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# Epibiont Guilds as Paleoecological Tools in Environmental Analysis: An Example From Modern and Ordovician Shell Substrates

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# EPIBIONT GUILDS AS PALEOECOLOGICAL TOOLS IN ENVIRONMENTAL ANALYSIS:

## AN EXAMPLE FROM MODERN AND ORDOVICIAN SHELL SUBSTRATES

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## Abstract

Paleocommunities of encrusting organisms exhibit characteristics that allow comparisons of modern and fossil systems and subsequent environmental analyses. Encrusting organisms attach to a substrate that is generally limited in area. Interactions between bionts and the host organism, and bionts and the environment, are preserved on epibiont encrusted fossils. Modern biont communities from known environments can be compared to fossil biont communities in order to determine the ancient environment experienced by that fossil. Using epibionts as a tool in paleo-environmental analyses employs the somewhat problematic idea that the present can be used as a key to the past. I suggest that by using guilds (as opposed to species) of bionts, defined by parameters of lifestyle and habitat, the present can be a key to the past with regard to encrusting communities.

A modern data set from off the coast of Lee Stocking Island, Bahamas, was used in this study. *Mytilus edulis* shells were experimentally deployed at seven depths from 15m to 275m for a period of two years. After retrieval by the SSETI team, I collected epibiont data from a total of 52 disarticulated bivalve shells.

To test the method of guild use in paleoenvironmental analysis, I used a fossil data set from the Richmond Group in Indiana, Ordovician in age. I obtained *Rafinesquina alternata* shells from three shell beds in one rock outcrop and collected epibiont data from a total of 208 of these articulated shells.

I compared epibiont data from the modern and Ordovician data sets using a number of different variables, including: presence of guilds, percent area of shell covered by guilds, relative abundance of guilds, and guild richness. I analyzed results for significant differences in order to determine if the Ordovician data were similar to data from any of the modern environments.

In addition to an analysis of the environment experienced by the Ordovician *R. alternata* and its encrusting organisms, I will explore several larger concepts. One major question is what parameters will be most useful in the comparison of guilds of encrusting organisms that are separated by a gap of 400 million years. I will also address the viability of using guilds as a tool in making comparisons of once living assemblages across such a large time span. Finally, the underpinning assumption of this research, that the modern can be used as a model for the past, will be discussed.


## Introduction

Comparisons of paleocommunities serve as useful tools in the analysis of both modern and geologic environments. Epibionts include any species that utilize the hard parts of organisms as a substrate on which to grow. Biont communities share three important characteristics. First, epibionts cement to their substrate and remain

permanently *in situ*. Second, the substrate is usually limited in area; therefore, each fossil substrate supports its own isolated 'island ecosystem'. Finally, biont growth varies with environment, so fossil bionts reflect the processes operating within ancient environments. These characteristics may allow inferences about fossil systems to be drawn based on modern models. The present as a key to the past is a crucial paleontological tool, but one fraught with difficulties. Comparison of epibiont communities may provide a relatively reliable way to employ this method. Determining the utility of epibionts as a means to draw comparisons across geologic time requires studies of both fossil and modern biont systems. Meaningful comparisons across longer spans of geologic time also require the development of guidelines to classifying bionts. These guidelines should not depend upon identification of species, as the same species will not exist, or may be significantly changed in lifestyle or habitat, between modern and ancient communities. I propose the use of guilds, defined by critical lifestyle parameters, as a means of classifying and comparing assemblages. Guild comparisons across long spans of geologic time may be more stable in terms of reflecting environmental parameters, thereby rendering epibiont communities a powerful paleoecological tool. I will use guilds to compare biont assemblages on modern *Mytilus edulis* shells with biont assemblages on Ordovician *Rafinesquina alternata* shells in order to decipher the Ordovician environment and determine the utility of guilds as a tool in environmental analysis.

*Past Work*

Epibionts have been colonizing biogenic hard parts since major fossil accumulations first began appearing in the early Cambrian period (McKinney, 1996, and

references therein). Extensive research on fossil epibionts and epibiont communities has been conducted over the past century with a variety of goals. Most numerous among these have been studies on the autecology of the host species (Ager, 1961; Richards, 1972; Pope, 1976; Kesling, 1980; Powers and Ausich, 1990; Spjeldnaes 1984; and others). Life position, hydrodynamics, and diet of host species have all been hypothesized from epibiont data. Work done by Ager (1961) on the epibionts on a Devonian spiriferid was one of the first studies to use epibionts as an indicator of the traits of a host organism, including symbioses of host and biont. Other research has focused on the ecology of the epibionts themselves, including recruitment rates, community interactions, host specificity and symbioses, and substrate specificity (Richards, 1972; Spjeldnaes, 1978 and 1984; Kesling, 1980; Lidell and Brett, 1982; Buss and Yund, 1988; McKinney, 1996; and others). Finally, epibionts have been used as a high-resolution sedimentological tool and indicator of environments of deposition (Seilacher, 1960; Bordeaux and Brett, 1990). While historically, epibionts were considered imperfections on fossils, and were often cleaned off during preparation for museum collections (Buss and Yund, 1988), they have increasingly gained recognition in paleontology and are now used in a large number of studies.

The literature on modern biont communities is extensive, but of particular interest to this study is research concerned with preservation and taphonomy. The rise of experimental taphonomy in the past few decades has led to an increasing number of studies on modern encrusters. The Shelf and Slope Experimental Taphonomy Initiative (SSETI) has played a large role in the accumulation of epibiont data. SSETI was created in 1993 in order to record taphonomic processes in a wide range of locations and depths,

on a variety of natural materials, and over a long period of time. Experimental arrays deployed by SSETI included shell material, wood, crab, and urchin carcasses either contained in mesh bags, tethered to poles, or freely scattered. Deployment and retrieval were accomplished via submersible, and SCUBA at the shallowest site. Deployment sites were located along two transects off Lee Stocking Island, Bahamas, and in 14 locations in the Gulf of Mexico. Environments included typical shelf and slope locations and atypical brine seeps, petroleum seeps, hardgrounds, a collapsed carbonate bank, carbonate sands, and deep-water reefs (Parsons, 1997). Depths ranged from 15m to 275m in the Bahamas, and 60m to 571m in the Gulf of Mexico (Parsons-Hubbard, 1999). Shells were deployed for a minimum of one year, while others are still deployed, for a total of 11 years thus far. The work done by SSETI fills a hole in the field of experimental taphonomy, which has primarily explored shallow-water taphonomic processes over short time intervals (Parsons, 1997)

Preliminary results from SSETI studies show trends in biont coverage on mollusc shells deployed at sites in the Bahamas from 15m to 210m for one and two years. Algal bionts dominated at shallow depths, resulting in correspondingly high percent-area coverage values compared to deep shells, which support no algal bionts (Parsons, 1997). Biont coverage was also found to change with differences in bottom type: encrusted shells were only rarely found on soft bottoms below wave base, more commonly occurring on hardgrounds or sandy bottoms (Parsons-Hubbard, 1999). Changes in biont diversity were observed with depth on gastropod shells after one year of deployment. Diversity was highest at 73m, a mid-range depth in the study, which had sites at depths between 15m and 260m (Walker, 1998). Finally, biont coverage was noted as affecting

other taphonomic characters, including breakage, discoloration and weight change (Staff et. al., 2002).

In a SSETI study of shells taken from the same transect and time interval as the shells in this study (Parsons-Hubbard et. al., 2001), taphonomy was found to be affected by a complex interaction of burial, sediment type, depth, and geography. Burial, however, was of primary importance. Degree of burial and biont coverage were inversely correlated, especially for preservable bionts. Rate of burial was also found to be relatively important. Sediment type, however, was not of much significance. This study by Parsons-Hubbard (2001) provides important insight into other taphonomic factors impacting the bionts themselves, and can be used to inform interpretations of ancient biont systems.

Outside of work done by SSETI, research on modern epibionts has included work done by Jackson (1977) on colonial and solitary encrusting organisms, and their growth and 'competition strategies' in a variety of marine environments. Martindale (1992) observed changes in both species and growth form of epibionts with changes in environmental factors including water turbulence and light. Epibionts in Martindale's study were from reefs of Barbados, but many of the same bionts (crustose coralline algae, bryozoans, foraminiferans, and serpulid worms) are found off the coast of Lee Stocking Island in the Bahamas.

The possibility of using epibionts as paleoecological tools has been explored by a few researchers. Fagerstrom (1996) used modern symbioses between bionts and their hosts as a possible analogue for ancient symbioses. He concluded that such a comparison is tenuous due to nutritional uncertainties. From the results of his test of symbiont analogues, he expressed concern over using the present as a key to the past in any

biological system. Buss and Yund (1988), however, had more positive results in their study of the colonial hydroid *Hydractinia*. They found that a modern model corresponded well with 'ancient' populations, but ancient in this study referred to populations ranging from only 100 to 150 years old. A study done by Martindale (1992) is the most relevant to this study as it compares calcified epibionts from modern reefs to bionts from the Pleistocene. The results of this work are promising, as he determined the modern model to be a reasonable analogue for ancient communities, and he went on to use bionts as an indicator of paleoenvironment in the Pleistocene reefs. He found encrusters to be reliable indicators of ancient sea level fluctuation and catastrophic events, due to the sensitivity of modern calcified epibionts to environmental fluctuations including changes in water turbulence and light.

In addition to past work on epibionts as taphonomic characters, one study done by McKinney (1996) explores the taphonomy of epibiont communities themselves. He asks the question, "How accurately do residual skeletons and borings in shells reflect the taxa, degree of cover, and ecological structure of the original living complex of encrusting organisms?" The results of this study provide useful background information for my research, and so will be briefly summarized here. Organic decomposition through time was simulated by application of a solution of sodium hypochlorite. After application, most surfaces were bare due to the much higher diversity and coverage by non-calcified species. Bare surfaces were most common followed by, encrusting bryozoans and bivalves occupying the second and third highest percentages of shell space. Other encrusting organisms totaled only 10.9% of shell space. Species totally eliminated by application of sodium hypochlorite included: unicellular films, mats, erect Hydrozoa,

erect Bryozoa, Gastropoda, and Ascidia. The "fossil" systems, as compared to the living biont communities, showed percent area covered by bivalve bionts to be ten times as great, and significant increases occurred in Annelida and Cirripedia percent areas as well.

The community comparison aspect of my study has received considerable attention from other researchers in the field of ecology. The concept of a niche has been used to describe organism interactions in a community, but it has been used in two distinctly different ways and remains a confusing term. In a study of living bird assemblages, Root (1967) developed the concept of the guild. He uses the guild to define a group of organisms, not necessarily of the same species, who utilize the same set of resources in the same way. Since the introduction of the concept, the use of guilds has gained popularity. J. A. Fagerstrom has utilized the concept to describe reef communities through time (1987, 1991, 1994), and Gwen M. Daley (2002) has used guilds in paleoecological studies of Pleistocene shell beds.

While epibiont studies are abundant, and some research has explored the value of epibionts as paleoecological tools, there are significant questions yet to ask. My research explores the possibility of extending the applicability of epibiont community models beyond the Pleistocene to ancient communities hundreds of millions of years old. In so doing, I will also address the question, so central to much of paleontology, "*is the present a key to the past?*"[1], at least with respect to encrusting communities.

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[1] *The present as a key to the past* is a concept originally created by James Hutton in 1795 and later developed by Charles Lyell in 1830. Hutton called his concept "uniformitarianism" and "gradualism" and Lyell expanded the idea with the recognition that catastrophic events interrupt long periods of relative stasis.

*Goals*

In order to determine the value of bionts as paleoecological tools over a long span of geologic time, I propose stepping beyond comparisons at a species level to comparisons at a guild level. Guilds will be established based on critical lifestyle and habitat parameters, and both modern and ancient bionts will be classified as members of a guild. The modern biont data come from the results of a study of experimentally deployed *Mytilus edulis* shells conducted in the summer of 2003 at Oberlin College. The ancient biont data will come from an epibiont study on *Rafinesquina alternata*, a brachiopod from the Upper Ordovician of Indiana.

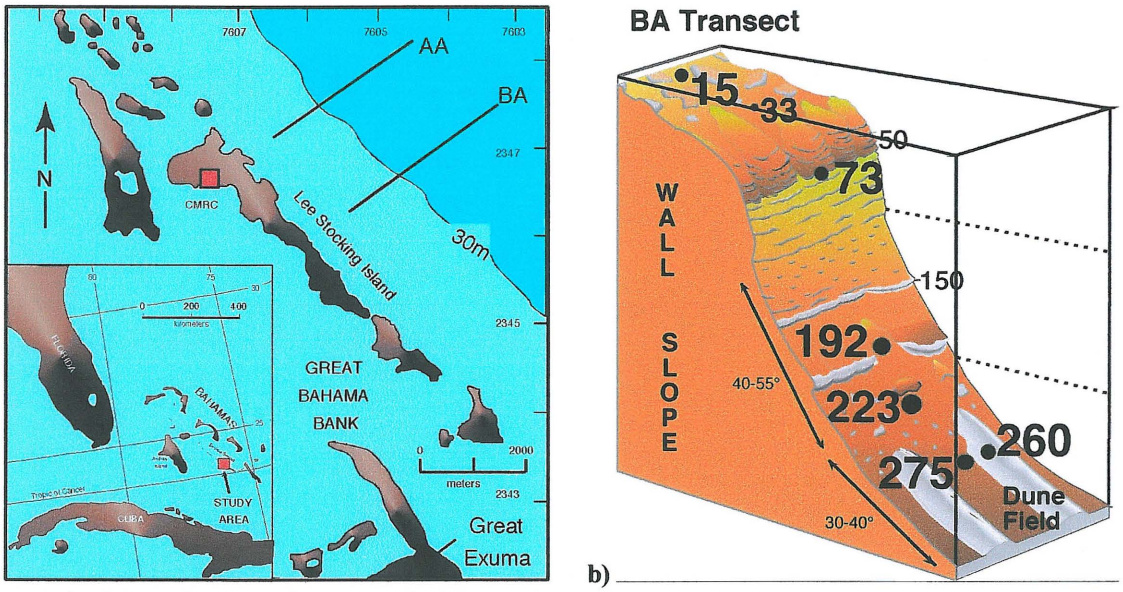
My primary goal in this research is to determine the viability of the use of guilds as a tool in using modern biont communities to understand their ancient counterparts. I will attempt an analysis of the Ordovician environment using results from guild comparisons. From these comparisons, I will determine if guilds are useful as paleoecological proxies.

## Methods

*Modern Epibiont Analysis*

Shells of the mollusc *Mytilus edulis* were deployed in 1996, as a part of a larger experimental array, by the Shelf and Slope Experimental Taphonomy Initiative (SSETI). Shells were deployed at five sites off the coast of Lee Stocking Island, Bahamas, along the BA transect, for a period of two years (Fig 1 a,b). Site locations ranged from 15m to 275m along a continental shelf and slope profile and exhibited various environments of

deposition (Table 1). Generally, the Bahamas environment is one of clear water, with entirely carboniferous sediment and no terriginous mud. A total of 52 *Mytilus edulis* shells were retrieved, corresponding to 5-10 shells per depth location (Table 1).

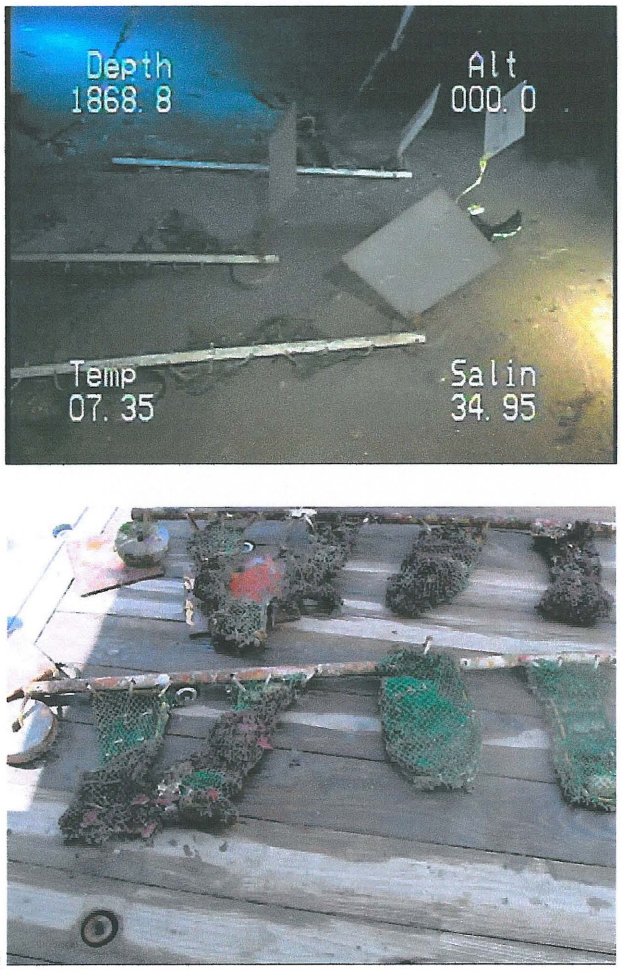



**Figures 1.** a) Location map of transects showing position of BA transect straddling the shelf-slope break (AA transect was not used in this study) and b) cross-sectional profile of BA transect. Depths listed are in meters below sea level. Environments at each depth are illustrated along profile. Both figures provided by Parsons-Hubbard.

**Table 1.** Descriptions of depth locations along BA transect and the number of *Mytilus edulis* shells retrieved from that depth which were used in modern study. A total of 52 modern shells were used in this study. Adapted from Parsons-Hubbard, 1999.

| Depth | Location | Site Description | Number of Shells |
|---|---|---|---|
| 15m | Sand channel and mud hill | Open sand bottom with migrating ripples and a low-relief mud hill stabilized by gorgonians. Macrofauna include a diverse gorgonian assemblage. | 10 |
| 33m | Sand channel | Rippled sand between patch reefs. *Halimeda* is common. | 9 |
| 70m | Wall | Narrow ledge on the wall. Associated fauna include plate corals, sponges, gorgonians, and encrusting algae. | 8 |
| 192m | Talus | Shingled rock and boulder strewn slope with stalked crinoids, crabs, and sea whips. | 5 |
| 223m | Talus | Talus strewn slope with carbonate promontories on a fine sandy bottom. | 5 |
| 260m | Crest of dune | Crest of relict dune aligned parallel to dip of slope. The sparse macrofauna includes crabs, holothuroids, and sea whips. Tracks and trails are common. | 5 |
| 275m | Trough of dune | Trough of dune with sparse macrofauna same as for 260m site. | 10 |

Deployment and retrieval at all sites was accomplished via submersible, except for 15m sites that were collected by SCUBA. Shells were deployed in mesh bags attached to1.2-m PVC rods (Fig. 2 a,b). A polyethylene float was suspended above the rod to aid in relocation of the array (Parsons, 1997).




a)

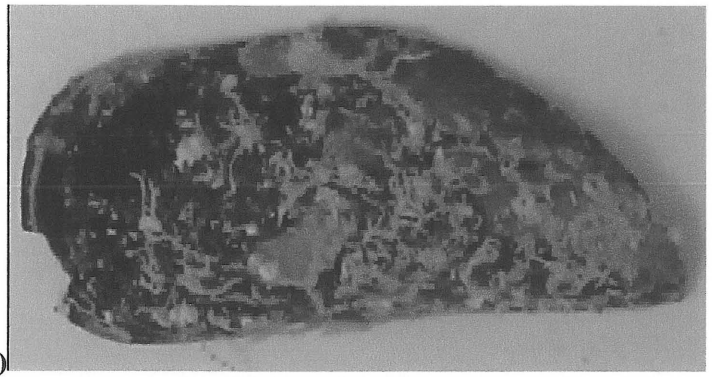
b)

**Figures 2.** a) Photo of SSETI experimental array during deployment. Mesh bags are tethered to poles and plates are floating above. Shells were contained in the bags. b) Experimental arrays after retrieval. Note encrustation of mesh bags by red algae, sponges, and other encrusters. Both photos provided by Parsons-Hubbard.

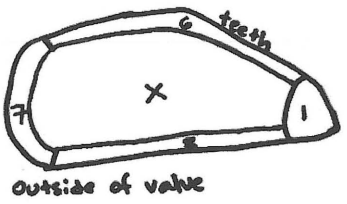
An initial taphonomic study was conducted within 48 hours of retrieval, during which time shells were stored in chilled seawater. Shells were subsequently stored in

70% ethanol solution until further lab work could be conducted (Parsons-Hubbard, Personal communication).

In the lab I examined each biont-encrusted valve (Fig. 3 a,c) using a dissecting microscope at powers up to 180x, except for some species of coralline algae and foraminifera, which were identified using a scanning electron microscope. Biont coverage was recorded as percent-area coverage estimates, with the exception of foraminifera, whose small size resulted in fractional percent-area coverage values. Foraminifera were counted for frequency of occurrence per shell area. Estimating percent-area coverage as opposed to counts of individuals eliminates the problem of defining the boundaries of the individual, which can be ambiguous when bionts are colonial or multinucleate protists. Bionts were recorded within separate shell areas on both the inside and outside of the disarticulated *Mytilus edulis* valve, as illustrated in Figure 3 (b,d). Shell areas, as opposed to whole shell, were used in counting biont percent cover in order to determine whether bionts were preferentially settling and or growing into one are of the shell or another.



a)

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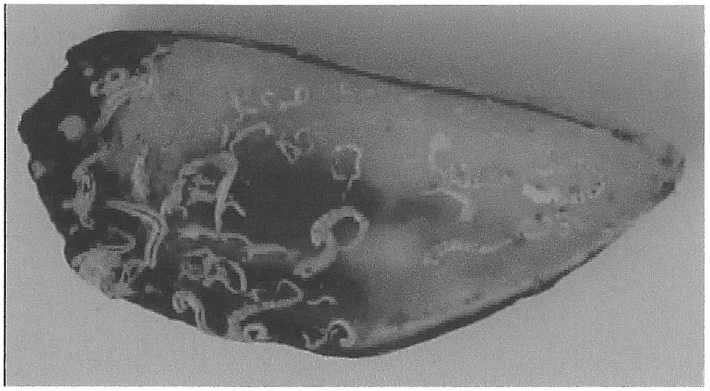
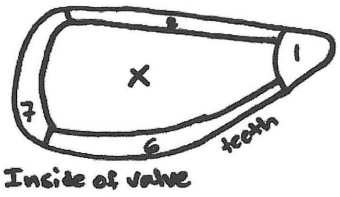


c)




d)

**Figures 3.** a) Photo of *Mytilus edulis* shell after retrieval. Serpulids, spirobids, and algae are readily apparent encrusters. b) Sketch of shell areas used during data collection for outside of valve. c) Photo of inside of the valve of the same *M. edulis* shell after retrieval. Note encrustation by brown striped serpulids and white keeled serpulids, as well as serpulid scars. d) Sketch of shell areas used during data collection for inside of valve. Photos provided by Parsons-Hubbard, 2003.

Identification of bionts was accomplished using the Treatise on Invertebrate Paleontology, specifically Part C, Protista (Moore, 1964), as well as the taxonomic work of Winston (1982, 1984, 1986 (a,b) on the bryozoa, and Loeblich and Tappan (1988) on the foraminifera. Shells had been examined, while fresh, by the SSETI team (primarily C. Brett) to identify fleshy, non-skeletonized bionts prior to storage in ethanol (Parsons-Hubbard, personal communication). Additionally, previous work done by Dr. Parsons-Hubbard was used as a preliminary source, in almost all biont identifications. Occasionally, direct comparison to specimens in the Paleontology collection at Oberlin College was useful. Often, bionts were identified as morphospecies because identification by shared morphology was possible, but positive identification to the species level was

not (e.g. serpulid identifications, as well as for some foraminifera). "Morphospecies" are defined based on morphology, whereas "real" species are defined based on reproductive isolation and/or phylogeny. Also, I use "biont" and "epibiont" interchangeably because the majority of the bionts found on shells were epibionts, but it should be noted that "bionts" includes both "epibionts" and "endobionts".

Using Microsoft Excel, I first reduced data by applying an algorithm to convert shell-area percentages to whole shell percentages (Appendix I) and then summing values for identical bionts, resulting in whole-shell percent area coverage values for each biont morphospecies. These values were averaged for all shells present at a given depth (5-10 shells at each depth). Data were analyzed for morphospecies richness on whole shell, percent area cover of whole shell, and percent area cover by shell area. Error bars were calculated for data using Students T-distribution with a probability level 0.05 (i.e. 95% confidence interval of the mean).

An analysis of 'morpho species-richness' was also conducted for each depth location. Species richness refers to the number of different species (or morpho-species) occurring in a sample. Two separate analyses were done, one including non-preservable bionts and one excluding them. Bionts considered to be non-preservable include algae (with the exception of coralline algae), hydroids, ascidians, agglutinated serpulids, agglutinated worm tubes, microscopic foraminifera (agglutinated and otherwise), and egg masses. Microscopic foraminifera are included in the non-preservables due to their susceptibility to detachment from the substrate during the process of fossilization or during the process of cleaning the fossil in preparation for study. Again, this judgment was made with the goal of comparisons with fossil systems in mind.

Shells were deployed in mesh bags, creating an artificially cryptic environment and nesting of valves in the bags, essentially eliminating the possibility of using coverage by individual shell area (such as edge or umbo) in a comparison with fossil systems. Based on the overall lack of significant differences between depths when analyzed by shell area, and the bias created by the mesh bags, it was clear that whole shell area values would be more useful in comparison with ancient data. When biont cover was assessed by shell area, we found few significant changes with depth, confirming this observation.

After Guilds were established, modern bionts were placed into guilds for further analysis and eventual comparison to the ancient data. These analyses will be discussed in the guilds section.

