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Bad-Boy Bryozoan Biomarkers: Cheilostome Distribution Patterns Along a Bahamian Depth Gradient

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ABSTRACT

In 1993 and 1994, the Shelf and Slope Experimental Taphonomy Initiative (SSETI) deployed thirty-five samples of sea urchins along the continental shelf/slope of the Bahamas in an effort to explore the paleoecology and taphonomic potentials of shallow water carbonate environments. Samples were retrieved at 1-, 2-, and 6-year intervals for examination and comparison of epibiont accumulation.

Tests and spines of the sea urchin *Eucidaris* were examined for encrusting cheilostome Bryozoa. Specimens were identified to the genus level. Assessment of abundance and distribution patterns with water depth shows that cheilostomes are prevalent in photic waters, and lacking at depth. Burial of substrates limits bryozoan settlement patterns in shallow waters but not below the photic zone. Preliminary results indicate that cheilostomes may be useful biomarkers, at least in modern environments.

INTRODUCTION

Some people call them sea mats. Others refer to them as moss animals. They are the Bryozoa, sessile, aquatic animals belonging to the super-phylum Lophophorata. These colonial organisms are predominantly marine creatures, although freshwater species exist as well. In its entirety the phylum Bryozoa is incredibly diverse, with at least 3,500 living species, and over 15,000 fossil species (Prothero, 1998). This variety is reflected in the multitude of morphological forms that inhabit an equally diverse range of environments. Bryozoans are often found as encrusting layers on rocky surfaces and shells in the sublittoral zone. They also develop as brittle, branching colonies that stand erect in the water column at great depths (Ryland, 1970). Their prolific nature has both secured them a position in fossil carbonate limestones (Pinna, 1990), and lead to the burdensome fouling of ship bottoms and water intake pipes (Ryland, 1970). Bryozoans have even extended into the world of medicine as potential synthesizers of anti-cancer drug compounds (Newman, 1996).

Paleoecology seeks to identify and reconstruct the physical and biological communities of the past in order to infer their ecological and evolutionary significance. Examining organismal patterns of distribution and abundance provides insight into the intricate workings and preservation of habitats through time. This thesis explores the ecology of encrusting bryozoans belonging to the order Cheilostomata, the dominant bryozoan lineage of Cenozoic times (Robison, 1983). Two main objectives lie at the heart of the project: First, to determine the degree to which extant Bryozoa reflect the physical and biological conditions of the environments in which they live. Second, to assess the potential that this contemporary model has as a paleoecological tool for understanding similar communities in the fossil record.

Cheilostomes were selected for study because of their pervasive nature. They are found on a variety of substrates and are common in both shallow and deeper waters. In addition, they have a calcitic skeleton, which increases their chances for incorporation in the fossil record. Thus the cheilostomes appear to be

be ubiquitous and distinctive representatives of community dynamics across environmental gradients, with high potential for retaining the taxonomic richness of a community assemblage. Accordingly, in a manner similar to the treatment of index fossils, the Bryozoa have the capacity to serve as sensitive indicators for a wide range of physical and biological parameters.

BACKGROUND

Morphology

Despite their abundance in the marine realm, bryozoans are little known in comparison with other habitat-associated metazoans. The reason for this has to do primarily with size. Individual bryozoans, or *zooids* (Fig. 1) have bilateral symmetry and are generally 1 mm or less in length. Together, a colony of encrusting cheilostomes looks like a cluster of miniature boxes (Fig. 2). Whole colonies grow to as much as 1/2 meter, and contain anywhere from a few to millions of individuals (Prothero, 1998). Their size thus requires the use of a microscope to examine internal zooidal composition. Each zooid is enclosed in an external skeleton and body wall called the *zooecium*. This skeleton can vary in composition from soft tissue to a rigid calcitic structure, and is extremely useful in taxonomic identification. The skeleton of the colony is the *zooarium,* which consists of both individual zooid walls as well as *extrazooidal* parts that simply provide additional support to the colony (Robison, 1983).

Characteristic zooidal anatomy includes a mouth that opens into a u-shaped gut within the body, or *coelom*, of the animal. The digestive tract ends in an anus that sits just outside a ring of filter-feeding tentacles called the *lophophore* (Fig. 1). It is this feeding apparatus that links bryozoans with the other lophophorates, brachiopods and phoronids. And it is the location of anus in relation to the lophophore that generates the alternate term for Bryozoa, Ectoprocta, meaning 'outside anus' (Ryland, 1970). In addition there is a small central ganglion that serves as a nerve center. Bryozoa lack specialized excretory, respiratory, or vascular systems. Respiration and excretion take place by diffusion through the body wall (Robison, 1983).

As colonial animals, the entire complex is a genetically similar unit (Prothero, 1998). However, varying environmental conditions necessarily stimulate unique functional adaptations for individual species within specific habitats. Cloned individuals often have different phenotypic expressions, whether

ontogenetic or environmentally induced, which result in zooids with different morphologies and functions, or *polymorphism.* Zooids specialized strictly for feeding are called *autozooids.* Other specialized zooids in which the mechanism for feeding is incomplete or absent are lumped as *heterozooids.* These include *avicularia* (Fig. 1) for defense and predator determent, *vibracula* for cleaning the colony surface of debris, and *kenozooids* for filling space and providing colonial support. Together the individually specialized zooids enable the colony to function as a whole unit, e.g. the heterozooids depend on the autozooids for nutrients (Silén, 1977). Polymorphism permeates roughly 75 percent of tropical, cheilostome species (Prothero, 1998). Increased zoarial diversity is interpreted as a sign of favorable growth conditions (Moyano, 1979, in Smith, 1995).

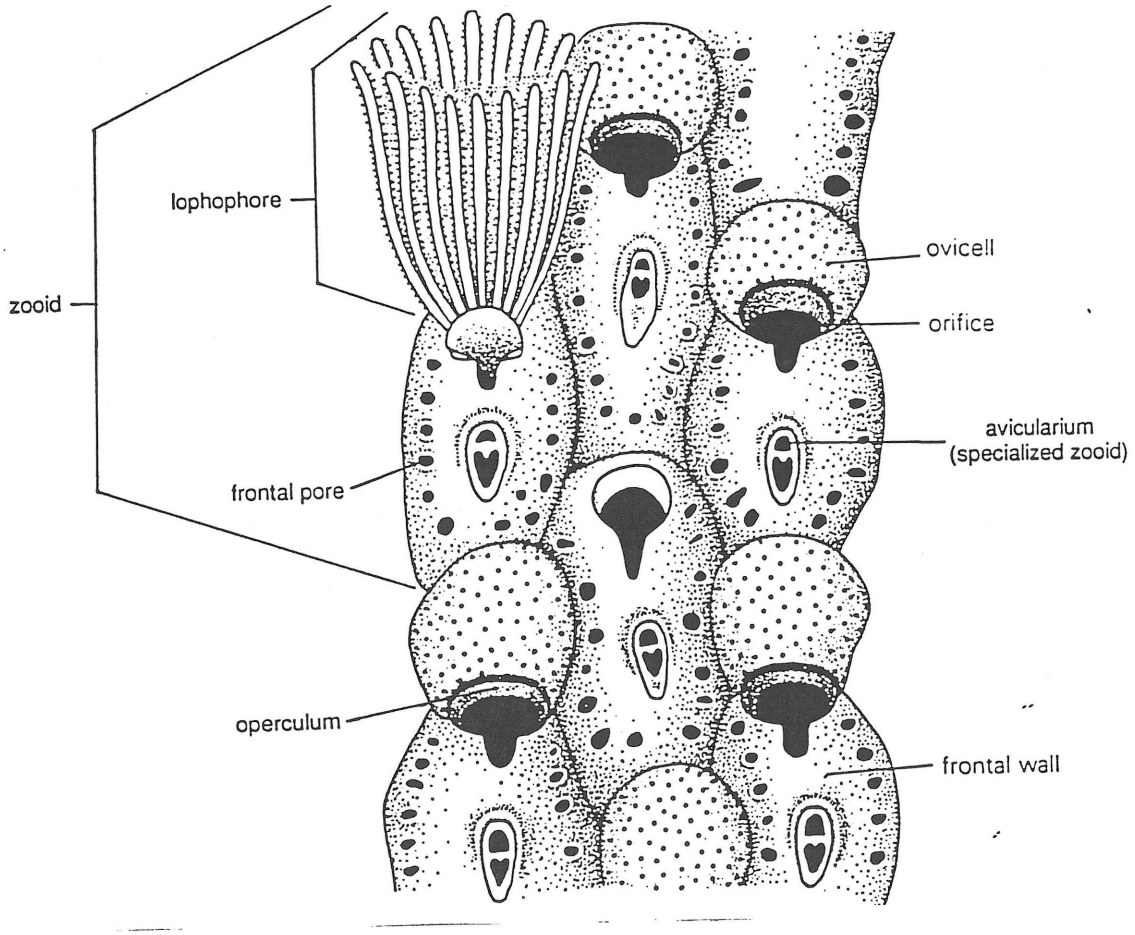


Figure 1. Skeletal structure of the cheilostome *Smittoidea marmorea,* showing distinctive anatomical features utilized in bryozoan identification. (Adapted from Clarkson, 1993).

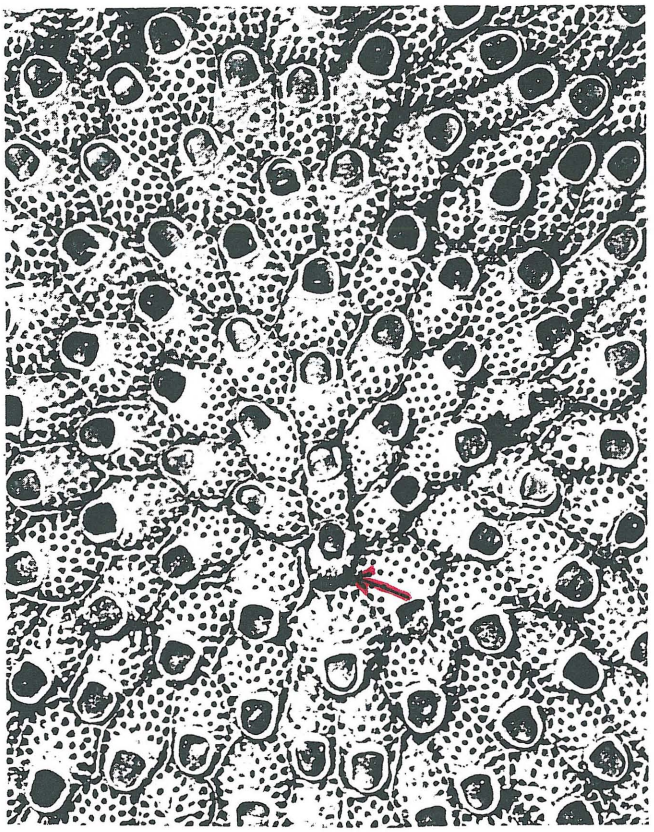


Figure 2. Aggregate of *Cryptosula,* an encrusting cheilostome, showing box-like individuals in a colonial arrangement. Arrow indicates ancestrula, the first zooid of a colony. (From Boardman and Cheetham, 1987).

Reproduction

Bryozoa are both sexual and asexual and most are hermaphroditic. In general, sexual reproduction is for the generation of new colonies, while asexual budding allows growth within the colony. Some species have adopted the sexual tactic of broadcasting egg and sperm into the water column where fertilization takes place. More commonly eggs are brooded in a reproductive chamber called the *ovicell* (Fig.1), into which sperm are captured for fertilization to form a larval zygote. This free-swimming larvae metamorphoses into a primary zooid, or *ancestrula* (Fig. 2), which settles on a substrate and becomes the basis for a whole new colony (Prothero, 1998). All additional zooids of that colony are

produced by budding new parts asexually, farther and farther from the point of origin (Ryland, 1970). Since cloning is the main process by which the colony expands in size, if a piece is broken off or destroyed by predation, the detached modules can grow and form a new colony (Jackson, 1983).

Systematics

Bryozoan evolutionary history cannot be fully interpreted without a thorough understanding of the phylogenetic relationships. Yet classification within the phylum Bryozoa is anything but standard. An evolutionary convergence in zooidal morphology and colony form and the conservatism of stenolaemate and gymnolaemate polypide organization has resulted in a lack of understanding of phylogenies at higher taxonomic levels (McKinney and Jackson, 1989). Several different systematic formats proposed within the last fifty years exhibit distinct organizational patterns due to differences in character weighting and emphasis. The most recent and comprehensive cladistic analysis is Anstey's (1990) scheme (Fig. 3).

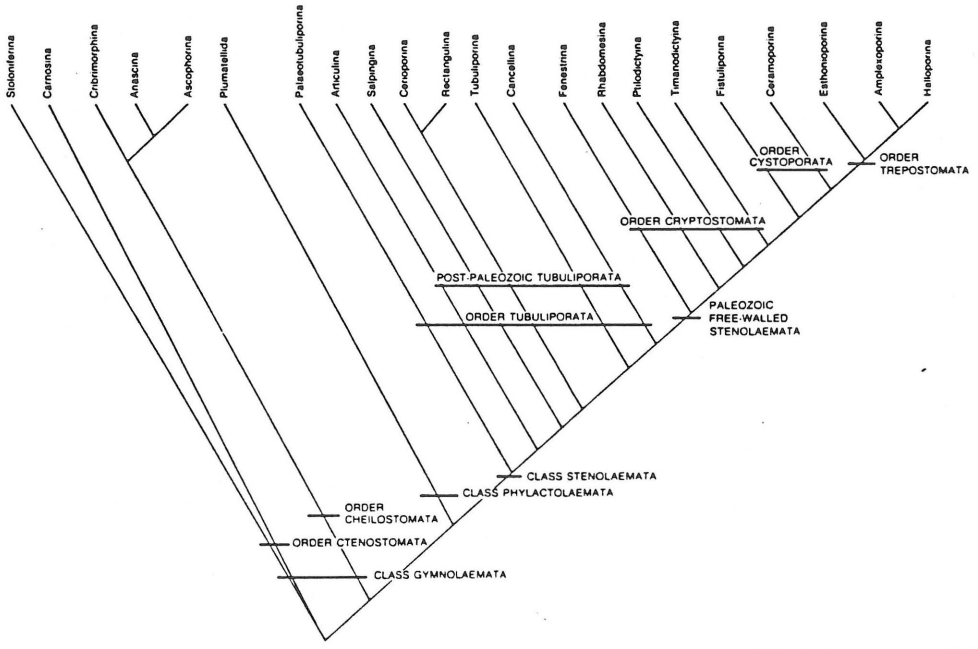


Figure 3. Anstey's (1990) cladistic analysis of the phylum Bryozoa, showing major lineages and evolutionary divisions.

Most bryozoan taxonomy relies on external differences in skeletal morphology, primarily because bryozoan soft parts are not preservable (Prothero, 1998). McKinney and Jackson (1989) questioned the reliability of taxonomic identification on skeletal morphology alone and suggested phylogenetic analysis based on molecular similarity. Although this method would be beneficial for living bryozoans, it is useless among extinct taxa, which comprise a majority of the bryozoan lineage. There is much subjective interpretation in the process of identification and correlation between taxa, particularly when examining disarticulated fossil fragments. Consequently, bryozoan phylogenetic relationships and higher level taxonomy are a tangled mess. The systematic scheme followed in this study is outlined below after Prothero (1998).

The phylum Bryozoa is divided into three classes:

Phylactolaemata (Recent) are freshwater forms without a skeleton. The lack of calcified hard parts excludes it from the fossil record, although fossil *statoblasts*, dormant reproductive buds, have been found from the Mesozoic (Boardman and Cheetham, 1987). Being non-preservable, they were not included in this study.

Stenolaemata (Lower Ordivician-Recent; 750 genera) dominated the bryozoan world in Paleozoic times, with only one order, the cyclostomates, surviving through to the Cenozoic. They are characterized by elongate, tubular zooids, which lengthen with development, the long axis oriented at an angle to the direction of colony growth. Basal and vertical walls are rigidly calcified. The tentacles are extruded by using muscles to squeeze a membranous, fluid-filled sac, which when deformed forces the lophophore through the orifice at the outer end of the skeletal tube.

The Stenolaemata are sub-divided into five orders:

Cyclostomata/Tubuliporata (Early Ordovician-Recent; 250 genera)*
Trepostomata (Ordovician-Triassic; 200 genera)
Cryptostomata (Ordivician-Permian; 90 genera)
Fenestrata (Early Ordivician-Permian; 100 genera)
Cystoporata (Early Ordivician-Triassic; 100 genera)

* Included in this study

Gymnolaemata (Upper Ordivician-Recent; 650 genera) comprise the bulk of the living bryozoan diversity. Their zooecia are generally box-to-sac-shaped or short cylinders, with the long axis roughly parallel to colony growth direction. Zooidal body walls range from entirely organic to rigidly calcified. Zooidal body size is fixed early in ontogeny and colony growth is achieved by adding discrete zooecia, rather than accretion at the edge of a tube. Lophophore extension is achieved by muscular deformation of the vertical or frontal wall. Additional characteristics are interzooidal communication by a *funicular* network through tissue-plugged pores in the zooidal walls, and abundant zooidal polymorphism.

There are two gymnolaemate orders:

Ctenostomata (Upper Ordivician-Recent; 50 genera)
Cheilostomata (Upper Jurassic-Recent; 1000 genera)

The majority of the research presented in this thesis is based upon the Cheilostomata. A few of their defining features include:

-- zooidal walls are box-like, calcified, may be flexible or rigid, and perforated by numerous pores (Fig. 1).
-- the *orifice* Fig. 1) is frontal, and closed by a proximal, chitinous, hinged *operculum* (Fig. 1). Cheilostome is Greek for 'lip mouth'.

-- polymorphism is varied and prolific in the form of autozooids and heterozooids, e.g. *avicularia* (Fig. 1).

-- specialized reproductive *ovicells* (Fig. 1) are often present.

-- they are the most diverse group of living Bryozoa, having radiated in the Cretaceous into three suborders, Ascophora, Anasca, and Cribrimorpha, which are distinguished by frontal calcification and the method of lophophore protrusion.

