GEOSPATIAL ANALYSIS OF ECOLOGICAL ASSOCIATIONS AND SUCCESSIONS IN MIDDLE
DEVONIAN BIOHERMS OF THE GREAT LAKES REGION

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ABSTRACT

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Corals and stromatoporoids often built biohermal complexes, which preserve intrinsic and extrinsic controls, dictating reef development. Devonian bioherms from the Appalachian, Michigan, and Illinois Basins were evaluated to compare community compositions and detect similarities between successional buildups and localities. Species abundances, environmental parameters, and successional models described reef morphology and development within and between basins. Localities were analyzed by taking photographs, documenting environmental parameters, and identifying corals to a species level. Photographs included 1m² quadrats, used in Coral Point Count with Excel extensions (CPCe) to acquire total percent of coral species and stromatoporoids as a proxy for abundances. Data matrices were created to run diversity indices, cluster analyses and multivariate techniques to interpret intrinsic and extrinsic controls affecting bioherms. Intrinsic factors, include species present and community interactions between organisms. Extrinsic controls such as lithology, grain size, and environmental energy, largely affect the construction of reefs. Documentation of coral-stromatoporoid complexes revealed geospatial and temporal trends across the Great Lakes of North America. Cluster analyses demonstrate extrinsic controls such as biogenic carbonate texture and basin type dictate community composition. Ordination techniques revealed the importance of lithology, biogenic carbonate texture and substrate type as the driving forces during reef development. Investigation of bioherms in the Great Lakes region were used in a comparative approach to recognize spatial and temporal trends, providing a better understanding of reef ecology, biodiversity, and evolution during the supergreenhouse climate of the Middle Devonian.

I would like to dedicate this thesis to my loving husband, Kevin, for his endless support to follow my dreams. I would also like to thank my family and friends for their kindness, patience, and dedication throughout graduate school. Without their love and cherished support, I would not have completed my educational journey and be where I am today.

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CHAPTER I. INTRODUCTION

The Middle Devonian was a critical time for reef expansion that led to many preserved paleocommunities across North America, specifically within the Great Lakes region. These rock units represent an interval of non-glacial greenhouse deposits that are primarily subtidal ramp and platform carbonates with mixed deposition of siliciclastics and carbonates (Brett et al., 2011). The Devonian is colloquially known as the “age of the corals” due to the overwhelming abundance of corals and stromatoporoids in shallow restricted or open ocean settings (Goldstein, 1985). Mid-Paleozoic reefs show major expansions in latitude, thickness, and areal extent of organic buildups. Many reef complexes from the Emsian to the Givetian were larger than the biggest reef today, the Great Barrier Reef of Australia. These dynamic stromatoporoid-coral metazoan reefs may display fundamental differences in reef development and skeletal building. These sedimentary basins in Eastern North America provide latitudinal and temporal gradients for comparison (Copper, 1994).

A lack of polar ice during the Eifelian kept the shallow waters warm and hermatypic corals were able to extend throughout tropical habitats, making North America an ideal location to study the structure of bioherms from the Paleozoic (Martin, 2002). Bioherms refer to biogenic structures characterized by an accumulation of biomineralized material with limited internal structure. These organic accumulations can vary from small patch reefs to large reefal communities with topographic relief (Reid, 1994). More generally, reefs are any three-dimensional accumulation of marine organisms, and are favored in passive margin settings with open circulation and sufficient nutrients (Copper and Scotese, 2003). The biogenic structures in the mid-Paleozoic were primarily constructed by stromatoporoids, rugose and tabulate corals; these groups originated in the Ordovician and remained diverse throughout the Silurian and into

the Late Devonian. The Eifelian to the Givetian stages during the Devonian represent a pivotal time of reef growth and development. They mark the peak in Phanerozoic reef development, before the Famennian crash of stromatoporoids and corals, which were later replaced by calcimicrobial reefs (Copper and Scotese, 2013). Copper (1994) showed on a global scale that reefs did not die out at extinction events, including the Early Cambrian, Late Ordovician and Late Devonian, but approximately 0.5 to 1 million years prior, suggesting reef ecosystems are sensitive to environmental changes. Studying Middle Devonian corals and stromatoporoids before the crash of metazoan reefs will therefore help identify parameters that affect biohermal construction, including environmental conditions and biological factors.

Reefs have been around for over 3.5 billion years and have responded to environmental factors affecting growth and zonation (Wood, 2011). Today reefs are a high priority for researchers investigating the effects of global warming by considering growth, successional changes, and overall community function occurring in modern reef ecosystems. By observing past reef ecosystems we can make prediction of threats to modern reef ecosystems. We can advance our understanding of biotic responses to climate change by focusing on controlling factors of reef development in ancient ecosystems. During globally warmer periods reefs show high-latitude distributions, are less isolated, display different species, and may have significantly different construction types and shapes (Kiessling et al., 2002). Given what we know from warm time intervals, we can focus on the geospatial and temporal distributions of corals and stromatoporoids that reflect these characteristics.

Despite the Middle Devonian being a time of great reef expansion, the ecology and evolution of small bioherm communities are not well documented, in North America. These epicontinental basins may display fundamental differences in reef development and skeletal

building. In this study, investigation of the bioherms of the Appalachian, Michigan, and Illinois Basins is used in a comparative approach to document spatial and temporal trends in order to provide a better understanding of reef ecology, biodiversity, and evolution during the supergreenhouse climate of the Middle Devonian. The fossil reefs of interest provide key insights regarding the interactions between species during the building process, how physical parameters affected vertical zonation, and whether the buildups were mediated by allogenic or autogenic factors during this period.

CHAPTER II. PREVIOUS WORK

Geologic Setting

Factors such as tectonics, subsidence, and sedimentation can affect reefal buildups and how they develop, and therefore produce basinal differences that may affect bioherm communities. During the Devonian, eastern North America was part of Laurentia, which was colliding with the Avalon continent producing the Acadian Orogeny. This resulted in mixed deposition of siliciclastics and carbonates to the west (Brett et al., 2011). The tectophases of the Acadian Orogeny triggered subsidence associated with tectonic loading, which divided eastern North America into several subbasins (Figure 1) (Brett et al., 2011).

The Appalachian Basin represents a foreland depression while the Michigan and Illinois are intracratonic. The convergent plates, creating the Acadian Orogeny, produced deformation to the west; causing depression and flexuring of the continental crust (Einsele, 1992). The Appalachian foreland basin was created on the craton side, parallel to the mountains due to isostatic adjustments from mountain movement and uplift (Einsele, 1992). The intracratonic basins are found on continental margins and form from weak lithospheric crusts shifting downward (Einsele, 1992).

Recent paleomagnetic data place eastern North America (the Great Lakes region) approximately 35° south of the equator during the Middle Devonian (Brezinski et al., 2008). The semi-restricted basins during supergreenhouse conditions extended the range of several reef building species to latitudes 65° north and 55° south of the equator, due to warmer currents and upwelling nutrients (Copper and Scotese, 2003). By contrast, modern reefs are confined to less than 30° latitudes according to Copper and Scotese (2003).

Figure 1: Paleogeography of Middle Devonian North America. Sedimentary basins and tectophases of the Acadian and Caledonian Orogenies are labeled. Modified from Blakey (2016).

Regional Stratigraphy

Depositional sequences and correlations of units across the Appalachian, Michigan, and Illinois Basins from the late Emsian to the Givetian stages are shown in Figure 2 with field locations displayed in Figure 3. The Appalachian Basin was mainly a carbonate setting during the early Eifelian, which is represented by the Onondaga (Limestone) Formation. Deposition shifted to siliciclastic-dominated units in the overlying Marcellus Subgroup of the Hamilton Group, as siliciclastic sediments were shed from the Acadian orogeny (Ver Straeten et al., 2011). The Marcellus Subgroup contains the Union Spring Formation and Oatka Creek/Mount Marion Formations, which are represented by limestones interbedded with shale deposits, marking deep-water facies. The overlying Skaneateles Formation shifts from fossiliferous shell-rich carbonates to alternations of black shales and mudstones (Brett et al., 2011).

The Appalachian Basin was studied near its northern extent in Marblehead, Ohio at the Lafarge Marblehead Quarry. Marblehead stratigraphy starts with dolostones of the Lucas Formation within the Detroit River Group. The Columbus Formation follows with mostly limestones and interbedded chert. Bailey (1968) interpreted the relationship between the Detroit River Group and the overlying Columbus Limestone as a transgressive sequence in a marginal sea resulting in open ocean sedimentation. The depositional environment of the Columbus Limestone was normal marine subtidal conditions (Pieton, 1996). Following the Columbus Limestone, the Delaware Formation outcrops in several areas and records the transition from the Eifelian stage to the Givetian stage. The Givetian sequence ends with the Plum Brook and Prout Formations. The Appalachian Basin was connected to the open ocean, the Rheic Sea, and was divided from the intracratonic Michigan Basin by a higher topographic feature, the Findlay Arch (Figures 1, 3).

The Michigan Basin included study areas from two northern sections near Alpena, Michigan and a third site near Whitehouse Quarry in northwestern Ohio. The northern Alpena location consists of the Eifelian Detroit River Group with the Sylvania Sandstone and the younger Lucas Dolomite units (Sparling, 1985). Overlying the Detroit River Group is the Dundee (Limestone) Formation, a highly fossiliferous unit that contains the Rogers City and Reed City Members. The Dundee is described as a graded-upward sequence with lighter coarse-grained limestones to darker fine-grained limestones associated with scattered chert found near the margins of the basin (Gardner, 1974). Following the Rogers City Member, the Givetian is represented by several transgressive and regressive cycles in the Bell Shale, Rockport, Genshaw-Ferron Point, Newton Creek, and the younger Alpena Formations (Janssens, 1970 and Brett et al., 2011). Near Whitehouse, Ohio, the stratigraphic sequence demonstrates minor differences compared to the northern Michigan localities. The Eifelian includes the Detroit River Group and the younger Dundee Formation, which is followed by a large unconformity (missing the late Eifelian and early Givetian). The Silica Shale and Blue Limestone make up the remaining Givetian stage and are equivalent in age to the Plum Brook Formation from the Appalachian Basin. The Michigan Basin is divided from the Illinois Basin by a higher topographic feature, the Kankakee Arch, which may have been breached during high eustatic sea level (Figure 3).

The Illinois Basin includes several locations that were analyzed, including the Falls of the Ohio in Clarksville, Indiana, and two sites within Kentucky, Fork Bear Creek (Bear Creek) and Champions Trace near Louisville, Kentucky. The Emsian and early Eifelian are represented by the Jeffersonville Formation, which is made up of limestones with intertwining coral beds that unconformably overlie Silurian strata (Hendricks et al., 2005). A large unconformity of middle Eifelian age separates the Jeffersonville from the Sellersburg (North Vernon) Formation. Clastic

mudstones and limestones are dominant, representing the Speeds, Silver Creek and Swanville Members within the Sellersburg Formation. The top of the Sellersburg Formation is marked by a large unconformity of middle Givetian age. The Illinois Basin is separated from the Appalachian Basin by a topographic high, the Cincinnati Arch (Figure 3).

All three basins underwent constant shifting from coral-stromatoporoid carbonates to alternating siliciclastic organic-rich shale deposits (DeSantis et al., 2011). The basins represent restricted and open ocean environments that may have different sea level histories, resulting in localized variations in reefs rather than global eustatic sea level (Corlett and Jones, 2011a). The variations in depositional environments, tectonics, eustatic sea level changes, and sea chemistry affected fauna assemblages and reefal complexes in each basin.

Economic Geology

Historically the Middle Devonian units within all three basins have been studied by oil companies seeking potential oil reservoirs (Curran and Hurley, 1992). These formations do contain oil, but it is often too costly and difficult to extract (Wright, 2006). Rock quarries deployed the use of the limestone formations for building stone and cement. Since the 1900s, the limestone has provided agricultural lime as well as crushed gravel and aggregate for concrete (Conkin et al., 1998). The Lafarge Marblehead Quarry in Ohio and the Besser Museum in northeast Michigan (which received blocks donated by Lafarge Alpena Plant and Specification Stone Products of Alpena) show prime examples of Middle Devonian rocks with coral and stromatoporoid buildups.