*Ancient: Field Collection*

A collection of the articulate brachiopod *Rafinesquina alternata* was used in this study. I collected a set of these shells from the Tanners Creek Formation of the Richmond Group, Upper Ordovician in age. The Richmond Group outcrops in the Cincinnati region of southern Ohio, along the Ohio River in Ohio and Indiana, and in areas of Kentucky (Fig. 4); (Fenneman, 1916; Richards, 1970). Where well developed, the Richmond attains thicknesses of up to 91m. (Fenneman, 1916). The sample locality, Hannah's creek, is located in Roseburg, Indiana, off IN 101 (Fig. 5).


**Figure 4.** Map of outcrop area of the Richmond Formation. Dark lines indicate county borders and dashed lines encompass outcrop areas. Scale shown at bottom right. Arrow points to approximate location of my collection area (Roseburg, IN). (From Richards, 1972)

**Figure 5.** Photo of Bridge crossing Hannah's creek off IN 101, Roseburg IN. Cutbank is approximately 50 meters upstream from bridge, on left side of creek (when facing upstream).

Classification of the Richmond Group has undergone frequent changes over the last century, as summarized by Richards (1970). The Richmond Group is Upper Ordovician in age (approximately 450 ma) and is suggested to span a length of only 5-15 million years (Richards, 1970). Schemes for the division and nomenclature have been

<table>
<tr><th>Meek and Worthern (1965)</th><th>Nickles (1902)</th><th>Twenhofel et al (1954)</th><th colspan="2">Fox (1962)</th><th>Hatfield (1968)</th><th colspan="2">Richards (1972)</th></tr>
<tr><td rowspan="7">Cincinnatian Series<br>(≈ 450 ma)</td><td rowspan="7">Richmond Group</td><td>Elkhorn Fm.</td><td colspan="2">Elkhorn Fm.</td><td rowspan="2">Whitewater Fm.</td><td rowspan="3">Whitewater Formation</td><td>Upper Member</td></tr>
<tr><td>Whitewater Fm.</td><td rowspan="3">Whitewater Fm.</td><td>Upper Member</td><td>Saluda Member</td></tr>
<tr><td>Saluda Fm.</td><td>Saluda Mbr.</td><td rowspan="2">Saluda Fm.</td><td rowspan="2">Lower Member</td></tr>
<tr><td rowspan="2">Liberty Fm.</td><td>Lower Mbr.</td></tr>
<tr><td rowspan="2">Waynesville Fm.</td><td colspan="2" rowspan="2">Tanners Creek Formation</td><td rowspan="2">Tanners Creek Fm.</td><td colspan="2" rowspan="2">Tanners Creek Formation</td></tr>
<tr><td>Arnheim Fm.</td></tr>
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**Figure 6.** Nomenclature of divisons of the Richmond Group as defined by Nickles (1902), Twenhofel (1954), Fox (1962), and Richards (1972). Shells collected from the Tanners Creek Formation, a designation agreed upon in all of the latest schemes. Table adapted from Richards (1972).

offered by Twenhofel, *et. al.* (1954), Fox (1962), Hatfeild (1968), and Richards (1972): (Fig. 6).

The lower Richmond Group, including the Tanners Creek Formation and some of the Liberty Formation, is characterized by greenish-blue, evenly bedded, and highly calcareous shale (Fenneman, 1916). The limestone in this section is gray to buff in color and is generally nodular and discontinuous (Fenneman, 1916). Fossils common to the lower Richmond include the brachiopods *Thaerodonta, Plaesiomys, Hebertella,*

*Rafinesquina, Catazyga, Strophomena,* and *Hiscobeccus* as well as the horn coral *Streptolasma*. There are also occurrences of molluscs, echinoderms, bryozoans, and trilobites (Totten, 1987).

The Whitewater formation, above the Tanners Creek Formation, is characterized by coarser particle size; however, silt and clay sized particles are still present (Richards, 1970). A distinct middle member of the Whitewater, the Saluda, contains abundant colonial corals and is composed of massive dolomitic limestone and calcitic dolomites. Symmetrical ripple marks and desiccation cracks are common (Richards, 1970). The Saluda is lens shaped regionally, pinching out between Brookville and Richmond, Indiana (Totten, 1987).

All *Rafinesquina alternata* used in this study were collected from the Tanners Creek Formation, a unit agreed upon by the three most recent schemes. The Tanners Creek Formation reaches up to 70m in southeastern Indiana outcrops. During the Upper Ordovician, this area was located in the low latitudes of the Southern Hemisphere and experienced a humid, tropical climate (Betz, 1987). The Tanners Creek Formation is interpreted as having been deposited in a shallow, regressive epi-continental sea, contained between the rising Appalachian Mountains from the Taconic Orogeny, to the east, and the nearby Cincinnati Arch, to the west (Fox, 1962). The Richmond Group thickens eastward, indicating the Appalachians as the primary contributor of terrigenous sediment. The Richmond Group is thought to reflect a shallow, quiet water, offshore environment experiencing slow sedimentation rate (estimated at 1cm/1000yrs) of mixed siliciclastic muds and carbonate sediment (Richards, 1970). The entire Richmond Group is thought to have been below wave base, with patches of carbonate sand and gravel sized

sediment over a largely muddy bottom. Events including storm re-working, tsunamis, and "submarine swells" have been suggested by various authors to have occurred in the Richmond Group, and may account for local concentrations of carbonate material into what is now discontinuous limestone layers and nodules (summarized in Richards, 1970). Ford (1967) placed the entire Cincinnatian series within the photic zone based on the presence of fossils requiring light , nutrients, currents, and appropriate salinity and temperatures in order to survive. It can also be inferred that Fox (1968) placed the Tanners Creek Formation in the photic zone, based on his statements about the fossils found in the formation requiring more or less light and what that indicates about depth of the bottom environment.

The lower part of the Tanners Creek Formation appears to represent a deeper water environment, while the upper Tanners Creek reflects a shallowing trend. Evidence for water depth comes from the greater proportion of shale in the lower Tanners Creek and limestone in the Upper Tanners Creek Formation. Additionally, the Upper Tanners Creek contains more abraded fossils and a greater abundance of fossils in general (Richards, 1972).

*Ancient: Rafinesquina collected in the field*

On October 19, 2003, my advisor Dr. Parsons-Hubbard and I collected bulk samples from Hannah's Creek in Roseburg, Indiana off IN 101 (Fig. 4, 5). Samples were collected from the cut bank of a bend in the creek, approximately 50m upstream from the road crossing (Fig. 7). *Rafinesquina alternata* shells were collected from three individual layers and later lab analyses of encrustation were done by layer. The bottom layer

contained 111 shells, the middle layer contained 52 shells, and the top layer contained 45 shells, for a total of 208 shells in the Ordovician data set.

**Figure 7.** Photo of outcrop area. Samples collected from three shell beds within cutbank of Hannah's Creek, approximately 50m upstream from road. Photo is looking upstream, away from the road, and cutbank is visible at base of hill in photo.

The outcrop was shale and mixed shale-limestone layers, light grey in color. Fossils were common both in the outcrop and the float. Samples were collected from three shale-rich shell beds. Six bags of approximately 900mL (900 cubic cm) of shell and shale material were collected from each layer for a total of 18 bags and 16,200mL (16,200 cubic cm). When collecting samples, we attempted to get large chunks of the shale layer and not just individual fossils (Fig. 8, a). Layers were measured down from a limestone marker bed (chosen as a convenient reference independent of water level in creek) shown in Figure 8

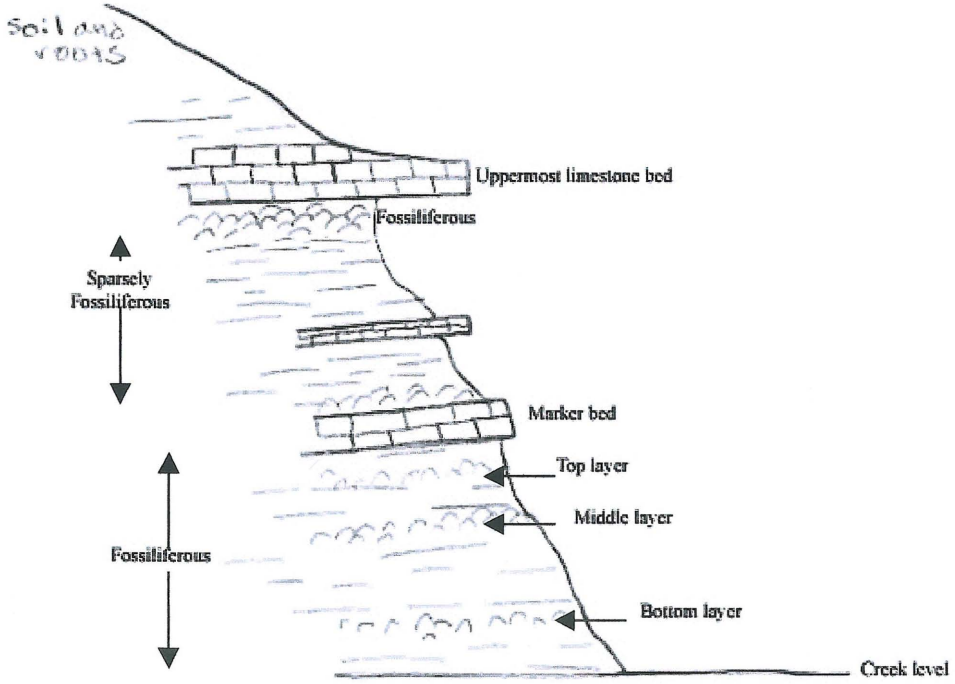
(a,b,e). The top layer was located 10-15cm down from the marker bed, the middle layer 24-25cm down, and the bottom layer 55-60cm down. Each layer was approximately 5-8cm thick but variable, overall shaley in composition but with nodules of limestone or more dolomitized material. Fossils were abundant and were falling out whole into the creek bed and float (Fig. 8 c,d). Often *R. alternata* shells were stacked in layers, and many fossils showed some breakage or fracture. In addition to *R. alternata*, fossils in these beds included various species of ramose bryozoans ranging from 'sticks' 1mm in diameter to large leaf-like forms 1.5cm thick and 3-4cm wide. Brachiopods were also abundant, including *Zygospira modesta, Dalmanella meeki, Platystrophia clarksvillensis, Herbetella occidentalis,* and *Plaesiomys subquadrata.* Individual *Cornulites,* a tube-shaped organism commonly thought to be an annelid worm, but recently considered by Vinn and Mutvei (2004) to be more closely related to the Lophophorates, were also found, presumably detached from their original location encrusting a shell.

**a)**


b)

c)

d)




e)

**Figure 8.** Photos of collection layers and marker bed. Above marker bed, outcrop is shaley and sparsely fossiliferous. Near roots at top of outcrop a normally graded fossil bed occurs. a) Photo of collection process and bags of material. Bags are placed along layer from which they were collected. Blue backpack is sitting on the marker bed. b) Photo with all three layers and marker bed. Has red hammer handle at the marker bed, the point at the top layer (10-15 cm below marker bed), the chisel at the middle layer (25cm below marker bed), and the blue hammer point at the bottom layer (60cm below marker bed). Take your pick for scale; c) General photo of outcrop material. Shale and limestone visible as well as imbrication of brachiopods. d) Photo of middle bed with pencil for scale. e) Sketch of stratigraphic section of collection outcrop. Marker bed and three collection layers marked.

Fossils were separated from the shale material by heating in 90° C water with approximately one third of a cup of Borax (sodium tetraborate decahydrate) for a period of 12-24 hours. The material, contained in a strainer, was then rinsed with cold water to remove loosened shale, and fossils were extracted by hand. Many fossils were unavoidably broken by this process, and many larger chunks of what appeared to be more dolomitized material would not release their fossils; however, a large number of whole or nearly whole *R. alternata* shells were obtained. These were cleaned further using a paintbrush, toothbrush, fingers, and water. A total of 208 *Rafinesquina alternata* shells were recovered from the layers, 104 of which were encrusted (Table 2).

**Table 2.** Total number of *Rafinesquina alternata* shells collected from each shell bed, and number of those shells with bionts present. Totals number of Ordovician shells (from all beds) and number of those shells with bionts present given at bottom.

| Layer | Total Number of Shells | Number of Encrusted shells |
|---|---|---|
| Bottom | 111 | 39 |
| Middle | 52 | 37 |
| Top | 45 | 28 |
| TOTALS | 208 | 104 |

Bionts were identified using the following sources: The Treatise on Invertebrate Paleontology (Moore, 1953), PhD thesis by Richards (1970) on brachiopod species of the Richmond Group, Fossils of Ohio (Feldman, 1996), and specimens from the Paleontology collection at Oberlin College, which were used for direct comparison. Additionally, a set of *Rafinesquina alternata* in the Paleontology collection at Oberlin College served as preliminary set of data on which to first identify bionts. 75 of these shells were collected at the Hannah's Creek locality, and of these, 70 were in usable condition for biont identification

Bionts could often be identified only to the genus level, and most bryozoans were identified as morphospecies, although some were identifiable to the genus level.

Morphospecies classifications were based on colony form and height off substrate. Identified bionts were placed into guilds based on characters of lifestyle and habitat.

Epibiont data for these shells was collected using the same method as for the modern the study. Shell areas were defined for *R. alternata* as illustrated in Figure 9.

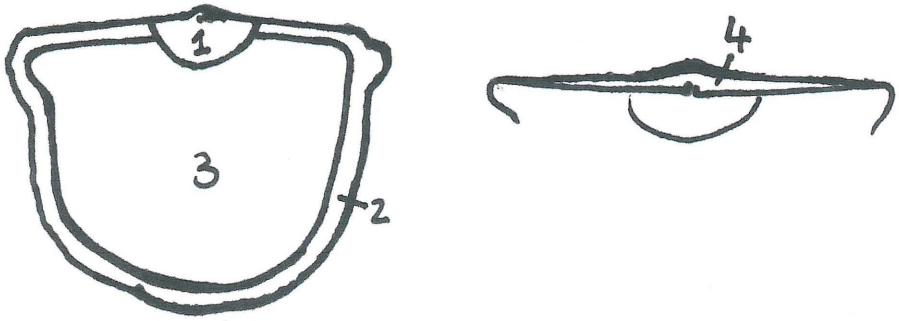




**Figure 9.** a) Two *Rafinesquina alternata* shells encrusted with *Petrocrania scabiosa* and *Trypanites,* convex valve of both shells is shown. From the Oberlin College Collections; b) Diagram of shell areas used during data collection for *Rafinesquina alternata*. Areas for convex and concave valves were the same.

Bionts were recorded using percent area coverage estimates both by whole shell and by shell area within each layer.

Analyses of ancient biont data were the same as those done for modern biont data. An initial assessment of the proportion of shells with encrusting bionts was conducted for each layer (bottom, middle and top) (Fig 14, 15). Average percent area of whole shell encrusted was determined for each layer, as was percent cover by shell area. Morphospecies richness was also determined for each layer. Error bars were calculated using a Student T-test with a probability level of 0.05 (i.e. 95% confidence limits of the mean).

After the construction of guild categories, based on information on all preservable bionts (i.e. those with attached mineralized skeletons), identified in both modern and ancient studies, ancient bionts were placed into guilds and analyzed further, including a comparative analysis with modern data. These analyses will be discussed in the Guilds Section.

## Guilds

*Creation of Guilds*

A simple comparison of species from modern encrusting communities to species from ancient encrusting communities clearly is not viable. As Valentine and Jablonksi (1993) noted, "removal, addition, and substitution of species within marine community associations is common in nature and in fact is the rule over time." Over 400 million years of time, it is unfeasible to use species as the unit of comparison. An alternative use

of niches as a unit of comparison is confusing due to the variable use of the term in ecology. As explained by Root (1967) the term niche originally was used in reference to "the functional role, particularly in trophic interactions, of a species within a community". Those factors that bound a 'functional role' had not been adequately defined, which led to confusion in the literature. In 1957, Hutchinson and Macfadyen independently defined the niche as "the range and combination of environmental conditions that permit a species to exist indefinitely," (Root, 1967). A few of these conditions will be critical to the success of the species, and will thereby define the fundamental niche. The Hutchinson Macfadyen model, however, requires the consideration of the taxonomy of species in defining the niche. A comparison between modern and ancient epibiont communities cannot rely on the use of the niche classification due to its reliance upon taxonomy.

The concept of guilds of living assemblages, as proposed by Root in 1967, can provide a meaningful unit of comparison. He defines a guild as "a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." According to this definition, the same species can be a member of more than one guild, and communities are composed of interacting guilds (Root, 1967). Guilds prove more useful than species or niches as a unit of comparison when the communities of interest exhibit a high degree of diversity and preservation due to the complexity that would be involved with either smaller-scale unit (Fagerstrom, 1994). While the ancient shells had neither high diversity nor excellent preservation, the modern

shells exhibited both. The guild concept, therefore, certainly simplifies an analysis of the modern communities.

Bambach (1983) suggested that in addition to basic habitat and food source characters that normally define a guild, a dimension for large morphologic differences, or bauplan, should be added. While essentially this adds a taxonomic factor back into the classification of guilds, it is not the primary factor, and can still include more than one species. Root's original definition of guilds (1967) actually leaves room for this extension to the bauplan of the organism. He states that not only are environmental resources critical to guild distinction, but also the way in which the organism uses those resources, a factor partially dependent on morphology and phylogeny.

I defined guilds based on those unique characters of habitat, lifestyle, food sources, and bauplan that were distinguishing differences between bionts or groups of bionts. The resulting scheme of 14 guilds (Table 3) fits both Root's definition of a guild and Fagerstrom's (1994) suggestion for the use of hierarchical factors in guild classification. My hierarchical factors were chosen after an analysis of biont habitat, food resources, and morphology. The use of guilds justifies identification of bionts at the morphospecies level, as the factors used in guild classification are specific to morphology and not reproductive isolation or phylogeny (used in definitions of "real" species).

**Table 3.** Guild names, definitions based on critical characters, and associated code. Guilds assigned only to preservable bionts. There are a total of 14 guilds. Photos of selected guild members in Appendix II.

| Code | Guild Name | Characters Used in Defining |
|---|---|---|
| A | Filter Feeding Colonial Thin Crust | Food Source – Filter feeding close to substrate<br>Morphology - Colonial |
| B | Filter Feeding Colonial, <1mm | Food Source – Filtering within 1mm of substrate<br>Morphology – Colonial |
| C | Filter Feeding Colonial, 1-2mm | Food Source – Filtering between 1 and 2mm off substrate<br>Morphology – Colonial |
| D | Filter Feeding Colonial, 2mm | Food Source – Filtering at 2mm off substrate<br>Morphology – Colonial |
| E | Filter Feeding Colonial, 8-10mm | Food Source – Filtering up to 8-10mm off substrate<br>Morphology – Colonial |
| F | Running Bryozoan | Food Source – Filtering less than 1mm off substrate<br>Morphology - Zooids separated in a branching pattern across substrate. |
| G | Dissolution Bryozoan | Food Source – Filtering, unknown height above substrate. Likely quite small.<br>Morphology – trace of branching bryozoan in shell – dissolution of shell or faint trace |
| H | Serpulid and Filter Feeding Solitary Biont 1-2mm | Food Source – Filtering 1-2mm above substrate<br>Morphology – One location of food acquisition, solitary; tube-like morphology. |
| I | Mollusc and Brachiopod <1mm | Food Source – Filtering less than 1mm above substrate<br>Morphology – Solitary, has two valves. |
| J | Mollusc and Brachiopod 2mm | Food Source – Filtering 2mm above substrate<br>Morphology – Solitary, has two valves. |
| K | Ichnofossil | Food Source – Unknown<br>Morphology – Circular to elliptical borings in substrate. |
| L | Photosynthetic Diffuser less than 1mm | Food Source – Combination photosynthesis and diffusion through cell membrane at less than 1mm off substrate.<br>Morphology – not specified |
| M | Photosynthetic Diffuser, 2mm | Food Source – Combination of photosynthesis and diffusion at 2mm off substrate.<br>Morphology – Not Specified |
| N | Photosynthesizer, less than 1mm | Food Source – Only photosynthesis<br>Morphology – Less than 1mm off substrate |

*Habitat: Shell Substrate*

Habitat is largely the same for all bionts in this study because all bionts used either the *R. alternata* or *M. edulis* shells as their substrate (as the shells compose the data sets). The modern mollusc and ancient brachiopod are comparable as substrates even though their shells differ in composition and morphology. A brief summary of the shells is useful to determine the validity of such a comparison.

*Rafinesquina alternata* were concavo-convex strophomenid brachiopods. As described by Schwimmer and Sandy (1996), they have a semicircular outline truncated by a straight hinge line and have roughly equal dimensions of width and length.

Ornamentation consists of numerous fine ribs radiating outward from the umbo on both valves. The concave valve in *R. alternata* is the brachial valve and the convex valve is the pedicle valve. Both valves are pseudopunctate. *R. alternata* were adapted to live on muddy bottom types (Richards, 1972).

*Mytilus edulis* is a member of the family Mytilidae, class Pelecypoda (the bivalves), and phylum Mollusca. Their geologic range is from the Upper Jurassic period to recent (Linne, 1758). They are equivalve, but inequilateral in shape. The shell consists of an outer layer of fine, radially oriented needles and an inner pearly layer. The hinge margins are smooth and the surface has fine radial ribs. Shell is generally wedge shaped and elongate, and has a well developed periostracum (Moore, 1969).

Composition of *Rafinesquina alternata* and *Mytilus edulis* shells differs as well. This difference in shell composition could create differences in biont preference, especially for endobionts; however, I found nothing in the literature specifically listing this as a result. And interestingly, I found ichnofossil data to be quite similar between the modern and the Ordovician (Fig. 33). *Rafinesquina alternata* shells were calcitic while *Mytilus edulis* shells were aragonitic. Epibionts will, however, be affected by the presence of the periostracum in the *Mytilus edulis* shells. It is, in fact, hypothesized that the purpose of the periostracum is prevention of recruitment of biont larvae. It is not known if a periostracum existed on *Rafinesquina alternata* (it is non-preservable).

Despite these differences similarities in gross morphology (concave-convex shape; rounded, thin edges; fine radial ornamentation) and size make the comparison reasonable. Also, all the problems associated with the comparison create a bias against my hypothesis, so if my hypothesis still proves viable it can at least be known that the

results are not an artifact of the differences in substrate. It is possible that a comparison of different shell species would yield even more positive results.

The location of the biont on the shell, either on the umbo, edge, or center of the valve (or interarea for *R. alternata),* is recorded as a part of data collection; therefore, a preference for shell area does not need to be used in creation of guilds. Also, preference for location on the shell will vary with shell species, due to differences in morphology and hence water flow around the valve, as well as due to different locations of inhalent and exhalent siphons, which often attract bionts. If the *Rafinesquina alternata* were alive during biont encrustation, settlement and growth patterns would be different than if the brachiopod were dead. Location on the shell will not be a factor considered in guild creation.

*Food Resources: Height Above Substrate*

Given similarity in habitat, factors concerning food resources or gross morphology of the biont must be used to define guilds. Food resources, for the majority of bionts examined, come from water that is in direct contact with the biont. Some modern bionts either photosynthesize or have photosynthetic symbionts, but filter-feeding or direct diffusion are the norm for bionts in this study. Height above the substrate, then, is the limiting factor in resource acquisition.

Due to the host shell's location at the sediment water interface, the water bringing nutrients to the bionts will be a part of the boundary flow layer. Flow at the benthic boundary layer exhibits the "no slip condition", in which a fluid directly in contact with a solid surface does not slip relative to that surface. (Denny, 1951) Water at the sediment

water interface also has some degree of viscosity. These two factors, in combination, decelerate water flow along the seabed. Water motion experiences a maximum degree of slowing directly along the interface, and becomes progressively faster as it gains height in the water column (Denny, 1951). The implication of this trend in water velocity for bionts is that more food and nutrients are cycled through the column further from the substrate during a given period of time. Additionally, even actively filter-feeding bionts have a difficult time obtaining nutrients from the laminar flow boundary layer; those bionts that act as "roughness elements" increase the turbulence of the boundary flow layer and increase circulation of nutrients (Denny, 1951). Again, height off the substrate influences the organism's ability to gain access to food, this time because of increased water turbulence rather than velocity (Denny, 1951)

Because of the relationship of water velocity to height above substrate (Fig. 10), small changes in height above substrate have potential to significantly impact access to nutrients by increased velocity in the water column and increased turbulence.

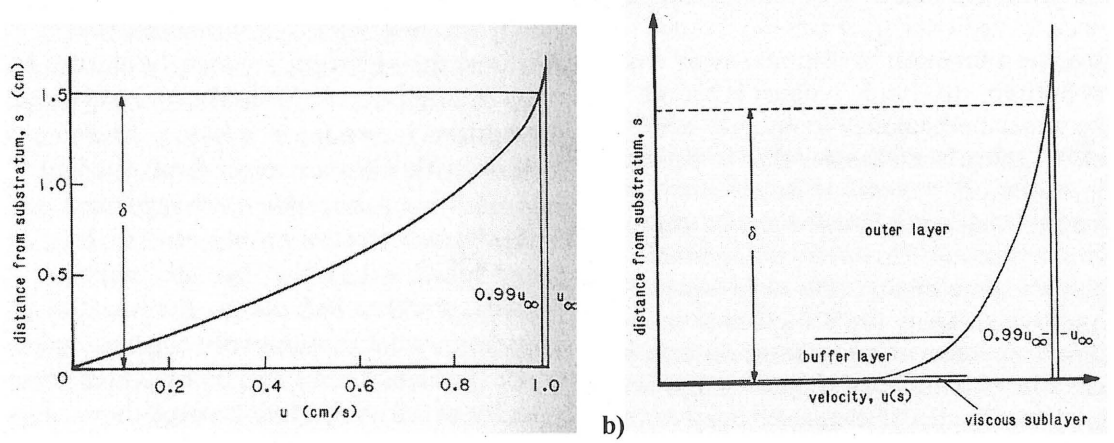



**Figure 10**. a) The laminar boundary layer. Water velocity as a function of distance from the substratum is calculated for a point 10 cm from the leading edge ($u_\infty$ = 1cm/s). $\delta$ is the boundary layer thickness. b) The turbulent boundary layer on a smooth plate. Although the turbulent boundary layer may be thicker than it's laminar counterpart, high velocity is reached much nearer the substratum. Figures from Denny (1951).