Fossil History

As previously noted, the calcareous Ectoprocts are well-represented in the fossil record. Taxonomic identification is based on preservable skeletal parts. The oldest known fossil bryozoans date from the early Ordovician. If they existed in Cambrian or Precambrian times, no preserved evidence remains (Boardman and Cheetham, 1987). Throughout geologic times the two major marine bryozoan groups have been the tubular stenolaemates and the box-like gymnolaemates (Fig. 4).

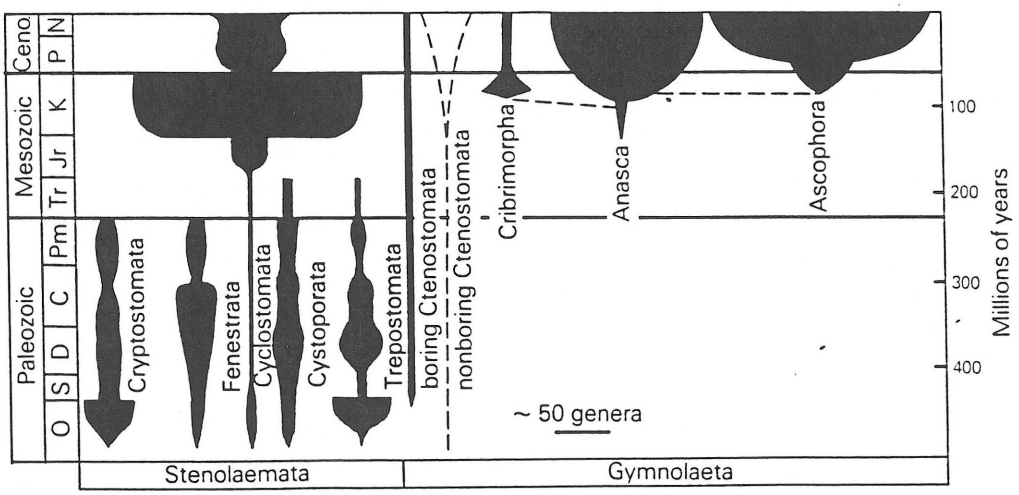


Figure 4. Diagram showing the temporal ranges and diversity of major bryozoan groups. Stenolaemata (left); Gymnolaemata (right). Note the prominence of cheilostomes in Cenozoic times. (From Boardman and Cheetham, 1987.)

Both have illustrious fossil histories. The stenolaemates radiated quickly in the Paleozoic, which is evidenced by their prominence in Paleozoic rocks, making up large parts of reefs, limestones and mudstones. Both robust and delicate forms, characteristic of shallow, high energy and deeper, lower energy environments, respectively, were plentiful (Boardman and Cheetham, 1987). Despite the bountiful presence of Bryozoa in marine limestones and calcareous shales such as the Silurian of England and North America (Pinna, 1990), most Paleozoic genera are long-ranged and facies-controlled, and therefore poor stratigraphic indicators (Clarkson, 1993). The Permian extinction terminated all but the cyclostomates. They subsequently thrived throughout the Jurassic and Cretaceous, but were severely reduced in the K/T extinction event, only to diversify again through the Cenozoic to the present, although to a much lesser extent. They are no longer dominant (Boardman and Cheetham, 1987).

The Gymnolaemata on the other hand picked up where the stenolaemates left off. Calcareous cheilostomes first appeared in the oceans in the Upper Jurassic with *Pyriporopsis portlandensis* (Pohowsky, 1973), then expanded greatly in late Cretaceous and Tertiary times with the decline of the cyclostomates (McKinney and Jackson, 1989). The cheilostomes subsequently diversified into three prominent suborders. The cribrimorphs were important in the Late Cretaceous but declined in recent times, while the Ascophora and Anasca are very important in the modern. Like their modern descendants, the majority of fossil cheilostomes were shallow water species (Boardman and Cheetham, 1987)

It is suggested that the highly successful cheilostomes arose from the earlier, uncalcified gymnolaemates, the ctenostomes (Clarkson, 1993). There are fossil indicators of ctenostomes from the late Ordivician, but these exist exclusively as distinctive borings of uncalcified zooids on carbonate substrates. Non-boring, non-calcified bryozoans are rare as fossils and known only from the Jurassic and Cretaceous (Boardman and Cheetham, 1987).

The cheilostomes examined in this study have fossil histories ranging from Eocene to Recent times.

Evolutionary Trends

As a colonial unit made up of discrete individuals, mutation and individuation act at the singular zooid level, while natural selection functions at the level of the bryozoan colony (Schopf, 1977). This second part has interesting implications about the role coloniality plays in the evolutionary process, a process that has produced an extensive assortment of bryozoan forms. Jackson and Cheetham (1995) examined cheilostome lineages and noted that Bryozoan evolution is characterized by periods of stasis punctuated by rapid evolution rather than gradual progression and speciation.

There are several trends that developed throughout bryozoan evolution. One significant development is the movement of more erect species to calmer, deeper water, while encrusting forms flourish in the shallower, high energy zones. This circumstance is a widespread adaptive feature that pervades numerous marine phyla. More specific to the research presented here, it is believed that 1) development of box-like zooecia with increasing calcification through time, and 2) increased integration of zooids, allowed for a more robust zooecium and greater feeding efficiency. These in turn led to the cheilostomes' dominance and diversification in the Cenozoic, having outcompeted the cyclostomes. Horowitz and Pachut (1996) proposed that the stout, box-like zooidal construction is a trait that even relates directly to the Late Paleozoic stenolaemate success, since the cheilostomes probably evolved from the Stenolaemata.

Additionally, zooidal integration is intimately connected with an increase in polymorphism, for the autozooids must filter enough water to support the non-feeding zooids as well. Thus, the higher the degree of zoarial diversity, the higher the degree of integration, with the most integrated colonies behaving like individual organisms (McKinney and Jackson, 1989). Improvement of the colony as a living mechanism allows for a greater competitive and regenerative capacity (Jackson, 1983).

Ecology

Bryozoans are found on all types of hard substrates, ranging from sediment to rocks, shells, wood, and even seaweed or algae. Almost all are immobile, although there are a few that creep about or live in the spaces between sand grains. Overall the Bryozoa are highly abundant and diversified, occurring at both nearshore and abyssal depths (the deepest was recorded at 8500 m (Prothero, 1998)) and at any latitude, from polar to equatorial seas. The majority, however, are found in shallow, coastal regions of tropical and temperate waters, where oscillating water movements predominate and keep the water relatively clear. Continuous sediment cover is detrimental to bryozoan survival (Prothero, 1998).

Modern reef-dwelling bryozoans are most commonly found in cryptic habitats including caves, crevices, the protected undersides of corals, and the shells of other invertebrates (McKinney and Jackson, 1989). Such microenvironments offer calm refuge from the immediate high energy surroundings, allowing delicate morphologies to potentially be preserved in a shallow setting (Smith, 1995). Unlike corals, the Bryozoa are too small to produce massive reef structures, but in trapping fine particulate matter they often contribute as sediment binders to overall reef framework (Clarkson, 1993).

As filter feeders, Bryozoa use their lophophore of ciliated tentacles to generate currents which funnel water into the mouth where it is strained for food particles (Winston, 1977). A healthy diet includes mainly microscopic phytoplankton, in addition to unicellular algae, diatoms, and other small (< 50 microns) planktonic organisms. They themselves are common prey for grazing organisms such as sea urchins, polychaetes, fish, and starfish.

Few bryozoans are intertidal, due to very high wave energy and desiccation between tides. Rather it is the sublittoral zone, particularly depths less than 100 m, that is most populated, this being a region of high illumination that supports an abundant microplanktonic food source (Ryland, 1970). Bryozoa themselves are not light-dependent and therefore are less light/depth restricted than organisms with algal symbionts. Below the photic zone, fauna decrease

substantially in numbers and importance with increased depth, in parallel with the similar decreasing trend of a living photoplanktonic food source (Clarkson, 1993). In this way, bryozoan depth ranges are useful in understanding the distribution patterns of the organisms they eat.

Distribution

There are several factors which control bryozoan distribution patterns, including temperature, salinity, wave energy, currents, sediment input, availability of substrate, and competition for resources. While it is clear that it is the combined effect of many influences acting together that governs distribution, the relative importance of each factor is unknown (Jackson and Winston, 1982).

Soule *et al.* (1979, in Smith, 1995) investigated bryozoan ecology at Long Beach, California and concluded that temperature was most important in determining bryozoan distribution. Understanding the role of temperature is often difficult because thermal tolerance varies significantly at the species level (Smith, 1995). Species that occur at a wide range of bathymetries can tolerate broad temperature ranges (Ryland, 1970). As a phylum, the Bryozoa can survive in water temperatures from -15 to 40 C.

Likewise, there is a correlation between distribution and salinity. Most Gymnolaemates are restricted to values near normal sea water of about 32-37 ppt (Smith, 1995). Hypo- and Hyper-saline species are present but rare, and the effect of reduced salinity is a depletion of faunal diversity (Ryland, 1970).

The role of wave action on species distribution is double-sided. Turbulence serves the useful purposes of mobilizing free-floating organisms, scattering reproductive larvae, supplying fresh oxygen, and bringing food to the passive suspension feeders (Ryland, 1970). Yet there are limits beyond which the degree of wave agitation can be productive, and storm events can cause damaging results such as failure to produce successful offspring, or skeletal breakage (Denny, 1988). Local coastal morphology is crucial in determining how wave energy is enhanced or attenuated (Ryland, 1970).

Water currents provide the favorable effects of waves, without the destructive element (Moore, 1973). Habitat selection may be influenced by the type and size of food available, in which case such currents are essential to filter feeding success (Buss and Jackson, 1981). Some of the largest abundances and diversities of Bryozoa are associated with high water transport rates distinctive of intake conduits, large channels, and narrow coastal bays (Ryland, 1970). Loss of currents to convey suspended food particles justifies a deficiency of sessile fauna in deeper waters (Clarkson, 1993).

Currents also play an active role in transporting sediment, particularly in shallow waters. Sediment migration can cause daily fluctuation between high and low burial signatures. In a study of sediment deposition in bryozoan habitats, Lagaaij and Gautier (1965) found that high rates of sediment input, in conjunction with low currents to remove the suspended material, can result in the smothering of sessile animals like bryozoans, interfering with feeding and respiratory mechanisms (Smith, 1995). Moore's (1973) studies off the northeast coast of Britain found the highest bryozoan diversities in clear water. In congruence, Ryland's (1970) study of the Mediterranean "provides clear factual evidence of the absence of bryozoans from areas of rapid silt accumulation." Analysis of the fossil record shows that when sedimentation rates exceed 1 meter per 1000 years bryozoans are generally absent (Lagaaij and Gautier, 1965). Species that do survive sediment laden areas are equipped with powerful vibracula to clean off surface accumulation, or develop erect morphology thereby avoiding particle accretion on horizontal surfaces (Ryland, 1970).

Bryozoan population distribution is strongly influenced by the nature and availability of substrate. Hard substrates offer the greatest stability in nearshore environments, and are associated with higher diversities than soft substrates like mud and algal material (Moore, 1973). Bryozoans often inhabit ephemeral materials like shells and kelp because 1) such substrata is usually readily available, and 2) the Bryozoa are outlasted by competitors on more stable surfaces (Clarkson, 1993). Most bryozoans are somewhat specific in choosing a

support to settle upon, which is important in limiting depth ranges. Bryozoans living on plant and algal material are restricted to the photic zone. Likewise, those that affix themselves by roots are more common in fine deep sea oozes where the sediments are not stable (Ryland, 1970). Larval preference for specific substrates helps in the selection of proper habitat conditions, and is useful in the identification of specimens in the fossil record.

Within benthic communities it is common for several organisms to occupy the same substrate and even be overgrown by other animals. Jackson (1977) found that greater than 95% of the cryptic substrate in Jamaican reef environments was occupied by colonial animals. Thus, there is intense competition for growth space between bryozoans and other sessile animals like sponges, algae, and tunicates (Boardman and Cheetham, 1987). Too many animals competing for the same substrate and the same food supply creates strenuous growth conditions (Buss, 1979). Bryozoans themselves are not good competitors and will usually lose a battle for growth space to other encrusters like sponges and cnidarians. (McKinney and Jackson, 1989)

Other disturbances such as predatory grazing and substrate movement also affect distribution patterns and reduce abundance (McKinney and Jackson, 1989).

Growth Form

The same factors that determine distribution patterns also govern colony shape, since growth strategies are defining characteristics of species type. Colonies range from encrusting to erect, to free-living, to rooted in soft sediment, each form reflecting an organization adaptive to a different ecological niche (McKinney and Jackson, 1989). Although colony shape by itself is not an indisputable paleoecological indicator, one is able to make general depth and substrate inferences based on growth type (Labracherie, 1973).

Nearshore environments are characterized by encrusting forms, while deep sea forms are more often brittle and erect. An encrusting lifestyle is vulnerable to sedimentation and overgrowth, and limited to resources that settle to the sea

bottom. Yet encrusters are able to withstand higher wave energies and grazing pressure, as well as reproduce faster (McKinney and Jackson, 1989). Both single and multi-layered encrusting sheets and mounds are common, the latter being more prevalent on substrates limited in size (Clarkson, 1993). Rigidly erect forms can get closer to food and nutrients and are not susceptible to sediment burial (McKinney and Jackson, 1989), but are restricted to low energy environments because they are more vulnerable to damage by currents (Cheetham and Thomsen, 1981). Some erect colonies are non-calcified, flexible forms that can withstand moderate current strengths (McKinney and Jackson, 1989).

Harmelin (1975, in Smith, 1995) opposed the traditional relegation of encrusting forms to shallow and erect forms to deep sea habitats. He contended that encrusting should correlate with low energy environments because that way nutrients could settle out onto a flat colony. Likewise, if erect forms are designed for catching food from moving water masses, quiet waters should not correspond to erect growth. Because observation most often reveals encrusters at shallow and erect-forms at depth, it is concluded that the detrimental effect of sediment cover at depth mandates an erect lifestyle, and the wave energies in shallow zones necessitate encrusting.

Smith (1995) wisely warns that in the present it is common to see several different growth forms within a single habitat. One should thus be weary when looking in the fossil record of inferring environmental conditions based on analysis of growth form or substrate selection alone. Combinations of different aspects of paleoenvironments produce more reliable results.

This study only examines encrusting cheilostomes, primarily because rigidly erect cheilostomes are not common in tropical seas at depths less than 100 m (Jackson, 1984). Even within the specific category of encrusters, distinctive environmental differences are reflected morphologically. The strongest, most-heavily calcified types, such as the ascophorans, live in turbulent zones, while delicate morphologies like those of the cribrimorphs are inclined toward sheltered cavities and other cryptic habitats isolated from conditions at the open surface (Clarkson, 1993). Sheltered areas of this nature may actually invoke an increase

in genera abundance (Smith, 1995). In general, encrusting bryozoans will settle wherever there is accessible, hard substrata and an absence of suspended sediment (Ryland, 1970).

METHODS

Field Analysis

In 1993 and 1994, SSETI deployed thirty-five samples of sea urchins at sites along the continental shelf/slope on the Atlantic side of Lee Stocking Island in the Bahamas (Fig. 5A). The area studied is characterized by a reef terrace slowly deepening from shore to the shelf break near 33 m depth, subsequently dropping rapidly along a steep (> 60°) slope to depths in excess of 250 m (Fig. 5B). Carbonate sand channels between patch reefs compose the shallow terrace sediments, with storms serving as a key mode of sand transport. The slope is mostly hard rocky carbonate outcrops covered with a veneer of sand-sized sediment moved from shallow water. Stalked crinoids are abundant where the slope begins to lessen around 250 m depth. Large dunes (5-10 m high) partially stabilized by authigenic cements, remnants from a glacial low stand of sea level, are common below the crinoid zone. Neither terrigenous sediments nor fresh water are influential constituents in the region studied.

The deployment sites were at depths of 15, 30, 73, 88, 210, 264, & 267 meters and 15, 30, 70, 183, 222, & 226 meters along two transects, North and South, respectively. (Figs. 5A & 5B). Each depth site contained, among other experimental assemblages, four bagged sample arrays, each individual array being composed of four mesh bags attached to PVC rods (Fig. 6). The mesh bags simulated cryptic conditions that are found in protected reef habitats. One of the four mesh bags on every array contained frozen sea urchins, including a single *Eucidaris tribuloides* specimen, commonly referred to as the pencil urchin (Fig. 7). *Eucidaris* does not occur locally in Atlantic waters, but is useful as a natural experimental substrate that can be kept consistent at all depths. As McKinney and Jackson (1989) commented, "By far the most deserving material for...investigation [of bryozoan fossil assemblages] is the epifauna of shells and skeletal debris where encrusting bryozoans have most prospered since the end of the Ordivician."