Stage	Conodont	T-R Cycles	Indiana	Michigan	Ohio		New York	Relative Sea Level		
			Southeastern	North Central	Northwest	North Central	Central			
Givetian	<i>ancinus</i>	IIal	Blocher	Thunder Bay	"Little Rock Creek"	Prout	Tully Formation			
		Ii	Portwood	Potter Farm			Moscow Formation			
		Ih		Norway Point						
	<i>rhencus</i>		Beechwood	Four Mile Dam	Tenmile Creek	Prout	Moscow Formation			
				Alpena Formation			Ludlow Formation			
		Ig	Beechwood	Newton Creek			Tenmile Creek		Prout	
	<i>timorensis</i>			Genshaw-Ferron Point	Silica Shale	Plum Brooke	Skaneateles Formation			
		If	Swanville	Rockport Quarry			Blue Limestone		Blue Limestone	Oatka Creek Formation
			Silver Creek	Bell Shale					Delaware Formation	Union Springs Formation
	<i>hemitrematulus</i>		(Deputy)	(Halihan Hill)						
Ie		Speeds	Rogers City Formation							
<i>enz.</i>										
	<i>koekeliannus</i>									
		<i>auriculatus</i>								
<i>coztatus</i>				Jeffersonville Formation	Dundee Formation	Dundee Formation	Columbus Formation		Onondaga Formation	
	<i>patulus</i>									
Emsian										

Figure 2: Stratigraphic Units for the Middle Devonian of Eastern North America. Conodont zonations (left) modified from DeSantis and Brett (2011) and Brett et al. (2011). The Middle Devonian sea level curve on the right shows an overall sea level rise from the Emsian to the Givetian, modified from Aitken et al. (2002).

Figure 3: Locations of Field Sites. Paleogeographic basins and topographic highs are indicated. Note that Besser Museum and Rockport Quarry in northern Michigan and Champions Trace and Fork Bear Creek in Kentucky are designated by single points.

Paleontological Background

Michigan Basin

Two formations within the Traverse Group were observed, the older Rockport Formation and the younger Alpena Formation. During the Middle Devonian the Michigan Basin was located approximately 25°-30°S of the paleoequator and was a closed basin with limited ocean access. Occasionally the isolated basin was breached during high sea level periods through the Findlay Arch in Ohio and the Kankakee Arch in Illinois (Edinger et al., 2002). Although this basin was mostly secluded, it provided an ideal habitat for several large reefal communities as well as small biohermal buildups.

Older reefs within the Rockport Formation have been previously observed by Cookman (1976) and Spruit (1981) near Alpena, Michigan. The dark organic muds contain overturned and *in situ* *Hexagonaria*, *Favosites*, and several solitary rugose corals (Cookman, 1976). The shale lenses interbedded in limestones are associated with low to moderate energy on a shallow marine carbonate platform with high faunal diversity and composition (Cookman, 1976). The presence of abraded lamellar stromatoporoids, stromatoporoid debris and toppled solitary corals suggests transportation from high energy conditions (Cookman, 1976 and Spruit, 1981). The fine-grained mud matrix surrounding the local buildups indicates a quiet offshore environment, thus showing evidence of both lower and higher energy conditions with excellent nutrient circulation. The binding of sediment created a firm substrate for smaller bioherm buildups, which coincided with a regressive interval. The flatter architecture of these buildups within the Rockport Quarry indicates that they represent a biostrome rather than a biohermal reef.

The younger Alpena Formation was stromatoporoid-dominant with tabular and laminar forms associated with lower nutrients (Bates and Brand, 1991). Reefs in the vicinity of Alpena reached heights over 10 meters with a base width of more than several hundred feet and slopes as large as 30 to 40 degrees (Grabau, 1902). Stumm (1969) described Michigan bioherms as smaller buildups that contain a higher faunal diversity than previous reefs from the Silurian. Bioherms exposed near Alpena, Michigan consist of massive growth forms including dominant types such as the colonial rugose coral *Hexagonaria* and the tabulate coral *Favosites* (see Appendix A for a full faunal list), typically surrounded in crinoid debris (Stumm, 1969). The dense reefs on the eastern flanks of the Michigan Basin making up the Alpena Formation were sculpted by high energy wave conditions, constructing internal features and high slopes.

Near the northwestern extent of the Michigan Basin, Meyer (1989) recorded Givetian aged bioherms within the Medusa Quarry of northwest Michigan. These reefs are smaller in size compared to the eastern Alpena localities, reaching a maximum height of 4.5 m, 75 m wide and 250 m long. The buildup of the small patch reefs first began with massive corals, predominantly *Hexagonaria*, localized thickets of *Thamnopora*, and several stromatoporoid species. Over time stromatoporoids become the dominant type, changing from massive to lamellar growth forms, with a minor presence of *Hexagonaria* as the only other framebuilder (Meyer, 1989). The depositional setting and general coral composition is similar to the eastern side of the basin, with patch reefs developing on the carbonate shelf in shallow subtidal conditions.

The southern extent of the Michigan Basin is preserved in northwestern and north central Ohio. Previous studies are from Grand Rapids and the abandoned Whitehouse Quarry in Ohio. Reid's (1994) study focused on units exposed at Grand Rapids, which were described as representing a lagoonal environment with hypersaline conditions. Those extreme conditions

made it difficult for many species to survive, which explains why gastropods, ostracods, stromatolites, and algae were the only fossils found (Reid, 1994). Whitehouse Quarry is situated on the western flank of the Findlay Arch and has been frequently studied (Stauffer, 1909; Basset, 1935; Janssens, 1970; Camp and Hatfield, 1991; Bose, 2006; Wright, 2006). Each time Whitehouse has been examined, more species have been added to the ongoing faunal list for the Dundee Formation, which shows a typical Paleozoic fauna (Appendix B). The units at Whitehouse consist of several smaller patch reef buildups that do not have large vertical or horizontal extents, unlike barrier reefs (Copper et al., 2002; Wright, 2006). Successive coral frameworks are not present and have empty spaces as well as sediment between each colony (Wright, 2006). The establishment of patch reef corals began on a firmground substrate on top of a shell pavement layer (Wright, 2006). They were deposited between storm and fair-weather wave base in the inner shelf facies on a carbonate ramp (Bose, 2006).

Illinois Basin

Divided from the Michigan Basin by the Kankakee Arch, the Illinois Basin is exposed in Indiana and Kentucky. The Jeffersonville Formation outcrops at Falls of the Ohio State Park during low river conditions uncovering flat beds that have been studied frequently (Perkins, 1963; Greb et al., 1993; Hendricks et al., 2005; Goldstein, 2013; Bulinski et al., 2015; Jeffery et al., 2015). The Jeffersonville Formation is described as fine-grained, medium gray, with fossiliferous packstones and grainstones (Greb et al., 1993). This formation has been divided into five biozones and includes the coral zone (the oldest of all the biozones). The coral zone was further divided into the lower and upper coral zones distinguished by coral fauna present (Appendix C).

The lower coral zone contains branching and large colonial corals, with both mound and mat-like stromatoporoids which are *in situ* (Perkins, 1963; Greb et al., 1993). The upper coral zone consists of many solitary rugose corals and branching corals that are often fragmented and not in growth position (Perkins, 1963; Greb et al., 1993). This difference suggests the environment of the lower coral zone had a low to moderate energy, while the upper coral zone had high energy causing fragmentation of the corals present. The coral assemblages at the Falls of the Ohio are interpreted as multiple generations of organisms due to dramatic ranges of colony sizes in corals and stromatoporoids (Jeffrey et al., 2015). Although the coral zone is ecologically diverse with respect to corals and stromatoporoids, there have been no other faunal elements observed (Jeffrey et al., 2015). The reefal buildups fit the description of a classic biostrome with limited three-dimensional framework, but the degree of patchiness across the formation is unknown (Bulinski et al., 2015). Little research has focused on the influence of storm activity and taphonomic conditions in this location. Goldstein (2013 and personal communication) noted at the Falls of the Ohio State Park that solitary rugose (often *Heliophyllum venatum*) and *Syringopora* species often grow on top of stromatoporoids, but never together. No actual numbers or statistics have been recorded, but it suggests that corals tend to grow not just on a sediment substrate but also on other organisms.

Appalachian Basin

The Appalachian Basin is divided from the Illinois Basin by the Cincinnati Arch and from the Michigan Basin by the Findlay Arch. The Marblehead locality is extremely close to the topographic high of the Findlay Arch. The Appalachian Basin was an open ocean basin with a connection to the Rheic Sea. Most studies pertaining to the Appalachian Basin come from field sites in New York; only a few researchers have observed outcrops in Ohio. Stewart (1955) noted

the presence of rugose and tabulate colonial buildups in Marblehead, especially *Eridophyllum seriale* and *Favosites (Emmonsia) emmonsi* (for full faunal list, see Appendix D). Briggs (1959) suggested that the presence of corals and stromatoporoids in Marblehead indicate an environment deposited in a hypersaline lagoon. The bioherms were deposited on a shallow carbonate ramp, above wave base in subtidal conditions (Briggs, 1959). The upwelling cool water from deeper environments created a nutrient rich basin, dominated by branching and dendroid corals (Bates and Brand, 1991). In a detailed study by Bjerstedt and Feldmann (1985), the Marblehead Peninsula was described as a fossiliferous packstone and grainstone facies with a diverse fauna residing on a subtidal bank with medium energy above wave base. Coarsening upward facies represent the younger Marblehead Member of the Columbus Limestone, a transgression and progradation of “normal-marine” facies, which were punctuated by episodic regressive cycles (Bjerstedt and Feldmann, 1985; Sparling, 1988).

Community successions have been recorded in the Appalachian Basin of New York (Onondaga Formation, Edgecliff Member) (Williams, 1980). She studied the Thompsons Lake reef, which is a patch reef formed on a carbonate shelf in shallow seas, an interpretation based on the lack of stromatoporoids and hardgrounds (evidence of deeper waters). The reef shows an elongated shape influenced by strong currents and storm generated waves (Williams, 1980). Community succession throughout the reef was driven by current patterns and biotic regimes altering the environment. Williams (1980) noted that this reef was not similar to most Middle Devonian reefs due to faunal differences and development characteristics related to the stronger affinity with patch reefs and not reefal complexes. This patch reef has a better correlation to the bioherms found within the Michigan and Illinois Basins and not true reefs observed in the Appalachian Basin of New York and in Australia (Williams, 1980; Corlett and Jones, 2011a).

Devonian Reefs

Bioherms

The term bioherm is used to refer to lens-like mineralized structures of biogenic origin embedded in rocks (Cummings, 1932). Bioherms and patch reefs have been well studied and cover 10 to 45% of the substrate and 40 to 80% of the solid reef mass in Devonian rocks (James, 1983). Organisms such as stromatoporoids and corals that make up bioherms played a significant function in building reef masses during the Middle Devonian. Modern and ancient buildups contain framework builders, often corals and stromatoporoids, plus binders, typically involving sponges, algae, bryozoans, and/or binding sediments. Other Devonian reef-inhabiting taxa included non-framework builders, such as brachiopods, gastropods, and crinoids, which resided on flanking beds and sheltered areas of the reef. Often, the skeletons of these taxa are fragmented and disintegrated, producing lime mud, carbonate sand and silt, which can be found in the sediment matrix between coral buildups (James, 1983). When considering environment, community, and evolution of reefal complexes, the uniformitarian approach is usually taken (James and Wood, 2010). Organisms that create these reefal structures fight for ecological space, incorporate sediment, and often build upwards. Fossilized reefs record the physical expression of the environment for an extended period in one place (James, 1983). Many small Paleozoic patch reefs and biohermal communities were skeletal structures on subtidal ramps and platform carbonates. Bioherms were dominated by solitary rugose corals, colonial rugose corals, tabulate corals, and stromatoporoid sponges (Figure 4). Middle Devonian bioherms were not constrained by light, heterotrophic, which exhibit many morphological growth forms (James and Wood, 2010). Corals and stromatoporoids can be found above or below storm wave base, usually in the reef core constructing the reef front and crest.

Figure 4: Middle Devonian Heterotroph Reef. Zoned cross-section of a marginal reef with associations to the environment, reef limestones, and coral morphology. Modified from James (1983) and Pomar et al. (2004).