Height above substrate will be used as to classify guilds in the following manner, and divisions will be "fine-grained" for the first few millimeters off the substrate (no bionts in either data set attained heights greater than 10mm off substrate). Notes on biont height were taken during data collection, and morphospecies were often defined using height for at least one parameter.

*General Morphology: Colonial Growth and Biont Phyla*

Coloniality is a critical morphological character of many modern and ancient bionts in this study. Colonial encrusting organisms have been shown to differ greatly in competitive ability from solitary encrusting individuals (Jackson, 1977). Also, colonial growth does not easily conform to guild parameters only involving height above substrate. Modern serpulids, for example, raise to the same height off the shell as ancient bryozoan colonies; however, the serpulids filter using only tentacles located directly at the top of their tube, while bryozoans have zooids filtering all over the surface area from the base to their maximum height. Clearly, surface area used for filter feeding is greatly different in these bionts, even though height above substrate is not. Coloniality will be another character of guild definition.

Finally, gross morphology, or bauplan, will be used as a distinguishing character of guilds. Bauplan is related, of course, to taxonomy to some degree. To avoid Guilds created around species distinctions this morphology axis in guild creation will be limited to the level of phyla.

While biont size is sometimes a part of a biont's gross morphology, it will not be used in guild classification. Colonial organisms are characterized by indeterminate

growth, so the use of biont size to distinguish guilds is only appropriate for a subset of the data.

*Guild Analyses: Modern, Ancient, and Comparisons*

A total of 14 guilds were created to encompass all preservable bionts from both the modern and ancient data sets (Table 3). Three of these guilds are found only in ancient communities and three only in the modern communities. A full listing of modern and ancient biont species identified and their associated guilds are given in Tables 4 and 5.

Data from modern *Mytilus edulis* was re-analyzed for total percent of shell surface covered by the new guild categories, and average guild richness on each shell was calculated. Error bars were calculated using a Student T-distribution with a threshold of 0.05 (i.e. 95% confidence limits of the mean). Overlapping error bars indicate a non-significant difference in data. Pie graphs were also used to show relative frequency of guilds in different environments (photic modern, non-photic modern, and buried modern). Relative abundance was calculated by finding the sum of the percent covers of each guild (i.e. the total area of shell encrusted by all bionts), and then dividing each guild percent area coverage by this value. An analysis of frequency of guild occurrence on shells was also done by environment. It should be noted that those species of modern photosynthetic diffusers occurring at deep depths are, in fact, only using diffusion for nutrient acquisition at those depths (Fig. 19).

Ancient bionts were re-classified as members of a guild (Table 5) and data for *Rafinesquina alternata* was re-analyzed for guild percent cover and richness by layer. Error bars were calculated using a Student T-test with a probability level of 0.05. Again,

overlapping error bars indicated non-significant differences between layers. Ancient data were then further reduced into one data set. Analyses of percent cover and richness of guilds was done for the combined Ordovician data set. Pie graphs were again used to show relative abundance of modern guilds in the Hannah's Creek samples. Relative abundances were calculated in the same manner as for modern guilds. Frequency of guild occurrence was graphed as well.

Comparisons between modern and ancient data sets were accomplished using the guild data. Differences were assessed using error bars calculated using Student T-distribution ($p > .05$). Pie graphs of relative abundances were used for a visual comparison of Ordovician to modern data.

**Table 4. Modern Bionts.** A total of 112 different species or morpho-species of bionts were identified on 55 *Mytilus edulis* shells. For each biont the species name is listed, if available, along with characteristics of the biont including: the phylum, whether or not it's preservable, if it is an epi or endo biont, and the code for its guild (See Table 3 for guild codes and classifications). Bionts organized alphabetically by phyla. Numbering is an approximate species count, as scars are numbered and therefore the same biont is counted twice. Photos of selected bionts given in Appendix II.

| | Species or Morpho-species Name | Phylum | Preservable | epi/endo | Guild |
|---|---|---|---|---|---|
| 1 | *Salmacinna* (fine anastomosing tubes) | Annelida (Polychaeta) | Yes | Epi | H |
| 2 | White keeled Serpulid | Annelida (Polychaeta) | Yes | Epi | H |
| 3 | Brown stripe keeled serpulid | Annelida (Polychaeta) | Yes | Epi | H |
| 4 | *Spirorbid* | Annelida (Polychaeta) | Yes | Epi | H |
| 5 | Agglutinated worm tube (possib. *Terebellid*) | Annelida (Polychaeta) | No | Epi | |
| 6 | Slender agglutinated worm tube | Annelida (Polychaeta) | No | Epi | |
| 7 | *Spionid* boring | Annelida (Polychaeta) | Yes | Endo | K |
| 8 | Serpulid tube scar | Annelida (Polychaeta) | Yes | Epi | H |
| 9 | *Spirorbid* remnant | Annelida (Polychaeta) | Yes | Epi | H |
| 10 | Rounded serp. with flared aperature | Annelida (Polychaeta) | Yes | Epi | H |
| 11 | Clear, keeled serpulid | Annelida (Polychaeta) | Yes | Epi | H |
| 12 | Coiled serp with excess CaCO3 over tube | Annelida (Polychaeta) | Yes | Epi | H |
| 13 | White calc. serp with fine annulations | Annelida (Polychaeta) | Yes | Epi | H |
| 14 | *Disporella* cf. *fimbriata* | Bryozoa | Yes | Epi | C |
| 15 | *Crepidocantha* | Bryozoa | Yes | Epi | B |
| 16 | *Crisia* (erect bryo) | Bryozoa | Yes | Epi | D |
| 17 | *Parellisina latirostris* | Bryozoa | Yes | Epi | B |
| 18 | *Hippopodina* | Bryozoa | Yes | Epi | B |
| 19 | Un-Identified Bryo stump or ancestrula | Bryozoa | Yes | Epi | B |
| 20 | *Schizoporella* | Bryozoa | Yes | Epi | B |
| 21 | *Amathia* (ctenostome) | Bryozoa | Yes | Epi | G |

| | | | | | |
|---|---|---|---|---|---|
| 22 | *Microporella umbracula* | Bryozoa | Yes | Epi | B |
| 23 | *Parasmittina signata* | Bryozoa | Yes | Epi | B |
| 24 | *Smittina* | Bryozoa | Yes | Epi | B |
| 25 | *Crepidocantha c.f. stigera* | Bryozoa | Yes | Epi | B |
| 26 | *Cribrilaria radiata* | Bryozoa | Yes | Epi | B |
| 27 | *Cleidochasma c.f. porcellanum* | Bryozoa | Yes | Epi | B |
| 28 | *"Cleidochasma" sp.* | Bryozoa | Yes | Epi | B |
| 29 | *Coelopora c.f. granulosa* | Bryozoa | Yes | Epi | B |
| 30 | Bryozoan remnant | Bryozoa | No | Epi | |
| 31 | *Hippothoa flagellum* (cheilostome) | Bryozoa | Yes | Epi | F |
| 32 | Unidentified Ctenostome Bryozoan | Bryozoa | Yes | Epi | G |
| 33 | Bryo w\ raised ridges, pores, & peristome | Bryozoa | Yes | Epi | B |
| 34 | *Aimulosia uvulifera* | Bryozoa | Yes | Epi | B |
| 35 | *Aetea cf. anguina* | Bryozoa | Yes | Epi | B |
| 36 | *Mollia patellaria* | Bryozoa | Yes | Epi | B |
| 37 | *Reptadeonella lostalata* | Bryozoa | Yes | Epi | B |
| 38 | *Plagioecia dispar* | Bryozoa | Yes | Epi | B |
| 39 | *Savignyella lafontii* | Bryozoa | Yes | Epi | F |
| 40 | *Canda simplex* | Bryozoa | Yes | Epi | C |
| 41 | "Bryo/Forma" | Bryozoa or | No | Epi | |
| 42 | Filamentous green algae | Chlorophyta (Algae) | No | Epi | |
| 43 | White ascidian with pebbly surface | Chordata | No | Epi | |
| 44 | Pink-orange solitary tubular anenome | Cnidaria (Anthozoa) | No | Epi | |
| 45 | Orange tubular, weekly colonial coral | Cnidaria (Anthozoa) | Yes | Epi | D |
| 46 | Hydroid | Cnidaria (Hydrozoa) | No | Epi | |
| 47 | *Planorbulina* | Foraminifera | Yes | Epi | L |
| 48 | *Gypsina c.f.plana* | Foraminifera | Yes | Epi | L |
| 49 | *Homotrema rubrum* | Foraminifera | Yes | Epi | M |
| 50 | *Carpenteria* | Foraminifera | Yes | Epi | L |
| 51 | *Saphulina* | Foraminifera | No | Epi | |
| 52 | Chitinous "Flask" | Foraminifera | No | Epi | |
| 53 | *Placopsilina* | Foraminifera | No | Epi | |
| 54 | *Cibicides sp.* | Foraminifera | No | Epi | |
| 55 | *Gypsina globularis* | Foraminifera | Yes | Epi | L |
| 56 | *Folliculinid* | Foraminifera | No | Epi | |
| 57 | *Cornuspiramia c.f. antillarum* | Foraminifera | No | Epi | |
| 58 | *Biarritzina carpenteriaeformis* | Foraminifera | No | Epi | |
| 59 | Branched, agglutinated foram | Foraminifera | No | Epi | |
| 60 | *Caribeanella* | Foraminifera | No | Epi | |
| 61 | *Discorbinellinae* | Foraminifera | No | Epi | |
| 62 | Cone attatched by flat side w\ sed. Halo | Foraminifera | No | Epi | |
| 63 | *Rotaliammina* | Foraminifera | No | Epi | |
| 64 | *Cibicides lobotulus* | Foraminifera | No | Epi | |
| 65 | *Haplophragmoididea* | Foraminifera | No | Epi | |
| 66 | *Cibicides cf. refrilgans* | Foraminifera | No | Epi | |
| 67 | Sediment Halo (foram popped off) | Foraminifera | No | Epi | |
| 68 | *Acervulina* | Foraminifera | Yes | Epi | L |
| 69 | *Tritaxis siphonifera* | Foraminifera | No | Epi | |

| | | | | | |
|---|---|---|---|---|---|
| 70 | *Spirillina vivipara* | Foraminifera | No | Epi | |
| 71 | *Ataxophragmitidae* | Foraminifera | No | Epi | |
| 72 | *Neoconorbina terquemi* | Foraminifera | No | Epi | |
| 73 | "Petal" foram | Foraminifera | No | Epi | |
| 74 | *Bueningia sp.* | Foraminifera | No | Epi | |
| 75 | *Saccaminidae* | Foraminifera | No | Epi | |
| 76 | Unidentified Textulariidae | Foraminifera | No | Epi | |
| 77 | *Trochamminidae sp.* | Foraminifera | No | Epi | |
| 78 | Chambered foram., old and eroded | Foraminifera | No | Epi | |
| 79 | *Melonis sp.* | Foraminifera | No | Epi | |
| 80 | *Planulina sp.* | Foraminifera | No | Epi | |
| 81 | *Tiphotrocha sp.* | Foraminifera | No | Epi | |
| 82 | *Possib. Strebloides or Discorbinoides sp.* | Foraminifera | No | Epi | |
| 83 | *Radulichnus* (rasping by grazing organisms) | Ichnofossil | Yes | Endo | K |
| 84 | Green Algae (Possibly *Ostreobium)* | Mollusca (Bivalvia) | No | Epi | |
| 85 | Spondylus-like bivalve (baby?) | Mollusca (Bivalvia) | Yes | Epi | I |
| 86 | *Terebratulid* | Mollusca (Bivalvia) | Yes | Epi | I |
| 87 | *Chama sp.* | Mollusca (Bivalvia) | Yes | Epi | J |
| 88 | *Anomia* base | Mollusca (Bivalvia) | Yes | Epi | I |
| 89 | Bivalve scar, possib. *Spondylus* | Mollusca (Bivalvia) | Yes | Epi | I |
| 90 | *Pododesmus sp.* | Mollusca (Bivalvia) | Yes | Epi | I |
| 91 | Vermetid tubes | Mollusca (Gastropoda) | Yes | Both | H |
| 92 | Fungal Filaments | Mycophyta (Fungi) | No | Endo | |
| 93 | Brown algal slime | Phaeophyta (Algae) | No | Epi | |
| 94 | White "styrofoam" sponge | Porifera (sponge) | No | Epi | |
| 95 | *Cliona* sponge boring | Porifera (sponge) | Yes | Endo | K |
| 96 | Red filamentous creeper | Rodophyta (Algae) | No | Epi | |
| 97 | Thick crust coralline (possib. *Titanoderma)* | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 98 | Slender erect coralline twig | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 99 | Peforate Coralline | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 100 | Boxy coralline | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 101 | Thick branching coralline | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 102 | Crumbly, branching coralline | Rodophyta (Coralline Algae) | Yes | Epi | N |
| 103 | Yellow-green slime with dots | Unknown | No | Epi | |
| 104 | Unidentified egg mass | Unknown | No | Epi | |
| 105 | Membranous green slime | Unknown | No | Epi | |
| 106 | Coarsely agglut. base w\ chitinous tube | Unknown | No | Epi | |
| 107 | Mass of finely agglutinated CaCO3 | Unknown | No | Epi | |

**Table 5. Ancient Bionts.** A total of 22 species or morphospecies of bionts on a total of 238 *Rafinesquina alternata* shells were identified. Species of biont is listed, when available, along with characteristics of the biont including: the Phylum, a description of biont, and the guild code of the biont. Guild codes area listed with names of guilds in Table 3. Numbering is approximate as scars are numbered and therefore the same biont may be counted twice. Photos of selected bionts given in Appendix II.

| | Name | Phylum | Comments & Description | Guild |
|---|---|---|---|---|
| 1 | *Cornulites richmondensis* | Annelida (debated) | Looks like ringed horn coral | H |
| 2 | *Cornulites richmondensis* | Annelida (debated) | Scar of Cornulites | H |
| 3 | Petrocrania Scar | Brachiopoda | Petrocrania Scar? Dark Circle | I |
| 4 | *Petrocrania scabiosa* | Brachiopoda | Reflects underlying shell topography | I |
| 5 | *Zygospira modesta* | Brachiopoda | Small with large ribs, fold & sucrus | I |
| 6 | Bryozoa A | Bryozoa | Thin Crust | A |
| 7 | Bryozoa B | Bryozoa | <1mm up off surface | B |
| 8 | Bryozoa C | Bryozoa | 1-2mm up off surface | C |
| 9 | Bryozoa D | Bryozoa | 2mm stick | D |
| 10 | Bryozoa E | Bryozoa | Ramose, 8-10mm up off surface | E |
| 11 | Bryozoa F | Bryozoa | Short zooids, 1-2mm up, colony crater shaped | C |
| 12 | Bryozoa G | Bryozoa | Rolling Hills avg of 1.5mm off, up to 3mm | C |
| 13 | Ctenostome Bryozoa | Bryozoa (Ctenostomata) | UnID'd. Dissolution branching pattern | G |
| 14 | *Ropalonaria venosa* | Bryozoa (Ctenostomata) | Dissolution, pinnate pattern | G |
| 15 | *Anolotichia ponderosa* | Bryozoa (Cyclostomata) | Hood-like lunarium, polygonal zooids | C |
| 16 | *Diastoporina flabellata* | Bryozoa (Cyclostomata) | Sub tubular zooids radiating from center of colony | C |
| 17 | *Stomatopora dichotoma* | Bryozoa (Cyclostomata) | Branching; zoids with some perfororations | F |
| 18 | *Atactoporella typicalis* | Bryozoa (Trepostomata) | Abundant acanthopores on zooids | C |
| 19 | *Halopora elegantula* | Bryozoa (Trepostomata) | Zoecia surrounded by mesopores | C |
| 20 | *Petroxestes* | Ichnofossil | Large elliptical borings, made by clams | I |
| 21 | Un-ID's Trace | Ichnofossil | Elongate, linear scar | I |
| 22 | *Trypanites weisei* | Ichnofossil | Circular or elongate borings, smaller than Petroxestes | I |

## Results

### *Modern Epibiont Study*

Differences in biont communities on whole shells exist with changes in depth (Fig. 11). Shells at 15m have significantly more surface area occupied by bionts than shells at any other depth. The average percent area covered at this depth is slightly above 60% due in part to overgrowth of bionts on top of one another, which results in some

shell areas having greater than 100% cover. Shells at 70m have the second most area covered by bionts. All other depth locations are similar in terms of total percent area encrusted, all having less than 10%. Shells located at 33m underwent extensive burial, which affected the total percent cover by bionts. It is also important to note that shells at 15m were often broken, leaving only the umbo (1A) region intact, therefore the total surface area of shell substrate is smaller at 15m. When biont cover is assessed by shell area (Fig. 12), we find few significant changes with depth. Significant differences between shell areas at 15m and 33m (buried environment) are indicated by non-overlapping error bars, but otherwise most error bars overlap between depths. There is a trend within depths to have most biont encrustation on the umbo at the 15m and 70m sites, and most encrustation in the central portion of the shell at deeper sites.

Significant differences in total area occupied by bionts with depth indicates the potential for comparisons to be made between modern and ancient shells at specific depths or in specific environments, as trends can be identified with depth. Where these bionts occur on the shell is less useful (Fig. 12). Also, percent of shell occupied by bionts is not significantly different for 192m – 275 m depths, regardless of changes in environment.

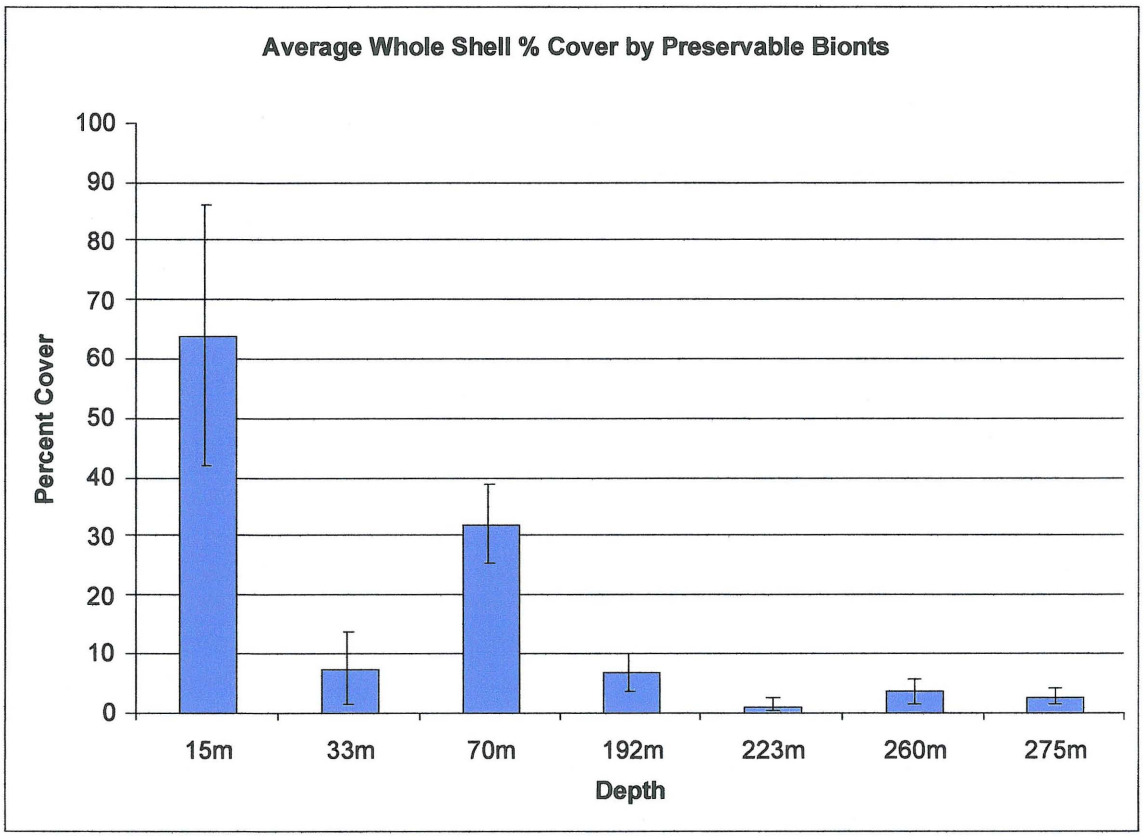



**Figure 11.** Percent of whole *M. edulis* shell encrusted by preservable bionts at each depth (15m-275m) along the Bahaman shelf and slope. Error bars are 95% confidence limits off the mean. Significant differences exist between columns with non-overlapping error bars. Note that 33m, 192m, 260m, and 275m all have overlapping error bars and so are not significantly different in average percent of whole shell encrusted by bionts. Shells at 15m experience the highest degree of encrustation.

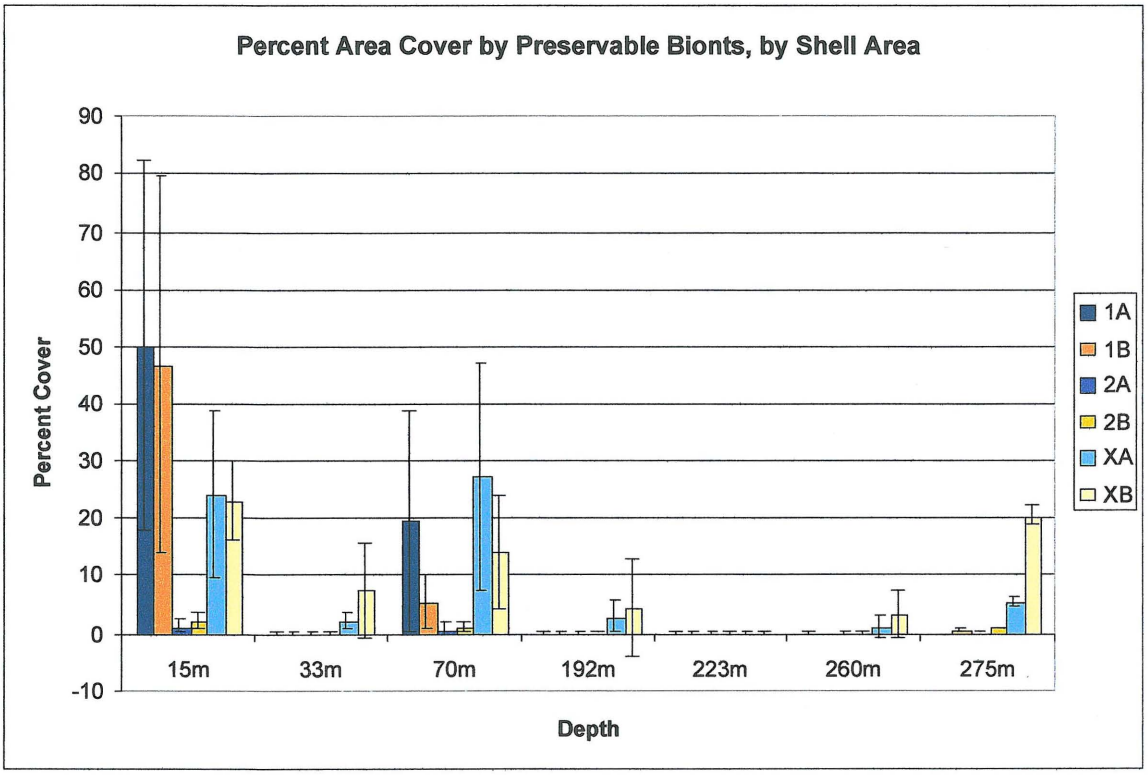



**Figure 12.** Percent of each *Mytilus edulis* shell area encrusted by preservable bionts at each depth (15m-275m). Error bars are 95% confidence interval of the mean. Shell area 1=umbo, 2=edge, x=central part of shell. A=exterior, B=interior. Numbers reflect mean cover on 5-10 shells per depth. Note the abundance of overlapping error bars and lack of a consistent pattern of significant differences. Also, the sample size of areas 2A and 2B at 15m and 70m are relatively small because the shells were often broken and missing those areas (the edge of shell).

An analysis of morpho-species richness was also conducted for each depth location (Fig. 13). Shells at 15m and 70m do not show significant differences in morpho-species richness, but they are both significantly higher (richness approx = 16) than richness values at all other depths (richness approx = 5). The trend in morpho-species richness with depth is similar to the trend in percent area coverage, with the 15m and 70m shells having the highest values, and all other depths being relatively similar.