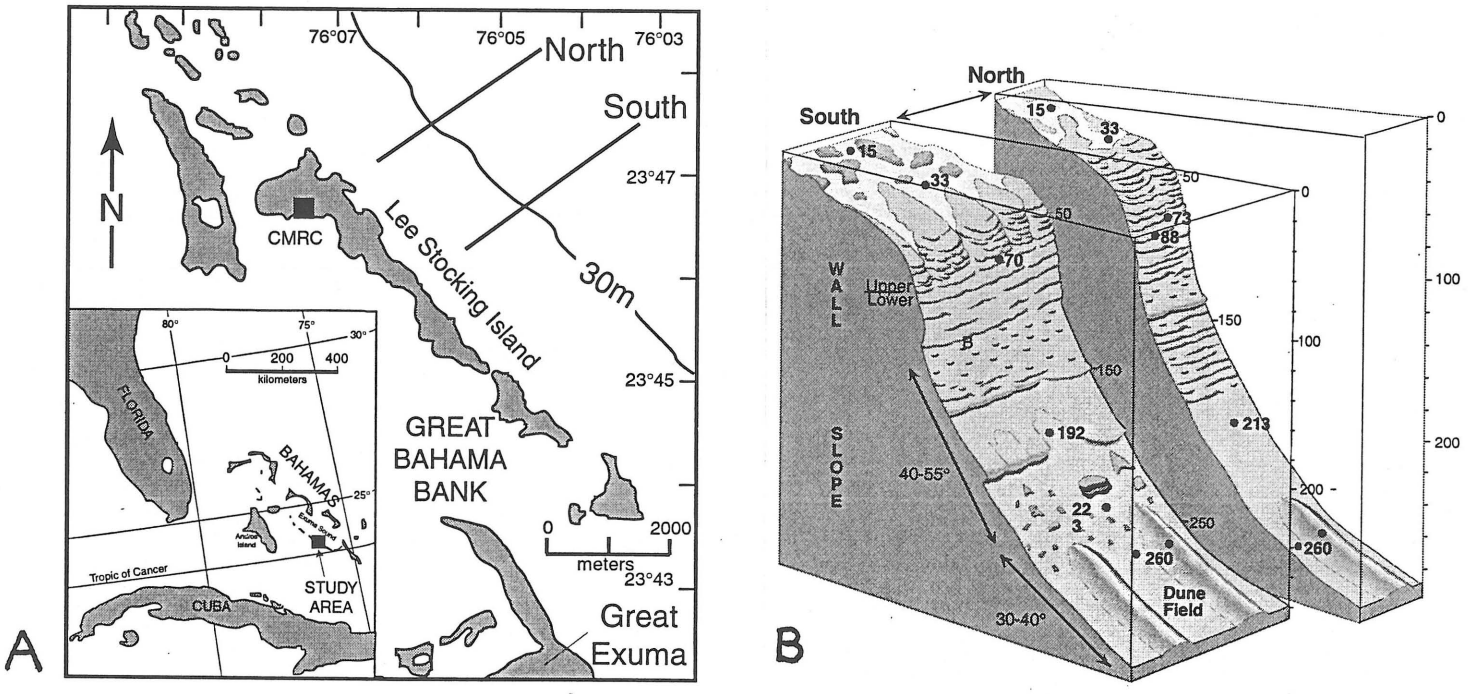


Figure 5. Location map of Bahamian sites. A) Location of transects North and South off Lee Stocking Island, Bahamas. B) Generalized slope profile of transects North and South showing the relationship among experimental sites. (From Parsons-Hubbard, NSF proposal, 1999).

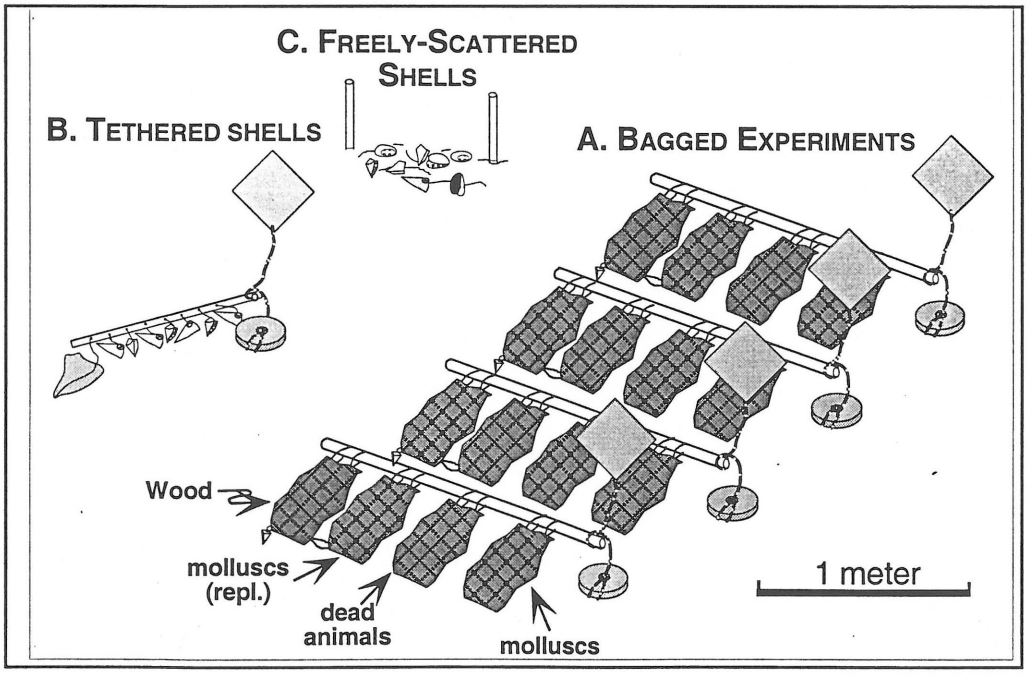


Figure 6. Site diagram for the experimental deployment showing different experimental arrays. A) Mesh bags contained shells, wood, and sea urchins (dead animals) attached to PVC pipe, with a weight and a marker float to aid in relocating the experiments. (From Parsons-Hubbard, NSF proposal, 1999).

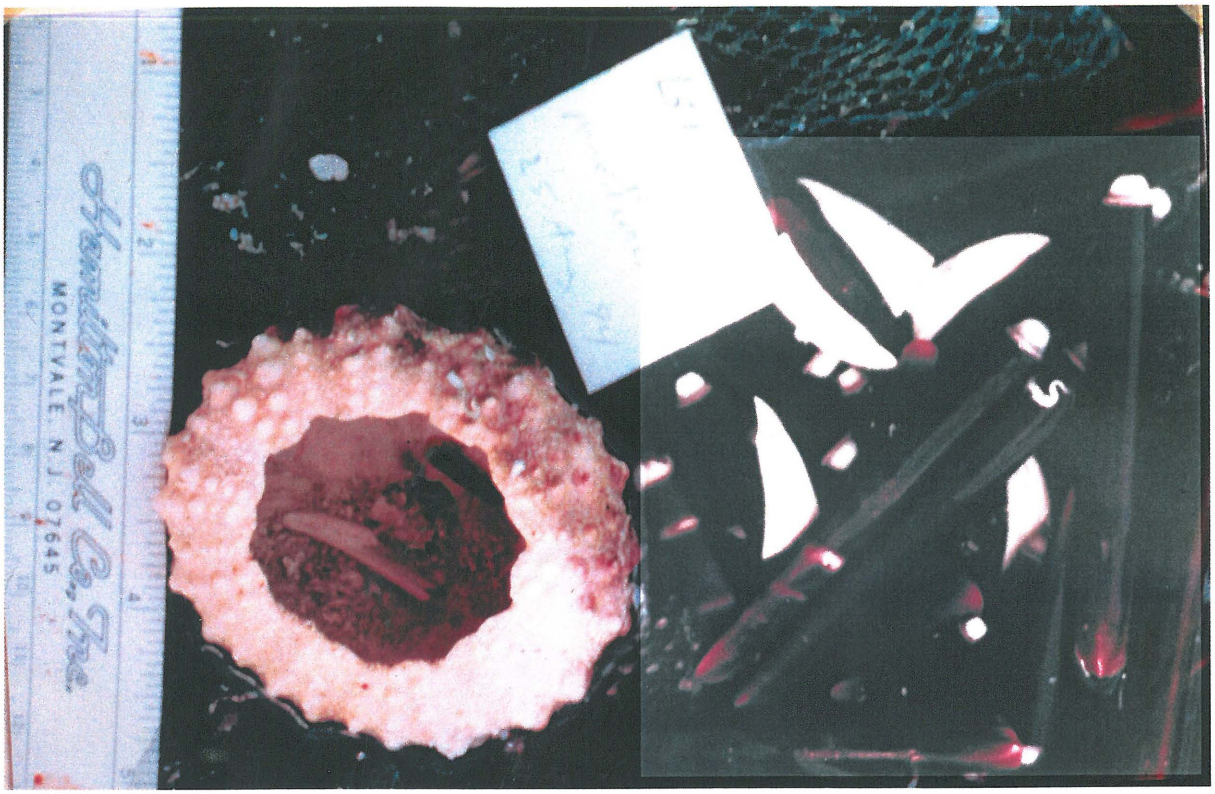


Figure 7. Photograph of test and spines of the sea urchin *Eucidaris tribuloides*, collected from a depth of 15m. This species is commonly referred to as the pencil urchin.

Bagged arrays were collected at 1-, 2-, and 6-year intervals from the North transect, and 1-, and 2-year intervals from the South transect. During each recovery interval, one bag array was collected from each site, analyzed, photographed, and archived. Assessment of physical and biological taphonomic alteration, epibiont and endobiont cover, and cursory identification of faunal assemblages was quantified immediately upon collection. Samples were subsequently frozen. All experiments were deployed and retrieved using the submersibles *Johnson Sea Link, Nekton Gamma, Nekton Delta* or *Clelia.*

Physical and chemical parameters were measured to document site characteristics. Sediment samples were collected from all locations. Salinity, temperature, and water current data were recorded with depth. Digital video record was taken of all sites prior to deployment and during retrieval to allow analytical description of experimental array movement and burial, in addition to changes in site conditions between retrieval intervals (Parsons-Hubbard, NSF proposal, 1999).

Laboratory Assessment

Thirty-five *Eucidaris* samples from 18 sites along both transects were analyzed in the laboratory. Urchin spines and tests were examined for encrusting cheilostome Bryozoa (Figs. 8 -11). Occurrence of a particular genus type on individual *Eucidaris* spines was tallied as a value of 1, regardless of how many distinct colonies of that type were present on the spine. In contrast, generic occurrence on the carbonate tests was counted for each colony observed. Two cyclostome genera, *Disporella* and *Berenicia,* were present at numerous sites, and counted as well. A single urchin test was accompanied by from 30 to 225 spines, depending on its size.

Only a gestalt feel for the character of entire colonies was visible to the unaided eye. Inspection of individual zooidal skeletal anatomy and taxonomic identification required the assistance of dissecting and scanning electron microscope (SEM) magnification. The following sources were utilized to identify specimens to the genus, and in some cases, the species level: Bock, 2000; Budd, 1999; Maturo, 1957; Osburn, 1940; Shier, 1964; Winston, 1982, 1984, 1986; Winston and Hakansson, 1986. Additional assistance was obtained by personal communication from paleobiologists and bryozoan experts Dr. Alan Cheetham of the Smithsonian Institution in Washington, D.C., and Dr. Paul Taylor of the Natural History Museum in London.

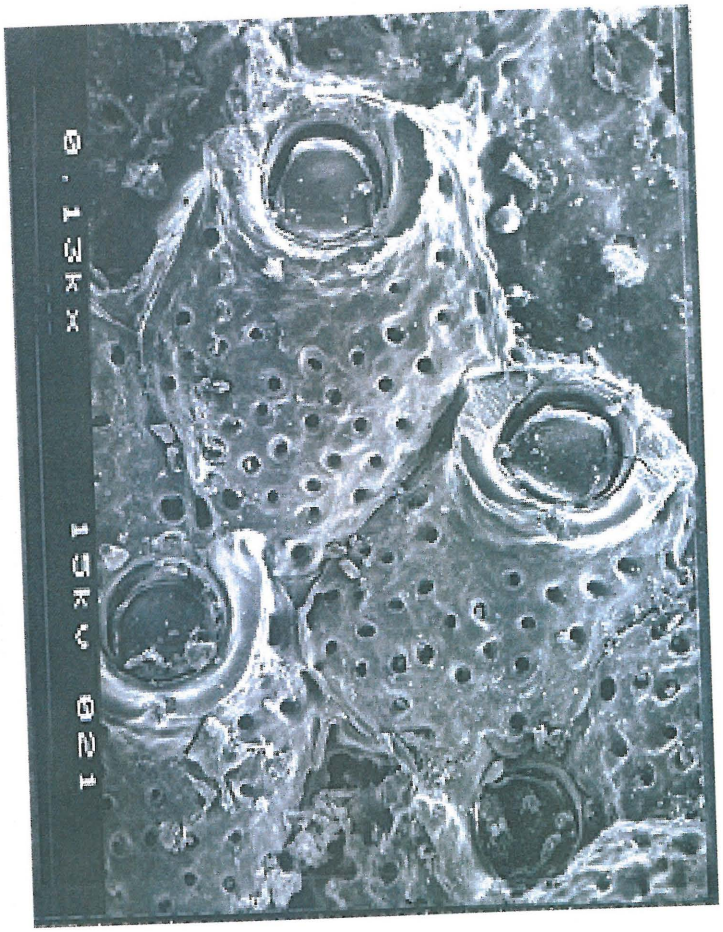


Figure 8. SEM photograph of *Exechonella antillea,* from 30 m. This specimen reveals well-preserved opercula within the main apertures.

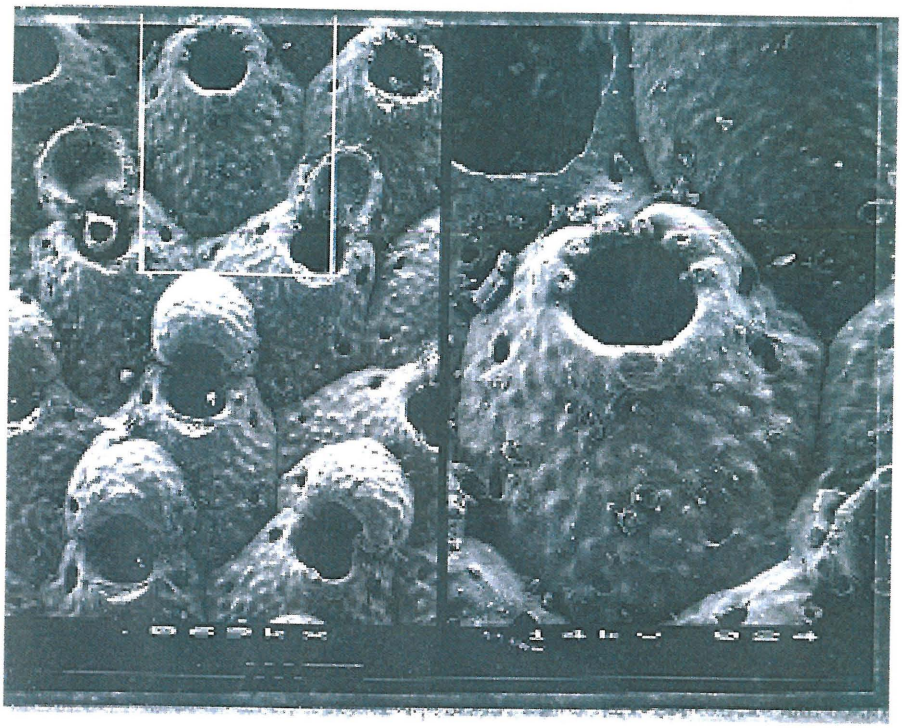


Figure 9. SEM photograph of *Aimulosia sp.,* one of the most common cheilostomes of this data set, collected from a depth of 15 m. Position of frontal pores, orificial spines, and sub-apertural knobby protuberance are all distinguishing features. The right panel is an enlargement of the area marked by the white box.

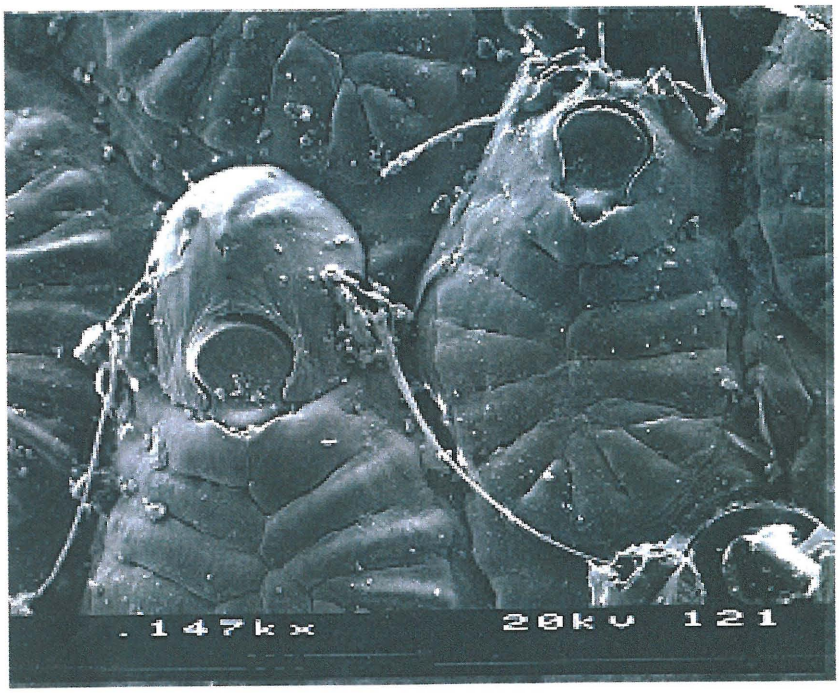


Figure 10. SEM photograph of an unidentified bryozoan from 70 m. Morphology is similar to that of the cribrimorphs. There is a strong possibility that this specimen represents a new species and maybe even a new genus.

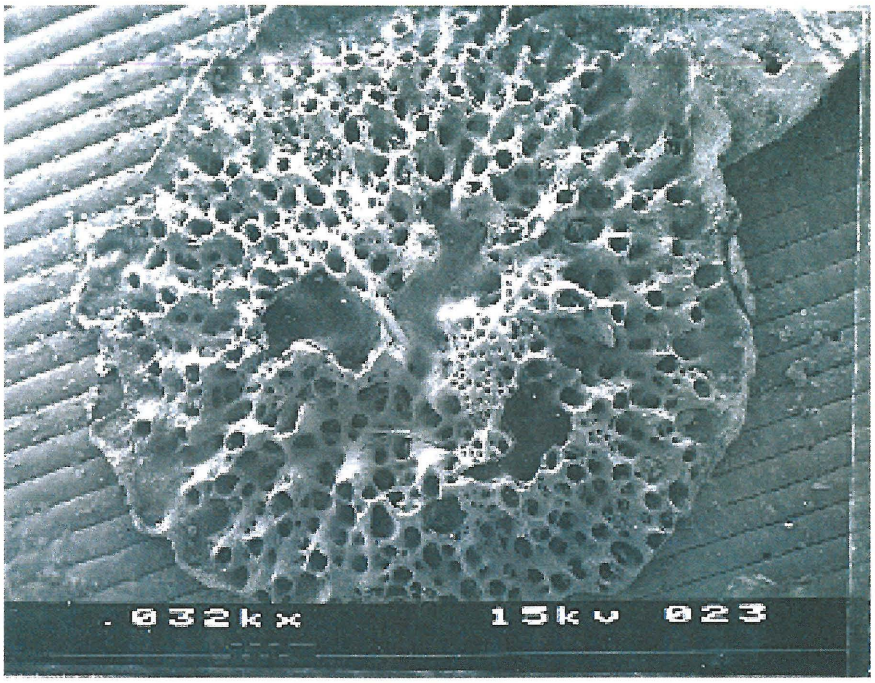


Figure 11. SEM photograph of *Disporella,* from 88 m. Not a cheilostome or even of the class Gymnolaemata, but rather of the order Tubuliporata within the class Stenolaemata. It is characterized by circular shape, with saucer-like margin, and rows of raised zooid tubes, most of which are destroyed on this specimen.