Comparing fossil stromatoporoids and corals to modern scleractinians can be problematic due to the unclear relationships between these fossil groups and symbiotic algae. Today symbiotic algae support controls on modern coral growth however, it is doubtful whether this was a factor for Paleozoic corals (Stearn, 1982). Comparison of fossil reef communities and associations to modern corals also include differences in substrate choice, attachment mechanisms, and role in reef construction (Scrutton, 1999). Modern corals prefer low nutrient conditions but require light for photosynthetic symbionts (algae), while Paleozoic reefs were more likely dependent on nutrients (Corlett and Jones, 2011b). Modern scleractinian corals grow rapidly, about 15 mm/year and decrease growth rates exponentially with depth and light (Wood, 2011). Ancient stromatoporoids and corals grew under different ecological conditions during the same time. Paleozoic coral-dominated reefs particularly preferred habitats with nutrient-rich waters while stromatoporoid reefs dominated in conditions with low nutrients in waters 30m deeper than corals (Corlett and Jones, 2011b). Stromatoporoids colonized several habitats during the Devonian in large and small reefal complexes. Stromatoporoids were the main frame-builders, while the corals still contributed but on a smaller scale, preferring turbid waters (DeSantis, 1996). Differences in substrate dominance are commonly due to stromatoporoids having higher growth rates than corals, solitary corals having faster rates than colonial corals, and stromatoporoids having a way to cement themselves to a hard surface (Scrutton, 1999).

When considering bioherms, looking at the specific dominant growth type is important. Growth forms provide evidence for environmental factors such as wave energy, sedimentation rates, and construction role in biogenic communities (Figure 5). Reef communities can be subdivided into units called guilds based on growth forms present and their role in the community structure (Weidlich, 2001). Growth forms with an erect skeleton belong to the

Middle Devonian Coral Morphology and Environmental Factors			
Growth Form		Environment	
		Wave Energy	Sedimentation
Delicate, branching	Low	High
Thin, delicate, platy	Low	Low
Globular, bulbous, columnar	Moderate	High
Robust, dendroid, branching	Moderate – High	Moderate
Domal, irregular, fasciculate, massive	Moderate – High	Low
Encrusting	Very High	Low
Tabular	Moderate	Low

Figure 5: Middle Devonian Coral Morphology with Associated Environmental Factors. Wave energy and sedimentation rates highly control growth types observed. Modified from James (1983).

constructor or baffler guild, consisting mainly of branching and dendroid forms (Scrutton, 1999; Weidlich, 2001). Growth forms that are laterally expanded with a high diameter-to-height ratio are part of the binder guild (Weidlich, 2001). The binder guild consists of colonies that require a lower sedimentation rate and spread laterally and vertically for space (Scrutton, 1999; Weidlich, 2001). The colonies within the binder guild are massive and can be further divided: 1) laminar, which are thin and sheet-like; 2) tabular, with a width-to-height ratios greater than 3; 3) domal, with a width-to-height ratio of less than 3; 4) bulbous, which has small width at the base and a larger width above mid-height (Scrutton, 1999).

Substrate choice is highly dependent on shape and growth of the coral, as well as environmental factors such as the presence of hard or soft sediment or skeletal debris (Scrutton, 1999). The fossil record commonly preserves interactions between organisms, including predator/prey, competition between or within species, or using another organism as a substrate. Skeletal metazoans often remain in place and are disturbed by bioeroders, encrusters, and storm activity (James, 1983). These disturbances sculpt and create internal cavities that can be filled or inhabited by other organisms or sediment (James, 1983). Frequently, stromatoporoids were employed as a substrate by other organisms, mostly because their growth forms were platy, massive, and lamellar with a large surface area. Colonial corals also share similar morphologies to stromatoporoids, especially massive and lamellar forms. Solitary corals or younger generation colonial corals exhibit the use of other organisms as a substrate. Some useful observations to make when observing this trend are whether or not the “substrate-coral” was alive or dead while the second organism settled on top (Goldstein, 2013). Once an organism is deceased on the sea floor, it becomes a substrate immediately. The corals and stromatoporoids competed for space on subtidal ramps often growing on sediment, dead or living sessile organisms. Corals and

stromatoporoids fighting for space will continue to grow around the new organisms, often resulting in irregular growth forms.

Similar to modern scleractinian corals, biohermal communities occupying North American shallow oceans during the Paleozoic competed for space. Although ancient reef systems were composed of different species, they underwent the same essential building processes and stages as modern reef systems. Documenting species interactions before the Famennian crash of corals and stromatoporoids is vital to understanding modern reef dynamics such as bleaching and decline of scleractinian corals. Comparing the succession of bioherm communities from the Appalachian, Michigan, and Illinois Basins will provide a better understanding of reef development and ecology during this supergreenhouse climate during the Middle Devonian.

Succession Models

Basinal differences and changes over time can affect the growth and development of successional reefal communities (DeSantis, 1996). Succession in reef complexes refers to the observed change through time within a biological community and can be applied to modern and ancient carbonate build-ups. Successions of reef and bioherm communities result in the replacement of one biocoenosis with new reef-building community species (James, 1983). Succession typically has a beginning and an ending point that characterize how reefs initiate, develop, and mature (Copper, 1988). The beginning starts with a suitable substrate. Reefal changes can then be intrinsic or extrinsic, internally or externally controlled (Walker and Alberstadt, 1975). Previous studies by Lecompte (1970), Walker and Alberstadt (1975), Hoffman and Narkiewicz (1977), and Copper (1988) have focused on Paleozoic reef communities, which helped develop reef succession models. The models include reef zonations

based on physical characteristics of reef development, coral shape, community interactions and environmental factors (Table 1).

Walker and Alberstadt (1975) recognized two types of succession, autogenic and allogenic succession. Autogenic succession, which is intrinsic and internal, occurs in relatively stable surrounding conditions and is community controlled. Change within a community can shift the local environment, thereby allowing other species to invade (Mewis and Kiessling, 2013). Other biological controls that are autogenic in nature are bioerosion and reef debris production, global carbon production, and biodiversity of framework species (Kiessling et al., 2002). Conversely, allogenic succession occurs when physical or extrinsic factors such as storm events or a change in sea level affect the community, resulting in a change in species composition (Mewis and Kiessling, 2013). The change occurs because the former species are no longer alive or present due to an external force; new species then arrive, colonizing on top of the old fauna. Physical changes in water depth (caused by eustatic sea level change) and turbulence are the main causes for changes in allogenic succession, although other contributors include changes in temperature, sedimentation rate, circulation, water chemistry, light, nutrients, tectonics, anoxic events, salinity, and open vs. enclosed systems (Kiessling et al., 2002).

Differences in autogenic and allogenic controls can be documented by observing the surrounding sediments. Binding sediments, skeletal debris from marine organisms, and orientation of fauna all indicate the degree of disruption of the bioherm and the allochthonous vs. autochthonous nature of bioherm sediments (Folk, 1959; Dunham, 1962; Embry and Klovan, 1971). Each layer within the framework represents a single community that can be analyzed to understand the stages from initial colonization to maturity (Hoffman and Narkiewicz, 1977). Walker and Alberstadt (1975) implied that the first three stages of succession are generally

autogenic with an increase in biomass and biodiversity. The last stage of succession has been deemed to represent an abrupt allogenic change, but can frequently be interpreted as a continued autogenic succession (Walker and Alberstadt, 1975). Because initiation and termination of bioherms can occur at any point during development, Hoffman and Narkiewicz (1977) suggested that biotic controls were less important, arguing physical changes are more influential on reef development. Abiotic controls do not always mean a step back in reef development, but can lay down the foundation for a new stage in the growth process (Hoffman and Narkiewicz, 1977).

Several models have been put forth in order to describe and summarize ecological observations at different stages of reef development. Lecompte (1970) broke down Paleozoic reef growth by noting differences in species composition across environmental gradients. Three zones were distinguished based on water turbulence and high to low energy environments. The first zone, the quiet water zone with little turbulence/low energy, was composed of tabulate and rugose corals. A subturbulent water zone with semi-high energy marks the second zone, which was inhabited mainly by tabulate stromatoporoids and abundant tabulate corals. Following this, the turbulent water zone was characterized by high energy and primarily consisted of domal stromatoporoids. Lecompte (1970) focused successional zonations on environmental energy and depth to describe biohermal activity in Paleozoic reefs.

An extensive model was put forward by Walker and Alberstadt (1975), who divided the type of succession into short-term or long-term successions. Short-term successions are rapid, short growth spurts in an unpredictable environment and fail due to allogenic (physical) catastrophe. Long-term successions are broken into autogenic and allogenic factors and into four distinct zones. The first zone is the stabilization zone, with the accumulation of a hardground, and is autogenic in character. This zone is the base of the reef, indicated by the scattered

accumulation of stabilized corals or stromatoporoids that can bind and stabilize the substrate (James, 1983). Second is the colonization zone, where most of the reef growth occurs vertically and horizontally, and which is usually autogenic. The colonization stage has a relatively low diversity and growth forms from branching thickets to massive or lamellar forms (James, 1983). Also autogenic in nature, the third diversification zone has the highest diversity of species and makes up the bulk of the reef mass. This stage often builds up to sea level, and thus has extensive vertical and lateral development, and a variety of reef-building taxa and growth forms. Finally, the last zone is usually an abrupt change from the diversification zone to the domination zone, which begins to show dominance in a single species and a decrease in other inhabitants. This zone can be subject to high turbidity, and can be characteristic of a continued autogenic or allogenic succession (Walker and Alberstadt, 1975). The first three zones all increase biological accommodation, diversity, and niche specialization (Mewis and Kiessling, 2013). The first two zones are considered pioneer stages, while the third is an intermediate stage before the climax zone (Walter and Alberstadt, 1975). Walker and Alberstadt (1975) interpreted these successional zones using species diversity, colonial growth morphology, framework species abundances, and autogenic or allogenic factors.

A third model was defined by Copper (1988), who simplified Walker and Alberstadt's (1975) four successional zones into two broad zones. Copper (1988) suggests succession is an orderly, predictable and directional pattern from pioneer to climax stages. These stages were divided by considering species-level factors as well as community-level factors that may influence reefal buildup. He defined the pioneer stage as a combination of Walker and Alberstadt's (1975) stabilization and colonization zones. The pioneer stage contains tougher species readily able to adapt to shifting substrates, showing rapid growth rates, a broad

geographical distribution, and low biomass (Copper, 1988). The climax stage is a combination of Walker and Alberstadt's (1975) diversification and domination zones. Climax species and communities tend to have reduced growth rates due to limited space, high biomass and large variations in shape and size of individuals (Copper, 1988). The pioneer to climax succession model was proposed in order to consider multiple factors affecting reef buildup, not just turbulence or allogenic versus autogenic factors. These enhanced models described by Lecompte (1970), Walker and Alberstadt (1975), and Copper (1988) will be used to describe bioherms from the Middle Devonian Great Lakes region.

Table 1: Successional Models. The observed changes in reef building specimens have been recorded in several different stages in order to collect data on interactions and different environments in which coral live. Modified by Lecompte (1970), Walker and Alberstadt (1975), Hoffman and Narkiewicz (1977), and Copper (1988).

Lecompte, 1970:

Zone	Energy	Framework Builders
Quiet Water Zone	Little	Tabulate and rugose corals
Subturbulent Zone	Medium	Tabulate stromatoporoids and corals
Turbulent Zone	High	Domal stromatoporoids

Walker and Alberstadt, 1975:

	Zone	Succession Type	Type of Buildup
Pioneer species	Stabilization Zone	Autogenic	Hardground development with coral and crinoid matrix debris
	Colonization Zone	Autogenic	Major reef growth, branching and encrusting organisms with building potential
Climax species	Diversification Zone	Autogenic	High diversity of tabulate and rugose corals and growth forms, reef zonation develops
	Domination Zone	Allogenic/Autogenic	Single species dominance, sheet tabulates and encrusters, loss of reef zonation due to buildup into surf zone

Successions are often autogenic, but can sometimes be influenced by allogenic controls.