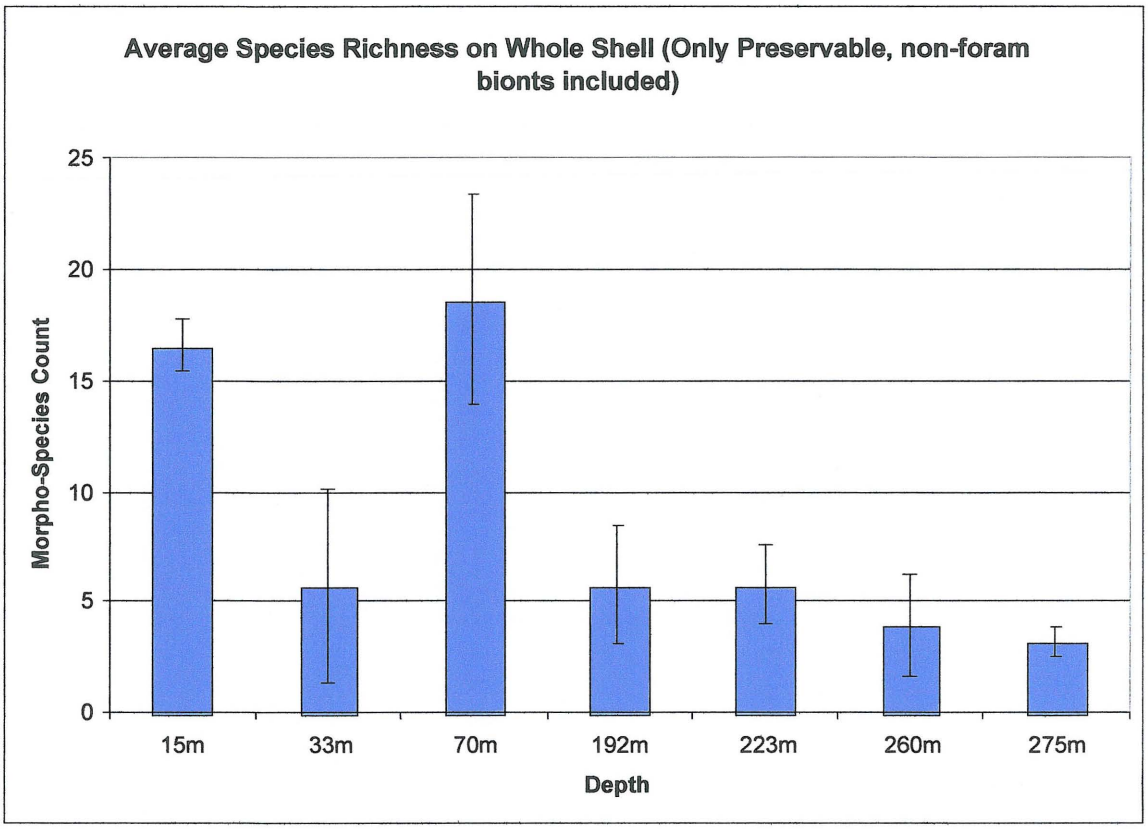



**Figure 13.** 'Morphospecies-richness' on whole *Mytilus edulis* shell by depth. Only preservable bionts were included. Error bars are 95% confidence limits of the mean. Note overlapping error bars between 15m and 70m depths, and between 33m, 192m, 223m, 260m, and 275m. Shells at 15m and 70m have significantly higher morphospecies richness from other depths.

*Ancient Epibiont Study*

The bottom shell layer at the Hannah's Creek outcrop yielded more than twice as many *R. alternata* shells, as well as the highest number of shells encrusted by bionts, for approximately equal amounts of material collected from each layer (Fig. 14). The number of encrusted shells from each layer is very similar, although the bottom layer has a slightly higher value. Due to the high number of unencrusted shells in the bottom layer, the proportion of encrusted shells from that layer is lower than from other layers, with the middle layer exhibiting the highest percentage of shells with bionts (Fig. 15).

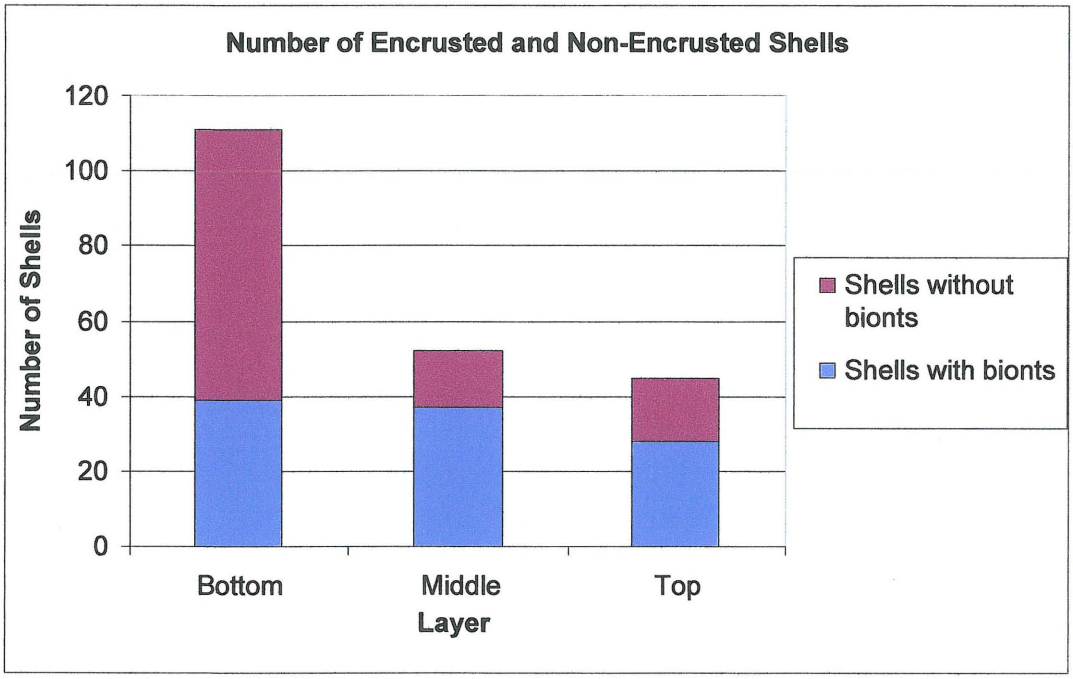



**Figure 14.** Number of encrusted and non-encrusted shells from each layer. Total number of shells represented by total height of each bar. The bottom layer contained the highest number of *R. alternata* shells of the three shell beds, as well as the largest number of encrusted shells. All three layers contained approximately equal numbers of encrusted shells.

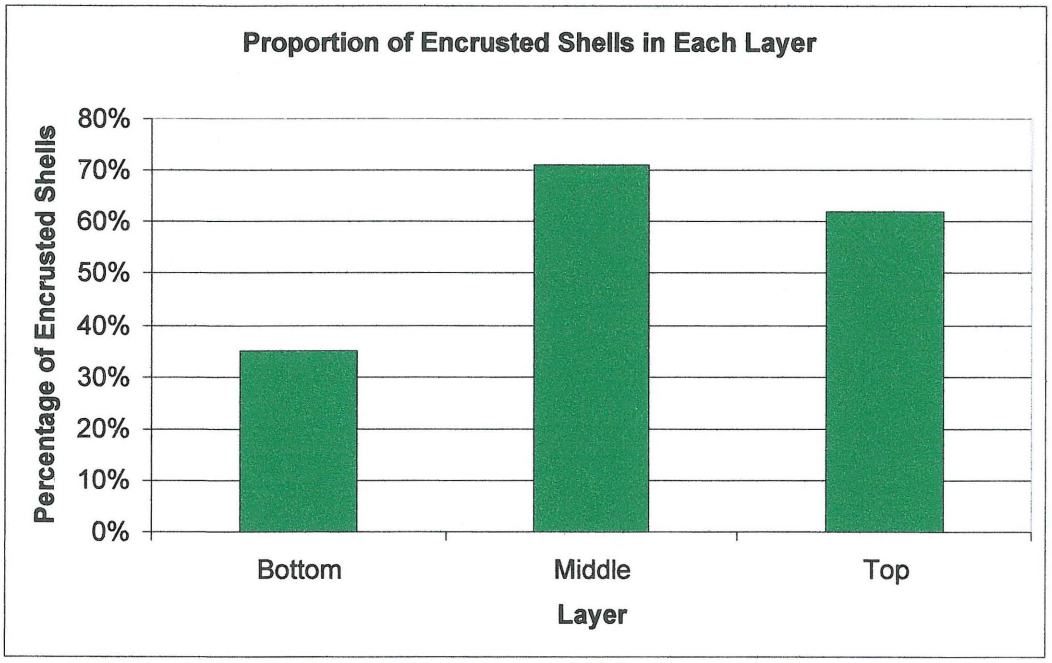



**Figure 15.** Proportion of shells from each layer that were encrusted. The bottom layer had the lowest percentage of its shells with bionts present, while the middle layer had the largest number at over 70% encrusted.

Despite having the greatest number of encrusted shells, the bottom layer had a lower mean percent area of shell occupied by bionts (Fig. 16). The top and bottom layers were significantly different with the top layer having a higher mean percent area cover, while the middle layer was not significantly different from either the bottom layer or the top layer. The high number of unencrusted shells in the bottom layer contributes to the low value for mean percent cover in that layer.

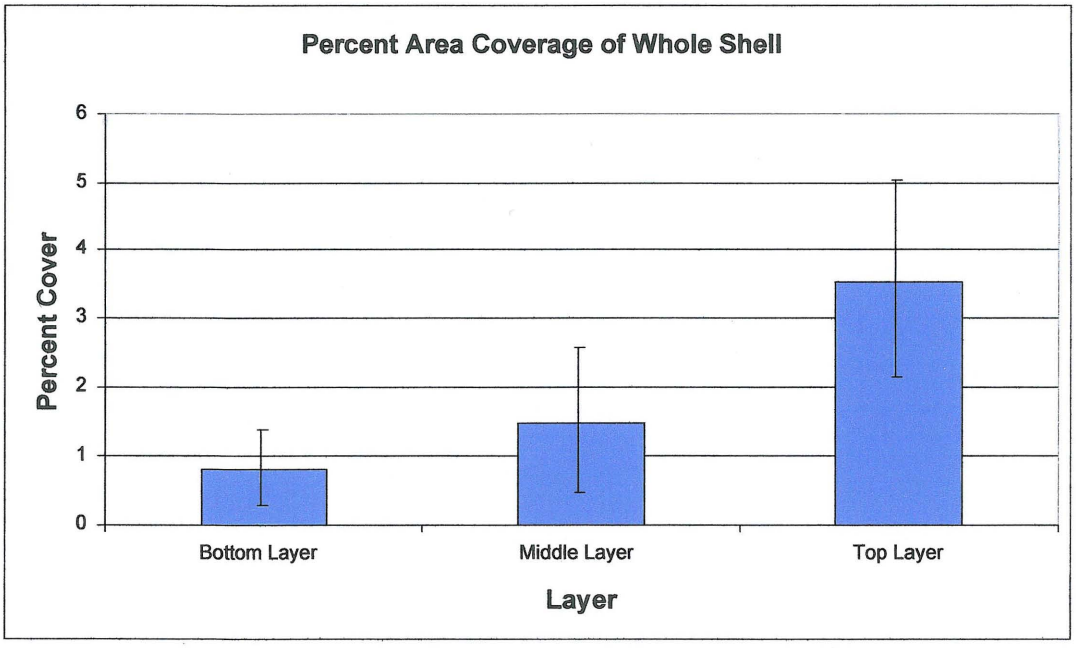



**Figure 16.** Mean percent of whole *Rafinesquina alternata* shell encrusted by bionts in each shell bed. Bottom layer contains an outlier (single biont) that biases the data in the direction of a greater difference from the middle layer. The bias is not great enough to change the bottom layer's relationship to either the middle or top layers, so it was left in the data set. The bottom and middle layers are not significantly different, and the middle and top layers are not significantly different, but the bottom and top layers are significantly different. Error bars are 95% confidence limits of the mean.

Significant differences in biont cover by shell area do not exist between layers, and a comparison by shell area will not be useful (Fig. 17). Encrustation of the interarea was observed only in the middle layer, and the percent area covered by bionts on the interarea and umbo regions was consistently low. Bionts were not found primarily in one region of the shell or another, demonstrated by the lack of significant differences between

shell areas within a given depth.

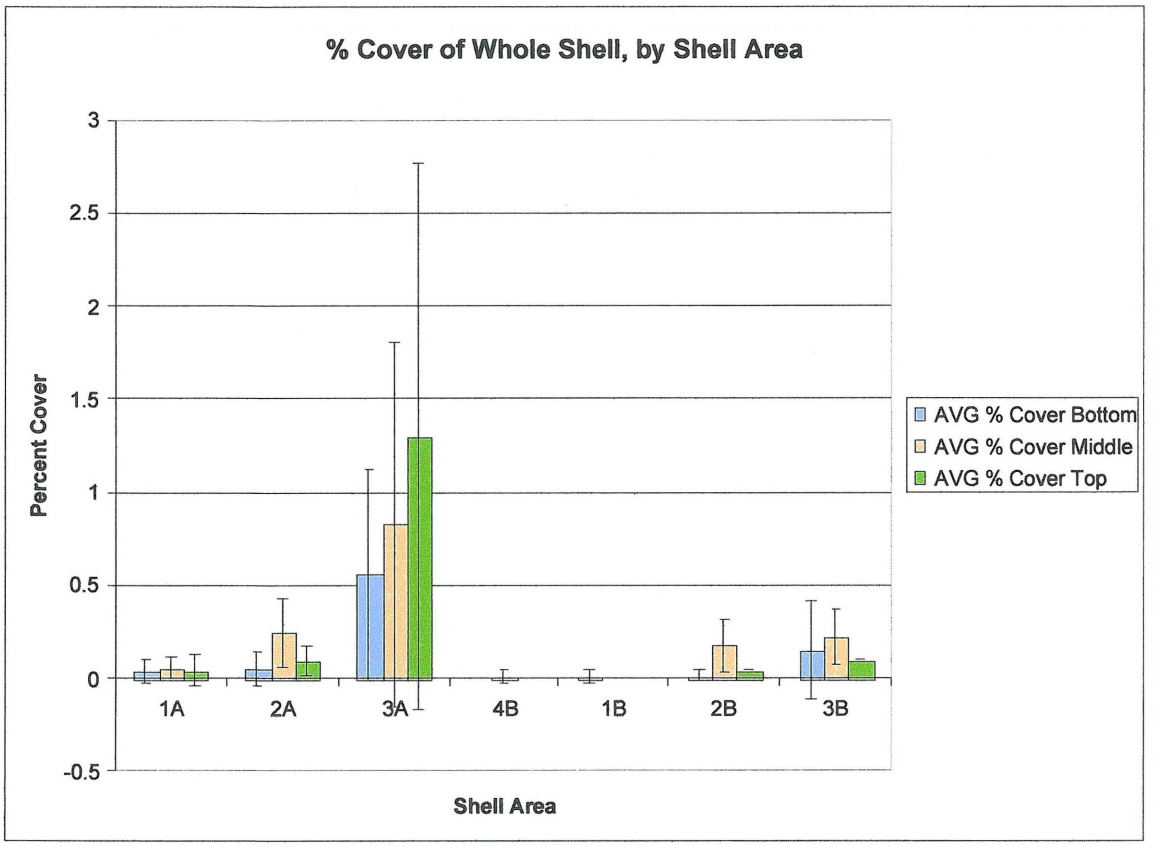



**Figure 17.** Mean percent of individual shell areas of *Rafinesquina alternata* shells encrusted by bionts. There is an outlier in bottom layer in area 3A (one large specimen of a bryozoan morpho-species); if the outlier is taken out, the value of percent cover of the bottom layer drops from 0.56% to 0.29%. There are no significant differences between layers within shell areas. There are also no significant differences between shell areas. Error bars are 95% confidence of the mean.

Mean morpho-species richness is significantly different in shells from the bottom and middle layers, with the middle layer having the highest value (Fig. 18). Morphospecies richness on shells from the bottom and top layers, and on shells from the middle and top layers, were not significantly different. Average morphospecies richness on an individual shell is lower than two in every layer, but the maximum morphospecies richness observed on a shell was only five.

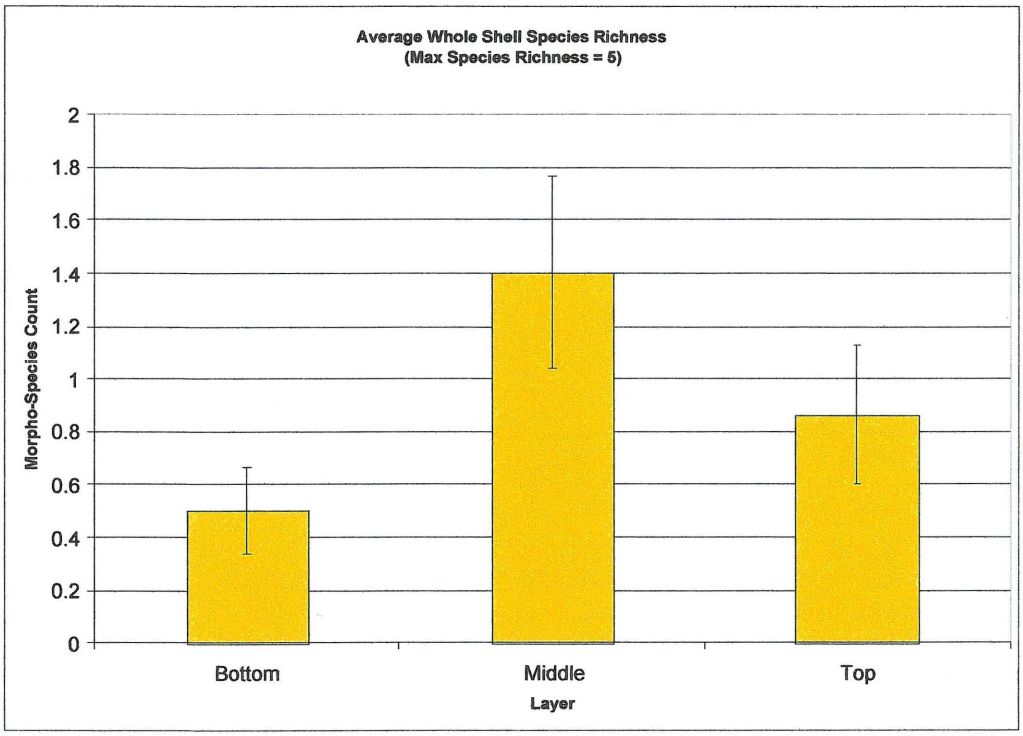



**Figure 18.** Mean 'morpho-species richness' on whole *Rafinesquina alternata* shells by layer. The maximum value for any single shell was 5 'species'. The bottom and middle layers are significantly different, but the middle and top layers, as well as the bottom and top layers, are not. Highest species richness occurs in the middle layer. Error bars are 95% confidence limits of the mean.

*Guild Comparisons*

Mean whole shell percent cover by guilds at modern sites was significantly different between depths. Within guilds, differences between the 15m and 33m sites often exist (Fig. 19). Likewise, differences exist between shallow depths (15m - 70m) and deep depths (192m-275m). Given these natural groupings, data can be further reduced into three categories: photic zone depths (15m and 70m), a buried shallow depth (33m), and non-photic zone depths (192m, 223m, 260m, and 275m). Data on modern guilds were grouped into these categories and re-analyzed.

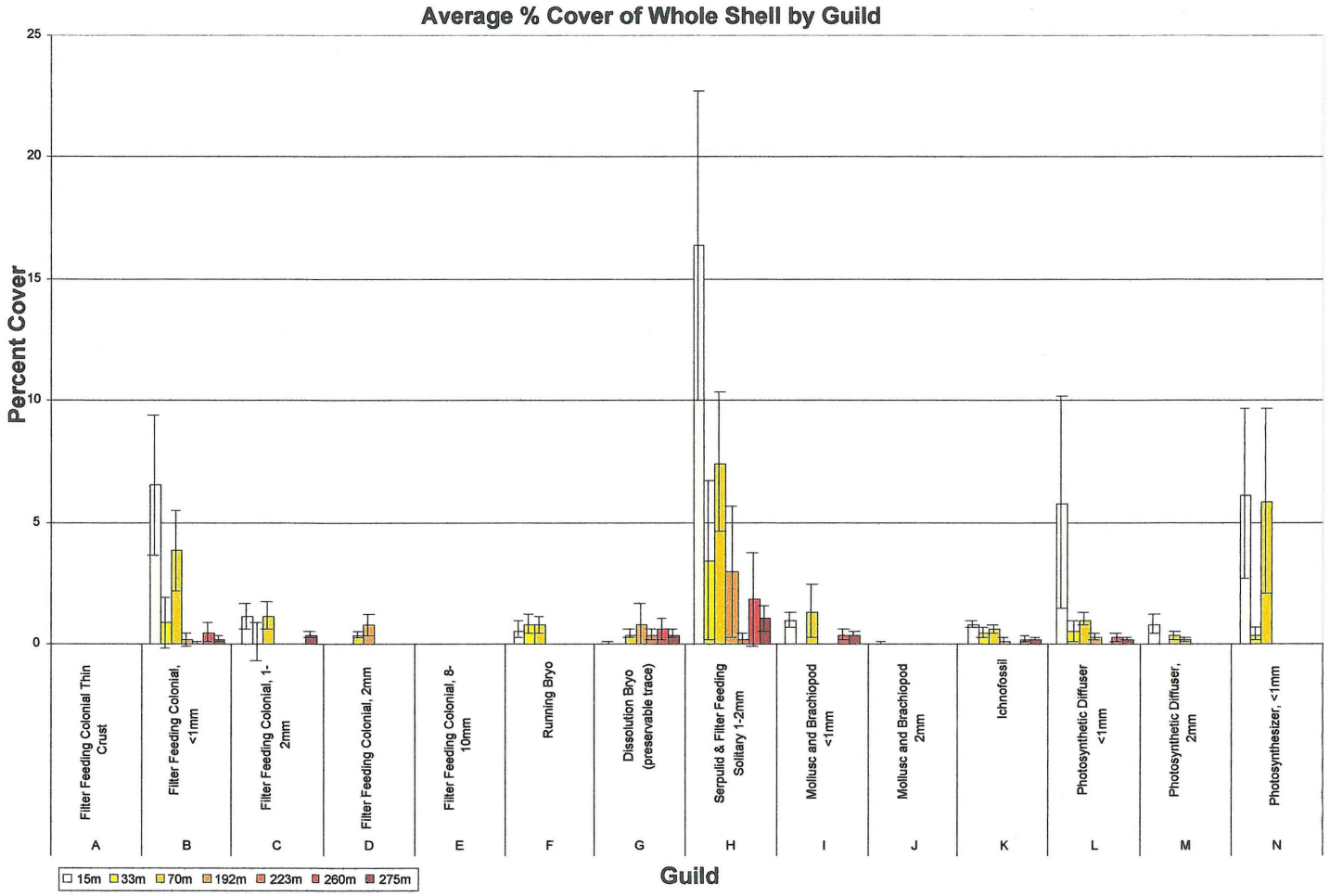



**Figure 19.** Comparison between depths of all biont guilds (by mean percent area of whole shell covered) on modern data set (*Mytilus edulis* shells). Error bars are 95% confidence limits of the mean. Empty guilds are those that are only occupied by Ordovician bionts (in this study). Overlapping error bars indicate non-significant differences between depths within a guild. Note the overlapping error bars in most guilds for 33m and 70m depths, as well as for 33m, 192m, 223m, 260m, and 275m depths. No significant differences between guilds exist. Largest mean percent cover is by Guild H at 15m. Note that values for photosynthetic guilds (L-M) at depths below the photic zone are present because of species that contain photosynthetic symbionts within the photic zone but not below. These values, then, do not represent bionts that are photosynthesizing but do represent bionts that photosynthesize when in the photic zone.

Grouping modern data into more general environments sheds light on some trends in the data (Fig. 20). Shells from the photic zone have encrusters from a larger number of guilds than from either of the other two environments (Figs. 20, 21), and frequently have significantly higher mean percent cover values as well. Non-preservable bionts, if they had been included, would have distinguished the photic zone even more. The highest mean percent cover by guild is by the 'serpulids / solitary filter feeders' guild (H);

however, the 'photosynthesizer' (L-N) and the 'colonial filter feeders less than 1mm' guild (B) are not significantly different from the serpulids, and so all three guilds occupy the highest percentage of shell area on shells from the photic zone. Shells from the buried zone do not often exhibit significantly different mean percent area coverage by guild values from shells in the non-photic zone.

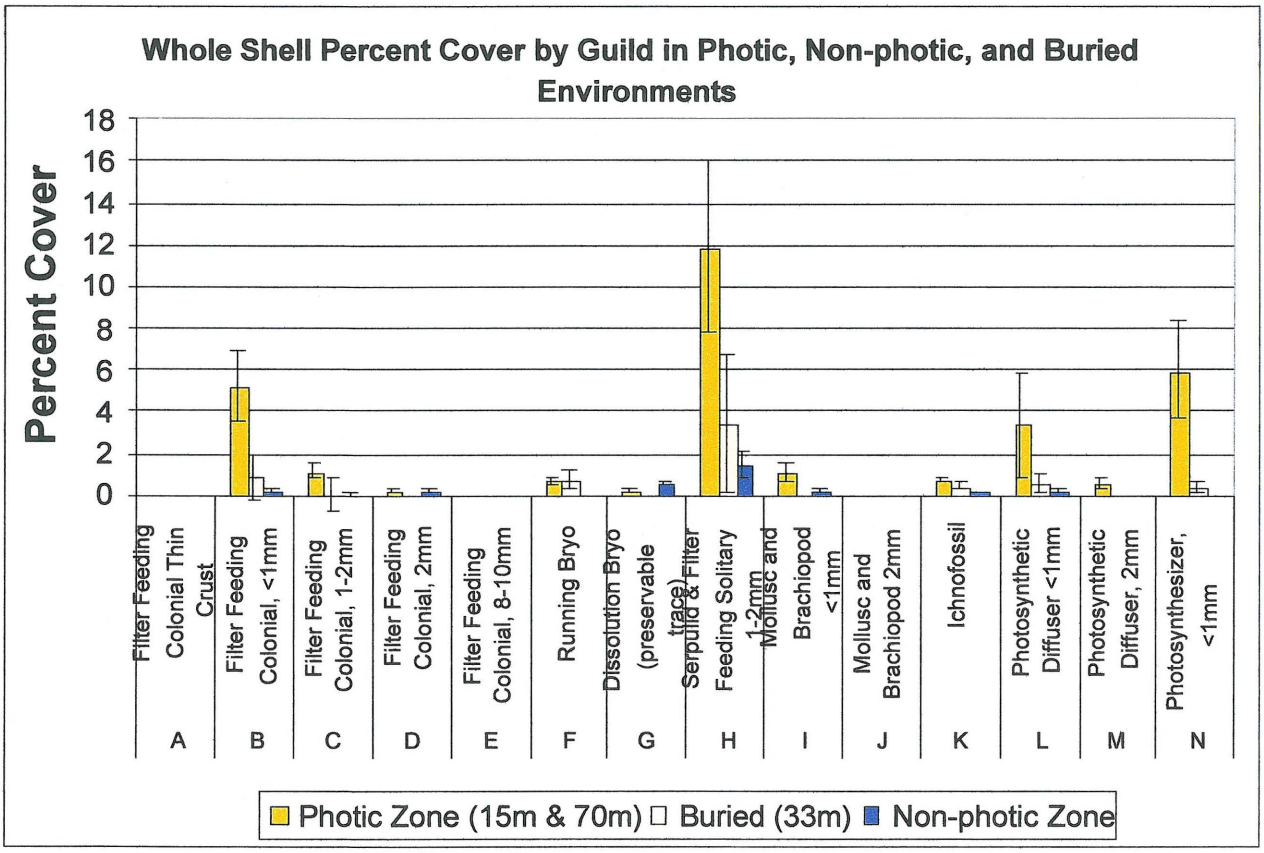



**Figure 20.** Mean percent of whole shell encrusted by guilds for three modern environments – photic, buried, and non-photic. Error bars are 95% confidence limits of the mean. The highest mean percent coverage is by Guild H in the photic zone. There are some significant differences in guild coverage with depth, indicated by non-overlapping error bars. Generally, guilds in photic zone and non-photic zone cover significantly different mean areas of shell.