Video record of deployment sites was analyzed for degree of sediment coverage with depth and location through time. Evaluation of array sediment cover through time is problematic. Video footage only represents the sediment cover accumulated at the moments of deployment and retrieval. Rates of accumulation, transport and removal between video capture events are unknown. This could lead to erroneous results for plots that have burial depth as a parameter because accumulation may have been constant between retrieval intervals, but it may also have been highly irregular. For example, it is possible that arrays were completely buried for most of a given time interval and exposed by the action of a storm only just before they were videotaped. Such a scenario may have occurred

when major hurricanes swept through the region in 1995 and 1996. The resulting plots would show low richness associated with low burial depth, thereby preventing the observation of a richness/burial depth trend where one might actually exist.

Total number of individuals and genus richness values were summed and used to generate diversity [$D_{Margalef} = (S\text{-}1)/\ln N$] and evenness [$E = H/H_{max}$] numbers for each site. Results were plotted for a range of water and burial depths. Data for all but the graphs involving sediment coverage were generated by combining generic values from both transects so as to increase the size of the data set for each depth, with the goal of revealing trends which accurately represent the environments from which they were gathered. For such joint-data graphs, 70 m data from the North transect were combined with 73 m data from the South transect and together called 70 m. Plots with burial depth as a parameter were generated for 1-, 2-, and 6-year intervals for both transects, i.e. no data were combined because of sediment cover variation between the two transects.

RESULTS

A total of 459 bryozoan specimens were tallied from the thirty-five sea urchins studied. These specimens were present on *Eucidaris* samples at all depths except 210 m, 226 m, and 267 m. Twenty-seven distinct genera were identified. Fourteen additional samples were too badly damaged to be identified.

Even with the combination of data from both transects, many 1- and 2-year trends do not develop significantly, or are variable. Conversely, the data from the 6-year interval, while only from the North transect, most often depicts the strongest trends. The reason lies in the number of specimens collected at each time interval. 1-year arrays collected from North and South transects together yield a total value of 64 individuals which fall into 12 distinct genera from 4 different depths. Similarly, 2-year arrays collected from both transects yield a total value of 171 individuals from 16 different genera at 5 different depths. The 6-year arrays, collected from the North transect alone, yield a total value of 207 individuals from 22 genera at 5 different depths. It is possible then, that low numbers of data points for some 1- and 2-year data may give misleading correlations.

Since this study focuses on abundance and diversity patterns with depth, a greater number of individuals, genera, and depths represented will produce a more complete data set, and when plotted, show more reliable relationships between the samples and their environment. The conclusions presented here will therefore rely more heavily, although not exclusively, on the trends observed from the 6-year interval. 1- and 2-year data will be addressed because they do represent the bryozoan distributions over shorter time intervals.

Depth Distribution

The distribution of genera by depth for 1-, 2-, and 6-year intervals, respectively, is presented in Figures 12A, 12B, & 12C. Taken together, these three graphs illustrate an increase in both genus richness and numbers of individuals through time and at shallower depths.

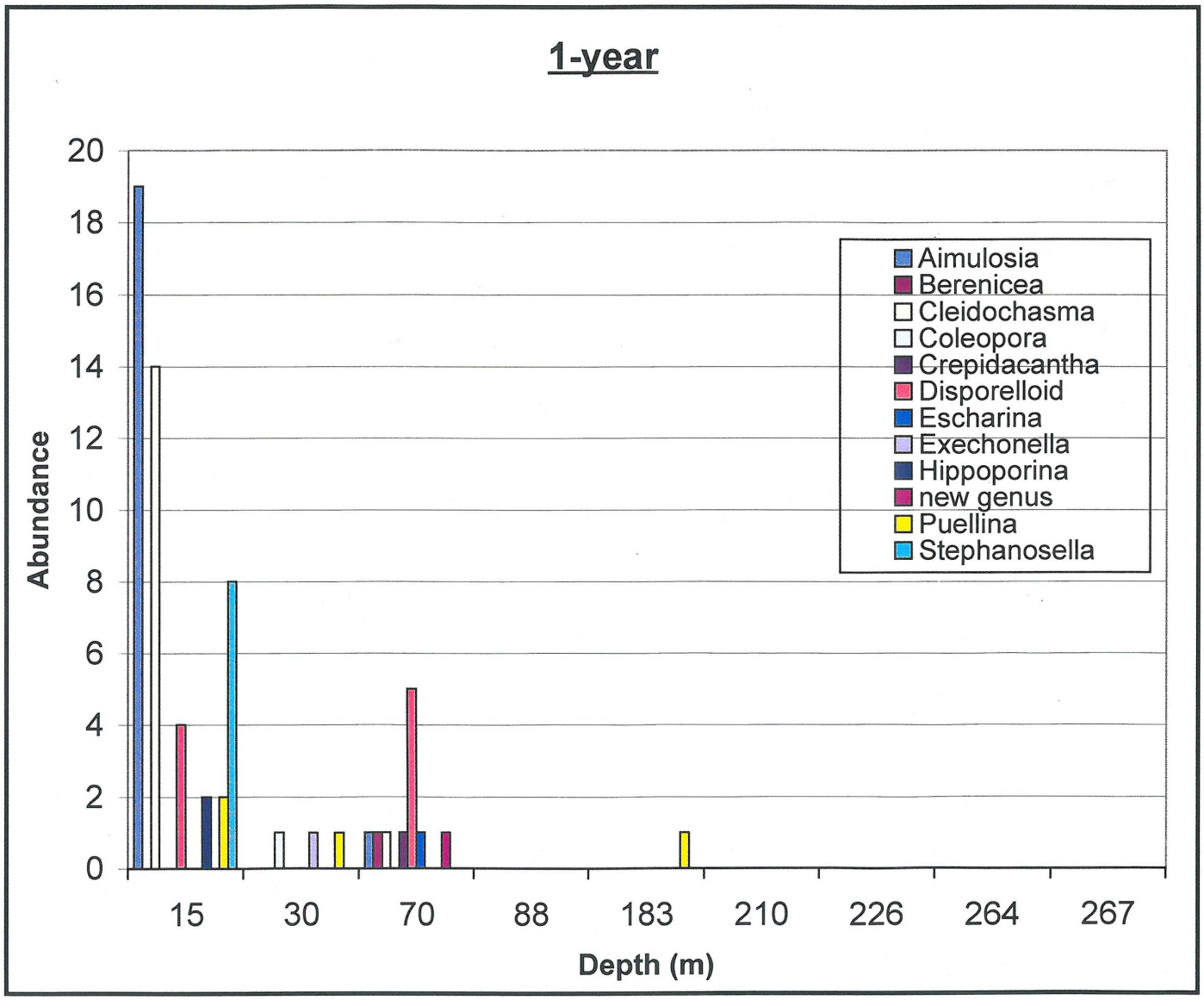


Figure 12A. Distribution of genera by depth for 1-year interval (data from both transects). 64 individuals from 12 different genera were identified. All but one specimen were collected within the photic zone (above 100 m).

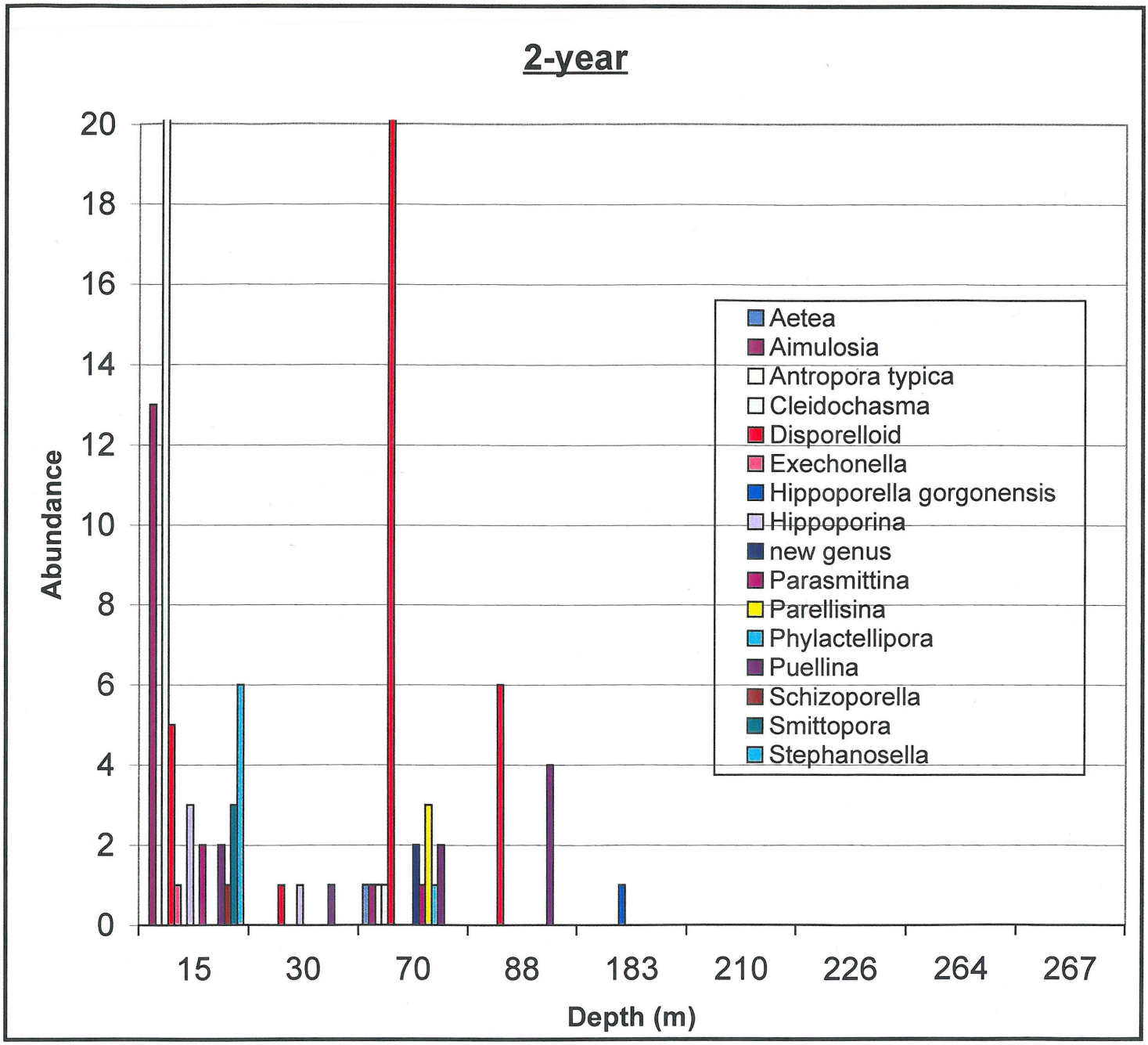


Figure 12B. Distribution of genera by depth for the 2-year interval (data from both transects). 171 individuals from 17 distinct genera were identified. All but one specimen were collected within the photic zone (above 100 m)

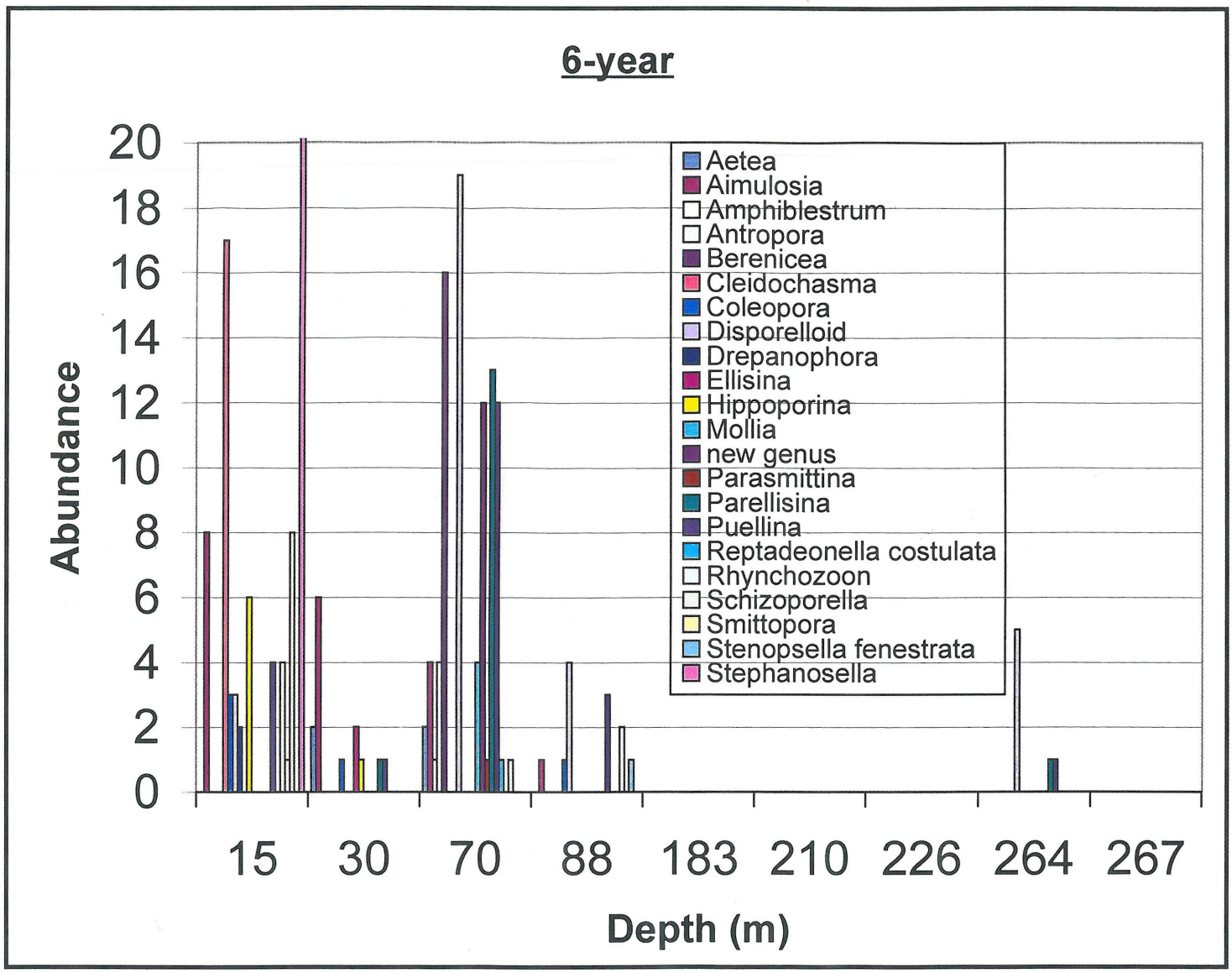


Figure 12C. Distribution of genera by depth for the 6-year interval (data from both transects). 207 individuals from 22 different genera were identified. All but 6 specimens were collected within the photic zone (above 100 m).

When combined, Figures 12A, 12B, & 12C collectively generate figures 13 and 14, which are two representations of genus distribution of all the specimens collected from all the water depths sampled at all time intervals. Figure 13 illustrates the depth ranges of individual genera, while figure 14 portrays what genera are abundant at each sample depth.

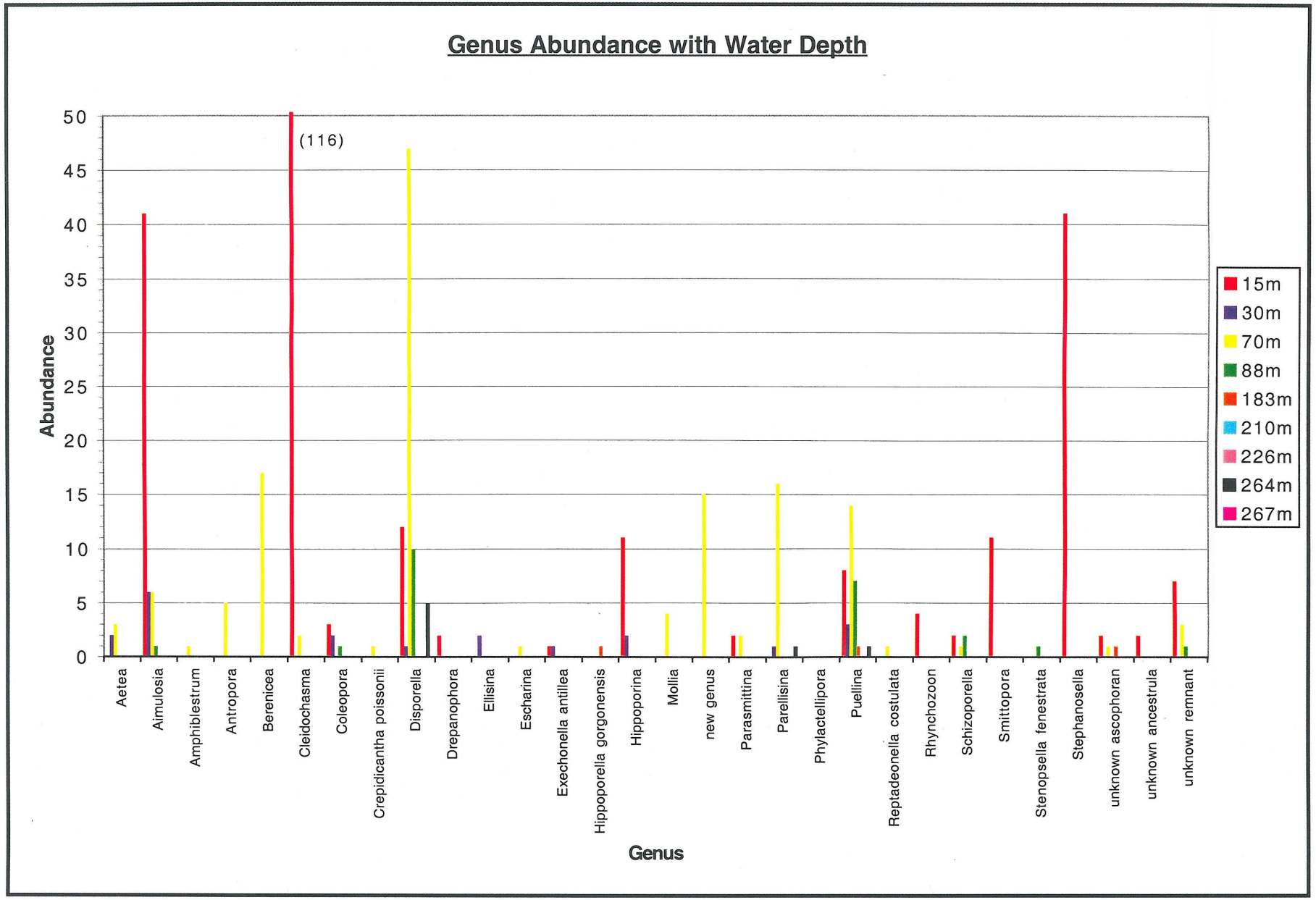


Figure 13. Histogram showing the depth ranges of individual genera, and their abundance at each depth (data from both transects). 459 specimens were counted. 27 distinct genera, including 1 new genus, were identified. Fourteen specimens could not be identified and were grouped as unknowns.