Hoffman and Narkiewicz, 1977:

Zone	Succession Type	Type of Buildup
Quiet Water Zone (Stabilization)	Allogenic	Tabulates in skeletal debris matrix, below storm-wave base
Subturbulent Zone (Colonization)	Allogenic	Tabular stromatoporoids, below wave base and above storm-wave base
Turbulent Zone (Diversification)	Allogenic	Massive stromatoporoids, development of reef zonation, above wave base
Surf Zone (Domination)	Allogenic	Diverse tabulate and rugose fauna, reef zonation continues to develop

Suggests mostly allogenic controls (instead of autogenic) and uses zones from a combination of Lecompte (1970) and Walker and Alberstadt (1975).

Copper, 1988

Community Factors	Pioneer	Climax
Community structure	Random	Planned, hierarchical
Net community production	High	Low
Total biomass	Small	Large
Area occupied	Small, incomplete	Full, 3D
Food changes	Simple, linear	Complex, webbed
Nutrient conservation	Wasteful	Conserving, recycling
External perturbation	Easily affected	Stable
Major controls	Extrinsic (physical)	Intrinsic (Biological)
Niches available	Few	Many
Symbioses	Few	Many
Competitive interactions	Few	Many
Species diversity	Low	High
Substrate type	Softground	Hardground
Sediment input	High	Low
Water depth	Deep	Shallow
Extinction vulnerability	High	Low
Population crashes	Common	Rare
Population sizes	Large, less efficient	Small, effective

Species-Level Factors	Pioneer	Climax
Species type	Opportunistic, generalists	Equilibrated, specialists
Niche specialization	Broad	Narrow
Species equitability	Unbalanced	Balanced
Species distribution	Eurytopic, ubiquitous	Stenotopic, Endemic
Spatial organization	Unzoned	Well zoned
Organisms	Small	Large
Morphology	Generalized, normal	Frequently aberrant
Morphologic variation	Low infraspecific	High infraspecific
Biotic organization	Solitary, ahermatypic	Colonial, clonal, hermatypic
Life cycles	Short, simple	Long, complex
Fecundity	High larval reproduction	Low larval reproduction rates
Growth rate	Rapid	Slow
Epibiota attached	Rare	Common, abundant
Geologic range	Long, slowly evolving	Short, rapidly evolving
Adaptations	Tolerant taxa	Niche adapted
Extinction probability	Low	High

Research Objectives

The aim of this project is to assess individual bioherms and patch reef communities in the Michigan, Illinois, and Appalachian Basins from the Eifelian to the Givetian stages of the Devonian Period. Despite the Middle Devonian being a time of great reef expansion, the ecology and evolution of small bioherm communities in epicontinental basins of North America are not well documented. There are five key aspects to understanding paleontological variations of ancient reefs.

First, how do reef community compositions vary geospatially and temporally among localities? By quantifying coral species abundances we can compare reef development and composition across all three basins and through time. Predictions include compositions changing through time at a single locality, and compositions varying between basins, which will display different species, guilds, morphology, and distribution. Localities that fall within the same basin, however, should reveal more similarities than differences, due to close proximity and faunal mixing. Second, what are the successional patterns of bioherms in each basin and are they allogenic or autogenic? I expect to see unique successional patterns at each location, due to distinct faunal compositions and environmental variables associated with successional stages. Locations controlled by allogenic factors will show physical disturbances, such as toppled organisms from storms, changes in sedimentation rates, and evidence of sea-level fluctuations. Autogenic factors affecting biohermal buildup are intrinsic and autogenic successional changes are driven by community composition, species interactions, reef debris, and bioerosion. Autogenic successions are noted when organisms are preserved in-growth position and there is a clear change in abundances or species without evidence of physical disturbances or extrinsic forces. Third, did environmental factors that differed among basins affect buildups? Ecological

associations affect reef buildup and by quantifying the environmental observations at each location, we can determine which factors may have been driving reefal communities in the Paleozoic. Fourth, is there a detectable gradient between more open versus closed basins? Nutrient availability plays an important role for all organisms, especially sessile corals, who rely on the circulation of nutrients. Differences in buildup may be attributed to varying nutrient conditions. Basins with a direct connection to a larger ocean, in this case the Rheic Sea, are expected to have higher nutrient levels; this includes the Appalachian and Illinois Basins. With the potential for high nutrient levels, open ocean basins would be host to large climax biohermal communities. More restricted basins that do not have corridors directly connected to the Rheic Sea, like the Michigan Basin, may have had limited influx of nutrients and circulation. I would expect to see pioneer buildups and environments that cannot support large reefal communities. Fifth and lastly, do successional models reflect environmental conditions, community composition, and provide a better understanding of reef ecology? Successional models summarize observations of ecological variables associated with the buildup processes of Devonian reefs, including energy, depth, and community characteristics. Each model focuses on different environmental factors and aids in the understanding of reef development. Answering these questions adds to the significance of this project by providing detailed descriptions of biohermal activity in the Middle Devonian of North America.

CHAPTER III. METHODS

Field Work

In order to determine the succession and ecological associations of bioherms in the Middle Devonian of the Great Lakes region, field sites were identified and then visited during the summer and fall of 2015. Bioherms were documented from sites within the Michigan (Alpena, Michigan and Whitehouse, Ohio), Illinois (Clarksville, Indiana and Louisville, Kentucky), and Appalachian (Marblehead, Ohio) Basins. Published data were also used to help constrain and identify local environmental conditions.

The Michigan Basin was studied by examining outcrops in north-central Ohio and northeastern Michigan, which helped document differences within the same basin. The first locality was at an abandoned quarry in Whitehouse, Ohio where the Dundee Formation (Eifelian in age) is exposed sporadically around the quarry. The second and third localities within the Michigan Basin were at the Besser Museum for Northeast Michigan and Rockport Quarry near Alpena, Michigan. Both areas consist of talus piles and large boulders with fossils that are no longer *in situ* due to quarry operations. The Besser Museum has an outdoor area with boulders from the Alpena Formation (Traverse Group) that were donated and transported from the active Lafarge Quarry in Alpena for safe amateur fossil collecting. Currently called the Rockport Recreation Area, the abandoned Rockport Quarry is also open for amateur collecting within the Traverse Group, but from the older Rockport Formation.

The Illinois Basin was studied in three different locations near Clarksville, Indiana and Louisville, Kentucky. The first locality was at the Falls of the Ohio State Park in Indiana where the Jeffersonville Formation is visible on the banks of the Ohio River. The second and third

localities, Fork Bear Creek (Bear Creek) and Champions Trace in Louisville, Kentucky, also represented the Jeffersonville Limestone.

The Appalachian Basin was represented by outcrops at the Lafarge Marblehead Quarry in Marblehead, Ohio. This locality is near the topographic high, the Findlay Arch, separating the Appalachian and Michigan Basins. This locality represents the northern extent of biohermal activity in the Columbus Formation within the Appalachian Basin.

Field work included the documentation of corals and stromatoporoids in vertical and horizontal outcrops in order to interpret zonations of bioherm complexes. Spatial relationships of reefs in all three basins were relatively easy to observe. Most of the beds are exposed due to erosion by glaciers, rivers, or quarry operations, leaving bedding surface horizons to be examined. To ensure comparable sampling, a counting method was employed for spatial observations by using 1m² quadrats to record corals. Quadrats were randomly laid down on horizontal exposures (and a few vertical outcrops), digitally photographed, and sketched in the field for later reference. Several close up photographs were taken of the corals and stromatoporoids within each quadrat to help with identifications back in the lab. Approximately 10-20 additional coral and stromatoporoid samples were taken from each locality and labeled for faunal identification purposes. Samples were not collected from the Falls of the Ohio State Park, due to collection restrictions on state lands.

In addition to basic field observations and faunal identifications, the matrix around build-ups, sedimentological features, and the architecture of the organic accumulations were described. The architecture of coral buildups includes growth shapes, community strategies, and interactions observed in the field or in the images. The closer individuals were to each other, the more corals and stromatoporoids had to compete for space, nutrients, and light. Noting how

much area the corals covered per quadrat also helped identify the successional zones, not just spatial associations. After the coral coverage was classified in each quadrat, the remaining area was represented by sediment and reef debris. Lithology ranged from mudstone, limestone, and dolostone, which were often void of any other organisms. Whitehouse Quarry, Rockport Quarry, and the Besser Museum sites showed crinoidal fragments within the matrix. Spatial relationships among corals living in the same region were recorded by observing trends of coral buildups. Cases where the corals and stromatoporoids were preferentially growing on top of other organisms, specifically other corals or stromatoporoids were noted. Instances where sediment had accumulated between each new buildup were also recorded.

Temporal patterns were harder to document. Few exposed outcrops displayed successional patterns in vertical sequences at all locations. The best vertical succession was observed at Besser Museum. The imported boulders were excavated from a nearby quarry and represented a true climaxing coral reef in the domination stage of development. Incomplete 3D reefal exposures on these boulders permitted determination of temporal and spatial associations of corals living in close proximity. Since they were transported, it was difficult to delimitate and retrieve geologic information about the area from which they came, including the precise age and location.

Three Paleozoic basins were identified to study biohermal activity within the Middle Devonian. Within these sites, 7 localities were investigated and data were taken from 34 pseudo-replicates (quadrats). All digital images, sketches, and field notes were brought back to BGSU's geology laboratory for further identification, description, and analysis. Additional hand samples were also collected from all field locations (except Falls of the Ohio State Park) to aid in species identifications.

Laboratory Work

Once hand samples and images were transported to BGSU, photographs were organized in relation to location. To accomplish this, PowerPoint files were made for all localities, permitting the aggregation of photographs, annotations, and labels. The PowerPoint slides were organized by quadrat and some close up photographs were added to aid in the description of buildups and faunal identifications. After the photographs were organized, identifications were made using classifications from previous studies by Stewart (1955), Ehlers and Kesling (1970), Stumm (1950, 1954, 1961, 1969), and Goldstein (2010).

After the completion of the species identifications, a counting method determined the area of coral substrate coverage in all 34 quadrats. These areas were used as a proxy for species abundances. Coral Point Count with Excel extensions (CPCe) from the National Coral Reef Institute, Nova Southeastern University Oceanographic Center, was used to obtain coral and stromatoporoid area coverages from each location. Originally designed by Kohler and Gill (2006), CPCe is utilized as a tool for modern coral counting and ecological purposes. CPCe is a common procedure to get an estimate of benthic marine community populations from either images or videos (Kohler and Gill, 2006). Using this modern coral and substrate coverage program, a coding system was developed for all Middle Devonian species observed within all three basins. Each species was assigned a two to three letter species code to be added for “simple-click species and substrate labeling” within the program (Kohler and Gill, 2006). The scale on each photograph was defined and then area coverage was determined. Identifications made in the previous PowerPoints helped locate and identify corals and stromatoporoids. The extent of each coral and stromatoporoid exposure was manually digitized in CPCe to define the outline, which calculated the area. Areas were then filled in with associated colors on the image and coded accordingly by species (Figure 6 and Figure 7). The quantified area coverages were

recorded in an Excel spreadsheet. Species present multiple times within a quadrat were added together for total exposure and presence. The entire dataset from CPCe for coral abundances includes the basin, sampling location, quadrat, species present, coral type/sponge (CR – Colonial Rugose; SR – Solitary Rugose; T – Tabulata; SS – Stromatoporoid Species), area cover (cm²), and percent area coverage (Appendix E).

While recording the coral area coverage, quadrats were simultaneously analyzed to determine the substrate on which corals preferred to grow, either sediment or other organisms (mainly corals and stromatoporoids). Growth substrates were recorded by counting the number of times corals and stromatoporoids were growing on top of another coral or stromatoporoid (strom) mass. Observed contacts specifically include: coral-on-coral growth; coral-on-strom; strom-on-strom; or strom-on-coral contact. Documenting the sediment association was simple: “NO SED” referred to no sediment between coral species and direct competition for space; “SED” indicates the identification of sediment between coral buildups and no direct species competition. The observations were made using all 34 quadrats from all seven locations. To closely examine the interactions between the corals, stromatoporoids, and associated sediments, the images were enhanced using PowerPoint, Adobe Photoshop CS6, and CPCe. Due to the complex bioherm communities and lack of exposure from buildup, not all the interactions could be observed. However, most of the build-up data and sediment relations were visible and recorded in an Excel spreadsheet (Appendix F).