Guild richness analyses for the modern data show significant differences between depths, and follow the same pattern as percent area covered by guild (Fig. 21). Natural groupings of samples into photic zone (15m and 70m), shallow buried (33m), and non-

photic zone (192m-275m) seem to occur. While guild richness values for shallow buried and non-photic zone are similar, the buried shells are quite different from neighboring depth locations above and below it and will be therefore be kept separate.

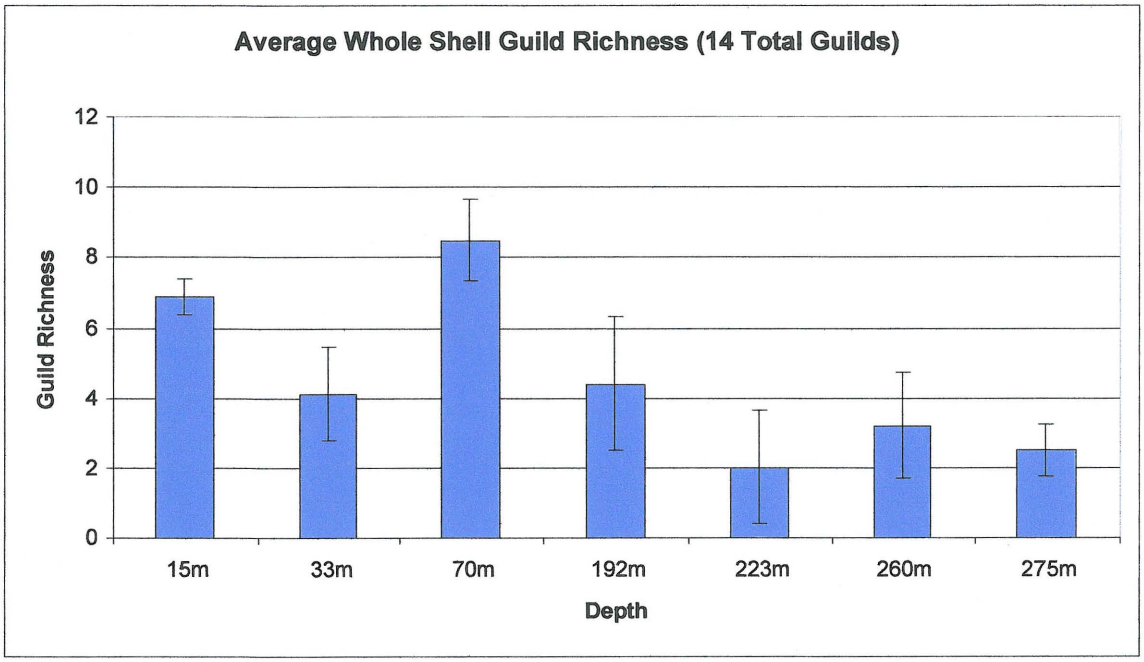



**Figure 21.** Mean whole shell (*M. edulis)* guild richness at each depth in modern study. 15m and 70m depths are not significantly different. 33m, 192m, 223m, 260m, and 275m are not significantly different. The largest guild richness occurs at 70m. Error bars are 95% confidence limits of the mean.

*Ordovician*

A clear decrease in guild richness occurs from photic to buried to non-photic zones (Fig. 22). The error bars on the buried and non-photic sites overlap, so the only significant change in guild richness occurs between the photic zone and all other sites. While the same trend shows up in the analysis of guild richness by depth, it becomes much clearer in the analysis by environment.

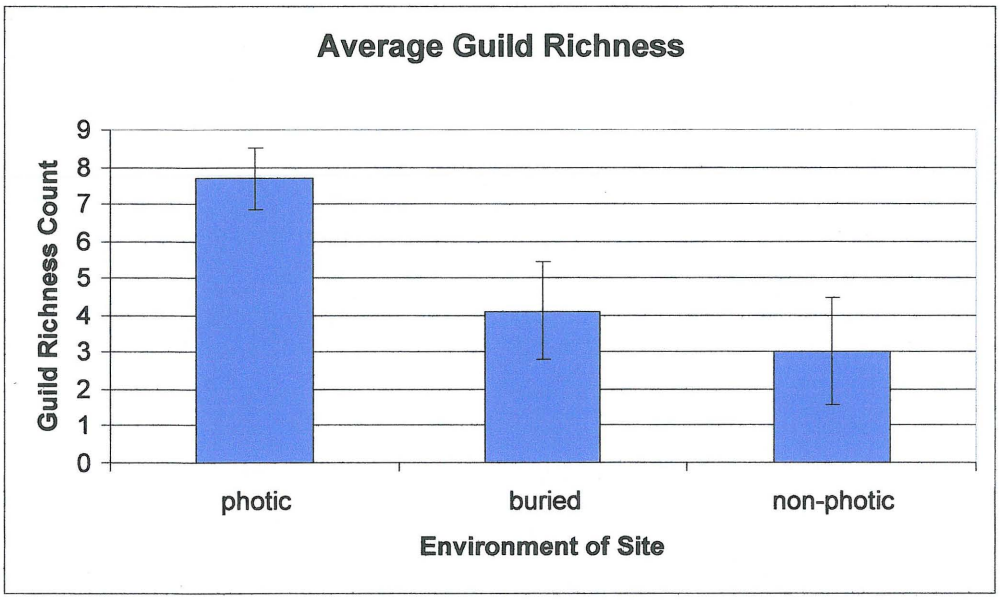



**Figure 22.** Graph of average guild richness on whole *Mytilus edulis* shells by environment: photic, buried, and non-photic. Richness was highest on average on shells from the photic zone. Richness on shells from buried and non-photic zones were not significantly different. Error bars are 95% confidence limits of the mean.

Mean percent cover on *Rafinesquina alternata* shells does not vary significantly with guilds (Fig. 23). One exception is by colonial filter feeders 1-2mm off the shell (guild C) which occupy the most surface in the top layer, and the lowest in the bottom layer. Colonial filter feeders 8-10 mm off the substrate were observed only on one shell from the bottom layer and occupied a large area on that shell. Several guilds were not occupied by bionts found on the *R. alternata* shells: the mollusc and brachiopod 2mm guild (J), and the photosynthetic guilds (L-M). The colonial filter feeders 1-2mm off the substrate had significantly higher mean percent area coverage values than any other guild (discounting the anomalous occurrence of guild E). All other guilds represented approximately equal areas of shell substrate.

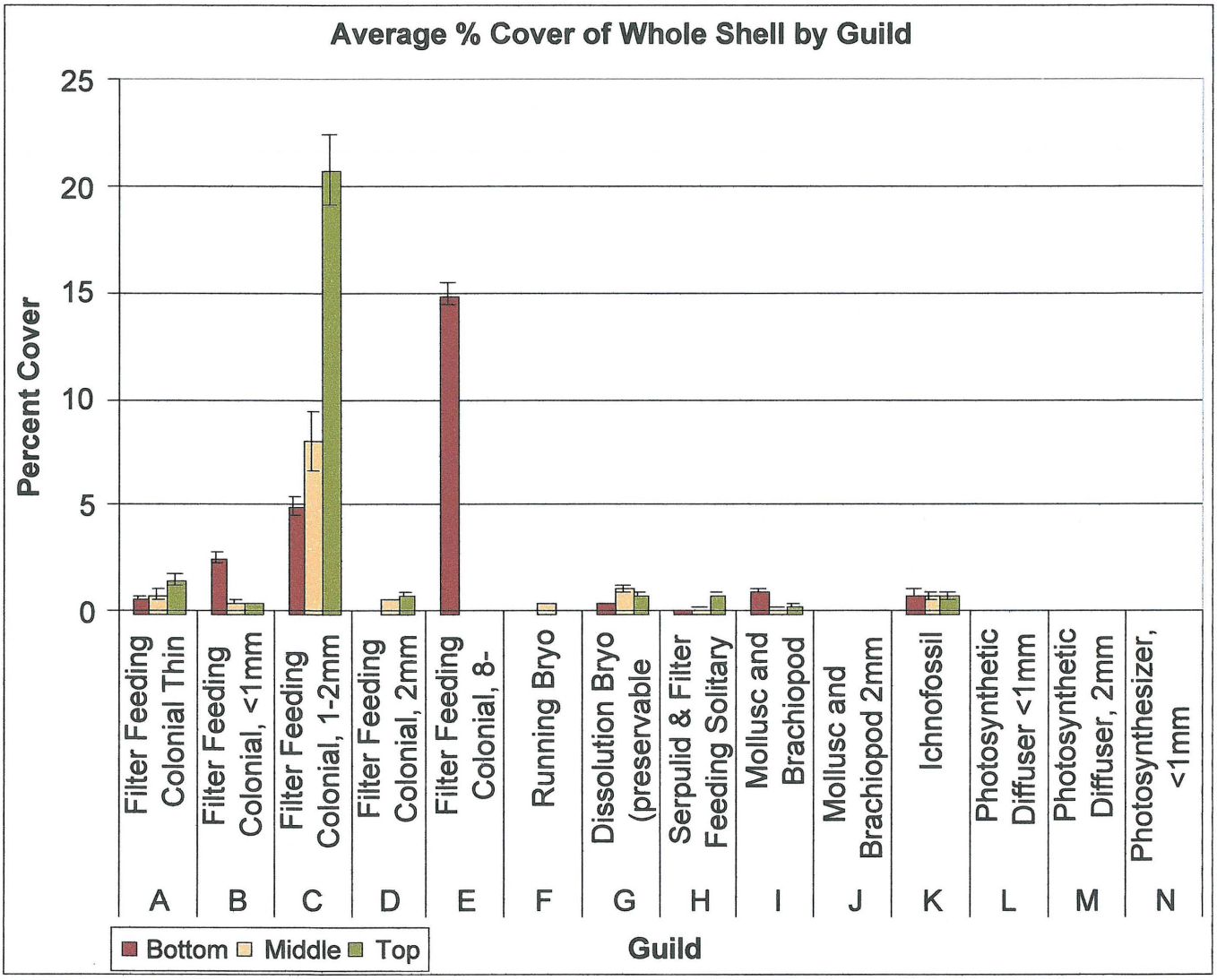



**Figure 23.** Graph of percent area of whole *Rafinesquina alternata* shells covered by guilds of bionts in each Ordovician layer (bottom, middle, and top). Significant differences between layers do occur within guilds, but not in a consistent pattern. The high percent cover by Guild E is due to the presence of a single specimen on a single shell in the bottom layer, and disregarding this outlier, Guild C covered significantly larger areas of the shell than all other guilds. Empty guilds are those only represented by modern bionts. Error bars are 95% confidence limits of the mean.

Mean guild richness (Fig. 24) falls between 0.5-1.5 guilds per shell. This reflects the fact that each shell harbors only one or two different guilds. The bottom and middle layers were significantly different, with the middle layer having a higher guild richness value. The middle and top layer, and the bottom and top layer, did not significantly vary in guild richness per shell. These layer differences follow the same pattern as mean whole shell morphospecies richness on *R. alternata* (Fig. 18).

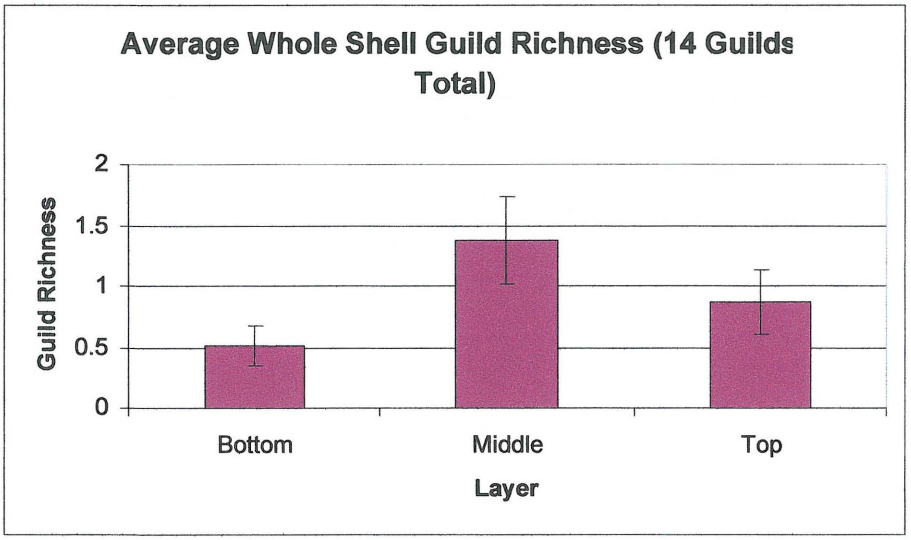



**Figure 24.** Mean guild richness on *Rafinesquina alternata* shells from the three Ordovician layers. Bottom and Middle layers have significantly different guild richness values, while the bottom and top, and the middle and top, are similar. The low values for guild richness per shell emphasize the fact that each shell usually supports only 1 or two guilds, and many shells in the data sets are free of encrusters. Error bars are 95% confidence limits of the mean.

Based on the results of the Ordovician data set, a problem arises when trying to reduce and condense shell bed data. Significant differences in percent area covered by biont species (Fig. 16) exist between the bottom and top layers, but not between the bottom and middle or middle and top layers. Even when the anomalous morphospecies of bryozoan (BrE), which occurs only on one specimen in the bottom layer, is thrown out, the difference between the bottom and top layers only widens. Still, because overlap in error bars exists between the middle layer and both top and bottom layers, it would be reasonable to combine the layer data into one ancient data set. When species richness between layers is compared (Fig. 18) a similar situation results. In this analysis, error bars between the bottom and top and between top and middle overlap, but not between bottom and middle. Yet, again, because each layer overlaps with at least one other, the three layers could reasonably be combined into one data set.

A more difficult problem arises when guild analysis is done for the Ordovician layers. While the average whole shell guild richness analysis does have overlapping error bars between layers, the percent area coverage analyses do not. Significant differences between layers in percent area covered by guilds exist in all guilds except for K, the ichnofossil guild. The question, then, is can the three layers, bottom, middle, and top, reasonably be combined into one data set. The motivation for such a combination is twofold. The first reason for combination is the observation made in the field during sample collection that all three layers seemed to be transported rather than *in situ*. Signs of transportation included shell breakage, the lack of shells or other fauna *in situ*, the presence of broken pieces of ramose bryozoans and disarticulated brachiopods, and the presence of shells in distinct beds in an otherwise fine grained and shaley outcrop. Also, the imbrication of brachiopods in each bed may indicate transportation. Transportation would eliminate the need to keep layers separate because the layers would not be reflecting an ancient environment in the first place, and could be combined into one large data set. The second reason for combination is that the error bars do not always overlap between the same layers: significant differences exist between the bottom and top in total percent area coverage but between bottom and middle in species richness. The inconsistency in layer overlap indicates the feasibility of treating all three layers together in comparisons with modern studies. This result (inconsistent differences based on error bars) may also be an artifact of a relatively small sample size. Although total number of shells collected is high (208), the sample comes from only three positions from each of three closely spaced beds. More extensive sampling might lead to complete overlap between layers. Finally, due to slight differences in lithology of the layers shells may

have been more or less subjected to preservational differences that may have biased the data towards increased or decreased biont cover. Preservational biases may have influenced guilds differently, as guilds reflect height off substrate and therefore may be more or less subject to scraping off during cleaning or during transport and burial. These biases may account for some of the smaller differences in error bars seen in Figure 23 (and 26). Based on this rationale, ancient data for guilds was combined into one data set for the Ordovician (Fig 25), for use in comparisons with the modern environments. The resulting average guild richness for the combined Ordovician data set is 0.92 (or 1guild per shell), with a confidence limit of 0.26.

The error bars on the graph of combined data for percent area cover do not overlap, which indicates that there is a significant difference between percent area covered by each guild. Of course, percent area covered is dictated by factors such as coloniality and overall growth form, or bauplan of the biont; therefore, error bars on this graph do not indicate much in terms of significant differences between the guilds. The relative shortness of the error bars to data columns does at least indicate reliable data for the ancient data set.

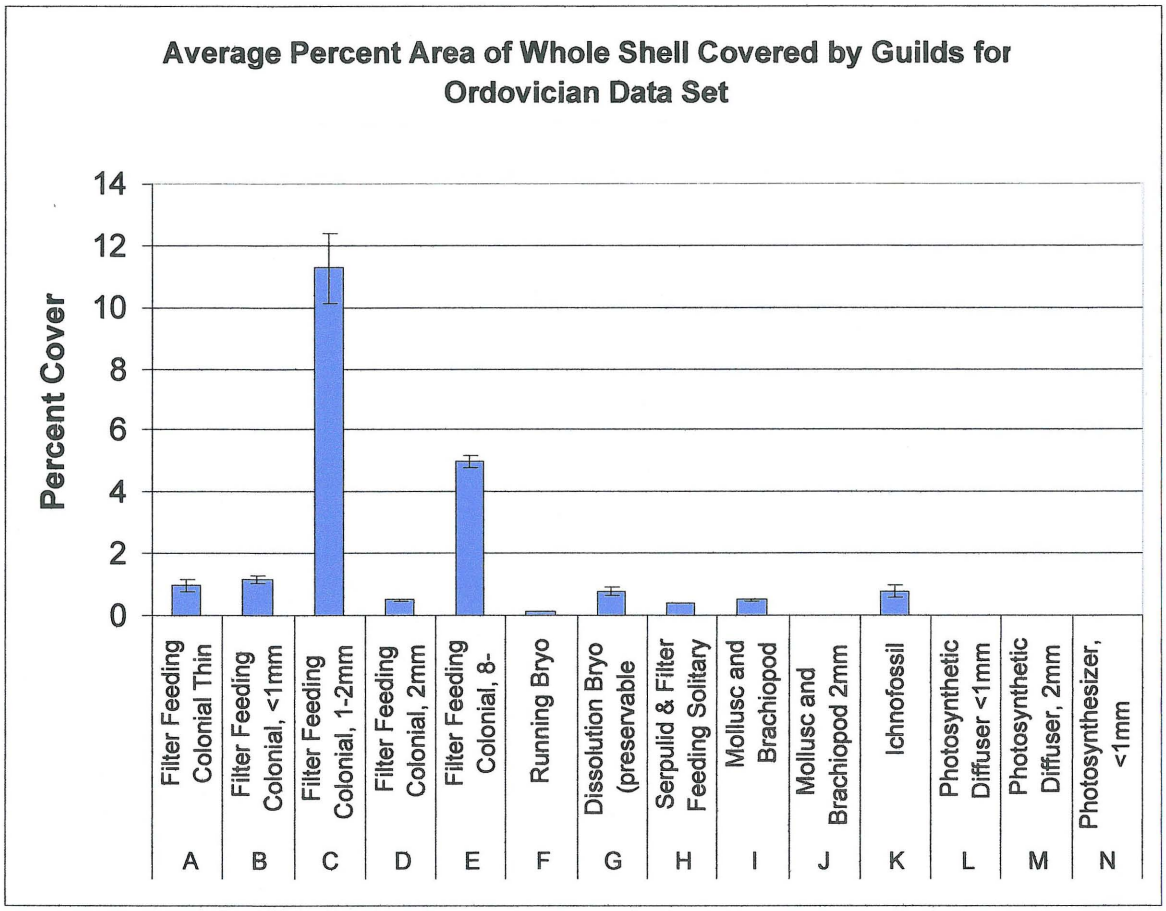



**Figure 25.** Combined data sets from bottom, middle and top layers into one Ordovician data set. Analysis is for mean percent of whole shell covered by a guild. Significant differences occur in between most guild covers, notably between Guild C, which covered the most shells area, and all other guilds. Guild E is an outlier (occurring on one specimen). Small error bars reflect the large size of data set when all shells from Ordovician are combined. Error bars are 95% confidence limits of the mean.

Guild comparisons between the modern and the ancient were made using the combined modern data (photic, buried, and non-photic) and combined Ordovician data (all layers) for percent area cover (Fig. 26). Similarities between the Ordovician and a modern environment exist, but the modern environment which most closely resembles the Ordovician varies with guild.

Guild A, E, and J are only represented in the Ordovician. Mean percent cover by Guild B is similar on the Ordovician shells to the Buried modern shells (Fig. 27). Guild C does not exhibit similarities between the Ordovician and any modern environment (Fig.

28). Guild D is not similar in percent coverage on the Ordovician and either modern environment. Guild F percent coverage is significantly different in the Ordovician and all modern environments. Guild G is represented equally in the Ordovician and non-photic zone (Fig. 30). Guild H percent area coverage is similar for shells from the Ordovician and the Buried shells (Fig. 31). The Ordovician data matches the non-photic zone for Guild I (Fig. 32). Guild J is unoccupied. Guild K occupies a similar total shell area in the Ordovician as in the modern photic zone (Fig. 33). The three photosynthetic guilds, L, M, and N, are occupied only in the modern data set (Fig. 26). Overall, the mean percent area occupied by guilds on shells from the Ordovician is most similar to shells from the buried environment and the non-photic environment. Of all the common guilds (8 in all), two guilds place the Ordovician within the buried modern environment, and two place the Ordovician within the non-photic modern environment. Only one shows affinities to the photic zone guilds (the ichnofossil guild, K).

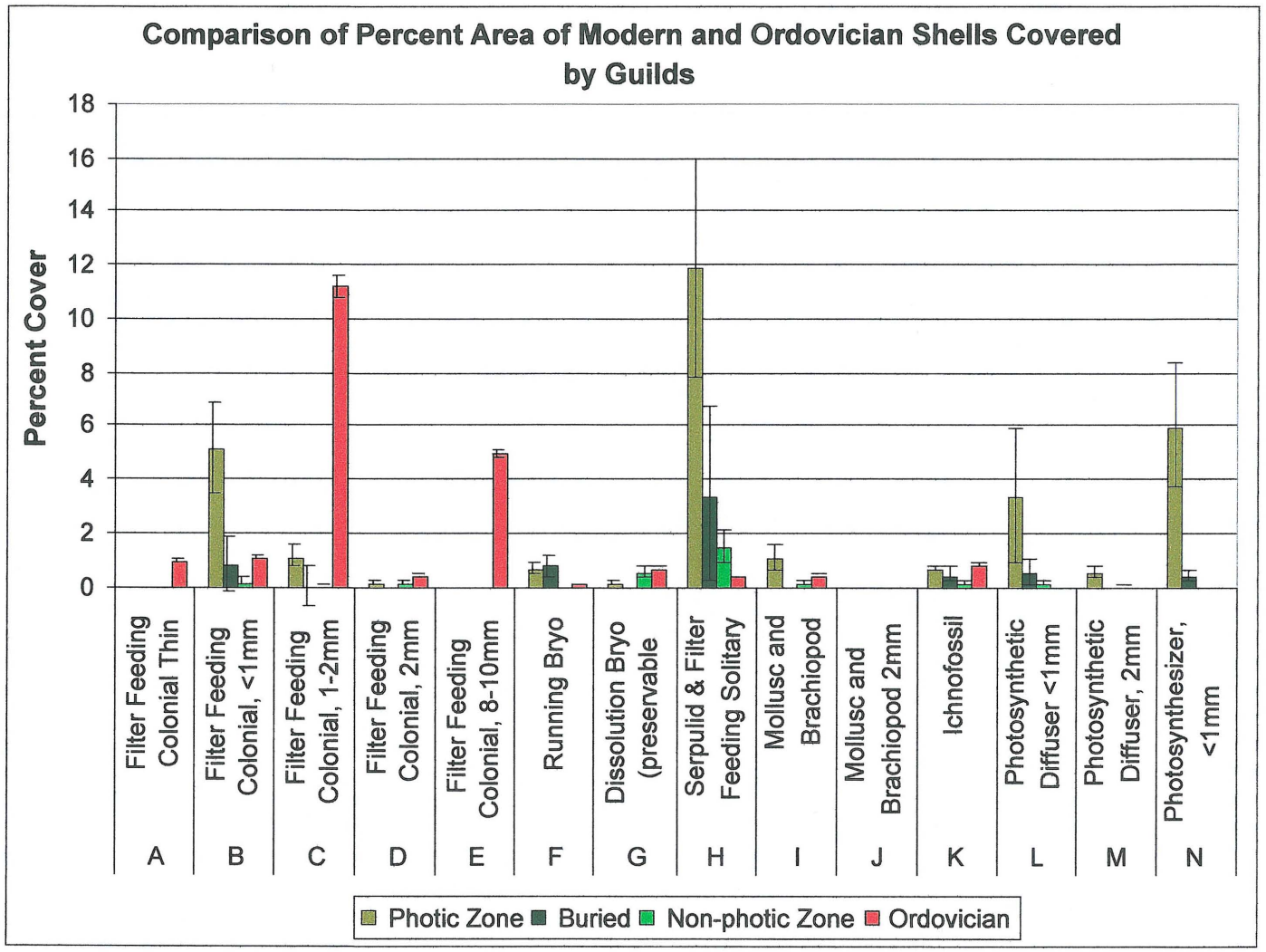



**Figure 26.** Comparison of mean percent cover of whole shell by guild in modern environments (photic, buried, and non-photic), and in the Ordovician data sets. The Ordovician data are similar to the photic environment in guild K (ichnofossil), similar to the buried environment in guilds B and H (colonial filter <1mm and solitary filterers), and similar to the non-photic in guilds G and I (dissolution bryozoans and molluscs/brachiopods). Error bars are 95% confidence limits of the mean.