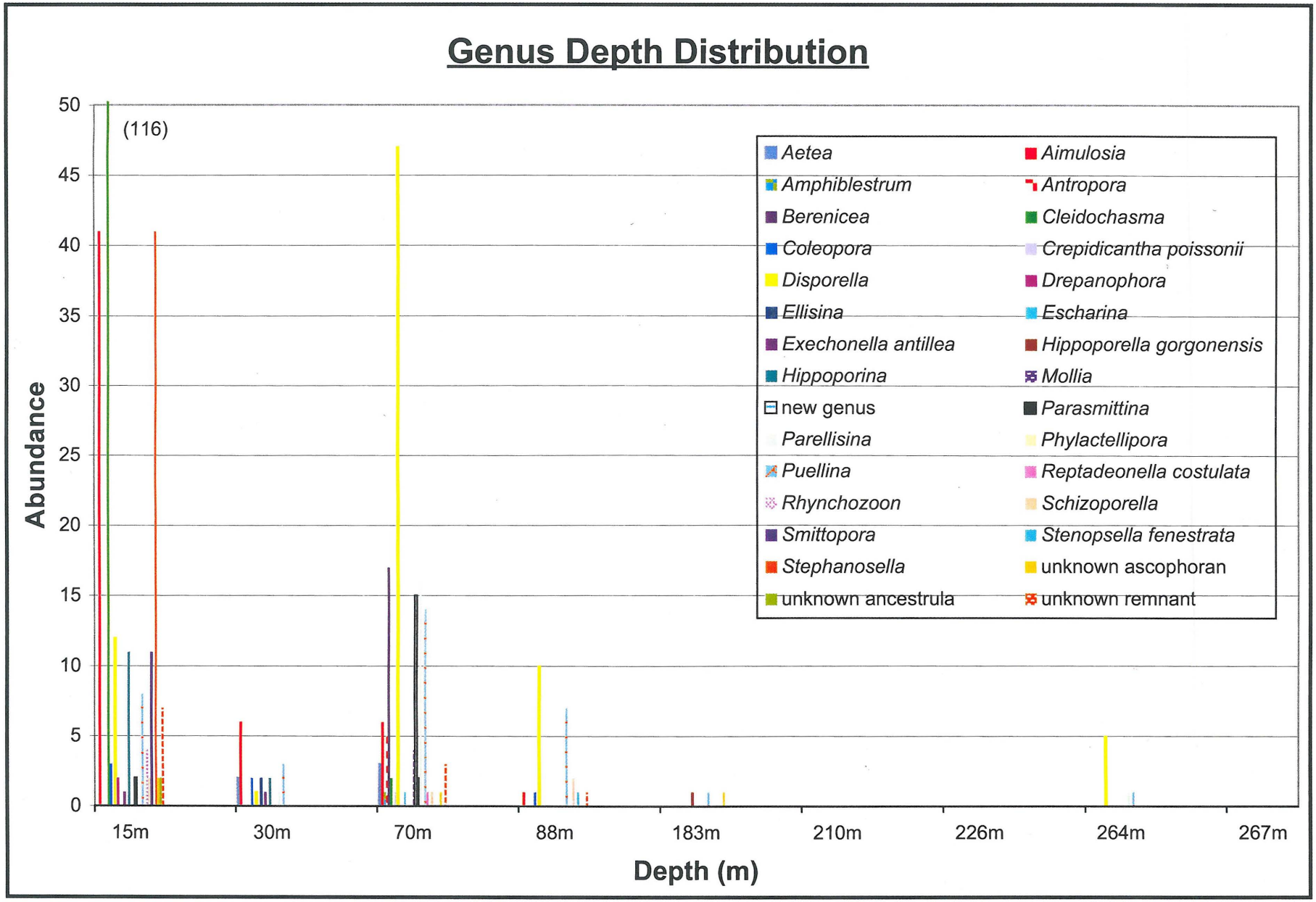


Figure 14. Histogram showing generic abundance at each sample depth (data from both transects).

In tabular form (Table 1) one can see that some genera are partial to shallow waters while others occur in both shallow regions and at depth: *Stephanosella* consistently appears only at the 15m sites, while *Puellina* is found from 15m down to 183m. Yet for most other genera, too few specimens were obtained to generate secure conclusions about the depth conditions to which each is partial. Conversely, from a broader prospective it is clear that an overwhelming majority of the specimens identified (irrespective of genera) were collected from sites within the photic zone (Fig. 15). Hence, specific genus distribution with water depth is a less distinct parameter than overall abundance patterns with water depth.

	15m	30m	70m	88m	183m	210m	226m	264m	267m
Aetea spp.		●	●						
Aimulosia spp.	●	●	●	●					
Amphiblestrum sp.			●*						
Antropora spp.			●						
Berenicea			●						
Cleidochasma spp.	●		●						
Coleopora spp.	●	●		●					
Crepidacantha poissonii			●*						
Disporella spp.	●	●	●	●				●	
Drepanophora spp.	●								
Ellisina spp.		●							
Escharina sp.			●*						
Exechonella antillea	●	●							
Hippoporella gorgonensis					●*				
Hippoporina spp.	●	●							
Mollia spp.			●						
new genus			●						
Parasmittina spp.	●		●						
Parellisina spp.		●	●					●	
Phylactellipora sp.			●*						
Puellina spp.	●	●	●	●	●			●	
Reptadeonella costulata			●						
Rhynchozoon spp.	●								
Schizoporella spp.	●		●	●					
Smittopora spp.	●								
Stenopsella fenestrata				●*					
Stephanosella spp.	●								
unknown ascophoran	●		●		●				
unknown ancestrula	●								
unknown remnant	●		●	●					
	* signifies only 1 specimen identified for that genus								

Table 1. Observed depth ranges of individual genera (data from both transects).

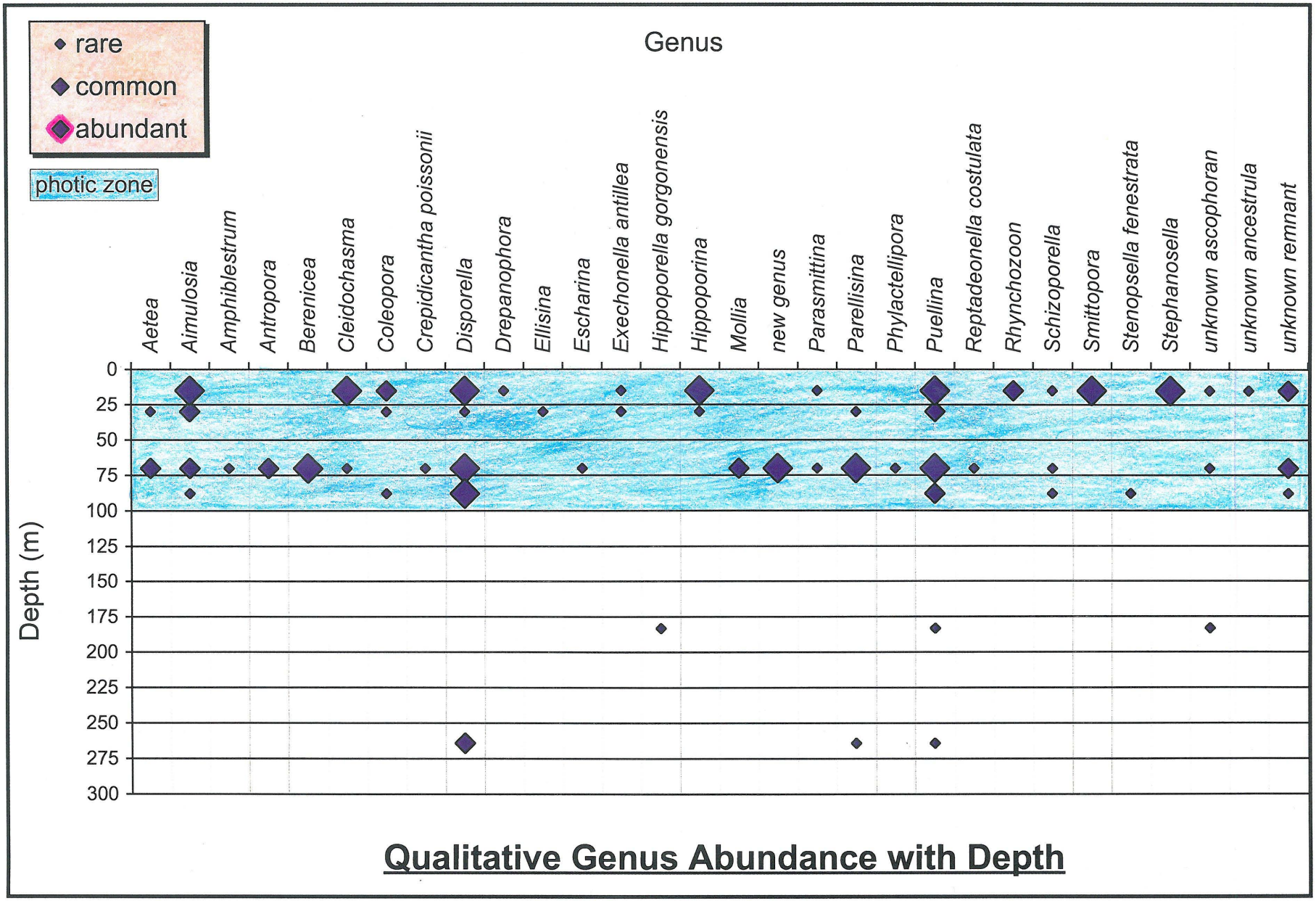


Figure 15. Qualitative analysis of relative generic abundance with depth (data from both transects). An overwhelming majority of the specimens identified were collected from sites within the photic zone (above 100 m).

Richness

Figure 16 shows richness (*S* = number of genera) vs. water depth for the combined North and South transects. 1-, 2-, and 6-year retrieval intervals all show a trend toward low richness at deep sites, increasing to greater richness at shallow depths. Richness increases faster in photic waters compared to the rate of increase at sub-photic depths. This is expected if we assume a greater nutrient abundance in shallow, photic waters. Consecutively shallower sites within the photic zone do not indicate a consistent increase in richness. Rather, the trend indicates the different richness potentials associated with bathymetric regions to which light can and cannot penetrate. Furthermore, total richness increases with time, as evidenced by significantly higher richnesses from the 2- and 6-year intervals than the 1-year period.

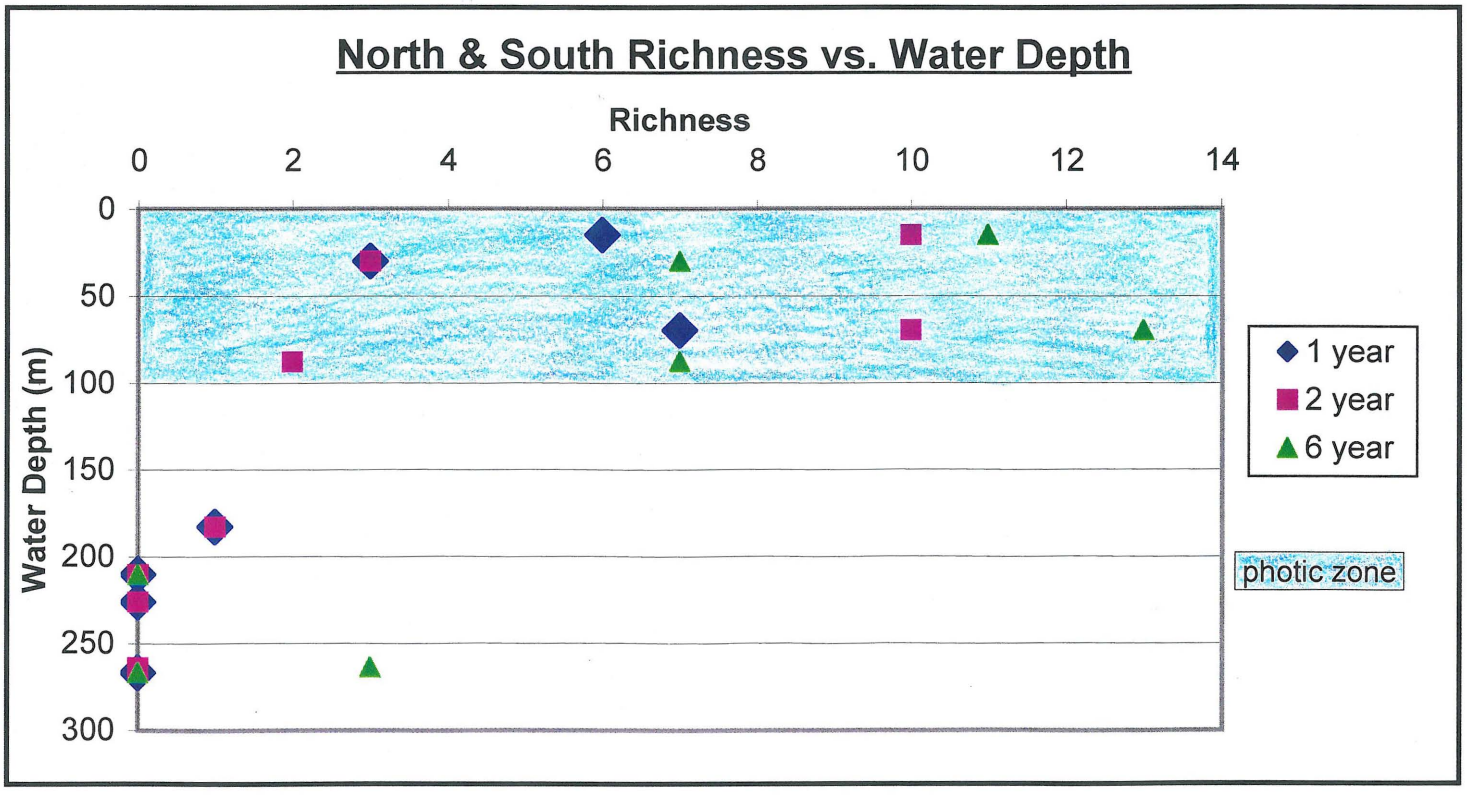


Figure 16. Richness vs. water depth (data from both transects). Lower richness occurs at deep sites, higher richness in shallow waters. Richness increases faster in photic waters. Total richness increases with time.

Diversity

Diversity (Fig. 17) was calculated for each depth using Margalef's index (Dodd and Stanton, 1990),

$$D_{MG} = (S\text{-}1)/\ln N$$

where S represents the total number of observed genera, and N is the number of individuals. High diversity is most often correlated with lower-stress environments. Diversity is derived from richness, and is generally preferred in statistical analysis because it corrects for sample size. The prevailing trend again reflects a profound difference between deep and illuminated waters, with lower diversity at greater depths and overall higher diversity at sites in the photic zone. Diversity, like richness, increases through time. Many of the deeper sites analyzed in this study were found to have zero richness. While zero richness is a plottable value, the concept of diversity is meaningless for a site with an absence of genera (e.g., all of the zero-richness sites are dropped from the diversity graph. A diversity value of zero corresponds to the presence of a single specimen, which would register as a value of 1 on the richness plot). Because most of the sites with no bryozoans were deep sites, the graph plotting diversity has only one or two points below the photic zone, and the resulting trends tell relatively little about the actual diversity at depth. Hence, for this study, the pattern of richness with respect to depth is more reliable than the related diversity values.