Figure 6: Coral Point Count with Excel Extensions (CPCe) Example from Besser Museum Location (BM2). Before species can be identified, the scale is set to the ruler in the image. Coral areas were digitized, coded, and area is determined by dividing coverage areas by quadrat area. Areas were compiled in an Excel file listing the species present and percent abundance.

CPCe Key:				
Code	Species			
FA	<i>Favosites alpenensis</i>	SE	<i>Siphonophrentis elongata</i>	
HA	<i>Hexagonaria alpenensis</i>	CA	<i>Cystiphyllodes americanum</i>	
FM	<i>Favosites mammilatus</i>	FD	<i>Favosites digitatus</i>	
		SS	<i>Stromatoporoid species</i>

Figure 7: CPCe Example from Rockport Quarry (RQ2). Additional species were identified in this quadrat. Species were manually digitized precisely to acquire coral areas. All area coverage data were recorded in Appendix E.

The build-up data and sediment associations helped classify the successional type of each quadrat by using the descriptions in the successional models put forth by Lecompte (1970), Walker and Alberstadt (1975), Hoffman and Narkiewicz (1977), and Copper (1988). Qualitative and quantitative data were used to describe successional zones. Qualitative data included detailed descriptions regarding coral growth morphology, framework species, and ecological factors associated with reef environments. Quantified data encompassed coral and stromatoporoid abundances and sediment associations/coral interactions. Successional zones were determined by synthesizing both qualitative and quantitative data associated with each location.

The build-up data were especially useful for distinguishing between pioneer communities and more complex reefs. Locations with fewer sediment associations were considered more complex due to having more area occupied by corals and stromatoporoids. Often these successions exhibited intrinsic controls, more niche availability, high competitive interactions, and higher species diversities (diversification zone) or were extremely dominant (domination zone). Quadrats with more sediment present between corals and stromatoporoids were interpreted as pioneer communities. More sediment is often associated with smaller coral area occupation, simple food chains, major extrinsic controls, few competitive interactions and low species diversity. Walker and Alberstadt's (1975) pioneer stages helped describe differences between initial buildup and continued biohermal growth and activity. Communities that display low diversities and a hardground fall within the stabilization stage. A hardground includes substrate observations comprised of crinoidal fragments or shell debris. If branching and encrusting organisms are present, display high growth rates or larger colonial organisms, then the colonization zone is observed. Bioherms that were complex were then further divided into

Walker and Alberstadt's (1975) diversification or domination successional zones. If we see higher species diversity, then the climax community is at the diversification stage. However, if the location is dominant with one or two species, than the successional zone observed is the domination stage. Lecompte's (1970) successional zones were determined by observing energy and depth at each location. Sites that had corals in growth position were interpreted as having lower current energy and being in deeper environments, suggesting the presence of the quiet water zone. If there were a few corals toppled over, but the majority were *in situ*, then the bioherm was at the subturbulent stage and in moderate depths. Communities that demonstrate drastic storm events and toppled corals were in high energy and shallow water environments, consistent with the turbulent zone interpretation. Successional zones following Lecompte's (1970) model were determined using this study and interpretations from previous studies to infer depth and energy.

In addition to species abundances (as measured by area coverage), environmental parameters for each quadrat were added to the data matrix for the ecological analyses. The environmental variables were derived both from previous studies at the localities and observations made for the present study. Environmental codes were created for each variable and added to the data matrix (Table 2). Environmental parameters include grain size, lithology, biogenic carbonate texture, environmental energy, substrate, and basin type (Table 3). A second data matrix was created to examine overall locality trends by averaging the quadrat abundances and environmental factors (Table 4).

Field and lab methods were used to determine successions and the ecology of Middle Devonian bioherms. If communities displayed low diversities, lots of associated sediment, few competitive interactions, small biomass and individuals, then the succession represented in a

pioneer community. In contrast, communities showing colonies with abnormal morphologies, a lot of competitive interactions, large biomass, and little sediment are climax communities.

Successional zones describe and summarize observations of ecological variables and community compositions, which can be compared between basins and other reefal communities, if described the same way. If allogenic factors are dominant, then observations include physical evidence of disturbances such as storm events, sea level fluctuations, species not *in situ*, and sedimentation rates. Autogenically driven successions are less obvious, but they often display little physical disturbances. Autogenic successions focus on community driven factors, bioerosion, carbon production, and often have *in situ* corals.

Table 2: Ecological Parameter Codes. Each environmental factor was coded as listed below and codes were included in the data matrix for the canonical correspondence analysis (CCA). The variable type or attribute scale was also defined as ordinal or nominal.

Environmental factors:	Code:	Variable type:
Grain size:		
Fine	1	Ordinal
Medium	2	
Coarse	3	
Lithology:		
Mudstone	1	Nominal
Limestone	2	
Dolostone	3	
Biogenic carbonate texture:		
Autogenic	1	Nominal
Allogenic	2	
Autogenic/allogenic	3	
Environmental energy:		
Low	1	Ordinal
Medium	2	
High	3	
Substrate:		
Softground	1	Ordinal
Firmground	2	
Hardground	3	
Basin Type:		
Closed	1	Nominal
Open	2	

Table 3: Environmental Parameters According to Location. Variables are the same in all quadrats associated with the locality. See Table 2 for meanings of code numbers. WQ-Whitehouse Quarry, BM-Besser Museum, RQ-Rockport Quarry, FO-Falls of the Ohio, BC - Bear Creek, CT- Champions Trace, MQ-Marblehead Quarry.

Environmental Parameters	Code	WQ	BM	RQ	FO	BC	CT	MQ
Grain Size	Grain	2	3	1	2	2	2	3
Lithology	Lith	3	2	1	2	2	2	3
Biogenic Carbonate Texture	BCT	1	1	2	3	3	1	1
Environmental Energy	Env E	2	3	1	2	2	2	2
Substrate Type	Sub	2	3	1	1	1	1	2
Basin Type	Basin	1	1	1	2	2	2	2

Table 4: Averaged Abundance Matrix and Environmental Parameters. The abundance data for each species are averaged across all quadrats in each locality. Abundances are reported in units of square meters. Type: T – tabulate coral, SR – solitary rugose corals, CR – colonial rugose coral, SS – stromatoporoid species. (Table 2 for environmental codes).

Species	Type	Code	WQ	BM	RQ	FO	BC	CT	MQ
<i>Acinophyllum mclarni</i>	CR	AM	0	0	0	0.598	0	0	0
<i>Acinophyllum segregatum</i>	CR	ASG	0	0	0	0	0	0	0.579
<i>Acinophyllum stokesi</i>	CR	AS	0	0	0	5.366	0	0	0
<i>Blothrophyllum romingeri</i>	SR	BR	0	0	0	0	0	0.318	0
<i>Cladopora imbricata</i>	T	CI	0	0	0	1.695	0.349	0	0
<i>Cladopora tela</i>	T	CT	0.077	0	0	0	0	0	0
<i>Cystiphyllodes americanum</i>	SR	CA	0	0	0.149	0	0	0	0
<i>Cystiphyllodes hispidum</i>	SR	CH	0	0	0	1.0769	0	0	0
<i>Cystiphyllodes infundibuliformis</i>	SR	CYI	0	0	0	0	1.271	0	0
<i>Cystiphyllodes nanum</i>	SR	CN	0	0	0	0.4773	0.324	0	0
<i>Eridophyllum seriale</i>	CR	ES	0	0	0	0	0	0	16.842
<i>Favosites (Emmonsia) emmonsi</i>	T	FE	3.155	0	0	0.384	0	0	5.282
<i>Favosites (Emmonsia) epidermatus</i>	T	FEE	0	0	0	1.402	1.22	0.749	0
<i>Favosites (Emmonsia) ramosa</i>	T	FER	0	0	0	0.865	0	0	0
<i>Favosites (Emmonsia) tuberosus</i>	T	FET	0	0	0	0	1.736	0	0
<i>Favosites alpenensis</i>	T	FA	0	0.279	0	0	0	0	0
<i>Favosites biloculi</i>	T	FB	0	0	0	0	1.234	6.167	0
<i>Favosites digitatus</i>	T	FD	0	0	4.287	0	0	0	0
<i>Favosites hemisphericus</i>	T	FH	0	0	0	0	0	0	0.669
<i>Favosites limitaris</i>	T	FL	0.327	0	0	0	0	0	0
<i>Favosites mammilatus</i>	T	FM	0	0	1.658	0	0	0	0
<i>Favosites nitellus</i>	T	FN	0	0	0.619	0	0	0	0
<i>Favosites ramulosus</i>	T	FR	0	0	0	1.83	0.289	0	0
<i>Favosites turbinatus</i>	T	FT	0	0	0	0.065	1.06	3.472	0
<i>Heliophyllum venatum</i>	SR	HVN	0	0	0	0.527	0.312	2.228	0
<i>Heliophyllum verticale</i>	SR	HV	0	0	0	0.198	2.229	2.387	0.152
<i>Heterophrentis irregularis</i>	SR	HI	0	0	0	0.553	0.159	0.335	0
<i>Heterophrentis simplex</i>	SR	HS	0.154	0	0	0	0	0	0
<i>Hexagonaria alpenensis</i>	CR	HA	0	31.403	0	0	0	0	0
<i>Hexagonaria anna</i>	CR	HAA	0.676	0	13.291	0	0	0	0
<i>Pleurodictyum cylindricum</i>	CR	PC	0	0	0	0.48	0	1.943	0
<i>Pleurodictyum planum</i>	CR	PLP	0	0	0	0	0	7.989	0
<i>Prismatophyllum ovoideum</i>	CR	PO	0	0	0	0	0	0	3.196
<i>Prismatophyllum prisma</i>	CR	PP	0	0	0	1.055	0	0	0
<i>Siphonophrentis elongata</i>	SR	SE	0	0	0.211	0.588	3.428	0.641	0
<i>Siphonophrentis yandelli</i>	SR	SY	0	0	0	0	0	0.471	0
<i>Striatopora bellistriata</i>	T	SB	0	0	0	1.274	0	0	0
<i>Thamnopora limitaris</i>	T	TL	0	0	0	2.117	0	0	0
<i>Zaphrentis gigantea</i>	SR	ZG	0.019	0	0	0	0	0	0.249
<i>Zaphrentis prolifica</i>	SR	ZP	0.082	0	0	0	0	0	0.01
Stromatoporoid species	SS	SS	1.654	9.599	0.972	16.135	12.983	0.304	0.231
Grain Size		Grain	2	3	1	2	2	2	3
Lithology		Lith	3	2	1	2	2	2	3
Biogenic Carbonate Texture		BCT	1	1	2	3	3	1	1
Environmental Energy		Env E	2	3	1	2	2	2	2
Substrate Type		Sub	2	3	1	1	1	1	2
Basin Type		Basin	1	1	1	2	2	2	2

Paleontological Data Analysis

Diversity metrics for each quadrat were calculated and compared between locations and basins to find the basins with highest diversity and dominance. The abundance data matrix (Appendix G) was analyzed using PAST 3.1 (Paleontological Statistics, Hammer et al., 2001). Community compositions were documented by taxon richness, Simpson's index, Shannon index, Brillouin index, and evenness measures for diversity. The diversity indices helped identify successional stages at each locality and add to the interpretation of the ecological factors dictating reefal structures.

Past 3.1 was also used to calculate two pairwise similarity metrics from the abundance data matrix (Appendix G). The Bray-Curtis similarity measure used the quantified areas as a proxy for the abundances for each species, whereas Jaccard used simple presence/absence of the species. Both metrics were used in order to check the validity of area as an abundance measure. The Bray-Curtis similarity is generally preferred because it includes species abundances and can therefore assess comparative degrees of evenness/dominance. If area is not an effective proxy for abundance, the simpler Jaccard similarity will provide meaningful support for patterns of comparison between sites. The Bray-Curtis and Jaccard similarity metrics were used for Q- and R-mode cluster analysis to find patterns between locations with similar faunal compositions and species with similar occurrence patterns.

