	RBCT	0.0	1.20	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SABELLID	SAB	0.30	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
GREEN ALGAE	AS	0.70	2.59	0.22	4.50	3.65	3.38	4.69	0.20
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORAL	AST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	EUS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	MAD	0.23	0.0	1.39	0.0	0.0	0.0	0.40	0.0
	PHYL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	TUB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BRYOZOA	WMB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	YGB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	LPB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CELL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CLEIDO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STYLO	0.0	0.0	0.0	0.0	1.63	5.08	1.16	0.0
	WSB	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	WBB	0.0	0.0	0.0	0.06	0.0	0.05	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FORAM	HOMO	0.01	0.01	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
HYDROZOA	STY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SCLEROSPONGE	CERAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	STROM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.10
BRACH	FREN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
BIVALVE	ISOGN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	CHA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OSTR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SERPULID	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04
	B	0.02	0.09	0.12	0.02	0.06	0.0	0.0	0.02
	C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	SPIR	0.12	0.06	0.02	0.15	0.16	0.0	0.01	0.08
	OTHER	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CORALLINE ALGAE	FCA	10.24	6.55	1.56	0.97	2.20	0.89	0.82	0.0
	PCA	1.00	0.39	0.90	9.52	0.0	4.72	11.60	1.73
OPEN SPACE		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL AREAS:		43.7	37.9	42.9	35.2	41.2	39.8	37.0	34.4