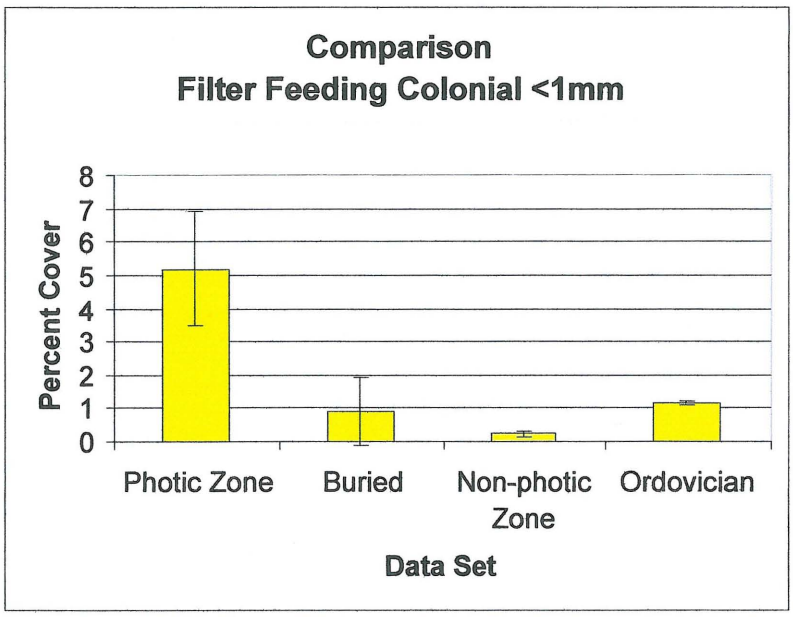



**Figure 27.** Mean percent cover (per shell) by filter feeding colonial <1mm guild (B). Shows similarities between Ordovician and modern buried environments. Error bars are 95% confidence limits of the mean.

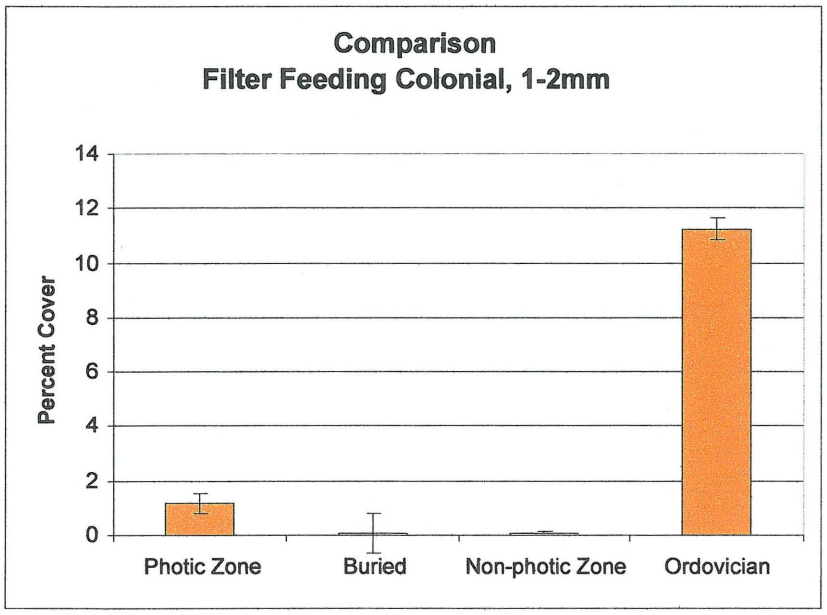



**Figure 28.** Mean percent cover (per shell) by filter feeding colonial 1-2mm guild (C). Graph shows no similarities between the Ordovician and modern environments. Note that percent cover by this guild in both the buried and non-photic zone is essentially zero. Error bars are 95% confidence limits of the mean.

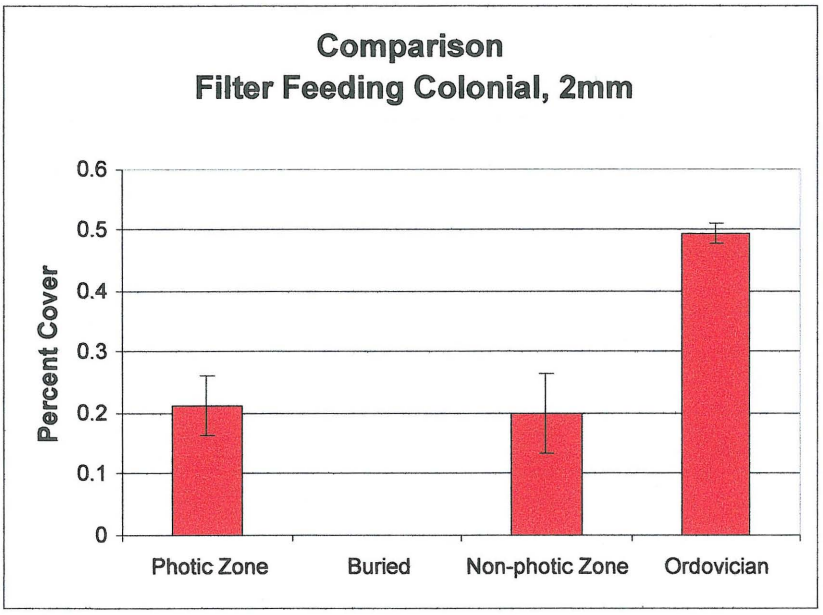



**Figure 29.** Mean percent cover (per shell) by filter feeding colonial 2mm guild (D). No similarities exist between Ordovician and modern environments. Error bars are 95% confidence of the mean.

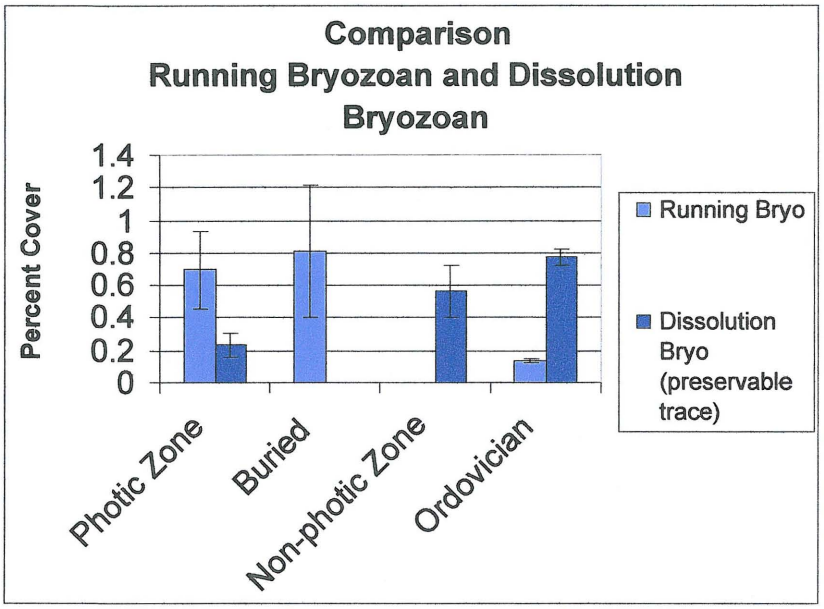



**Figure 30.** Mean percent cover (per shell) by running bryozoan and dissolution bryozoan guilds (F and G). Ordovician data is similar to the non-photic zone for dissolution bryozoa but is not similar to any modern environment for running bryozoa. Error bars are 95% confidence limits of the mean.

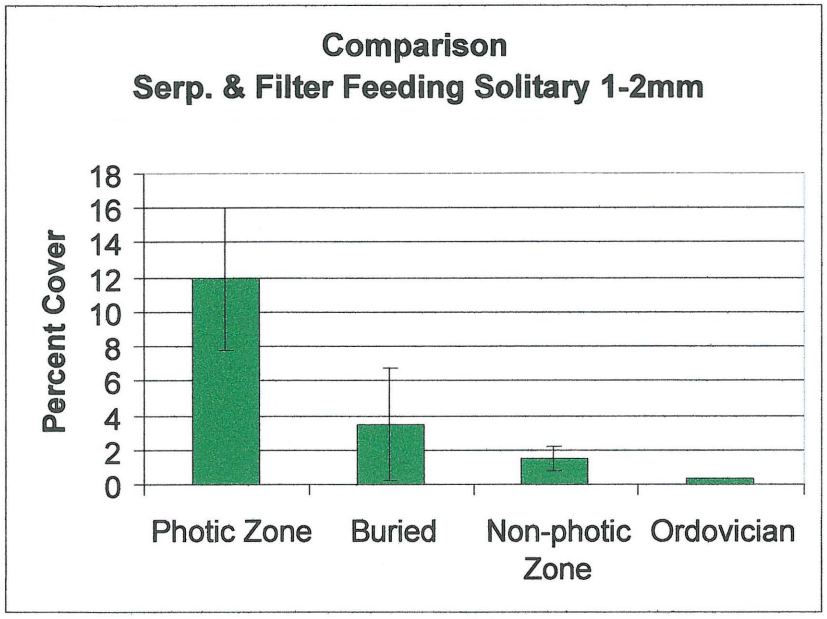



**Figure 31.** Mean percent cover (per shell) by serpulids and solitary filter feeders 1-2mm guild (H). Shows similarities between modern buried and Ordovician data. Percent cover in photic zone is significantly higher than in either other modern environment. Error bars are 95% confidence limits of the mean.

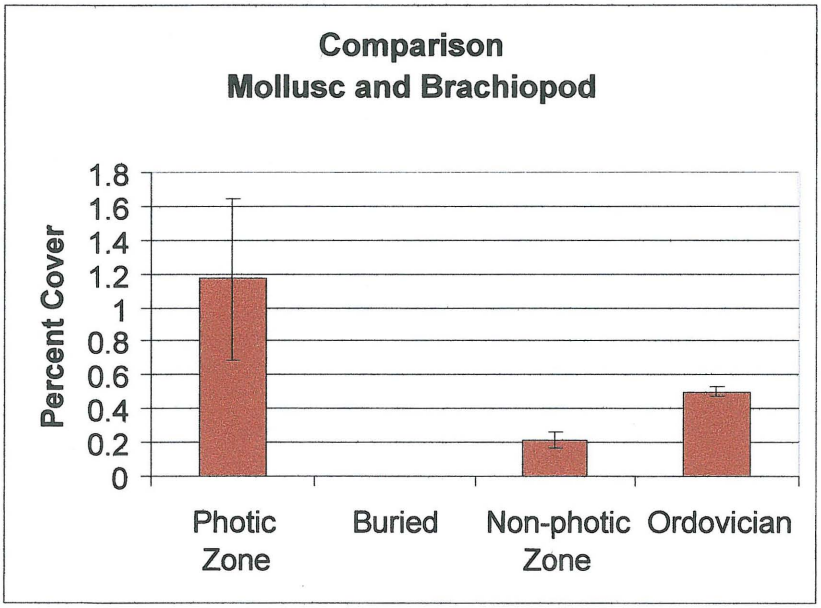



**Figure 32.** Mean percent cover (per shell) by mollusc and brachiopod guild <1mm (I). There are no similarities between the Ordovician data and any modern environment. Percent coverage by this guild is signifigantly higher in the photic zone than in either other modern environment. Error bars are 95% confidence limits of the mean.

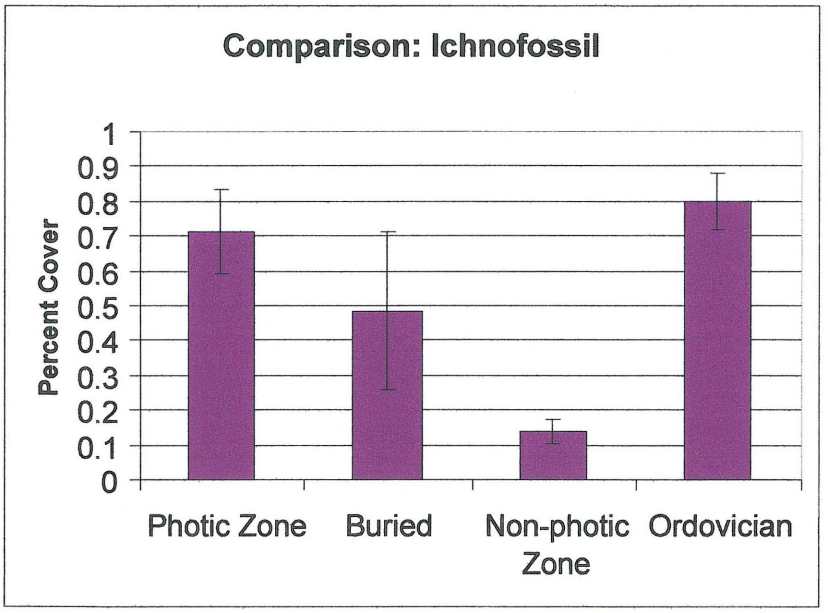



**Figure 33.** Mean percent cover (per shell) by ichnofossil guild (K). Ordovician data is similar to data from the photic zone. Error bars are 95% confidence limits of the mean.

Bionts in the Bryozoa guilds (A-G) share similarities in morphology and bauplan to a much greater extent than do other guilds. A comparison of the modern environments to the Ordovician data using a combined set of bryozoa guilds may demonstrate similarities not apparent in analyses by individual guilds. A combined bryozoan analysis, however, shows significant differences between the Ordovician and all modern environments (Fig. 34). The running and dissolution bryozoa are not as similar in morphology as the other guilds of bryozoa, so another analysis was done for bryozoa guilds excluding the running and dissolution bryozoa (Fig. 35). The trends apparent in this analysis were the same as shown in figure 34, with the guilds F and G.

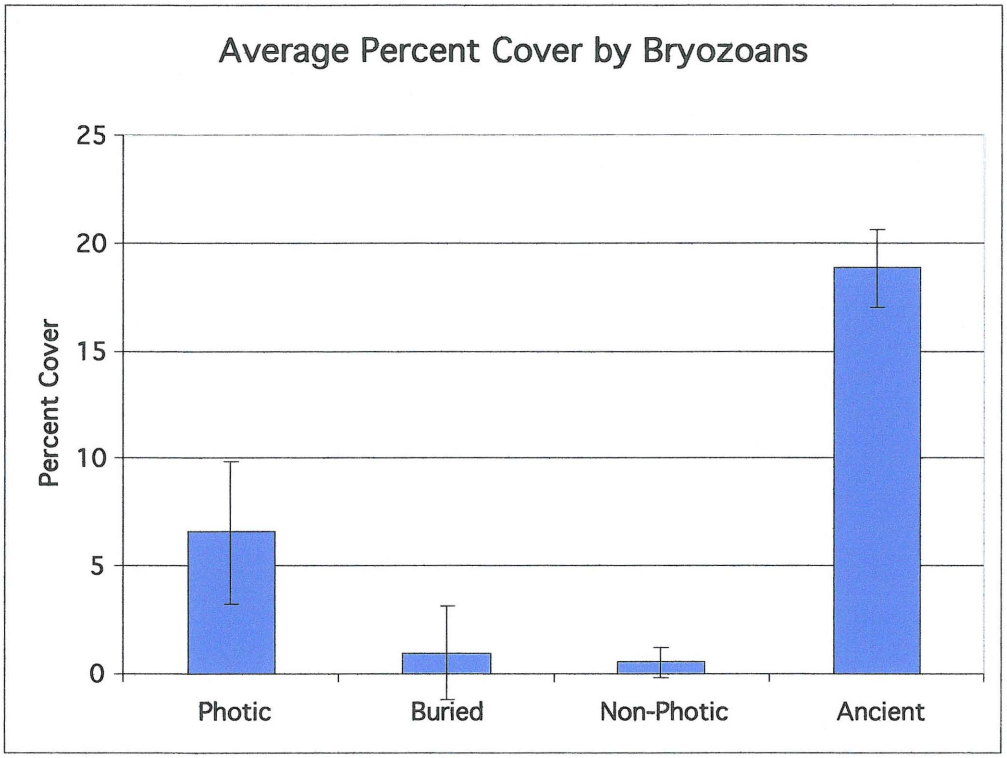



**Figure 34.** A comparison of mean percent of shell covered by bryozoans (Guilds A-G) on *M. edulis* and *R. alternata* shells from modern environments (photic, buried, and non-photic) and the Ordovician environments. The coverage of the Ordovician shells is much higher than in any modern environment. Bryozoans in the modern buried and non-photic environments occupy essentially equal areas of the shell. The closest match in bryozoan percent cover between the Ordovician and any modern environment is between the Ordovician and the photic environment, although this "match" differs by a factor of three. Error bars are 95% confidence limits of the mean.

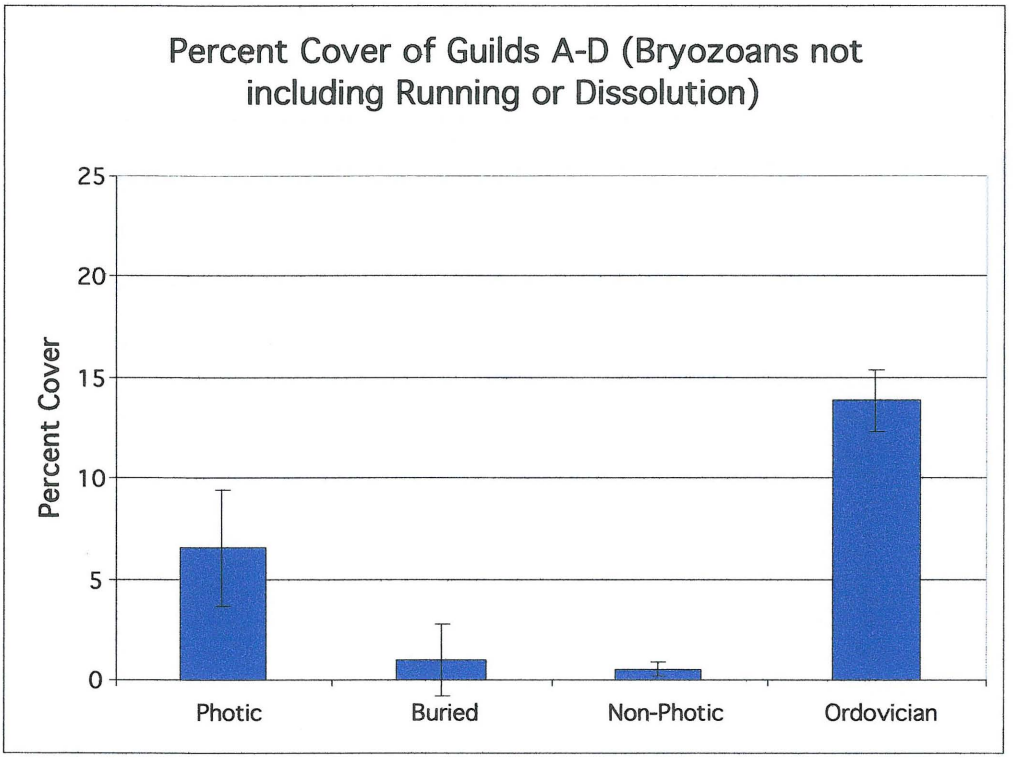
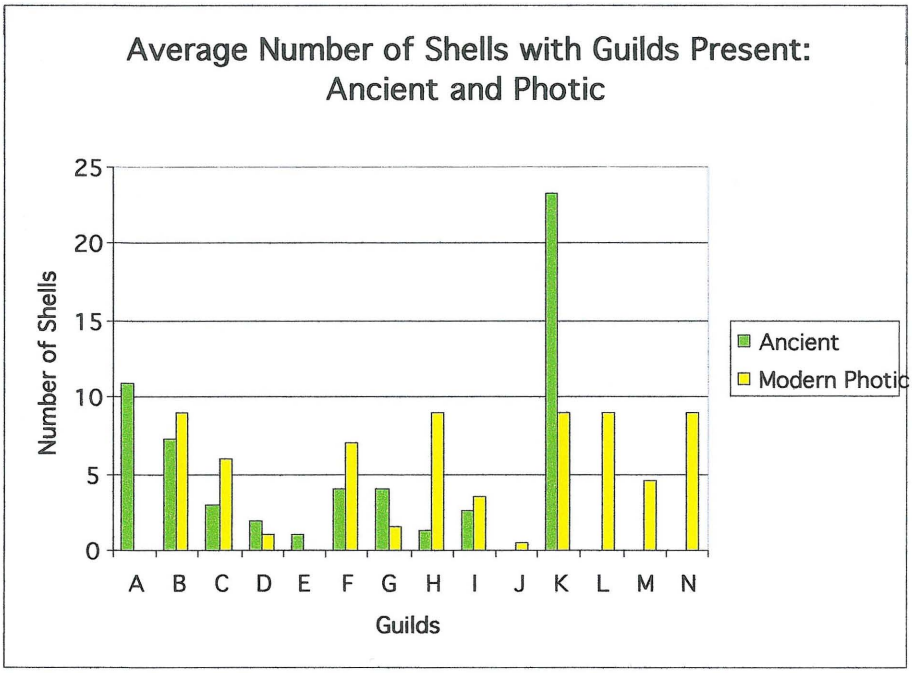



**Figure 35.** Mean percent cover (per shell) by bryozoa guilds, excluding the running bryozoa (guild F) and the dissolution bryozoa (guild G). Note similar trends as in Figure 32, which included guilds F and G. The Ordovician data is significantly different from the modern environments; exclusion of the two bryozoa guilds with a different bauplan did not affect results of this comparison. Error bars are 95% confidence limits of the mean.

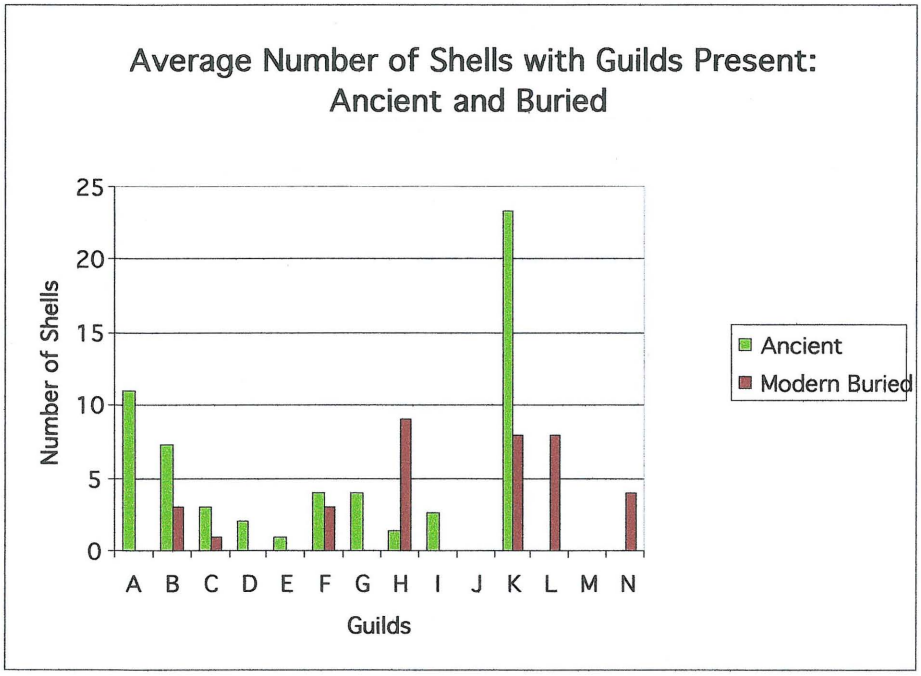
A more basic analysis of number of shells containing a guild (i.e. frequency of occurrence) was conducted for all modern environments and the Ordovician data set (Fig. 36). The photic zone shares a larger number of guilds, a total of 8, with the Ordovician than either of the other two environments (Fig. 36, a). The photic zone also is more similar to the Ordovician in overall frequency of shells supporting a particular guild (comparison of bar heights). The buried zone only shares five similar guilds with the Ordovician, and relative frequencies of all but guild F are more distant than in the photic zone (Fig. 36 a-c). The non-photic zone shares 7 guilds with the Ordovician, and except for guilds C and H, the relative frequencies in the photic are more similar to the Ordovician (Fig. 36 a-c). As the earlier analysis by percent area covered by guilds (Fig.

26) indicated a possible match between Ordovician data and a crossover of buried and non-photic data, a separate analysis was done for frequency of guilds in the Ordovician as compared with an averaged data set of buried and non-photic environments (Fig. 36 d). The resulting number of shared guilds is 8, equal to the number shared between photic and Ordovician; however, the relative frequencies (height of bars) within guilds are still closer in a comparison between the photic zone and the Ordovician.