Taxonomic compositions were analyzed using the standard multivariate ecological techniques of nonmetric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA). These techniques document and compare faunal associations within and between the basins to determine important contributing species within different stages of reef development. It is recommended that both ordination techniques be used to evaluate the

effectiveness of interpretations by thoroughly examining the original dataset to understand the environmental information it contains (Holland, 2006). Another data matrix was made that included environmental factors for each quadrat in order to perform a canonical correspondence analysis (CCA). The purpose of these multivariate ordination analyses was to determine successional patterns within these bioherms, environmental factors most affecting the communities, compositional and environmental differences between locations, and environmental and/or paleolatitudinal gradients within the region.

Nonmetric multidimensional scaling (NMDS) uses a distance matrix (any distance metric can be used) as input, and attempts to match rank order pairwise distances as closely as possible in the ordination. Stress levels, reflecting the degree of match, ideally should be lower than 0.10, indicating a good match of rank order distances. A Shepard plot also provides a visual expression of the quality of fit between the ordinated rank order distances and the original distances. NMDS captures relative differences but is an iterative process that may find only a local optimum. The axes are arbitrary and cannot be interpreted as environmental gradients, unlike DCA, which reveals linear trends in environmental factors.

Detrended correspondence analysis (DCA) is a multivariate ordination technique that tries to maintain the correlations between pairs of samples and species on an ordination plot. This technique is based on an eigenanalysis of the X^2 (Chi-square) distance matrix. Rare taxa are often exaggerated in samples due to rescaling factors with the method assuming the turnover rates along gradients are constant. The plots reveal patterns that may be interpreted as environmental gradients by referring back to the raw dataset and DCA scores. The data matrix does not include environmental factors in the matrix or calculation when projecting the new axes; rather, the assumed environmental gradients are interpreted from the DCA results.

Canonical correspondence analysis (CCA) is a multivariate ordination technique that incorporates environmental data into the input dataset to reveal gradients. The species abundance is presumed to be representative of a response to these gradients. Like DCA, CCA ordines localities and species along an environmental gradient while maintaining correlations between localities and species. This ordination technique can handle rare species and incorporates the known environmental factors associated with sites and species, instead of inferring those factors, as in DCA.

CHAPTER IV. RESULTS

Modest Devonian reefs consisting of small, scattered patch reef or bioherm communities were found throughout the basins, with one exception in Alpena, Michigan, which represented a larger true reef complex. All three basins show differences in reef structure, contributing species, associated sediment, and substrate type.

Successional Patterns

Before the successional patterns in each location were determined, diversity indices were calculated to determine which basin had the most diverse (or dominant) coral assemblage (Table 5). Diversity indices were based on area coverage as a proxy for abundance of coral and stromatoporoid species in each quadrat sample. The Simpson, Shannon, and Brillouin indices all indicate that the most diverse quadrat was in the Illinois Basin (Jeffersonville Limestone, Falls of the Ohio State Park quadrat 4). Shannon and Brillouin indices identify Falls of the Ohio State Park as the most diverse locality, while the Simpson and Evenness indices suggest that Champions Trace was more diverse. The Dominance index revealed that Besser Museum quadrat 4 (Alpena Formation) and Rockport Quarry quadrat 1 (Rockport Formation) showed the highest dominance and were therefore the least diverse. Besser Museum 4 showed abundant *Hexagonaria alpenensis* and stromatoporoid species, while Rockport Quarry quadrat 1 only had one species present, *Favosites digitatus*. Overall, the diversity measures indicate that the Illinois Basin had the greatest diversity while the northern part of the Michigan Basin showed the highest dominance.

Table 5: Diversity Indices by Quadrat. The most diverse site is the Illinois Basin in FO4 (highlighted in blue, red, and green). The Michigan Basin paleocommunities show the most dominance, in BM4 and RQ1 (highlighted in yellow and purple).

Quadrat	BM1	BM2	BM3	BM4	BM5	BM6	RQ1	RQ2	RQ3	RQ4		
Taxa_S	3	3	2	1	2	2	1	5	2	2		
Individuals	26	51	48	35	54	19	13	17	4	31		
Dominance_D	0.505	0.621	0.745	1	0.971	0.574	1	0.300	0.871	0.915		
Simpson_1-D	0.495	0.380	0.255	0	0.029	0.426	0	0.700	0.129	0.085		
Shannon_H	0.753	0.606	0.423	0	0.076	0.620	0	1.322	0.252	0.182		
Evenness_e^H/S	0.708	0.610	0.763	1	0.540	0.927	1	0.750	0.643	0.600		
Brillouin	0.448	0.477	0.355	-0.011	-0.029	0.406	-0.154	0.647	-0.254	0.039		
Quadrat	WQ1	WQ2	WQ3	WQ4	WQ5	WQ6	MQ1	MQ2	MQ3	MQ4	MQ5	MQ6
Taxa_S	2	4	3	4	2	3	3	4	4	4	4	8
Individuals	2	4	5	7	2	9	8	42	31	17	45	8
Dominance_D	0.616	0.319	0.455	0.529	0.689	0.532	0.477	0.476	0.594	0.378	0.757	0.262
Simpson_1-D	0.384	0.681	0.545	0.471	0.311	0.468	0.523	0.524	0.406	0.623	0.243	0.738
Shannon_H	0.572	1.204	0.892	0.884	0.490	0.702	0.822	0.862	0.743	1.070	0.523	1.514
Evenness_e^H/S	0.886	0.833	0.813	0.605	0.816	0.673	0.758	0.592	0.526	0.729	0.422	0.568
Brillouin	-0.177	0.286	0.248	0	0.029	0.211	0.382	0.572	0.444	0.662	0.241	0.371
Quadrat	FO1	FO2	FO3	FO4	FO5	FO6	FO7	BC1	BC2	CT1	CT2	CT3
Taxa_S	2	5	12	13	12	9	7	8	8	7	7	8
Individuals	48	38	47	46	28	8	26	17	25	23	28	10
Dominance_D	0.648	0.968	0.267	0.131	0.263	0.463	0.390	0.202	0.443	0.309	0.301	0.181
Simpson_1-D	0.352	0.032	0.733	0.869	0.737	0.537	0.610	0.798	0.557	0.691	0.699	0.819
Shannon_H	0.537	0.103	1.753	2.174	1.678	1.266	1.249	1.734	1.230	1.458	1.451	1.846
Evenness_e^H/S	0.856	0.222	0.481	0.677	0.446	0.394	0.498	0.708	0.428	0.614	0.610	0.792
Brillouin	0.412	-0.066	1.096	1.406	0.783	0.193	0.672	0.825	0.522	0.632	0.781	0.525

Each location was individually examined using abundances, diversity indices, environmental variables and coral descriptions to categorize successional zones (Table 6). The Dundee Formation at Whitehouse Quarry, which has a lower diversity of coral species, relatively small corals, and few successional organisms, falls within the pioneer stage. Wright (2006) and field observations from this study noted the presence of shell lags. These shell lags have been interpreted as the formation of a hardground on which corals grew. The guilds represented in this area range from the constructor guild with robust branching corals to the binder guild with massive coral, domal, and tabular stromatoporoid forms. Whitehouse Quarry represents a pioneer stage in the zone of stabilization in subturbulent waters and is interpreted as being autogenically controlled.

The other locations within the Michigan Basin, which are significantly younger (by ~2-3 million years) than the Dundee Formation, represent advanced successional stages when compared to Whitehouse Quarry. The Rockport Formation at Rockport Quarry was quite different from the other two localities within the Michigan Basin. The Rockport Formation is slightly older than the Alpena Formation and younger than the Dundee Formation at the southern Whitehouse location (Figure 2). The lithology at the Rockport Quarry was mudstone and the site showed evidence of allogenic influences. Most of the branching corals were broken and not *in situ*. There were few large colonial corals and stromatoporoids. These grew to be massive forms, both tabular and domal. Branching corals in this area ranged from smaller delicate forms to robust branching ones. Due to the greater presence of branching and small solitary corals, this assemblage is interpreted as belonging to the constructor or baffler guild. Rockport Quarry represents a facies in the quiet water zone as described by Lecompte (1970), the colonization zone (Walker and Alberstadt, 1975), and a pioneer community (Copper, 1988). The presence of

several fragmented branching corals shows evidence of storm activity and the site appears to have been above storm wave base.

The Alpena Formation blocks at the Besser Museum were consistent in having a low diversity throughout the location with a high dominance of stromatoporoids, *Hexagonaria alpenensis*, and *Favosites alpenensis*. These buildups were extremely large compared to the Whitehouse and Rockport locations. Growth forms are massive, domal (mostly *H. alpenensis* and some stromatoporoids) and tabular (stromatoporoids and *F. alpenensis*). The growth forms are consistent with the binder guild. Overall reef geometry was unobservable due to the transport of these large boulders to the museum. Corals showed 3D zonations and were fixed to hard substrates, including other coral organisms with or without binding sediments between buildups. The coral colonies persisted for a long time, displaying a stable environment with few niches or cavities found between them. The Besser Museum location therefore represents a true reef and not a patch reef or biohermal environment. The corals and stromatoporoids represent succession types within the turbulent zone, domination zone (more autogenetically controlled), and the community/species structure falls into the climax zone.

Bioherms observed within the Illinois Basin showed similar zoning in all three locations, Falls of the Ohio State Park, Champions Trace, and Bear Creek. Faunal assemblages, lithology, and other environmental factors were nearly identical. All three locations have a diverse faunal assemblage, which displayed complex and competitive interactions of large colonial rugose and tabulate corals and stromatoporoids. A moderate abundance of solitary rugose corals is also present in the basin. Growth forms of the larger colonial corals are massive, domal, tabular, and fasciculate. Branching corals were smaller and highly fragmented in more areas, representing delicate forms that could not withstand higher water energy. The presence of both branching and

large colonial corals indicates that this assemblage was a mix between constructor/baffler and binder guilds. This reef is interpreted as a biostrome due to the large horizontal distribution of corals and lack of topography. Bedding planes were relatively flat and showed little vertical buildup. Vertical and horizontal zonations were patchy with lots of sediment between individual corals and stromatoporoids. High diversities of corals helped classify these buildups at all three locations as successional stages within the diversification zone in turbulent waters as part of the climax zone.

The Columbus Limestone at Marblehead Quarry represents the northern extent of the Appalachian Basin during the Middle Devonian. This area was on the topographic high of the Findlay Arch, which was often breached during high sea level fluctuations, allowing exchange of water, nutrients, and fauna between the Appalachian and Michigan Basins. At first glance, the fauna at this locality indeed resembles that at Whitehouse Quarry (Michigan Basin), but after careful observations, a few differences were noted, including larger grain size, and larger colonial and solitary corals at Marblehead. The growth forms were massive and mostly domal for colonial corals and stromatoporoids, representative of binder guilds. No other organisms besides corals or stromatoporoids were found in this unit, unlike at Whitehouse where brachiopods, bivalves, and other invertebrates were found scattered throughout the formation. The fauna at Marblehead consists of several large colonial rugose and tabulate corals that are *in situ*. Some solitary corals were also *in situ*, suggesting a quieter water environment in the colonization and pioneer stages of development.

Table 6: Location Summary of Ecological and Successional Associations. All locations were analyzed for dominant coral sizes, growth forms, guilds, successional patterns as defined by Lecompte (1970), Walker and Alberstadt (1975), and Copper (1988) and whether the successions are controlled by autogenic or allogenic factors.