4g) SR125A1

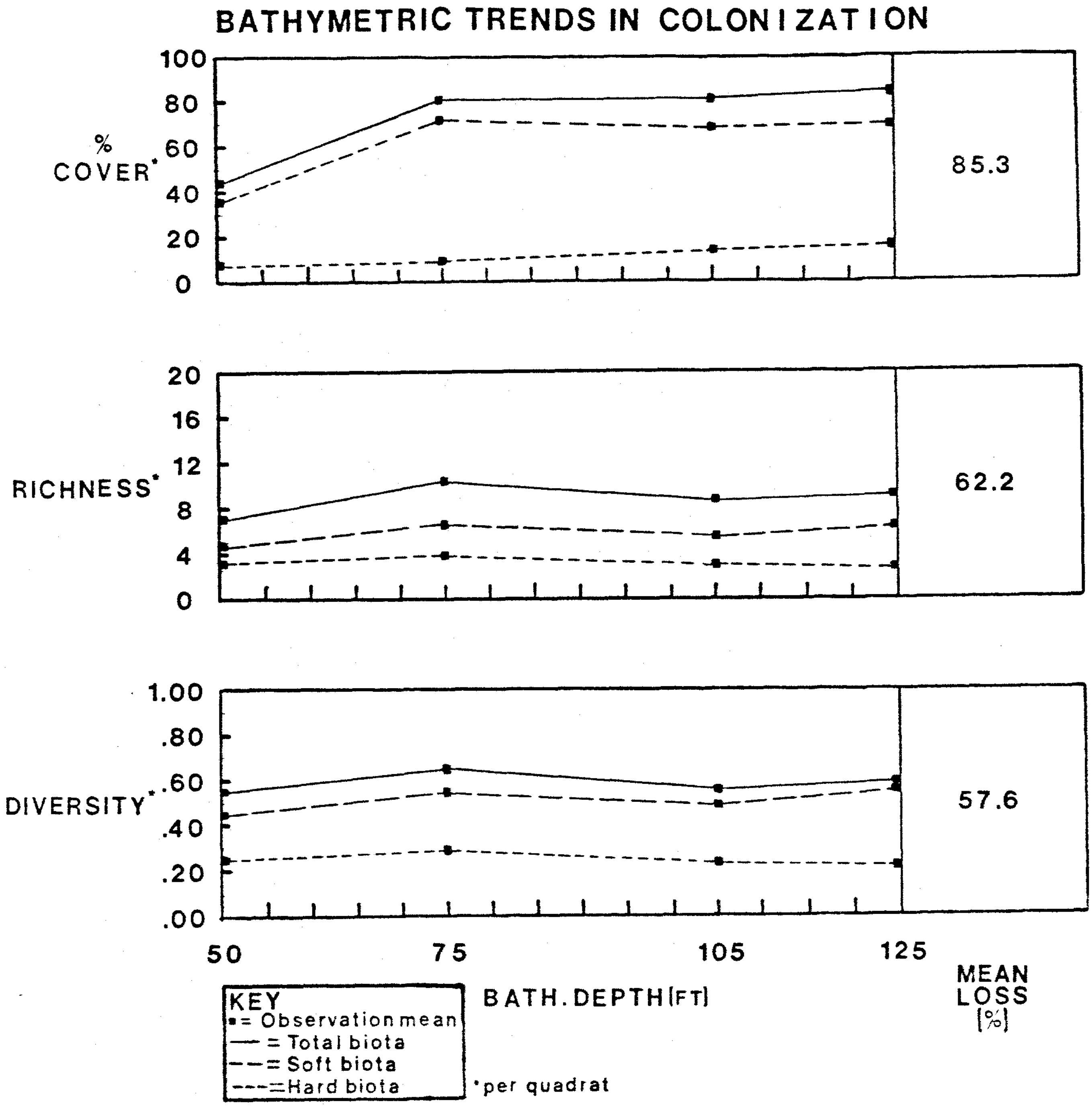


Figure 8. Bathymetric trends in each colonization index are considered for total organisms, and preservable (hard) and unpreservable (soft) components. Unpreservable organisms comprise the majority of biotas present, and thus parallel total trends. Preservable organism patterns vary discordantly from total organism trends. Points at which soft and hard component trends diverge indicate increasing levels of information loss. Mean percent information loss for the entire environment is listed to the right.

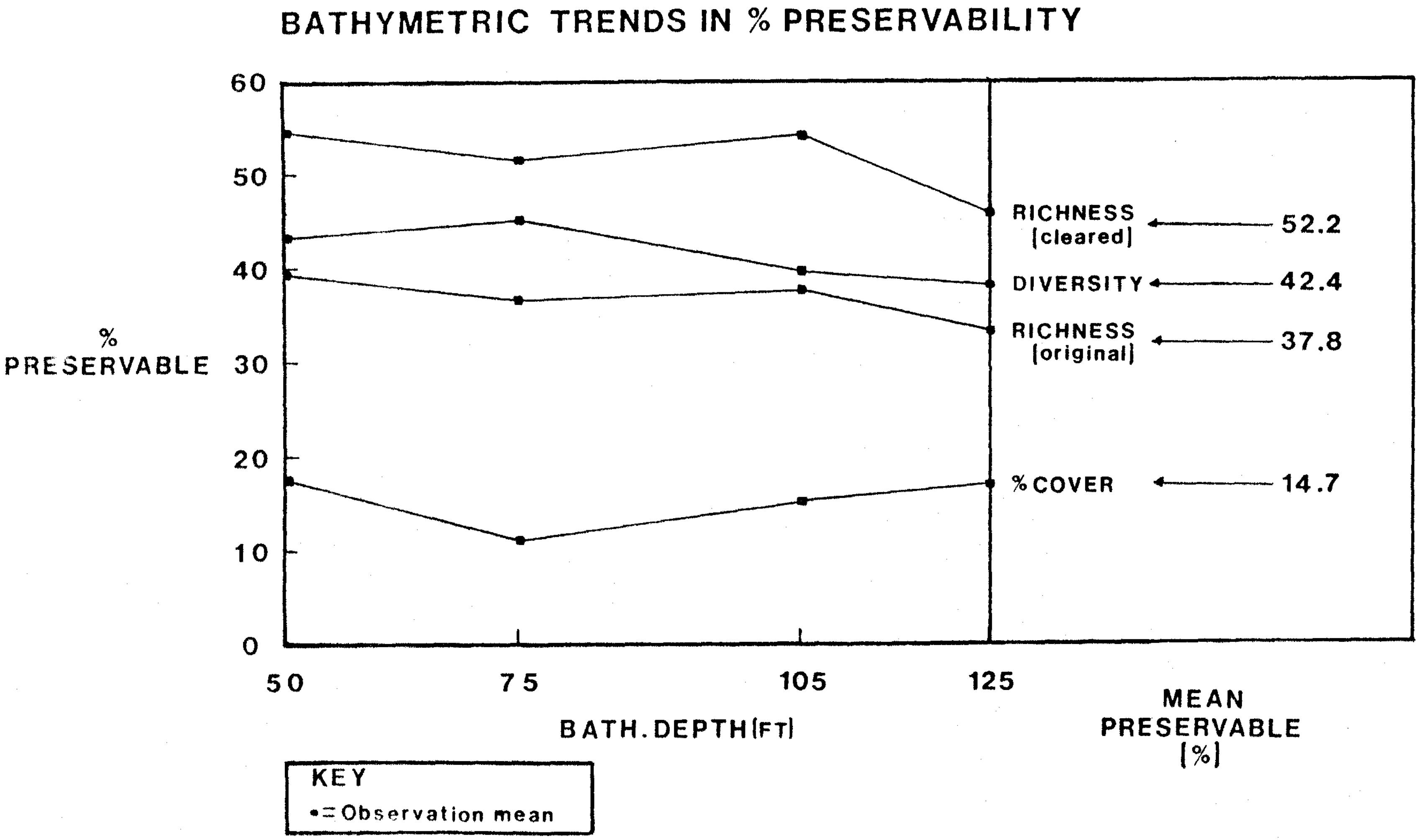


Figure 9. Bathymetric trends in percent preservability of colonization indices show these values to be affected by increasing water depth. Percent cover preservability remains roughly constant, due to the appearance of skeletonized sclerosponges, but would otherwise decrease markedly.