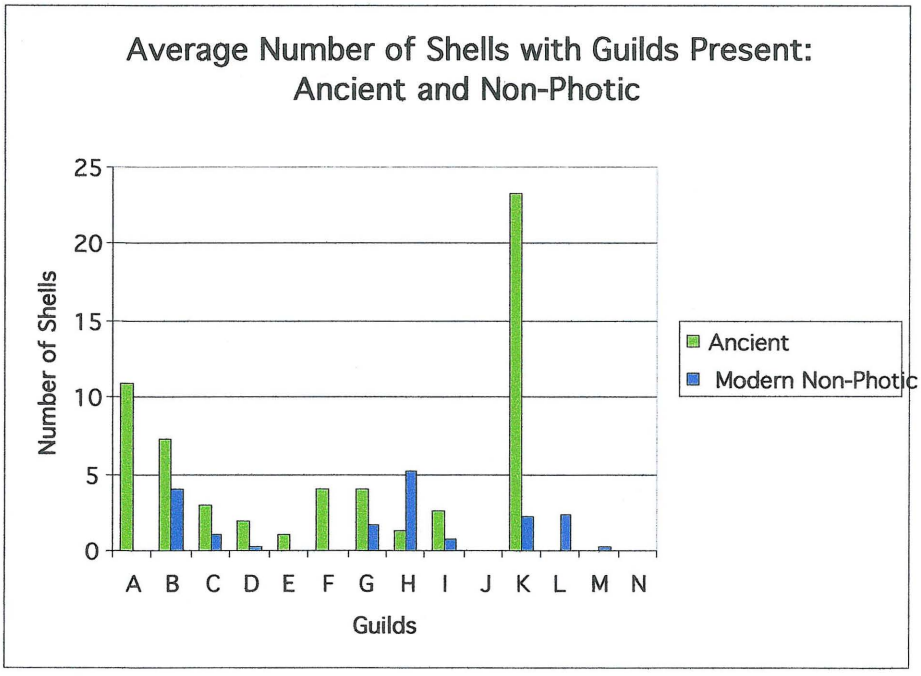


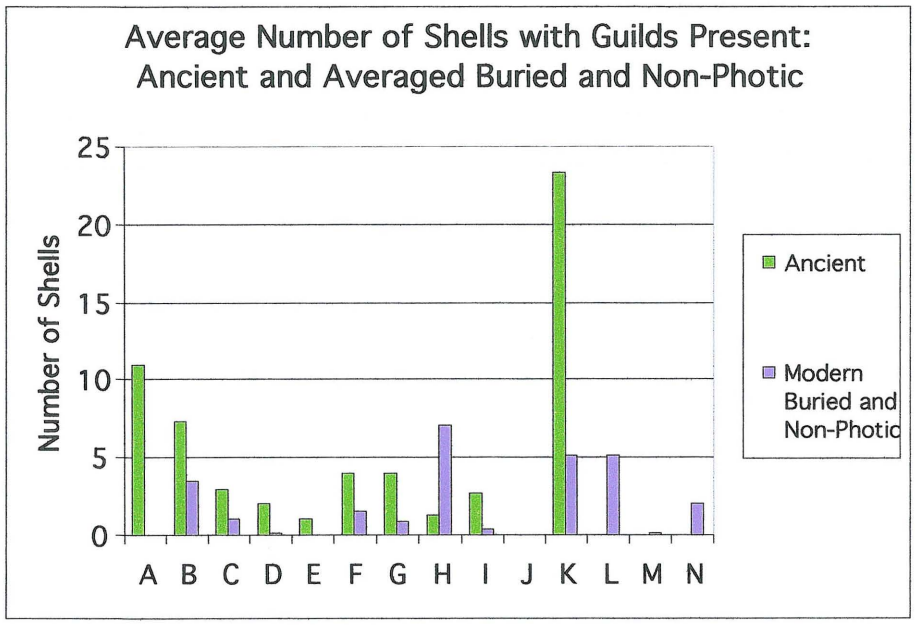

a)

b)


Average Number of Shells with Guilds Present:
Ancient and Buried
Number of Shells
25
20
15
10
5
0
A B C D E F G H I J K L M N
Guilds
Ancient
Modern Buried

c)


Average Number of Shells with Guilds Present:
Ancient and Non-Photic
Number of Shells
25
20
15
10
5
0
A B C D E F G H I J K L M N
Guilds
Ancient
Modern Non-Photic

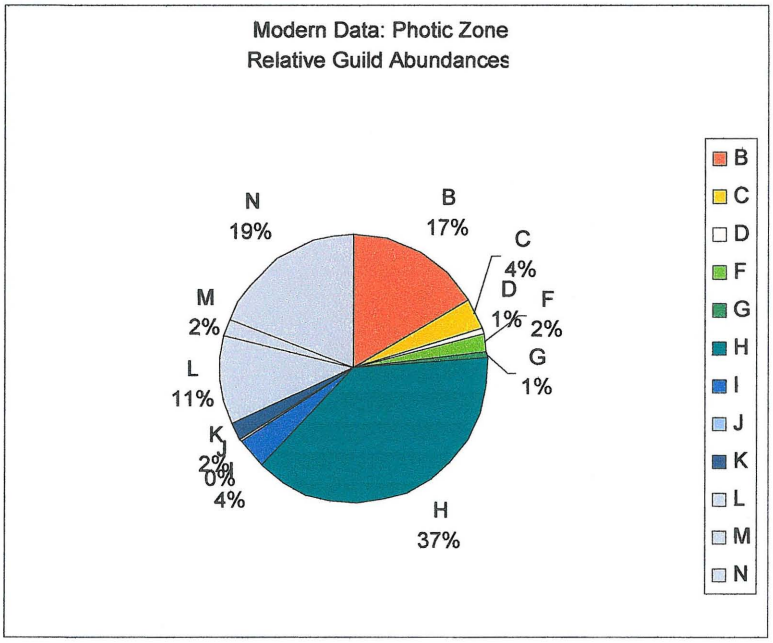



d)

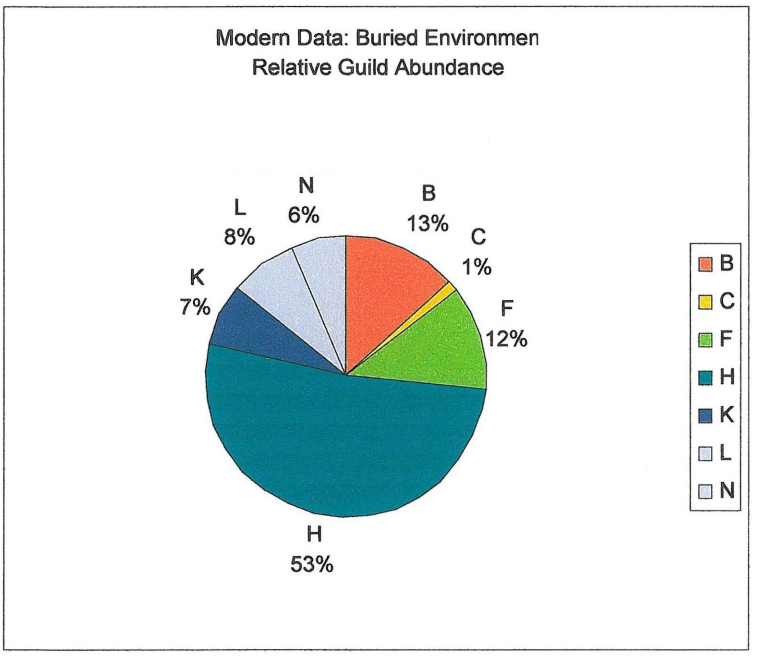
**Figure 36.** Comparison of number of shells containing at least one occurrence of a guild. a) Comparison of Ordovician with modern photic zone, b) comparison of Ordovician with modern buried environment, and c) comparison of Ordovician with modern non-photic environment. The photic zone and the Ordovician are the most similar in terms of number of guilds represented in both modern and ancient, and in terms of number of shells containing those guilds. When buried and non-photic data are averaged as in d), the similarity is not much improved. The photic zone remains a closer match by this analysis. Guild Codes: **A**-Thin Crust, **B**-<1mm, **C**-1-2mm, **D**-2mm, **E**-8-10mm, **F**-Running Bryo, **G**-Dissolution Bryo, **H**-Serpulid and Solitary filterer, **I**-mollusc and brach <1mm, **J**-mollusc and brach 2mm, **K**-ichnofossil, **L**-photosynthetic diffuser <1mm, **M**-photosynthetic diffuser 2mm, **N**-photosynthesizer.

Graphs of relative abundance of guilds indicate that the Ordovician data set does not match any modern environment (Fig. 37). Relative abundance is different than percent area coverage comparisons, because instead of simply amount of shell occupied by a guild, the proportion of total encrustation accounted for by one guild is shown. In all modern environments, serpulids and solitary filter feeders (guild H) account for the highest percentage of biont cover. This guild makes up only 2% of biont cover in the Ordovician. The difference, although quite large between all modern environments and the Ordovician, is smallest in the photic zone, for which Guild H is only 37% of the total as opposed to 47% or 53% in the other modern environments. In the Ordovician, the highest percentage of biont cover is by colonial filter feeders 1-2mm off the shell (c). The

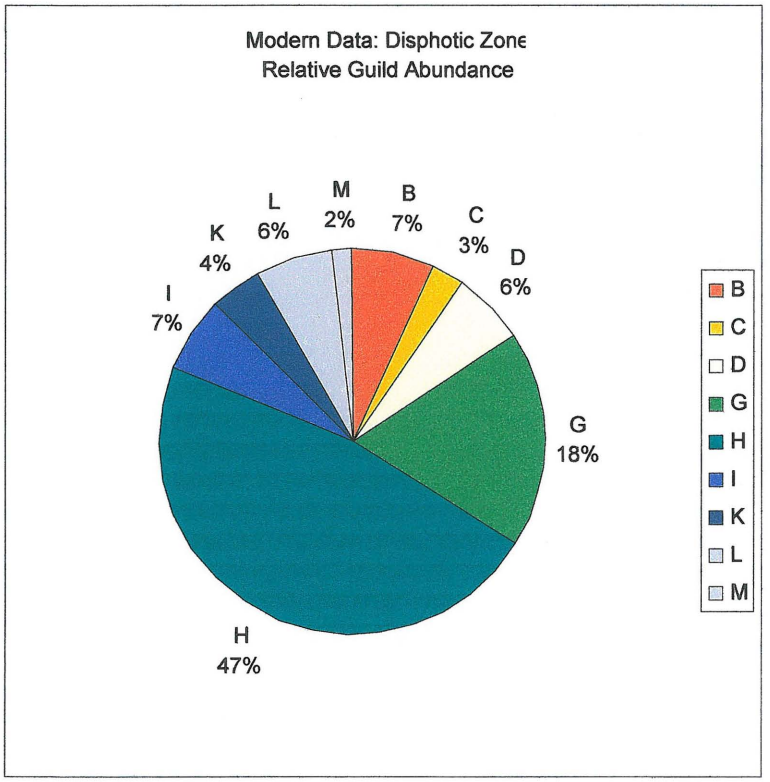
'colonial filter feeders less than 1mm off the shell' (B) are second highest in abundance in the Ordovician (not including those guilds with no counterpart in the modern, shown in grey on the chart). This guild is also the second highest in abundance in the modern photic zone and buried environments, but third in the non-photic zone. 'Dissolution bryozoans' (G) and 'ichnofossils' (K) tie for third in relative abundance on the Ordovician shells. 'Dissolution bryozoans' account for a large part of the modern photic encrustation (second in relative abundance) but 'ichnofossils' are much smaller in relative biont abundance in this environment. 'Dissolution bryozoans' make up a small percentage of biont cover in the other two modern environments, and 'ichnofossils' are only important in the buried environment (fourth in relative abundance). These comparisons indicate a closer match, in rank order of abundance, between the Ordovician and the modern photic environment. This trend is opposite to that seen in the comparisons of mean whole shell percent area coverage.



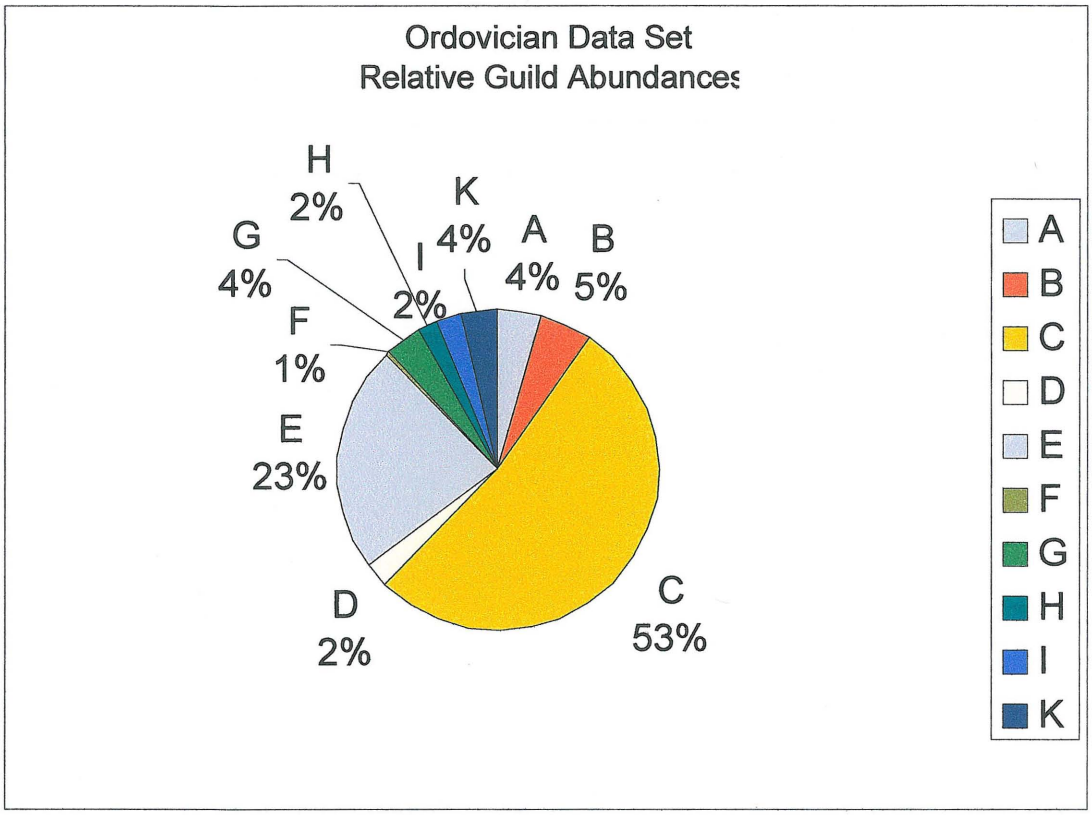

a)


Modern Data: Buried Environmen
Relative Guild Abundance
N 6%
B 13%
L 8%
C 1%
K 7%
F 12%
H 53%
B
C
F
H
K
L
N

b)


Modern Data: Disphotic Zone
Relative Guild Abundance
M 2%
B 7%
L 6%
C 3%
K 4%
D 6%
I 7%
G 18%
H 47%
B
C
D
G
H
I
K
L
M

c)




d)

**Figures 37.** Relative guild abundances for each modern environment and the Ordovician data set. The percent value refers to the percent of total guild coverage which that guild makes up. Letters in legend correspond to Guilds: **A**-Thin Crust, **B**-<1mm, **C**-1-2mm, **D**-2mm, **E**-8-10mm, **F**-Running Bryo, **G**-Dissolution Bryo, **H**-Serpulid and Solitary filterer, **I**-mollusc and brach <1mm, **J**-mollusc and brach 2mm, **K**-ichnofossil, **L**-photosynthetic diffuser <1mm, **M**-photosynthetic diffuser 2mm, **N**-photosynthesizer. All guilds found in only modern or only ancient data has been grayed. Shown in a) is the relative abundance of guild coverage in the photic zone. Guild H makes up the largest percentage of total encrustation, and guild B the second largest (not including photosynthetic guilds). Likewise, as shown in graph b) of the buried environment, Guild H account for most of the encrustation, with guild B in second. In the non-photic zone, graph c), guild H still accounts for the largest percentage of encrustation, but guild G is second to it. In the Ordovician data, graph d), the guild with highest relative abundance is guild C, and not including the outlier (guild E), guild B is second to it. Pie graphs normalize data, and low total percent area cover in the Ordovician is not apparent.

Finally, results of the analysis of guild richness in the combined Ordovician data set and the modern environments were compared (Fig. 38). The Ordovician data did not match any modern environment in a guild richness comparison; although it was most dissimilar to the photic zone and was relatively close in richness to both the buried and non-photic zones (which were not significantly different). Guild richness in the photic

zone is approximately twice as great as either other modern environment, and almost 8 times as large as the Ordovician data set.

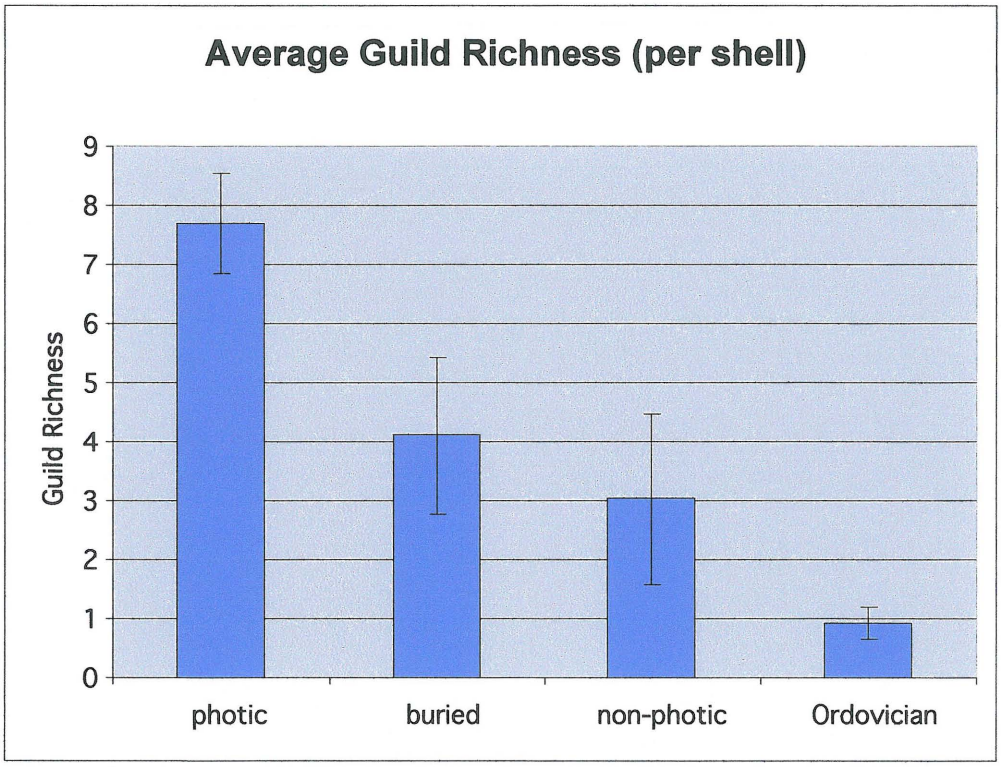



**Figure 38.** Comparison of mean guild richness (per shell) from Ordovician and modern environments (photic, buried, and non-photic). The Ordovician data do not match any modern environment, but are least similar to the photic environment. The buried and non-photic environments are not significantly different in this variable. Error bars are 95% confidence limits of the mean.

## Discussion

*Modern*

The results of modern data analyzed by depth (15m – 275m) indicated natural groupings of depths into photic, buried, and non-photic zones or locations (Fig. 9, 11, 17). While values of buried and non-photic data are similar, they were kept separate due

to results of previous SSETI research which indicated that degree of burial, in addition to depth (a proxy for light levels), is a primary taphonomic control affecting biont growth, particularly of skeletonized bionts (Parsons-Hubbard, 1999). Work by Martindale (1992) further justifies the grouping of modern depths into zones (15m combined with 70m and 192m combined with, 223m, 260m, and 275m). He found light to be the primary control on living assemblages of encrusting organisms. Despite widely different environments of deposition for each depth in the modern study (Table 1), sites at different depths within the non-photic zone were indistinguishable; sites within the photic zone were similar unless the shells had become buried. The buried site was kept separate. These groupings is justified by both the similarity in percent area coverage and species richness, as well as effects of burial and light on bionts (Martindale, 1992, and Parsons-Hubbard, 2001).

Salinity changes or temperature changes in ocean water with depth may also play a role in controlling biont coverage; however, a measurement of these variables along the BA transect during the time interval of this study show that both variables correspond roughly to the base of the photic zone (Fig. 39). While the cause of the changes in biont coverage and diversity cannot be known with certainty, and in fact, is probably controlled by all three, what is crucial to this study is that light, temperature, and salinity all change at approximately 100m, or with burial (in the case of light), and these changes are mirrored in the biont communities.

High percent cover in shallow depths is probably due to the presence of photosynthetic bionts, or organisms with photosynthetic symbionts. Other contributing factors may be higher water energy and turbulence (Fig. 10) and the presence of the picnocline at about the same level as the base of the photic zone (measured along the BA

transect during study interval; fig. 39). Percent cover at deep depths is relatively low, but diversity of biont morphospecies remains high.

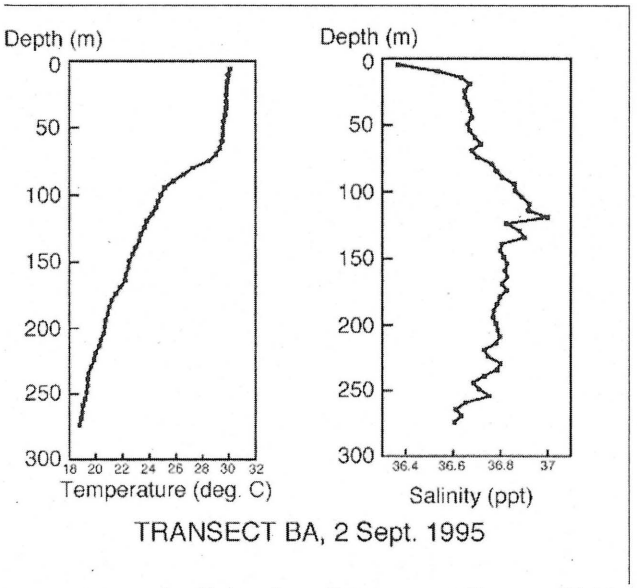



**Figure 39.** Gradient of temperature and salinity along BA transect. Parsons-Hubbard, unpublished data.

*Ordovician*

Results of the analysis of Ordovician data indicated that data from the three shell beds could be combined into one large Ordovician data set (Fig. 14, 16, and 20). Some significant differences were observed between data from the Ordovician layers, but for reasons outlined in the Results section, data was still combined. Although, the sample sizes used in the statistical analysis reflect only the variability within the data we collected, which was a relatively small sampling of the Tanners Creek Formation. More extensive sampling may result in smaller error bars and a more clearly homogenous Ordovician data set. An analysis of all fauna present in each shell layer, either for

percentage of each phylum or for species richness, could also provide some clues as to the legitimacy of combining these layers into one data set.

I could not find previous works that outlined legitimate reasons for the combination of fossils from separate beds into one data set; however, all studies I found that examined fossils used shells taken from outcrops without mention of specific beds in the outcrop. One study even used museum collections (Buss and Yund, 1988). Perhaps most important, the indication of transportation in the shell beds would argue against a separate environment of deposition for each bed. Non-overlap in error bars given transportation of material in beds may be random and not actually indicate significant differences in the beds. It may also be due to differences in transportation mechanisms. If transportation in one bed was a higher energy event than in another bed, the bionts on the shells in that bed may have experienced more breaking and fouling, leading to a taphonomic bias in the data, which would show up as differences in the beds by non-overlapping error bars.

*Comparisons by Guild*

Overall, a comparison of guilds of epibionts between modern and Ordovician shell data sets indicated a lack of correspondence of the data. Dissimilarity is inferred from both those results that clearly showed a wide difference in the data set as well as from the lack of consistent positive results between analyses. Given overall negative results, however, I believe that those positive results that were present may point simply to different environments of deposition in the modern and Ordovician, rather than a failure of the method used for comparison. The rest of this discussion will detail

interpretations of each analysis that led to the overall conclusion of negative results, but will also explore some of those similarities that did show up, possible biases in the data, and finally, a discussion of what the negative results can tell us.

Before a discussion of each analysis, one complexity involved in data interpretation should be outlined. Ordovician data was compared to modern data that was organized by "environment". Distinctions between environments fell naturally out of the results of modern data; however, the distinctions create complications for analysis. Two of the environments are distinguished on the basis of a single variable, light. The third environment, "buried", could occur in either a photic or non-photic depth. Yet, this complication can be resolved to some degree. First, burial created a difference in the results of modern data and therefore was acting as the primary control, or at least above the light factor. Second, if results of ancient data were to match with, for example, the photic zone and the buried zone in different analyses, then it could be interpreted as having experienced some degree of burial at a photic depth. If it only matched with the buried results, however, one could not determine whether it was buried at a photic or non-photic depth.

Comparison of the modern and Ordovician systems by percent area covered by different guilds does not consistently produce similarities between the Ordovician and any one modern depth zone or site (Figs. 24-31). There are guilds for which the Ordovician and modern environments overlap, however, the specific matching guilds change with the modern environment being compared. Filter feeders less than 1mm are not significantly different in percent area coverage between the Ordovician and the modern "buried" environment (Fig. 25). Yet when the guild being compared is bryozoa

that dissolve shell surface, the Ordovician overlaps with the non-photic zone (Fig. 28), and when the guild is "ichnofossil," it overlaps with the photic zone (Fig. 30). Overall, the Ordovician matches the modern buried environment for percent area covered by two guilds (B and H), and with the non-photic environment it matches with only one guild (G). The Ordovician data for percent area coverage only matches the modern photic zone for the ichnofossil guild. Ichnofossils may provide a somewhat less reliable percent area coverage value precisely because only a trace is preserved. The filtering portion of the organism could take up far more space than the trace alone. For these reasons and others, McKinney (1996) argues that ichnofossils should not be used in comparative biont studies. I think the abundance of ichnofossils on both modern and ancient shells warrant retaining the guild in my analysis, but since the only guild for which the modern photic zone is similar to the Ordovician is the ichnofossil guild, it is important to be cognizant of the shortcomings of this guild. While the Ordovician does not compare well with any modern environment, overall, based on comparisons of percent area coverage, the Ordovician seems to be most comparable to a combination of the modern buried and non-photic environments.