Locations	Whitehouse Quarry	Besser Museum	Rockport Quarry	Falls of the Ohio State Park	Fork Bear Creek	Champions Trace	Marblehead Quarry
Formation	Dundee	Alpena	Rockport	Jeffersonville	Jeffersonville	Jeffersonville	Columbus
Age	Middle Eifelian	Middle Givetian	Early Givetian	Middle Eifelian	Middle Eifelian	Middle Eifelian	Middle Eifelian
Basin	Michigan	Michigan	Michigan	Illinois	Illinois	Illinois	Appalachian
Colonial coral sizes	Small	Large	Medium	Large	Large	Large	Medium
Growth Forms	- Robust branching - Massive	- Massive - Domal - Tabular	- Robust branching - Massive - Tabular - Domal	- Massive - Domal - Tabular - Fasciculate - Delicate branching	- Massive - Domal - Tabular - Fasciculate - Delicate branching	- Massive - Domal - Tabular - Fasciculate - Delicate branching	- Massive - Domal
Guilds	Constructor and binder	Binder	Constructor and baffler	Baffler, constructor and binder	Baffler, constructor and binder	Baffler, constructor and binder	Binder
Diversity	Low	Low	Moderate	High	High	High	Low
Succession: Copper (1988)	Pioneer	Climax	Pioneer	Climax	Climax	Climax	Pioneer
Succession: Lecompte (1970)	Subturbulent	Turbulent	Quiet Water Zone	Turbulent	Turbulent	Turbulent	Subturbulent
Succession: Walker and Alberstadt (1975)	Stabilization	Domination	Colonization	Diversification	Diversification	Diversification	Colonization
Autogenic or Allogenic?	Autogenic	Autogenic	Allogenic	Autogenic and Allogenic	Autogenic and Allogenic	Autogenic and Allogenic	Autogenic

Paleocommunity Analysis

Cluster analyses using quadrat data from all basins reveal larger-scale patterns. The cluster analyses require less manipulation to the data and uses a direct measure of distances. Cluster analyses can compare 2D area representation using abundances (Bray-Curtis) and confirm trends with presence/absence metrics (Jaccard). Correspondence analyses (DCA and CCA) only use abundances, which can put more weight on species present, misinterpret patterns, or fail to account for preservational biases.

Q-mode cluster analysis, which clusters paleocommunities, was performed using both the Bray-Curtis (quantified abundances) and Jaccard (presence/absence) similarity metrics. The Bray-Curtis Q-mode cluster analysis (Figure 8) revealed an interesting division among basins. The division is driven by the presence of stromatoporoids and the successional patterns by Walker and Alberstadt (1975), suggesting a diversity-controlled pattern. The right side of the cluster diagram groups together localities (Marblehead and Whitehouse Quarries) that had few stromatoporoids and a low Walker and Alberstadt value. The cluster on the far left of the diagram, on the other hand, groups the localities (Falls of the Ohio and Besser Museum) that had a large abundance of stromatoporoids and a higher Walker and Alberstadt value. However, the only locality to not conform to this pattern was Rockport Quarry, due to a low Walker and Alberstadt value. *Siphonophrentis elongata*, a common species between Rockport Quarry and Falls of the Ohio State Park, had a large influence in the distribution of locations. Overall, this cluster is driven by species occurrences and diversity patterns explained through Walker and Alberstadt's (1975) successional model.

The Jaccard similarity metric was also used to produce a Q-Mode cluster diagram (Figure 9). The pattern derived from this presence/absence metric was slightly different; the biggest

Figure 8: Q-Mode Cluster Using Bray-Curtis Dissimilarity Metric. In general, quadrats plot by localities, which are designated by colors. Light green-Falls of the Ohio (FO) and Bear Creek (BC), red-Besser Museum (BM), yellow-Rockport Quarry (RQ), dark green-Champions Trace (CT), turquoise-Whitehouse Quarry (WQ), purple-Marblehead Quarry (MQ). Quadrats circled in red are outliers.

Figure 9: Q-Mode Cluster Using Jaccard Similarity Metric. In general, quadrats plot by localities, which are designated by colors (see caption for Figure 8).

division was between open and closed basin associations. The Illinois and Appalachian Basins are open basins, with their localities grouped to the left, leaving the Michigan Basin localities to plot on the right. Biogenic carbonate texture (allochthonous versus autochthonous) also plays a role in the separation between each location. The Michigan Basin units have more autochthonous textures, while the Illinois Basin units have more allochthonous textures, with the Appalachian Basin units falling in between.

The R-mode cluster analysis groups species with similar patterns of occurrence. This analysis was also completed using both Bray-Curtis and Jaccard metrics. The Bray-Curtis R-mode cluster analysis revealed a mixing of the species from different locations and basins (Figure 10). This cluster diagram does not show a clear geographic pattern, but appears to reflect local variations in species abundances, indicating the importance of local controls on community composition. The biogenic carbonate structure and successional stages are also contributing to the local patterns. Individual species rarely co-occur between basins, except between the Michigan and Appalachian Basins (Whitehouse and Marblehead Quarries). This mixing of species between localities is attributed to the flooding of the Findlay Arch during high sea levels. The Illinois Basin is unique with a very high coral diversity and most of the species found within the three Illinois Basin localities (Falls of Ohio, Bear Creek, and Champions Trace) plot close together. Jaccard R-mode cluster analysis (Figure 11) plots species from the same basin closer together and separates basin type (open versus closed). The basin type explains why the Illinois Basin localities and Marblehead Quarry plot close together, driving all the other locations to the right. The Illinois Basin species cluster on the left and had smaller calculated distances between them, due to the locations being extremely similar in composition. The Besser Museum and

Figure 10: R-Mode Cluster Using Bray-Curtis Dissimilarity Metric. Species plotted close to each other tend to co-occur. Brackets represent basins in which species were present, purple – Marblehead, turquoise – Whitehouse, red – Besser Museum, orange – Rockport, green – Falls of Ohio, Bear Creek, and Champions Trace. Species are color coded: turquoise – tabulates, red – colonial rugose, purple – solitary rugose, green – stromatoporoid species. For species abbreviations, see Table 4 above.

Figure 11: R-Mode Cluster Using Jaccard Similarity Metric. Species plotted close to each other tend to co-occur. For species abbreviations, see Table 4 above. For species and bracket colors, see Figure 10 caption above. Whitehouse and Marblehead show a larger mixing between species present while the three Illinois Basin locations show the same amount of mixing.

Rockport Quarry species form a cluster on the right of the diagram. Although they appear to plot close together, they have relatively low similarity values, suggesting strong differences between both localities.

The multivariate ordination techniques reveal other patterns in the data. Nonmetric multidimensional scaling was performed, again using the Bray-Curtis dissimilarity metric and the Jaccard similarity metric using both localities and species. The NMDS plot using the Bray-Curtis metric on localities shows a distinct separation between basins, with a little overlap between Marblehead and Whitehouse, as well as between the Falls of the Ohio and Bear Creek (Figure 12). The NMDS showed a low stress of 0.291. The Shepard plot (not displayed) revealed a little deviation, suggesting a reasonably decent match in rank order distances between the original data and the rank ordination. The NMDS plot using the Jaccard metric on localities showed a slightly lower stress at 0.277 (Figure 13). Illinois Basin localities plot close together, but have a larger spread of the data than with the Bray-Curtis measure. Marblehead and Whitehouse locations no longer overlap, appearing slightly farther apart than in the Bray-Curtis metric. Besser Museum and Rockport Quarry plot low and away from the other localities.

Figure 12: NMDS Plot of Localities Using Bray-Curtis Dissimilarity Metric. Samples from the same locality are indicated with convex hulls. The locations for the most part are separated, except for Whitehouse (WQ) + Marblehead (MQ) and Bear Creek (BC) + Falls of the Ohio (FO). The Rockport Quarry (RQ) quadrats show a large spread and are very different from all the other localities.

Figure 13: NMDS Plot of Localities Using Jaccard Similarity Metric. Samples from the same localities are indicated with convex hulls. Using this measure, based on presence/absence of species instead of abundances, there is no longer an overlapping between the Appalachian (MQ) and southern Michigan Basins (WQ), however Bear Creek samples still plot with the Falls of the Ohio convex hull.

NMDS ordination was used to examine patterns in the distributions of the species observed in all three basins. Using the Bray-Curtis metric (Figure 14), most of the species plot fairly close together except for a few outliers, including two coral species found at Besser Museum, *Hexagonaria alpenensis* (HAA) and *Favosites alpenensis* (FA). Both species plot close to each other on the far right of Axis 1, away from all the other species. Stromatoporoid species (SS) did not fall into the larger grouped population, plotting slightly higher on NMDS Axis 2; this separation may have been due to stromatoporoid presence at every locality. The NMDS Jaccard metric produced different results compared to the Bray-Curtis metric (Figure 15). Overall, species show a very wide spread. Species that plot closer to each other were consistently found within the same basin. Species that were outliers using the Bray-Curtis metric, *H. alpenensis* and *F. alpenensis*, now plot close to the other species. Jaccard outliers were *Favosites nitellus* (FN, Rockport Quarry) and *Heterophrentis simplex* (HS, Whitehouse Quarry); these species plot far away from all the other species due to their occurrence in a single quadrat. The stress values for the NMDS analyses on species were high, 0.646 (Bray-Curtis) and 0.612 (Jaccard), indicating these analyses do not represent rank order of distances between species very well and therefore may not be the best tool for analyzing these species data.

Figure 14: NMDS Plot of Species Using Bray-Curtis Dissimilarity Metric. The green circle represents the species plotting close together, while the red circles indicate outliers. *Hexagonaria alpenensis* (HA) and *Favosites alpenensis* (FA), on the far left, were both found only at Besser Museum and in large abundances. The one outlier plotting high on the y-axis are the stromatoporoids species (SS), which were found at all localities.

Figure 15: NMDS Plot of Species Using Jaccard Similarity Metric. This analysis shows a more even spread of the species data. The two outliers are *Favosites nitellus* (FN - Rockport Quarry) and *Heterophrentis simplex* (HS - Whitehouse Quarry), which were only found in small abundances in two separate single quadrats.

The detrended correspondence analysis (DCA) has the potential to reveal environmental gradients along the ordination axes. In DCA, 34.5% of the total variance is explained on Axis 1 and 26.5% of total variance is attributed to Axis 2 (Figure 16). Axis 1 reveals a large gradient based on lithology. In Axis 1, the mudstone represented in Rockport Quarry drives quadrats to the far left. Besser Museum and all three Illinois Basin localities plot in the center area due to a limestone matrix. Lastly, plotting on the far right are Whitehouse and Marblehead, which are more or less dolomitized. The basin type (open versus closed) may also be playing a factor in the distribution of quadrat data on Axis 1. The DCA spreads Whitehouse Quarry quadrats and pulls them towards the closed basin localities (high on Axis 1). The Illinois Basin localities, which fall in the open basin type along with Marblehead Quarry, plot low on Axis 1.

Axis 2 appears to display a gradient pattern represented by substrate and basin type. There is very little spread of the data on Axis 2, except for the placement of the Whitehouse and Marblehead quadrats. They tend to plot lower on Axis 2, possibly due to similarities in substrate type. Both exhibit firmgrounds, while all locations in the Illinois Basin and Rockport Quarry represent softgrounds and tend to plot in the middle of Axis 2. Besser Museum is a hardground and does not conform to the pattern, plotting in the middle of Axis 2. The major outlier not following the environmental gradients is Rockport Quarry quadrat 4, which may be plotting high on Axis 2 because of the presence of the rare species *Favosites nitellus* (FN), which had previously been an outlier in the cluster diagrams and NMDS. DCA is often criticized for the iteration process, which may exaggerate rare taxa, in this case rare taxa within Rockport Quarry quadrat 4). The DCA results for the species followed a similar pattern as the DCA localities plot (Figure 17). The species plot according to grain size on Axis 1 and by substrate and basin type on Axis 2.

Figure 16: DCA Ordination Plot for Localities. Lithology is the driving environmental gradient on Axis 1 with mudstone towards the lower end on the axis, then limestone, followed by dolostone with the highest values (WQ and MQ). It is difficult to distinguish what environmental gradient Axis 2 reflects. Substrate type seems to be the driving factor pulling Marblehead and Whitehouse closer together towards firmgrounds and driving the other locations higher on Axis 2 with the presence of softgrounds and hardgrounds.

Figure 17: DCA Ordination Plot for Species. Axis 1 reflects a lithological gradient (right to left: mudstone, limestone, and dolostone). Axis 2 reflects Lecompte's (1970) successional patterns. Axis 2 brings Marblehead (MQ) and Whitehouse (WQ) closer towards the lower Axis 2 values, while driving all other localities to the center of Axis 2. *Hexagonaria anna* (HAA) and *Favosites nitellus* (FN) from Rockport Quarry (quadrat 4) are causing this quadrat to be a large outlier that does not conform to the overall patterns observed.

Although DCA appears to reveal potential environmental gradients, it does not take all environmental parameters into consideration. Canonical Correspondence Analysis (CCA), however, uses the observed environmental data for each locality. In the CCA, 26.82% and 24.96% of the total variance was explained on axes 1 and 2, respectively. The CCA triplot (Figure 18) displays the localities and species, with environmental parameters indicated by lines that point in the direction of the most change, while the line length indicates the importance of the environmental factor. Locations (Figure 19) and species (Figure 20) were also plotted separately to visualize patterns associated with CCA.