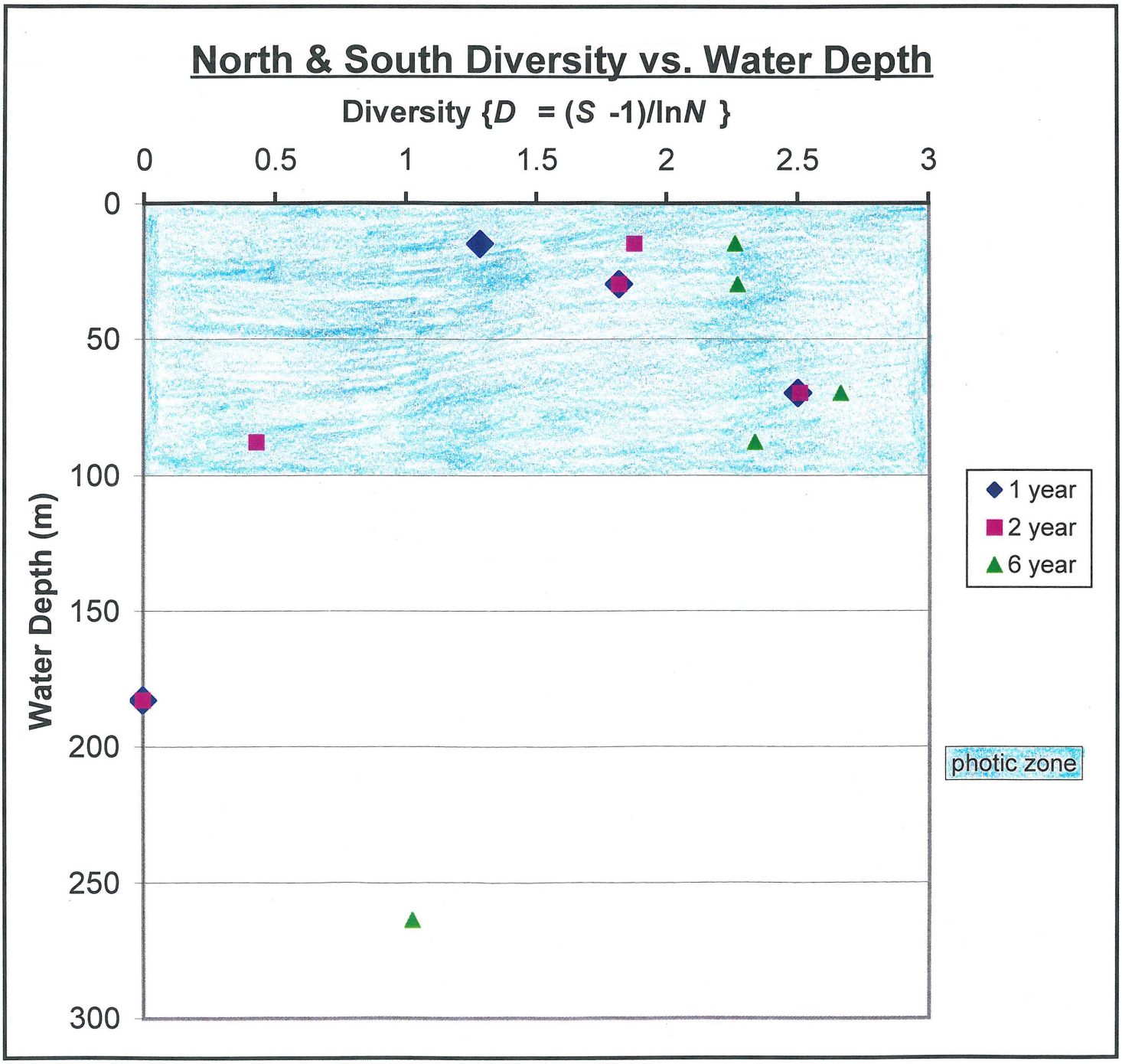


Figure 17. Diversity vs. water depth (data from both transects). There is a significant lack of diversity data at depth. In general, lower diversity occurs in deeper waters and higher diversity occurs in the photic zone. Total diversity increases with time.

Evenness

Evenness (Fig. 18) measures the ratio of the actual entropy of a community (*H)* to the entropy that would emerge if all the individuals of a community were divided equally amongst the associated genera (H_{max}). A value of 1 indicates perfect evenness, meaning genera at a given depth are equally abundant. A value approaching zero reflects decreasing evenness resulting from individual genera dominating a population.

$$E = H/H_{max}$$

Like diversity, evenness is in part derived from richness, and similarly, for values of richness equal to zero, evenness has no meaning. There is only one evenness data point below the photic zone and consequently accurate assessment of evenness varying as a function of water depth is severely limited. Only the 6-year interval exhibits the slightest possibility of a trend that increases in evenness from depth (point P) to photo-productive waters.

While evenness as a function of water depth is incomplete, evaluation of evenness through time is possible (Fig. 18). Comparisons yield the highest values of evenness at the 1-year interval, a wide range of values including both the lowest and highest end members of all three retrieval intervals at 2 years, and intermittent values for 6 years.

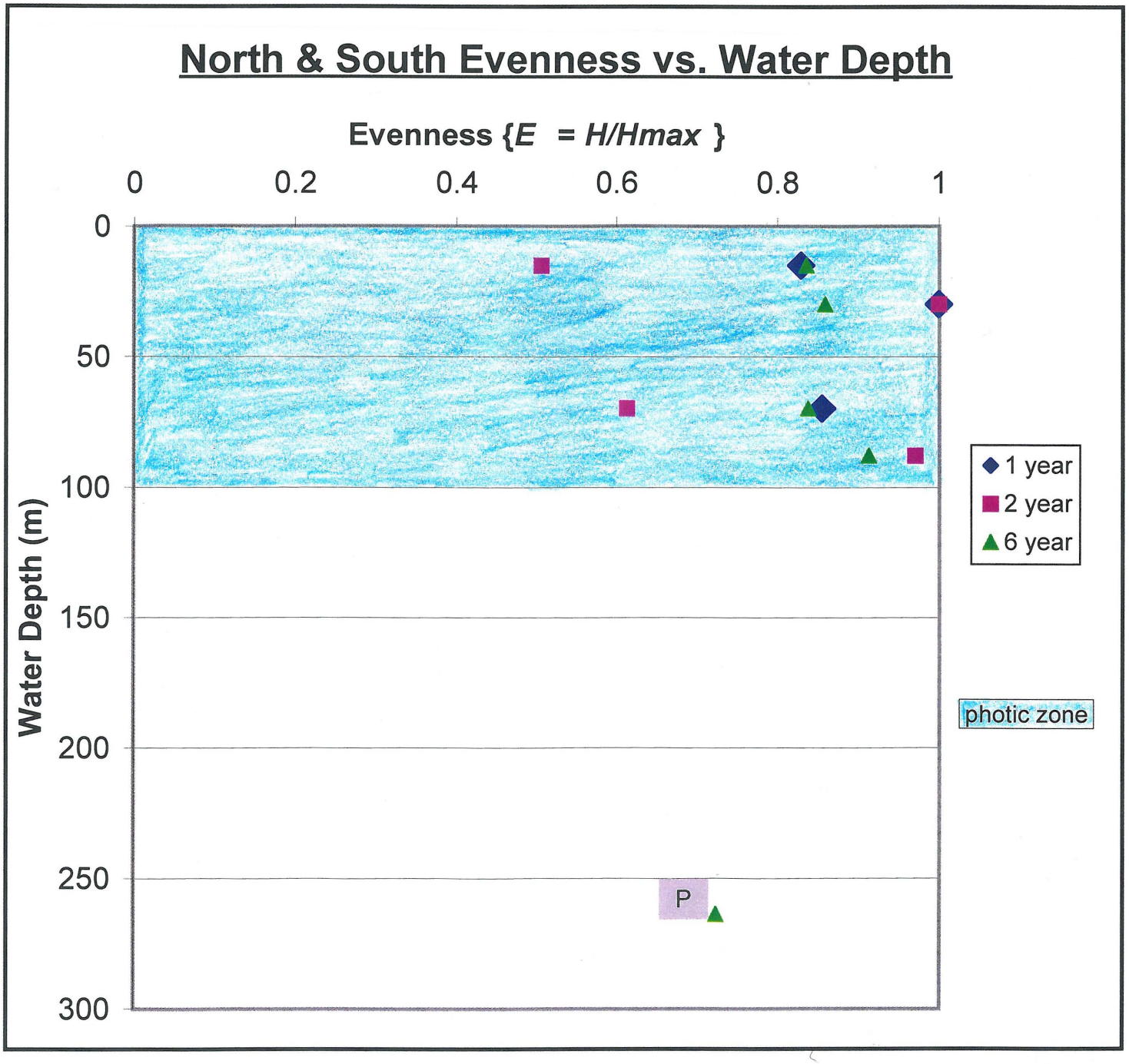


Figure 18. Evenness vs. water depth (data from both transects). There is a significant lack of evenness data at depth. Only the 6-year interval indicates a possible increase in evenness from point P at depth to data points in the photic zone. Evenness is greatest at the 1-year interval, both high and low at 2-years, and at intermediate values for 6 years.

Environmental Factors

Bryozoan distribution reflects a fusion of numerous biological and physical factors acting together. Even though no single parameter is responsible for bryozoan settlement patterns, it is useful to examine the distributing effects of individual components. This study considers the roles of temperature, salinity, wave energy, water currents, and sediment cover.

Temperature

Temperatures along transects North and South dropped from 30 to 19°C from the shallowest to the deepest sites (Fig. 19). Due to the Bahamas' geographic location, this range of values remains roughly constant throughout the year. The ranges of occurrence of bryozoans with respect to temperature have been shown to vary widely at the species level (Smith, 1995). This study made taxonomic identifications to the genus level. For that reason, even though it is likely that the observed decrease in temperature with depth influences Bahamian distribution patterns, the importance of this component could not be addressed.

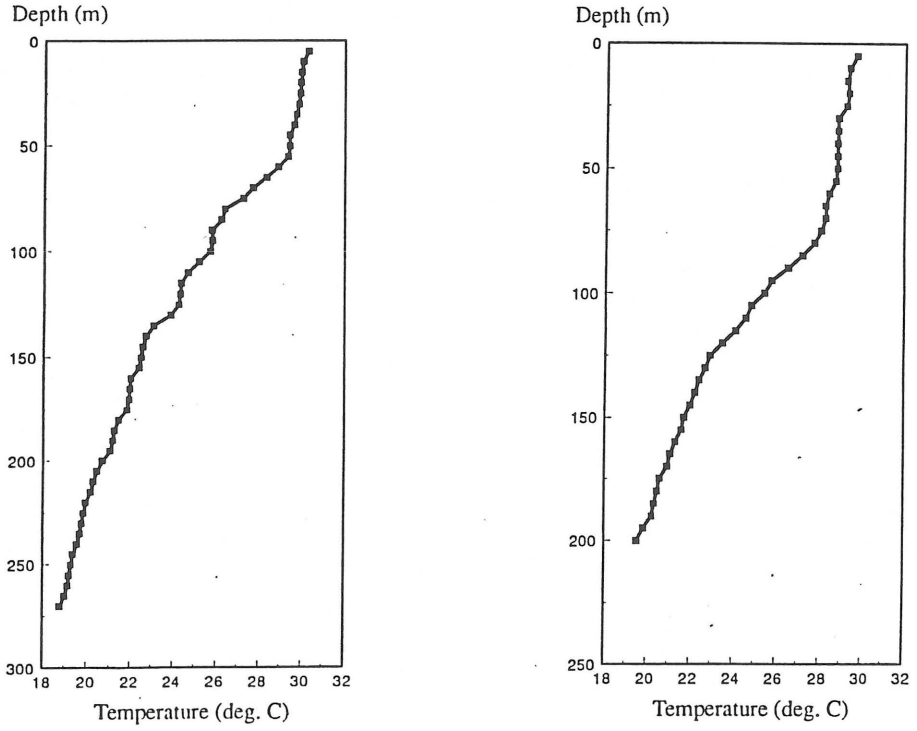


Figure 19. Temperature curves for Bahamian waters. A) North transect. B) South transect. Temperature decreases with water depth. Taxonomic identification to the species level is necessary to correlate temperature with distribution. The present study identified specimens to the genus level. Accordingly, the role of temperature is considered important in limiting bryozoan settlement, but could not be quantitatively assessed. (From Parsons-Hubbard, NSF proposal, 1999).

Salinity

Salinity (Fig. 20) does not vary appreciably in the range of depths investigated. The values for all experimental sites fall between 36.7 and 37.0 ppt. A salinity spike occurs from about 95 to 115 meters, but the continental slope at those depths is almost a vertical wall, which prevented deployment of arrays at the level of the spike.

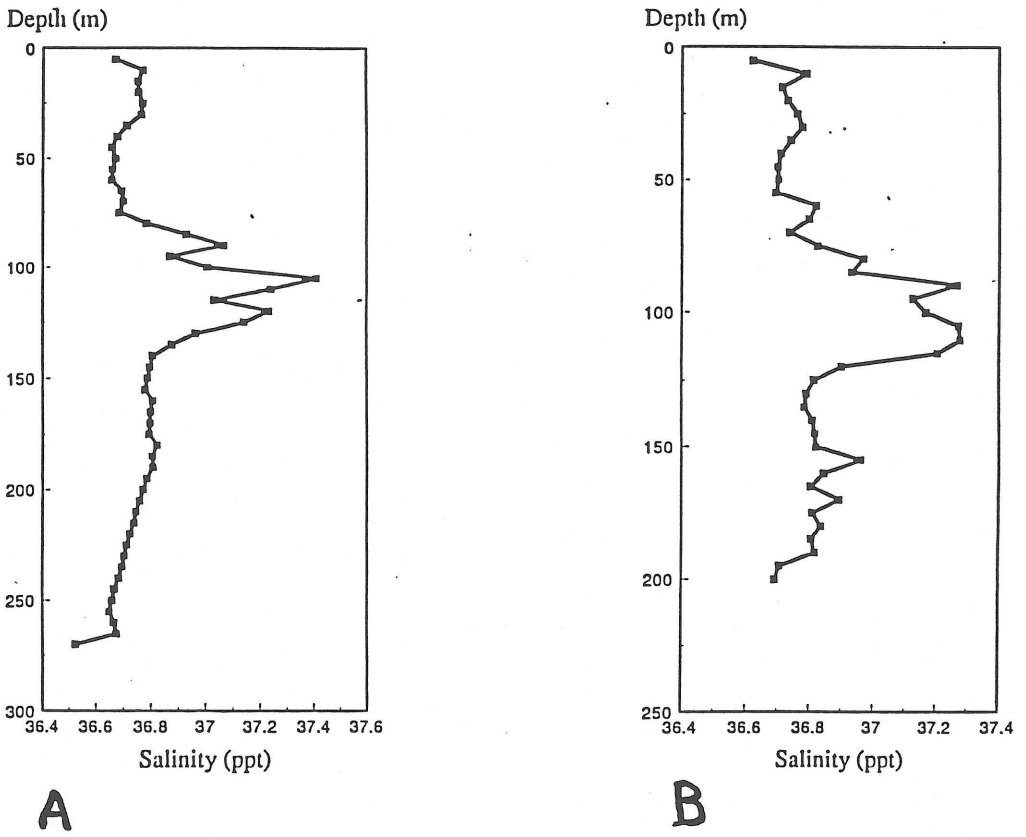


Figure 20. Salinity curves for Bahamian waters. A) North transect. B) South transect. Salinity is roughly constant for all sites sampled. No arrays were deployed within the ~100m depth zone characterized by a spike in salinity because the slope angles in that region are too steep. (From Parsons-Hubbard, NSF proposal, 1999).

Wave energy

The Bahamas is a region of intense tropical storm and hurricane activity which can create heavy waves that reach as deep as the 70 meter sites. Hurricane Aaron in August, 1995 blasted the Bahamas with windspeeds of 75 knots. In October, 1996, Hurricane Lili, a Category 3 storm, roared over the study area with winds in excess of 90 knots. Arrays deployed in shallow water (15 - 70 m) were likely affected by these events.

Water currents

Both shallow and deep sites are regularly affected by water currents that transport sand. 1993 North transect current meter data from 30 meters averaged 1.6 cm/s, with a range of .1 to 15.8 cm/s. Data from the same location in 1994 ranged from .1 to 15.9 cm/s, with an average of 2.6 cm/s. Average current increased again in 1995 to 3.3 cm/s, with a range of .2 to 13.1 cm/s. Similarly, 1994 South transect 30 meter data varied from .3 to 8.9 cm/s, with an average of 3.5 cm/s. 1995 data from the same location averaged 3.7 cm/s, with a low of 1.4 cm/s, and a high of 8.5 cm/s. 1993 North transect data from 257 meters averaged 3.0 cm/s, and ranged from 1.6 to 5.1 cm/s.

Burial Depth vs. Water Depth

Sediment coverage data along a range of water depths is displayed in Figures 21A & 21B for all time intervals of transects North and South. Data from the North 1-year interval (Fig. 21A) does not show any significant trend between water depth and sediment accumulation, all the sites in shallow and deep water being covered with less than .5 cm of carbonate sand. However, the 2- and 6-year data from North appear to yield a trend between water depth and sediment burial. Both high (points A & C) and low (points B & D) burial signatures are common in shallow waters, just as high (point E) and minimal (point F) burial values are present in deeper waters. Yet the range of burial values is greater in shallow water than in deep settings. That is, although both high and low accumulation occurs near the shore and at depth, shallow waters get higher highs than deep

waters. This reflects a possible trend of decreasing sediment burial with increasing water depth.