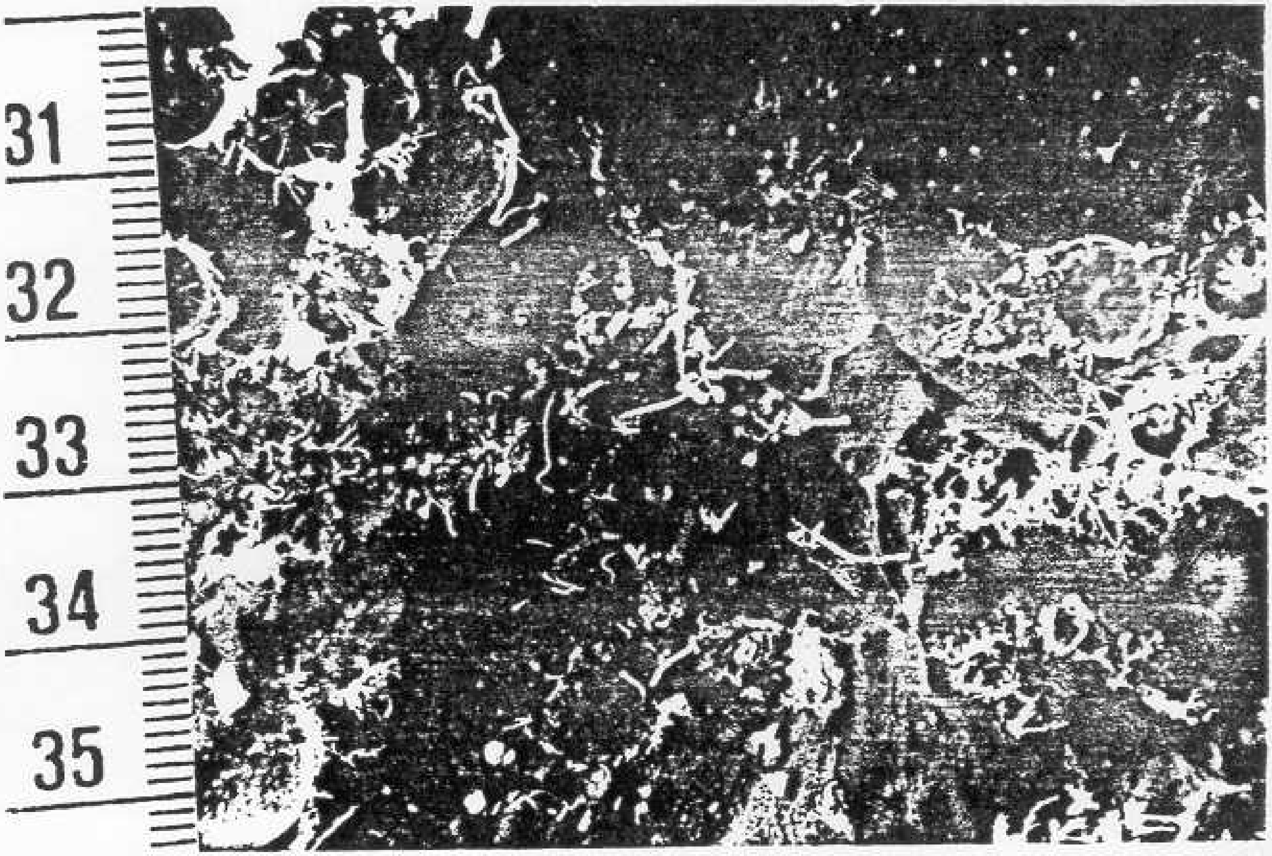


Figure 10a. An original quadrat photograph shows demosponges overgrowing solitary corals (SR75B2, #4).

Figure 10b. Clearing soft demosponges from the same quadrat as above shows previously hidden skeletonized organisms, including serpulid worms and relict corals. Varying degrees of corallite corrosion are seen, and suggest possible "biotic erasure" through demosponge encrustation.