Bryozoan guilds were analyzed together because it is the one set of guilds that is very similar between the Ordovician and today in functional morphology. The zooid shape, form, and encrusting patterns have changed relatively little over the past 400 million years (Photos in Appendix), and therefore the comparison of these guilds should be more relevant than comparisons of other guilds. The lack of a match between the Ordovician and any modern environment in bryozoa percent area coverage is perhaps more telling than analyses of other guilds.

A presence/absence comparison of the modern and Ordovician biont guild data (i.e. frequency of guild occurrence on shells) provides a different result from either of the other two comparisons thus far (Fig. 36). The Ordovician is more similar to the photic zone than to either of the other two environments when analyzed for this variable. The photic zone was a better match to the Ordovician even when buried and non-photic data were combined. An analysis for presence of a guild on shells from a certain environment is perhaps more useful than an analysis of percent cover because taphonomy can create a bias in guild coverage. Because guilds are partially classified by height above substrate and partially by bauplan of the biont, during processes of preservation and lithification, whole guilds of bionts may be more or less likely to be preserved. For example, thin crust colonial filter feeders are more likely to be obscured by sediment, while colonial filter feeders 8-10mm off the substrate are more likely to be broken off. A reduction in percent area coverage might not entirely remove a guild. At least one specimen of any single guild has some chance to make it through the fossilization process, even if most specimens are destroyed or hidden; therefore, while a percent area coverage analysis would indicate a much smaller representation of the guild, a presence/absence analysis would be relatively free of this taphonomic bias. However, mean frequency of guild occurrence on shells would average the data and retain that preservational bias. Even still, the bias would not be as great in this analysis as it is in percent cover or even guild richness analyses. Thus, the resulting match between the Ordovician and modern may have some validity, although this analysis did not produce an overall match between the Ordovician and any one environment.

Guild richness was also used to compare the Ordovician and modern biont data. Average guild richness (per shell) was significantly different between the Ordovician and all modern environments. It was closest to the modern photic zone, but the differences were still too great to make them comparable. Of course, the value for the Ordovician is an average that includes all the non-encrusted shells, resulting in an average guild richness of less than one. Since all modern shells were encrusted, these values are quite different. While this difference is explainable by the presence of non-encrusted shells in the fossil data set, it should not be analyzed for only encrusted fossil shells, because the un-encrusted shells are legitimate data points reflecting the environment in which they lived. No data is data in this situation, unless this is another trend resulting from a taphonomic bias operating between guilds.

A final comparison of relative abundance of biont data indicates a higher degree of similarity between the Ordovician data and the photic zone than the Ordovician and any other modern environment, but again, overall they are dissimilar. The relative abundance data cannot be subjected to a Students T-Test, therefore, these similarities cannot be analyzed for significance, but it is readily apparent that the values are still highly different. Relative abundance data, while argued by Daley (2002) as being a highly useful variable for comparisons of fossil assemblages, here proves useful primarily as a visual comparison of biont data. Also, because the data in relative abundance graphs are normalized, the low percent cover of Ordovician data is lost.

It is clear that each of these guild comparative analyses demonstrates some similarities between the Ordovician and different modern environments (Table 6). The photic zone is indicated in some, a crossover between non-photic and buried is indicated

in another, and some show no similarities at all. The question then becomes, does one analysis trump the others? As mentioned earlier, analysis by presence or absence of guild is more likely to be free of taphonomic bias, and analysis of percent cover of bryozoans may be more comparable across a long span of geologic time. Both of these analyses indicate no correspondence between the grouped Ordovician data and the modern data, regardless of the modern environment chosen for comparison. Even a cross of buried and non-photic modern environments did not yield values comparable with the Ordovician for the presence or absence of guilds per shell (Fig. 36). This may partially discount the results of the test of percent area covered by guilds that indicated a cross of buried and non-photic modern environments as being the best match to the Ordovician data. Regardless of which modern environment seems to be indicated as a better match above the other modern environments, overall, none of the modern data matches well with the Ordovician data.

**Table 6.** Summary of results of guild comparisons with Ordovician data. Those guilds that best match the Ordovician data for a given analysis are shown in cells. For example, the Filter Feeding Colonial <1mm guild is not significantly different between the buried modern environment and the Ordovician environment when analyzed for percent cover. Note the lack of a consistent pattern in guilds with depth or with analysis. Also, only percent cover analyses and relative abundance analyses indicate that no modern environment matches the Ordovician data. Photic seems to be a better overall match to the Ordovician than all other environments, although the ichnofossil guild should be treated with caution as an indicator similarity over a gap of 400 million years.

| | **Buried** | **Non-Photic** | **Photic** | **No Modern Env.** |
|---|---|---|---|---|
| **% Cover** | 1) Filter Feeding Colonial <1mm<br>2) Serpulid and Solitary Filter 1-2mm | 1) Dissolution Bryozoan | 1) Ichnofossil | 1) Filter feeding colonial 1-2mm<br>2) F.F. Colonial 2mm<br>3) Running Bryo<br>4) Mollusc and Brach<br>5) Total Bryozoan |
| **Frequency** | 1) Running bryozoans | 1) Filter Feeding Colonial 1-2mm<br>2) Dissolution Bryozoan<br>3) Serpulid and Solitary Filter 1-2mm | 1) Filter Feeding Colonial <1mm<br>2) F.F. Colonial 2mm<br>3) Mollusc and brach.<br>4) Ichnofossil | No match |
| **Other** | No match | No match | Total number of shared guilds | Relative Abundance (Not definitive) |

Other biases to the data in both the modern and Ordovician should be considered before a conclusion about the correspondence of one modern environment with the Ordovician data is drawn. First, *Mytilus edulis* have a periostracum, a proteinaceous shell covering, which has been hypothesized as functioning specifically to deter biont settlement and growth. The *M. edulis* shells used in the modern data set were dead and disarticulated before deployment. While the periostracum was preserved in many of the shells in lower energy environments, it was destroyed in the shallower, higher energy environments. This could have resulted in higher values for biont growth in the photic zone, with the exception of the buried site, in which the periostracum was always preserved. A bias towards larger percent cover by bionts in the photic zone decreases the

similarity between the photic and the Ordovician in four of the guilds, yet it increases the similarity in four of the guilds as well. So a periostracum on the dead *Mytilus edulis* shells does not bias the data in one direction. It is not known whether or not *Rafinesquina alternata* had a periostracum, as it is made of non-preservable proteinaceous material; however, as they are members of a different phylum than *M. edulis,* it is unlikely that they did. Additionally, several factors point to biont growth on *R. alternata* occurring after death of the host organism; therefore, even if a periostracum were present, it would not be re-grown after death and would not inhibit biont settlement. The factors that indicate encrustation after host organism death are the lack of clear organization of bionts by shell area (Fig. 17), a characteristic cited by Fagerstrom (1996) as being an indication of biont growth on a live shell, and research done by Richards (1972) that suggest that shells were flipped and exposed for a length of time after death and before burial. A periostracum on either the modern or ancient shells does not bias the data significantly in any direction.

Size of the data set for modern buried environments also could contribute to the negative results. Because only the 33m depth was buried, the size of the data set was much smaller than for either the photic or non-photic zones. This resulted in larger error bars and therefore overlaps with the Ordovician error bars in some cases. It is possible that if more shells were a part of the buried data set, the size of error bars would decrease and there would be no overlap between the Ordovician and this depth. Of course, it is also possible that if more shells were used in this data set, the values of biont cover would change, yet still overlap with the Ordovician. Based on personal observation of the

consistency of biont cover within all shells from the 33m depth, I think it unlikely that this would be the case.

Finally, it is important to realize that the depths that fall within the photic zone off the coast of Lee Stocking Island, Bahamas, are different than those that fell within the photic zone during the Ordovician in the region that is now Indiana. The water in the Bahamas is relatively clear, and the true photic zone extends down as far as 100m, and is disphotic to 300m. In muddier water, much shallower depths may not receive light. The Taconic Orogeny led to production of siliciclastic sediment deposited in the Richmond Group; however, as discussed by Richards (1970), sedimentation rate in the Richmond was thought to be relatively low. Yet, he also notes that *R. alternata* were adapted for life on muddy bottoms, so some decrease in light, even at shallow depths, seems likely. This only points out that one shouldn't expect the depth values between modern and fossil systems to correspond, as environments do not always correlate with depth.

In summary of the above discussion, the epibiont communities present on *Rafinesquina alternata* do not seem to correspond to epibiont data from modern environments (photic, buried, and non-photic) when analyzed by species, morpho-species, or even guilds of bionts. When different variables are analyzed, different results are found, and sources of error are not sufficient to explain inconsistencies. The most reliable analyses indicate a lack of correspondence between the Ordovician and any modern environment.

Several possible explanations could account for the source of these negative results. Are there changes in either preparation of fossils or analyses that could have been made to provide more accurate results? Are there other factors either of the environment,

the bionts, or the taphonomy that we did not account for? Was the environment experienced by the *Rafinesquina alternata* bionts simply different than any of the three modern environments? Are analyses of living assemblages not possible over a 400 million year time span, even when analyzed by guilds of bionts that are not dependent upon taxonomy?

The process of cleaning fossils was done carefully, by hand or with paintbrushes and toothbrushes. No obvious damage, such as scratching or abrasion, was done to any of the shells. Some sediment remained on shells due to these gentle cleaning techniques, and may have obscured bionts, as discussed in methods. Percent area coverage values were visual estimates, but the same method was employed in collection of modern data, so this should have biased the data in one direction for both data sets. Variables used in comparisons of modern and ancient data were relatively complete, and included presence/absence of guild, percent cover by guild, relative abundance by guild, and guild richness. Other variables for interactions between guilds or frequency of occurrence of individuals could have been also been used, but these are of secondary importance and are subject to significant sources of error during preservation and data collection. Changes in preparation and analysis are unlikely to account for the negative results of this study.

Factors of the Ordovician environment that bias the data could certainly exist; however, simply using past research on the Ordovician environment is not always useful because conclusions about the ancient environment are often drawn from these same types of data. Other factors of fossil biology unaccounted for in this study may affect our conclusions; however, it is unlikely that something like the filter-feeding area per

bryozoan zooid would change its guild classification. The comparisons with the modern data should still be valid. Finally, taphonomic processes, as mentioned earlier, certainly could impact our results, as they operate differentially between guilds. The analysis of guild presence / absence lessens the taphonomic bias, and yet results of this comparison still did not indicate any matches between the Ordovician and modern environments.

Two central questions remain. The first is whether negative results in this case are results themselves: did the *Rafinesquina alternata* shells simply experience an environment unrepresented in the modern data set? As discussed in the methods section, previous researchers have concluded that the Tanners Creek Formation represents a shallow marine environment experiencing a relatively slow sedimentation rate of mixed terrigenous / carbonate material. Fox (1968) and Ford (1967) believed the environment was within the photic zone, based on faunal assemblages. The difference in sediment type is a large environmental difference because terrigenous sediment often has adsorbed nutrients. The difference in the slope of the ramp or bottom is likely large, being shallow in the Ordovician and steep in the modern. So, the results of my analyses actually confirm the results of other researchers. The modern and the Ordovician environments were different. Some aspects of the environment, however, were similar. It seems likely that some degree of burial occurred in the Ordovician based on knowledge of a muddy bottom type (Richards, 1970). Those analyses that indicated a match with the modern buried site may be reflecting this similarity. Likewise, muddy water in the Ordovician would cut down on light penetration and those matches with the modern non-photic may be reflecting this environmental similarity. For this reason, I believe that the results of this study indicate both that none of the modern environments used were similar overall

to the Ordovician environment, and that the method of guilds as a paleoecological tool shows promise.

Finally, the question that is also a fundamental goal of this study: is it possible to make comparisons of guilds of bionts across a gap of 400 million years? While the negative results of this study may lead one to abandon the idea, I do not believe we should do so. The fact that a number of guilds were not significantly different across this gap in percent area coverage, richness, and relative abundance is encouraging. The problem does not lie in the incomparable nature of the data sets, rather, because the environment experienced by the Ordovician shells was likely different than the environment experienced by the modern shells, in any of the three environments, an exact match should not be hoped for. What would be interesting for further research would be an analysis of modern data for environmental factors that seem to control either percent area coverage or richness primarily. If it is known that certain environmental factors lead to certain trends in biont data (as opposed to whole environments leading to these trends), than even though the results of an analysis of percent coverage may differ from results of richness, these differences themselves may be attributable to differences in the environments. Or at least it could be known whether one set of analyses 'trump' another, and therefore environmental analysis should be done using only one variable for comparison. Or, a modern data set from a shallow, muddy sea bed could be used instead of a data set from a tropical reef setting. In general, an accumulation of data from diverse modern environments will offer a greater chance of positive results in comparisons to the Ordovician data.

While the shear number of variables that affect living assemblages, let alone fossils of once living assemblages, is vast, I believe comparisons of paleocommunities by guilds may allow environmental comparisons. Results of this study do not indicate the failure of the method but the need for consideration of the interplay of environmental factors and biont growth, as well as accumulation of modern data sets from a wide range of environments. Additional future research could also include a study of the effects of transportation of shells on epibionts. If some standard value for the resulting decrease in biont cover could be determined, it could be used to normalize the data and make degrees of encrustation between the Ordovician shells and modern shells more comparable. If no consistent value resulted from such research, an alternative study could be done with a data set restricted to fossils buried in life position.

## Conclusion

The use of guilds in a comparison of modern epibionts on *Mytilus edulis* shells and Ordovician epibionts on *Rafinesquina alternata* shells did not result in a match between the Ordovician and any one modern environment (photic, buried, and non-photic) from the Bahamas. These negative results are not a result of failure of the method, the use of guilds of bionts, used in comparisons. It is more likely that the modern data simply do not come from a comparable environment to the Ordovician. The use of guilds of bionts shows promise as a tool in paleoenvironmental analyses over long spans pf

geologic time, but large data sets must be accrued from a wide range of modern environments in order to have the breadth needed for realistic comparisons.

**Thanks**

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## Appendix I

An algorithm was used to convert percent area coverage values of shell area into whole shell percent area coverage values, for both *Rafinesquina alternata* and *Mytilus edulis* shells. For *R. alternata* I estimated the umbo (1A and 1B) to be 10% of total area of one valve. The edge (2A and 2B) I estimated to be 25% of each valve. The middle of the shell (3A and 3B) I estimated as occupying the remaining 65% of the area of the valve. Given that the whole shell is 100%, the pedicle valve (Side A) is 46%, the brachial valve (Side B) is 46%, and the interarea is the remaining 8%.

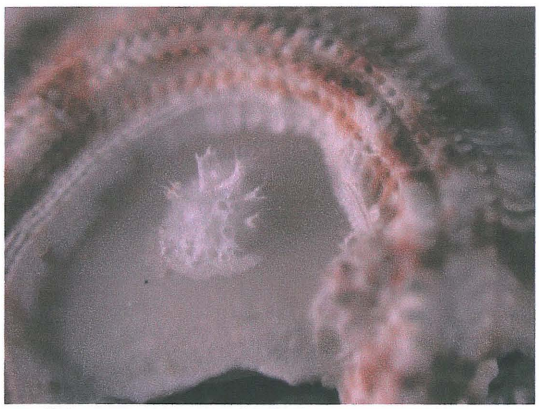
*Mytilus edulis* shells were estimated as having the umbo (1A and 1B) occupying 7% of either the outside or inside of the valve. The edge was broken into three separate areas for collection (Fig. ). Area 6 and 8 (A or B) I estimated as each being 5% of the total valve area. Area 7 (A or B) was approximately 3% of the total valve area. The middle of the valve (XA or XB) accounts for the remaining 80% of the valve area. As *M. edulis* does not have an interarea, the whole shell (100%) is made up of a 50% contribution by the outside of the valve (A) and 50% of the inside of the valve (B).

## Appendix II

An example of bionts from a subset of guilds for both the modern and Ordovician are pictured. These are not a complete set of biont photos.

*Modern Bionts:*

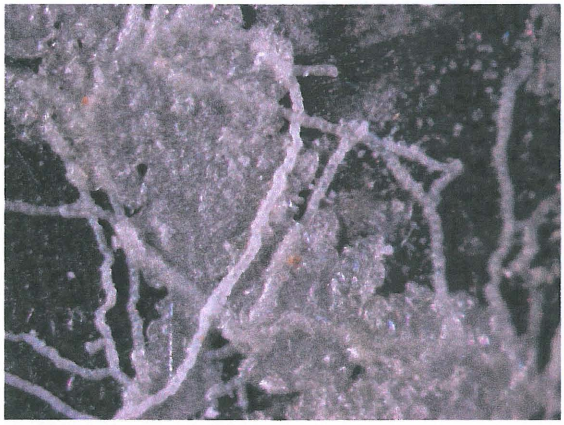
Guild B: *Cribrilaria radiate*



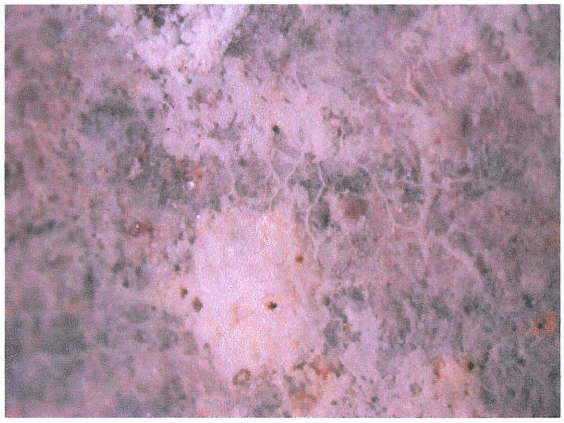
Guilds C,H: *Disporella* & 'brown stripe' serp.

Guild L: *Planorbulina*, Periostracum visible.

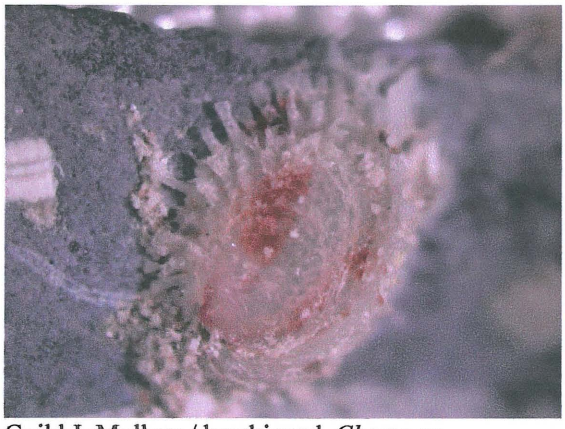
Guild M: *Homotrema rubrum.*



Guild N: Photosynthesizer <1mm
Thin branch and perforate.



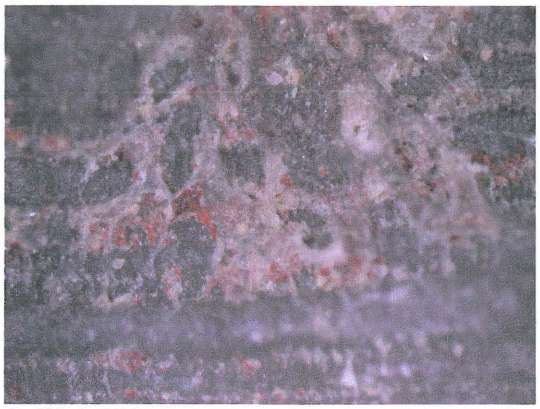
Guild N: Photosynthesizer <1mm
General shot of coralline encrusted surface.



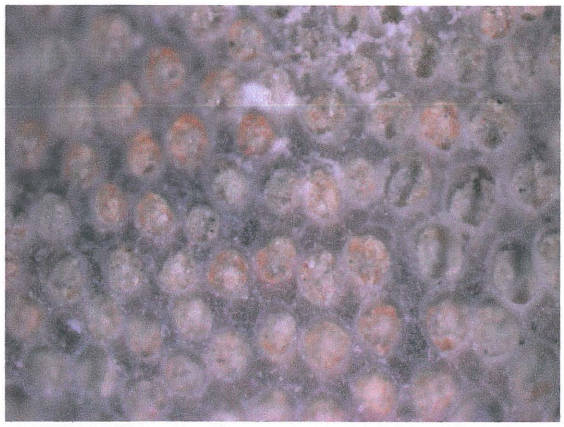
Guild J: Mollusc / brachiopod. *Chama sp.*

Multi-Guild Photo: Serp, foram, non-preservable
Flasks and bryozoan colonies pictured.

*Ordovician Bionts:*

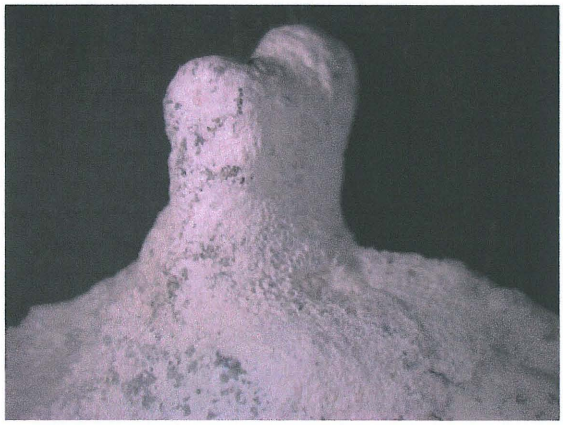


Guild A: Thin Crust Bryo, Bryozoan A

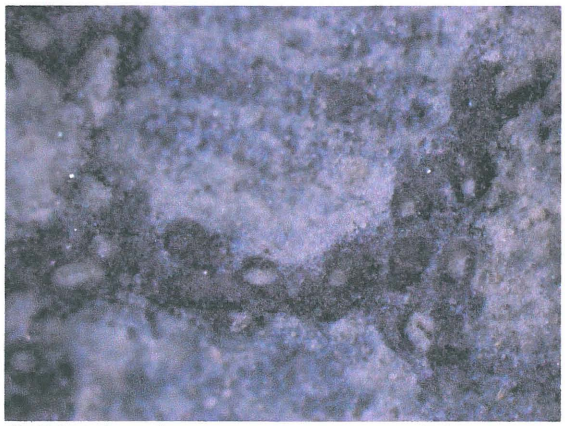


Guild B: Filter Feeding Colonial <1mm off surface, *Halopora elegantula*

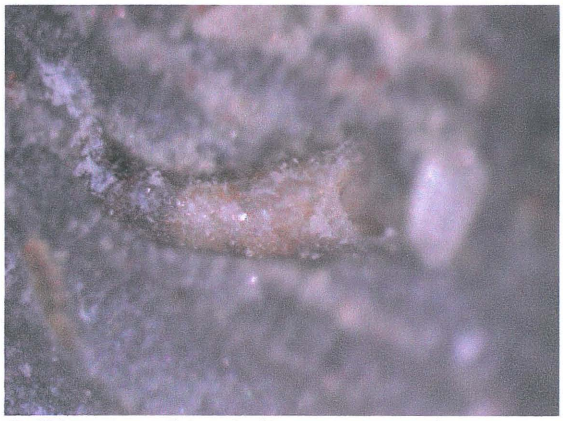
Guild B and C: Filter Feeding Colonial <1mm and 1-2mm, Bryozoa B and C



Guild E: Filter Feeding Colonial 8-10mm off surface, Bryozoan E.

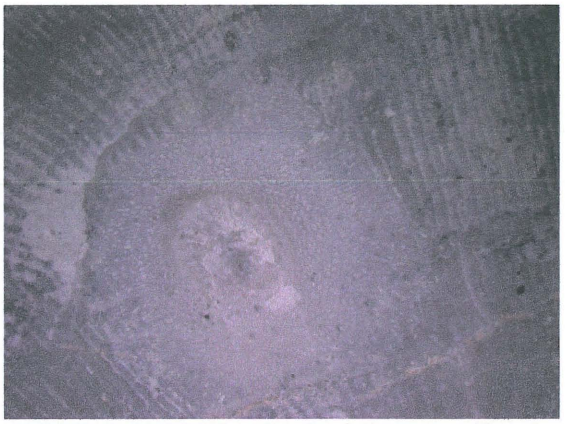


Guild F: Running Bryo, *Stomatopora dichotoma*

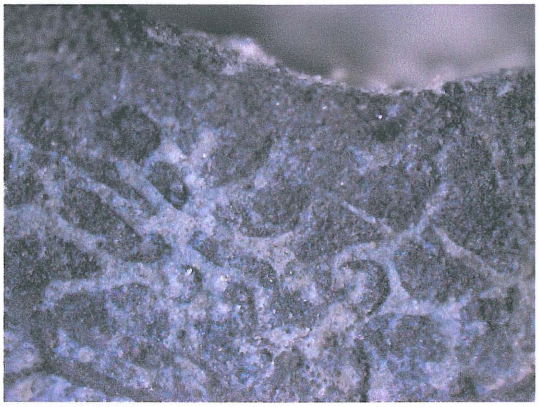


Guild H: Serpulid and Filter Feeding Solitary *Cornulites richmondensis*

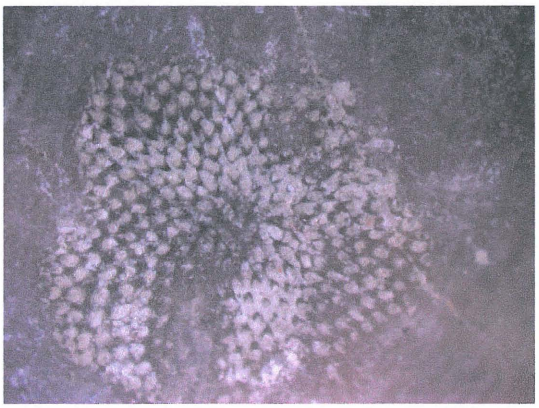
Guild I: Mollusc and Brachiopod,
*Petrocrania scabiosa*



Guild C: Colonial Filter Feeder 1-2mm up off surface
Bryozoan F



Guild G: Dissolution Bryozoan
Un-ID'd ctenostome bryo.



Guild C: Colonial Filter Feeder 1-2mm off shell
*Diastoporina flabellate*

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