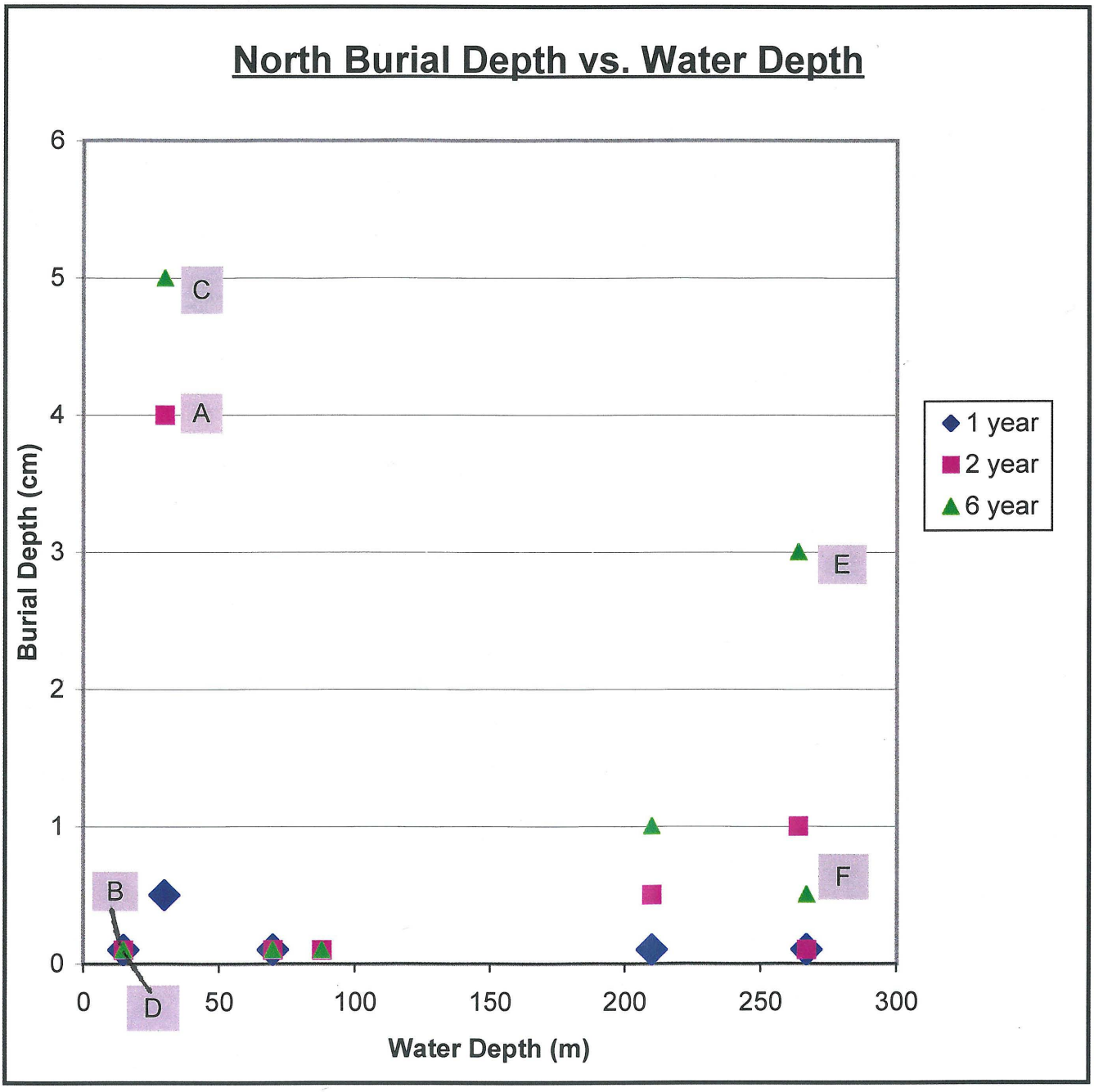


Figure 21A. Burial depth vs. water depth for the North transect. Sediment cover is greater in shallow waters, and decreases with depth. Two different arrays collected from the same depth may show completely different burial signatures, depending on whether or not sediment accumulation is removed by water currents, storm activity, or shifting of experimental arrays.

Analysis of South transect burial (Fig. 21B) with water depth shows an even stronger depth/burial trend. Points G & I and J & H respectively represent high and low burial values in shallow waters. Only low burial values are present at depth. Together then, retrieval intervals from both transects show that sediment coverage decreases with depth.

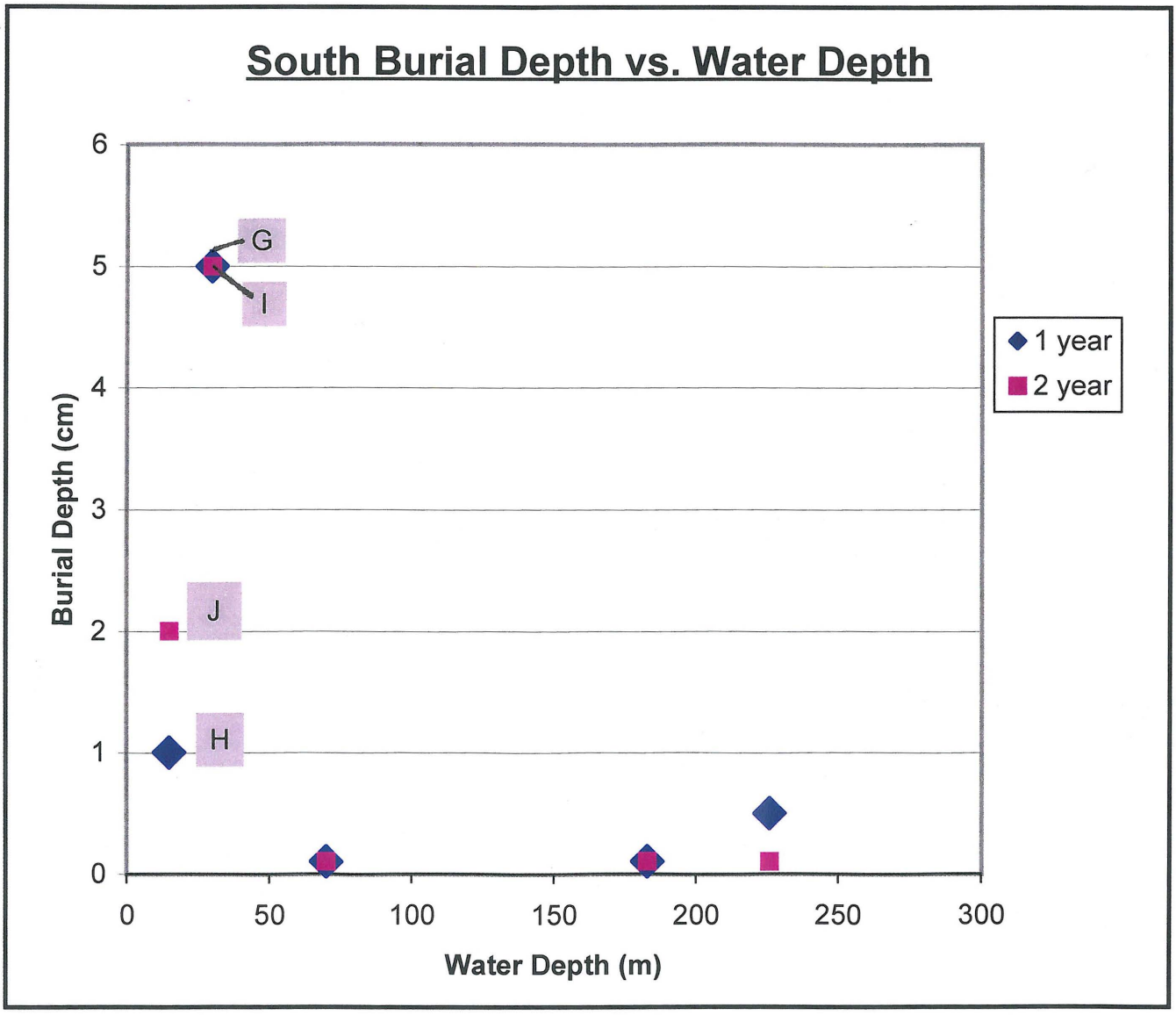


Figure 21B. Burial depth vs. water depth for the South transect. Again, there is a correlation between sediment cover and water depth. Sedimentation does not increase through time due to a loss of sediment accumulation from water currents, storm events and post-deployment shifting of collection arrays.

Burial Depth Through Time

It is also practical to look at how burial changes through time. When the 1-, 2-, and 6-year data at each depth site are compared, some data points show a general increase in burial depth through time, while other points do not reflect this increase. For example, sedimentation along the North transect (Fig. 21A) at the 1-year interval was low for all sites both shallow and deep. In contrast, at the 2-year interval there are nearshore and deep sites that show an increase in burial depth as well as sites that show no increase in burial depth. The 6-year interval displays analogous results of both high and low sedimentation at all depths.

The South transect (Fig 21B) does not indicate any noteworthy increase in sedimentation from the 1 to 2-year interval.

Burial Depth vs. Richness

Figure 22A shows North and South richness vs. burial depth.

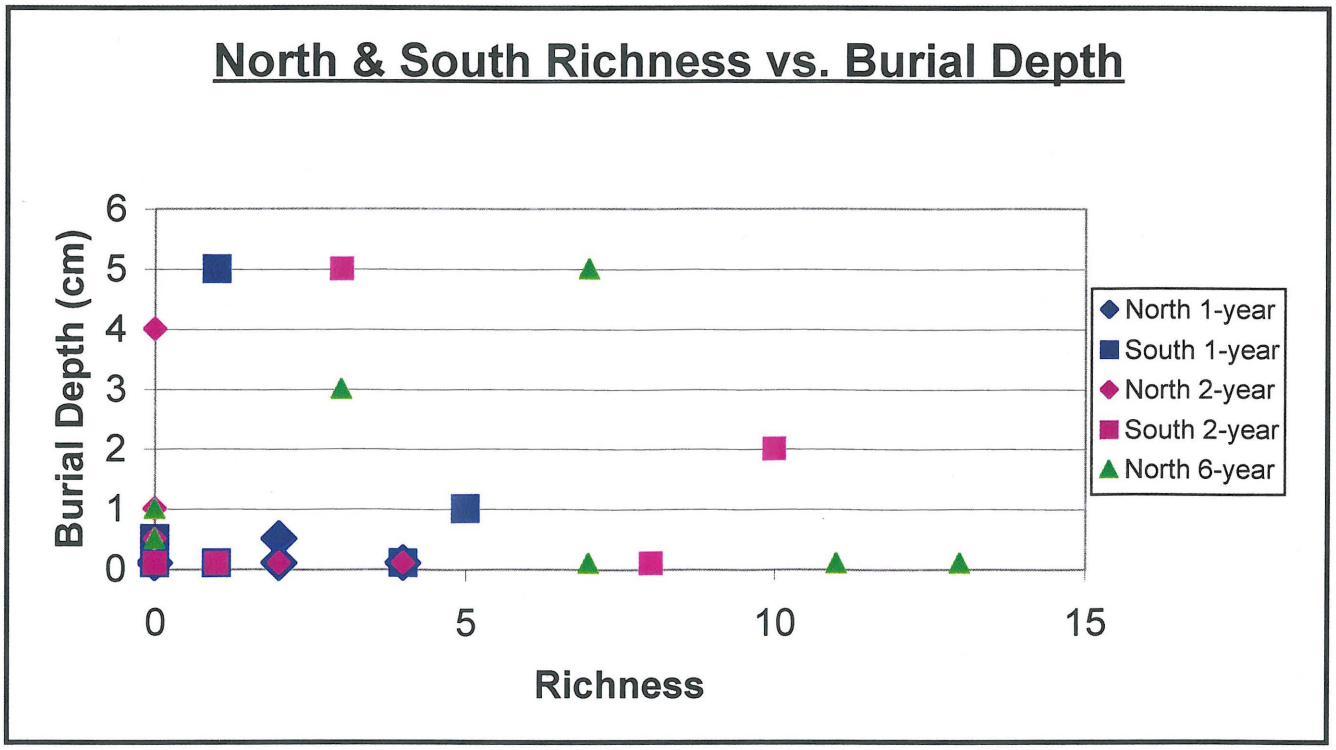


Figure 22A. Richness vs. burial depth (data from both transects). The graph does not show a significant relationship between richness and sediment cover, and therefore tells little about the influence of sediment on richness distribution.

The graph does not show a strong correlation between burial depth and richness. It appears as if greater richness might occur at shallower burial depths, but relatively low and high richness values are common at sites of both low and high sediment burial, particularly for the 6-year data. It is not discernable if sediment cover really influences richness distribution. This absence of a distinct trend is an artifact of graphing richness vs. depth values for sites at all water depths. When plotted for sites within the photic zone only, a more robust trend of higher richnesses at lower burial depths becomes evident (Fig. 22B).

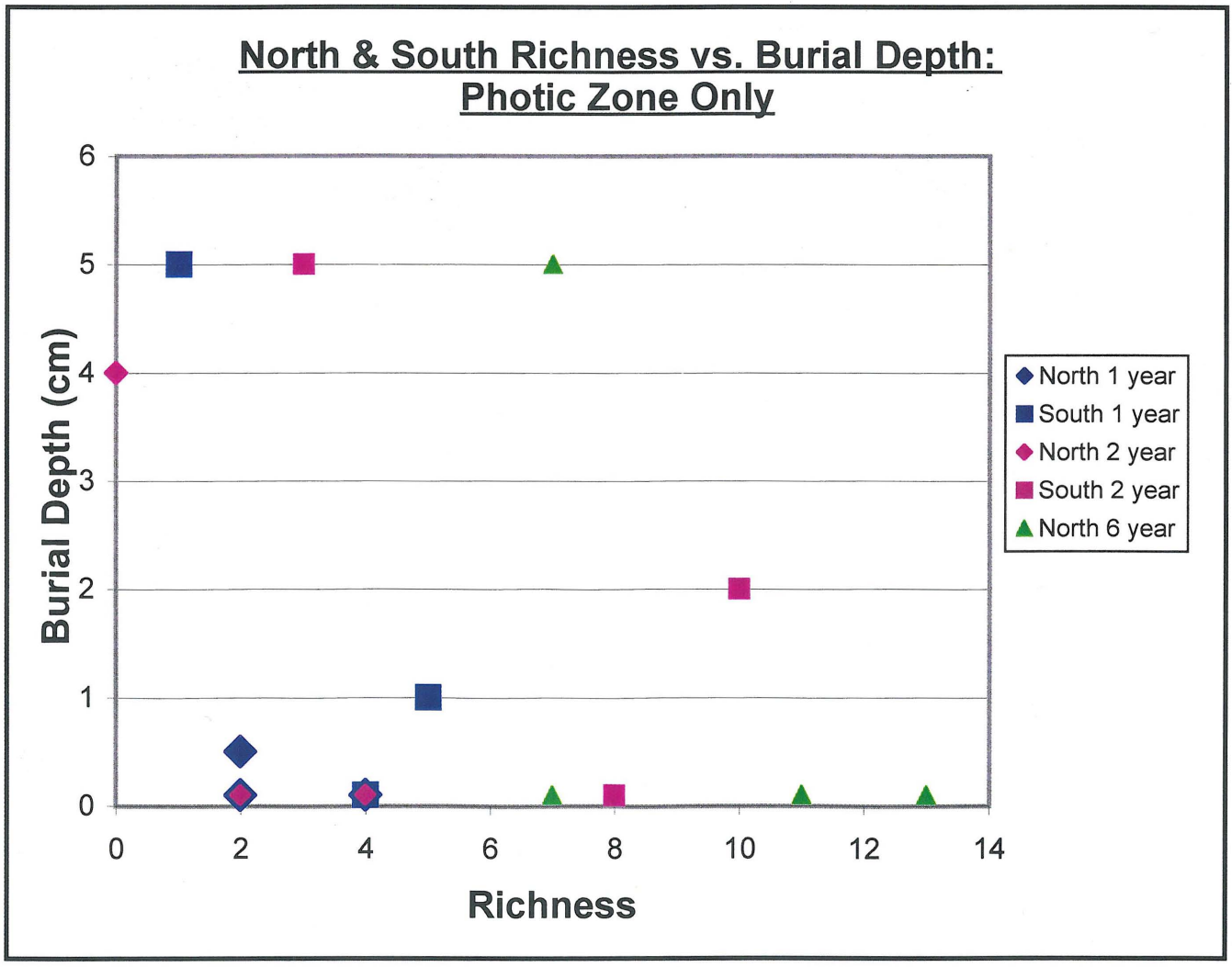


Figure 22B. Richness vs. burial depth within the photic zone only (data from both transects). Higher richness occurs at lower burial depths within photic waters, i.e. richness distribution may be a function of sediment cover. The trend of richness increasing with time is also apparent.

Supplementing this result is Figure 22C, which plots richness with burial depth for sites below the photic zone. All but one of the data points fall within a cluster of low richness associated with little burial depth, indicating the absence of a recognizable trend between richness and burial depth in deeper waters. The graph also reiterates the trend of increasing richness with time.

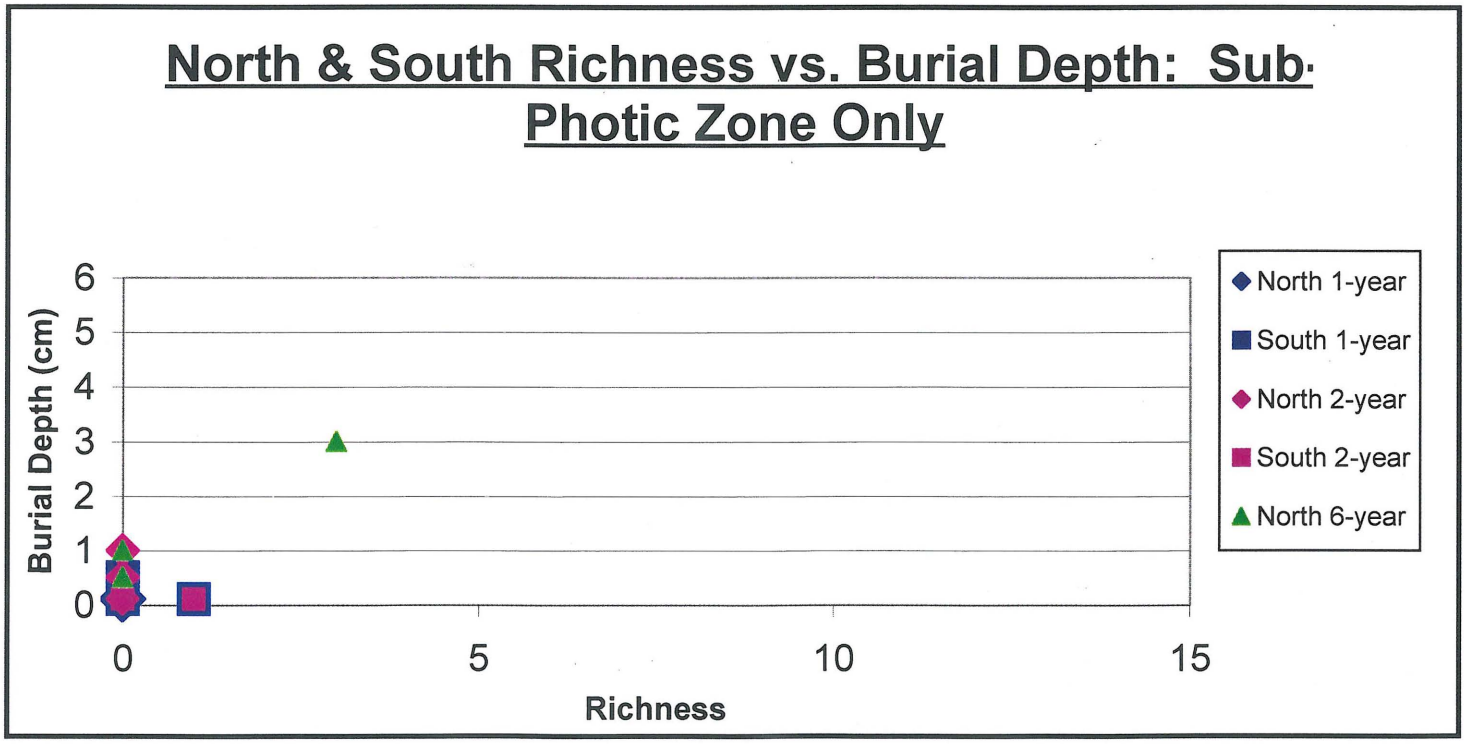


Figure 22C. Richness vs. burial depth below the photic zone (data from both transects). There is no apparent trend between richness and burial depth in sub-photic waters.

Together, Figures 23B & 23C suggest that in photic waters, burial depth is possibly a significant factor in determining richness distribution, while richness in sub-photic waters is not a function of sediment cover.

Burial Depth vs. Evenness

When burial depth is plotted against evenness (Fig. 23) scattered values of high and low evenness occur at both high and low burial depths. There is no apparent correlation between evenness and sediment accumulation.

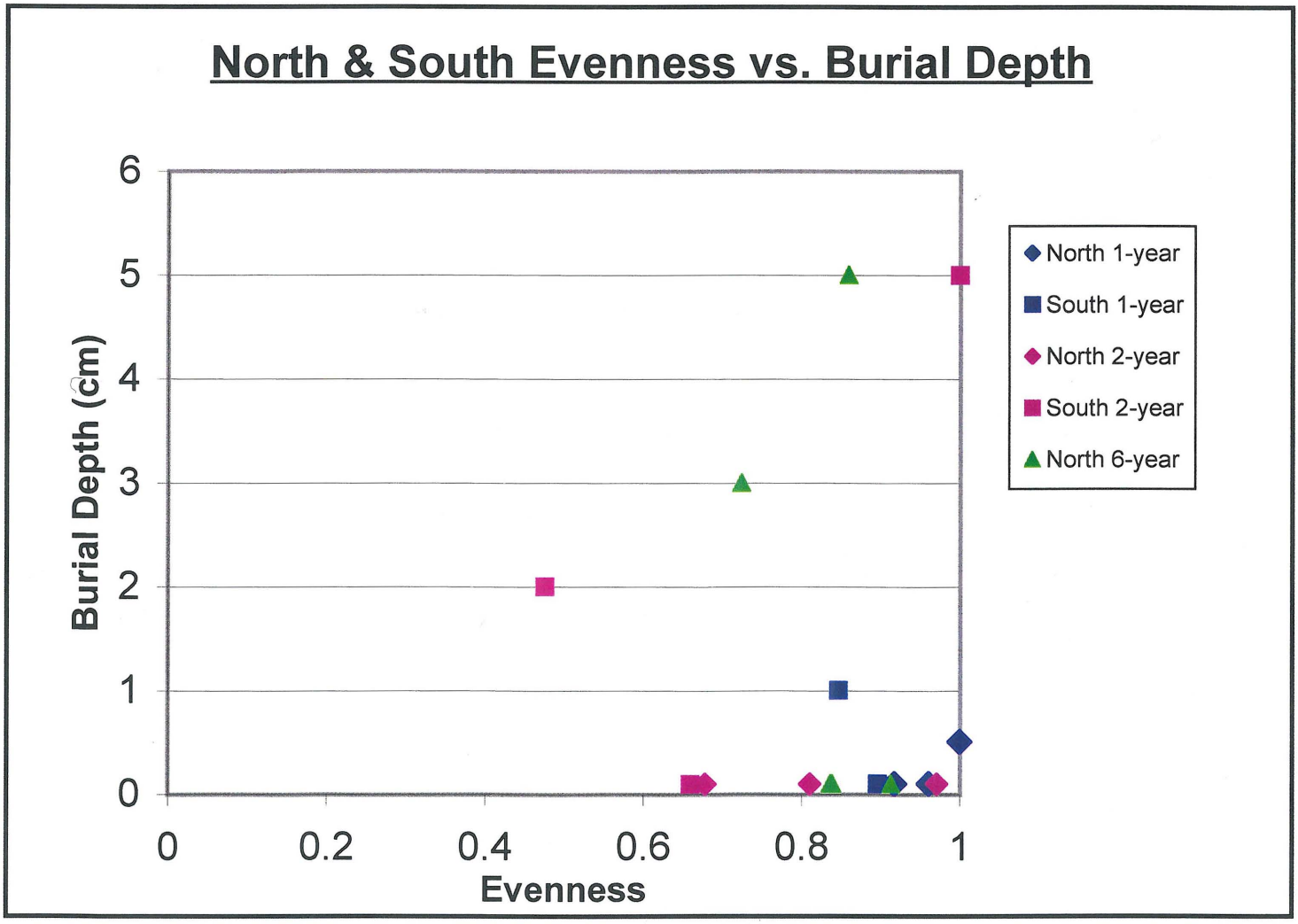


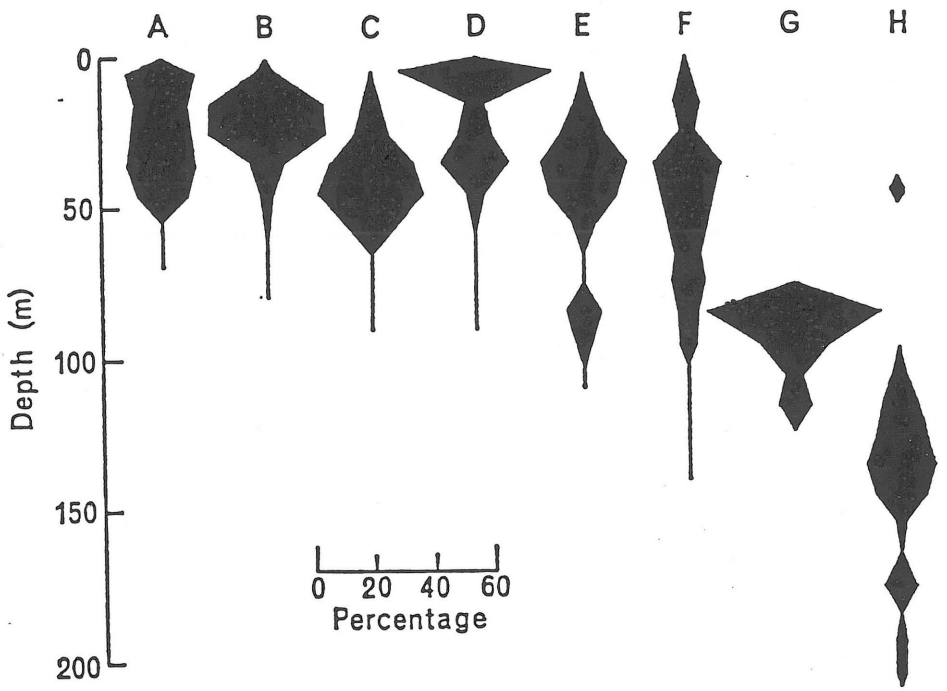
Figure 23. Evenness vs. burial depth (data from both transects). No recognizable relationship exists between evenness and sedimentation.

DISCUSSION

Depth Distribution and Light

The present study is unique in that it is the first of its kind to actually sample Bahamian bryozoans in deeper shelf and slope environments. The observed patterns of distribution presented here give experimental witness to the interactions of bryozoans along a depth gradient in the Bahamas. Specifically, generic distribution patterns are indicative of photic and non-photic bathymetric regions in the water column. High abundance and diversity occur in the photic zone. Relatively low abundance and diversity occur below the photic zone.

The fact that the majority of bryozoans collected were gathered within the top 100 meters is not unusual since the waters within the photic zone are the most nutrient rich and produce the greatest biomass. Yet until now this theory has never been scientifically tested in Caribbean waters for bryozoans. Very little work has taken place in sub-photic zone habitats. Studies performed by Gautier (1962, as described in Ryland, 1970) show that in Mediterranean settings the maximum abundance of bryozoans occurs within a range of 20-80 m, which correlates well with our data (Fig. 24). Two genus-types, *Schizoporella* and *Escharina,* occur in both the Mediterranean and Bahamian species lists. For both locations *Schizoporella* is associated with the photic zone, while the association of *Escharina* with sub-photic Mediterranean waters is in contrast to its Bahamian occurrence at nearshore depths. This difference could reflect a lack of enough *Escharina* individuals (only one was recorded) to conclude accurate depth affinities in the Bahamas. It is also likely that the physical parameters mediating the two environments differ significantly, especially in the sedimentation processes particular to each.



A *Margaretta cerioides*
B *Hippopodinella* spp
C *Schizoporella magnifica* (*Myriapora truncata* is similar)
D *Savignyella lafontii*
E *Schizomavella discoidea* (*Fenestrulina malusii* is similar)
F *Cellaria salicornioides*
G *Ramphonotus minax*
H *Escharina dutertrei* (occasional colonies occur at greater depths)
The bimodal distributions of D and E reflect the availability of suitable substrata.

Figure 24. Depth distribution of some western Mediterranean cheilostomes. As with the Caribbean data, the greatest diversity and maximum abundance of species lie within the photic zone. (From Gautier, 1962, in Ryland, 1970).

In addition to the photic zone serving as a nutrient source, there is possibly a connection between larval settlement patterns and photic illumination. Observations of several shallow water species show that light may initiate the release of larvae from the brood chamber (Ryland, 1977). Once free, the resulting larval behavior is also governed by light, and specimens exhibit several different phototaxes. The most common is for larvae to first display a positive phototaxis, being drawn toward the light, but subsequently develop a negative response before settling, as in *Hippothoa hyalina.* One beneficial result of this initial

positivity is to promote movement of larvae away from parent colonies which would compete for space and resources. The negative response that later develops is photokinetically related, influencing bryozoan settlement in shaded places like the undersides of rocks, overhangs, or experimental panels. Yet, this creates somewhat of a paradox. If light is influential in triggering larval escape, why then do the free larvae seek shaded substrate on which to settle? The answer may simply be that they colonize the lower surfaces of substrate because they are swimming upwards in response to light stimulation. More likely though, the deterrent effects of sediment accumulation on upper surfaces play a significant role in controlling settlement patterns. Regardless, it is light that draws the bryozoans to photic waters in the first place.

Other Environmental Factors

Although the data show clear distribution distinctions from photic to sub-photic waters, light is not the only significant factor dictating this trend. The presence of a distribution pattern that varies significantly with depth results ultimately from the interaction of several environmental factors within the water column. Of chief importance is salinity. While salinity does not appear to directly influence the settlement of adult bryozoans in the range of depths studied, the spike that occurs around 100 m may control larval distribution (Fig. 20). Specifically, enhanced salinity concentrations increase water density, and this density layer may serve as a boundary preventing larval passage into deeper waters. Of the 459 bryozoans tallied, only 10 were collected at sites below 100 m. This same density layer likely prevents many nutrients from raining down to greater depths as well. It is possible then that the varying distribution in bryozoans between photic and non-photic waters is largely an artifact of a restricting halocline.

As sedimentary environments, conditions in the Bahamas are quite uniform, ranging from carbonate sands to muds. The observation of low cheilostome

richness and diversity below the photic zone, increasing steadily to higher values in shallow waters is important in that it shows variability *within* a homogeneous sedimentary environment. Future work will compare these data to the clastic Gulf of Mexico and to Gulf carbonate sites, and it is expected that there will be significant differences between the distribution patterns observed in the two carbonate locations.

Sediment accumulation is significant in shallow waters. At depth, sediment is not an important factor. However, shallow waters do not necessarily imply burial, nor do deeper waters mean exposure. The observed variation in burial signatures between two different arrays collected from the same depth (Figs. 21A & 21B) is understandable in terms of water currents, storm activity, and shifting of experimental assemblages. Along the shallow reef terrace, sand ripples actively migrate with daily current activity, alternately covering and exposing sample arrays. Thus, experimental arrays at the same depth may reflect opposite burial signatures due to their position relative to the trough or crest of migrating sand channels.

It is likely that the wave energy associated with hurricanes Aaron and Lili also removed some of the sediment that previously accumulated. Furthermore, shifting of collection arrays along the seafloor at some point after deployment affects burial and therefore abundance. If arrays were tossed about by storm activity or tumbled down the slope, any prior accumulation would have been lost. Video analysis confirms that some slope arrays turned over. Beyond the shelf break, at depths below the base of storm activity, only currents and array movement affected burial patterns. In places where there were no significant processes of sediment removal, sedimentation rates remained constant throughout the experiment and thus burial increased with time.

The observed larval settlement patterns pose the question as to why genera are all evenly distributed at the start of the experiment, subsequently experience a decrease in some evenness values after a second year, and finally return to a more continuously even distribution after 6 years. Such patterns through time may reflect a burial signature, giving insight into whether or not burial

depth is a factor involved in evenness distribution. Intermediate disturbances in accumulation, like array movement and sediment removal by wave action, may be important in determining settlement patterns from year to year. However, figure 23 shows no obvious relationship between evenness and burial depth. Hence for point P, the lone evenness data point in subphotic waters (Fig. 18), we have eliminated sediment coverage as a causative agent for its relatively low evenness.

Grazing is not considered to be an important factor in this study. In natural marine settings bryozoans must combat the predatory jaws of fish and sea urchins. This experiment, however, used mesh bags to simulate cryptic environments, which protected encrusted bryozoans from most external predators.

Paleoecological Analysis

Looking in the fossil record one can find evidence for causes of bryozoan distribution patterns, assuming modern processes controlling distribution of benthic assemblages were also at work in the ancient (Jackson, 1983). Burial events, partial mortality, colony breakage, competition for growth space and predation all leave characteristic signatures.

Smith (1995) noted several concerns in making fossil bryozoan interpretations based on studies of modern species. Major problems exist with taphonomy. The fossil record is often incomplete or inaccurate, leading to biased interpretations of paleocommunities. It is important to know the fossilization potential of the fauna in question so that analysis can be made of what percentage of the original community is actually represented by the fossil assemblage (Schopf, 1978). Studies of cryptic environments in Salt River canyon, St. Croix, U.S.V.I. suggested that fossil assemblages of large, stable, cryptic environments are less preservable than smaller, ephemeral cryptic substrates like shells because the latter are more readily buried. For the communities that do get buried and at least have the potential to be preserved, as much as 62% of the originally observed taxa would be excluded from the fossil record due to the

nonpreservation of unskeletonized organisms (Rasmussen and Brett, 1985). It is for this reason that our study focused on bryozoans with preservable hardparts.

There is also the danger that uniformitarianism is being applied to a system in which evolution has occurred (Smith, 1995). The present may actually be much different than the past, in which case modern systems cannot simply be used to interpret fossil environments. Furthermore, it is possible that analysis of an ancient fossil community is actually an interpretation of a time-transgressive assemblage, i.e. there is no method by which one can tell what bryozoans were dead or alive at any given time. Thus an accurate picture of the true distribution pattern and the defining physical and biological parameters at any instant cannot be generated.

With these concerns in mind, we can use our modern bryozoan distribution model as a tool to reconstruct paleo-depth sequences of Cenozoic fauna. Eleven genera identified in this study have Cenozoic fossil histories. *Aimulosia* and *Aetea* both date back to the Eocene. *Cleidochasma, Ellisina,* and *Parellisina* are present in Miocene aged rocks. *Antropora, Crepidicantha, Escharina, Exechonella, Parasmittina,* and *Reptadeonella* all appeared in Pliocene times (Bock, 2000). Thus, Bahamian rock strata can be examined for similar taxonomic assemblages and distribution trends to differentiate between shallow and sub-photic settings in the past.

As this project is a continuous effort, hopefully spanning several decades, it will perhaps be useful in its implications of the rates at which fossil signatures develop in the geologic record. Does cheilostome colonization all occur quickly in the first 10 years and then remain constant, or is it something that develops gradually and changes with time? More generally, do the rocks document a temporally persistent or shifting assemblage? In most instances we cannot ascertain such things from the fossil record. The scale of geologic history is so great that the sediments layed down in 1-, 2-, and 6-year intervals effectively occurred simultaneously. Knowing the pace of modern substrate recruitment is very useful for interpretation of ancient settlement rates.

Finally, it is important to note that this project examines bryozoan distribution patterns that developed on a single type of substrata spread across a depth gradient. Therefore, the study only reflects the settlement patterns of Cheilostomes prevalent on *Eucidaris* tests and spines, a high-magnesium calcite material. However, Cheilostome distribution is only one part of a much larger experiment. Several other types of experimental substrate like wood and shelly fauna were also deployed at the same sites alongside the sea urchins, with the ultimate goal of evaluating the encrustation rates for a variety of materials. In addition, the settlement distributions observed at 1-, 2-, and 6-year intervals are most likely also connected to parameters beyond the scope of this study, including feeding patterns, substrate encrustation percentages, and predator-prey relationships. Future work combining ecological investigations of the entire community of organisms, their habitats, growth strategies, and interactions will be necessary to understand the dynamics controlling distribution patterns in tropical carbonate settings.

CONCLUSIONS

During early recruitment up through 6 years, cheilostome bryozoan diversity and abundance are low below the photic zone, and increase steadily in illuminated waters. Temperature is probably important in controlling settlement, but cannot be assessed without taxonomic identification to the species level. A halocline around 100 m serves to restrict passage of both nutrients and bryozoan larvae, and is fundamental in directing byrozoan distribution with depth. Sediment accumulation is directly connected to wave energy and water currents and burial appears to influence bryozoan distribution only at shallow depths, affecting richness but not evenness patterns. Comparison with data from the 8- and 10-year retrieval intervals will hopefully confirm these trends and uncover new patterns that generate a more complete picture of the modern.

Eleven genera identified in this study, *Aimulosia, Aetea, Antropora, Cleidochasma, Crepidacantha, Ellisina, Escharina, Exechonella, Parasmittina, Parellsina, and Reptadeonella,* all have Cenozoic fossil histories. With the aid of Smith's (1995) paleoreconstructive caution, we can look in the rock record and use fossil Bryozoa together with other benthic invertebrates to distinguish photic and sub-photic settings in tropical, carbonate paleoenvironments. Those environments can in turn be utilized to interpret global water depth changes throughout the Cenozoic era.

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