Lithology has the largest loading on Axis 1 (Figure 18), which is consistent with the results of DCA. This explains why Whitehouse and Marblehead, with extensive dolomites, plot close together and low on Axis 1. Rockport is singled out and plots alone in the center since it is the only location with mudstone. Limestone-rich Besser Museum localities plot with all three Illinois Basin localities towards the high end of Axis 1. The second largest environmental factor influencing the distribution of the data was biogenic carbonate texture, allochthonous versus autochthonous. Marblehead and Whitehouse Quarry plot low on Axis 1 and were both autogenic in nature. Rockport Quarry is allogenic and plots in the middle of Axis 1. All three Illinois Basin localities plot high on Axis 1 and represent both autogenic and allogenic influences. Besser Museum plots alongside Illinois Basin quadrats even though it is autogenic in nature. Besser Museum does not follow the biogenic carbonate texture gradient pattern. Instead Besser Museum is driven by the lithology factor. The type of basin, open versus closed, environmental energy, grain size, and substrate type were not as important as lithology and biogenic carbonate texture. This goes against the interpretations in the cluster diagrams, which were thought to be driven by open versus closed basins. However, CCA agrees with the cluster diagrams, revealing

biogenetic carbonate texture as an important influencing gradient. The CCA ordination of species (Figure 20) mirrors that of localities, as species from each locality plot together, in the same pattern as the localities.

CCA appears to be a more meaningful ordination technique compared to DCA. Environmental factors are incorporated into the analysis and explicitly tied to the ordination plot. DCA did reveal a lithology gradient, as did CCA. CCA displayed biogenic carbonate texture as an important factor, but DCA suggested that substrate type was more important. Contribution of environmental factors at different scales revealed differences observed in reef structure and reef communities. Local factors were important influences for the majority of these buildups and coral/sponge paleocommunities within each basin.

Figure 18: CCA Triplot of Localities and Species. Loadings for environmental parameters are indicated by black lines; line length indicates loading size, while direction indicates relative contribution to Axes 1 and 2 and direction of change. Abbreviations for environmental parameters: Grain – Grain Size, Lith – Lithology, BCT – Biogenetic Carbonate Texture, Energy – Environmental Energy, Sub – Substrate Type, Basin – Basin Type. Convex hulls were drawn and colored to easily identify all seven localities, see color key.

Figure 19: CCA Ordination Plot for Localities. On Axis 1, Marblehead and Whitehouse plot towards the left, while the Illinois Basin and the Besser Museum pull to the right. Rockport falls in the center on Axis 1, but plots extremely high on Axis 2. The other locations all plot towards the lower spectrum on Axis 2. Axis 1 represents lithologic differences, while Axis 2 is driven by biogenic carbonate texture.

Figure 20: CCA Ordination Plot for Species. All species plot in similar locations based on quadrat and overall location (Figure 19). *Favosites (Emmonsia) emmonsii* (FE) is found in Marblehead and Whitehouse, which is why it is not confined to a specific group. Stromatoporoids plot close to the Illinois locations and the Besser Museum, due to the large abundance from those sites.

Temporal and Spatial Patterns of Bioherms

Very few outcrops expose large vertical sections that would allow one to analyze and interpret different successional stages through time. The largest temporal observation in this study was at Besser Museum, where corals and stromatoporoids revealed successional trends on boulders just over 1m in height. The corals and stromatoporoids displayed a classic “keep up” reef pattern during a transgressive sequence. The “keep up” strategy is in respect to the corals, which are domal, tabular and show a trend of upwards building (rather than lateral spread), keeping up with the relative rise in sea level (James and Wood, 2010). The species present were building directly on top of other species, and the successional stage never changed, remaining in the domination zone for an extended period.

Combining the three localities within the Michigan Basin also provided a temporal gradient. Whitehouse Quarry exposes the Dundee Formation, representing the southern extent of the Michigan Basin, while the Rockport and the Alpena Formations represent northern extents. The Dundee Limestone is older (middle Eifelian) and successional models represent pioneer communities in the stabilization and subturbulent zones. About 2 million years younger (early Givetian), the Rockport Formation (Rockport Quarry) exposes another pioneer community but in the colonization and quiet water successional zones in the northern extent of the Michigan Basin. Near Rockport, the even younger Alpena Formation (Besser Museum; middle Givetian) was also examined. The Alpena Formation contains a true reef, which successional models describe as a climax stage in the domination zone within turbulent waters. Hence, all three Michigan Basin locations show unique and distinctive paleocommunities. The oldest Dundee Formation represents a pioneer community and the younger Rockport and Alpena signify a well established biohermal communities with higher successional stages. As conditions warmed during the

Middle Devonian, sea level was also rising. Corals may have favored closed basins on the northern extent of the Michigan Basin during transgressive phases. Environmental variables affecting corals were optimal, allowing for the colonization, diversification, and ultimately the domination of corals in the Michigan Basin.

Spatial patterns and extent of reef development were observed in all three basins, which provided a useful geospatial comparison of Middle Devonian bioherms. Middle Eifelian aged rocks, including the Dundee Limestone (Whitehouse, Michigan Basin), Columbus Limestone (Marblehead, Appalachian Basin), and Jeffersonville Formation (Illinois Basin localities) were compared. Marblehead and Whitehouse Quarry consistently showed similarities between environmental factors and species present. Both locations are in Ohio and separated by the topographic high, the Findlay Arch. Middle Devonian sea level curves show a global rise in sea level, supporting the idea that transgressive sequences breached the Findlay Arch, allowing for species mixing between the Appalachian and Michigan Basins. The Illinois Basin, however, is significantly different from the Appalachian and Michigan Basins due to different environmental variables affecting buildups, such as lithology and biogenetic carbonate texture, as well as the species present. Climax biohermal activity in the Illinois Basin also separates these complexes from the simple pioneering species in the Appalachian and Michigan Basins. This basin had a large diverse community that was equally allogenic and autogenic in nature, based on strom evidence and true successional species. The Dundee and Columbus Formations in Ohio show lower diversities and smaller area occupation of corals and stromatoporoids, suggesting little competition for space. The Jeffersonville Limestone, during the Eifelian, was a thriving ecosystem in a stable open ocean environment with optimum conditions for complex reef development. Although the Appalachian Basin was connected to the Rheic Sea, the Columbus

Limestone did not experience full open ocean conditions. The Columbus Limestone at Marblehead has previously been described as a lagoon (Briggs, 1959) and consequently secluded to a degree from the Rheic Sea.

Several factors affect the buildup of bioherms such as environmental variables and intrinsic controls, which can be at a community or species level. Environmental factors are strongly associated with the formation of bioherms and affect the build-up process in many ways. The Q-mode and R-mode cluster analyses showed that biogenetic carbonate structure and basin type (open versus closed basin) drove species compositions. According to the ordination techniques of DCA and CCA, lithology was the most important environmental parameter dictating relationships between basins and biohermal growth. DCA also revealed substrate type as an important contributing factor, while CCA showed that biogenic carbonate texture was more important. These ordination techniques showed that extrinsic controls such as lithology play a large role in biohermal construction, suggesting paleocommunities correlate with rock type. Intrinsic controls also seem to play an important role, according to Q-mode cluster analysis (Bray-Curtis), DCA, and CCA.

Devonian Bioherm Ecology

The true reefs and patch reefs in all three basins showed differences between basins determined by the successional zone or stage represented by the observed bioherms. Many factors affect the process by which corals colonize a suitable substrate and stabilize a biocoenosis. Not only does the substrate have to be ideal, but autogenic (species present) and allogenic factors also play a role. Physical and chemical parameters (allogenic) such as sea level fluctuations, temperature, nutrients, waves, and current action act as controls on growth space and morphology (Wang et al., 2012). All the corals in the studied localities resided in shallow subtidal environments on a carbonate ramp platform with significant nutrient supply and

wave/current action, except for Marblehead, which has been interpreted as a hypersaline lagoon by Briggs (1959).

The Appalachian Basin was studied at a location in the northern extent of the basin in the Columbus Formation. A single bioherm is represented at Marblehead Quarry in a lagoonal environment. The Columbus Formation and the Dundee Limestone (Whitehouse Quarry, Michigan Basin) are approximately the same age. Environmental conditions shared between both basins include similar lithology, biogenic carbonate texture and successional zones described by Lecompte (1970) and Copper (1988). Some species (*Zaphrentis prolifica*, *Zaphrentis gigantea*, and *Favosites (Emmonsia) emmonsi*) also occur in both localities, suggesting faunal mixing. Presumably the Findlay Arch was flooded during high sea levels and transgressive sequences allowing for mixing to occur between basins.

Whitehouse Quarry (also represented by a single bioherm) was more similar in composition and physical characteristics to Marblehead Quarry in the Appalachian Basin than to the other locations within the Michigan Basin. The younger Rockport Formation consisted of a single bioherm residing in deeper waters, comprised of robust and large colonial corals on a muddy substrate. Paleontological analyses consistently placed Rockport Quarry communities further from the other basins and localities due to the unique physical environment. The Alpena Formation also displayed a unique community, a true reef. Due to the transportation of the boulders, it is unclear whether this location represents a single reef or multiple bioherms. The reef revealed dominant corals (*Hexagonaria alpenensis* and *Favosites alpenensis*) and stromatoporoids, and occupied its own region in the analytical results. The basin with which it shared the most similarities was the Illinois Basin, according to DCA and CCA. Similarities between the Michigan and the Illinois reefs include substrate lithology (limestone) and high

successional zones (turbulent zone, climax zone, domination and diversification zones, respectively). Since lithology was an important factor affecting reef structure, these basins plotted closer when compared to the other identified bioherms.

The three localities from the Illinois Basin are in close proximity to each other and overlapped in every paleontological analysis. Bulinski et al. (2015) described the Falls of the Ohio State Park as a large biostrome. Due to the strong similarities between all three locations (Falls of Ohio, Bear Creek, and Champions Trace), the extent of this biostrome should be assessed. This biostrome potentially extended over a large area, representing a single biostrome at all three localities. Alternatively, if the biostrome does not extend to all localities, then it is possible each location represents its own patch reef. The bioherms and individual coral species thrived due to the upwelling and influx of nutrients in this open basin. The Jeffersonville Formation of the Illinois Basin is the same age as the Dundee (Whitehouse) and Columbus (Marblehead) Formations (Middle Eifelian). Complex reef development with a large faunal diversity was shown in the Jeffersonville Limestone compared to the low diversity pioneering communities in the Michigan (except Besser Museum) and Appalachian Basins.

CHAPTER V. DISCUSSION

Middle Devonian reefs in North America, specifically the Appalachian, Michigan, and Illinois Basins, have not been well documented. The five objectives of this project were addressed using area abundance data, environmental factors, and successional models to document and describe biohermal complexes. The ecology of coral and stromatoporoid communities in all three basins was interpreted using diversity indices, similarity metrics, and ordination techniques. Successional models (Lecompte, 1970; Walker and Alberstadt, 1975; Copper, 1988) should be used to describe any reefal or biohermal structure to summarize environmental observations and community compositions.

First, reef communities change geospatially and temporally among localities, which was observed and documented using paleontological analyses. The Q-mode and R-mode cluster analyses showed that biogenetic carbonate structure and basin type (open versus closed basin) drove species abundance and distribution patterns. DCA revealed lithology and substrate type were dictating relationships between basins. CCA suggests the most significant environmental factors associated with biohermal development were lithology and biogenic carbonate texture, confirming trends observed in DCA and cluster analyses. Extrinsic and intrinsic controls at a community or species level are strongly associated with the formation of bioherms and affect zonations. The ordination techniques showed that extrinsic controls such as lithology play a large role in biohermal construction, suggesting paleocommunities correlate with rock type. Abundances and intrinsic controls contribute to similarities between basins, according to Q-mode cluster analysis (Bray-Curtis), DCA, and CCA. Unsurprisingly, the Illinois Basin localities all plotted very close together since they are in close geographic proximity and fall within the Jeffersonville Formation. Marblehead Quarry and Whitehouse Quarry, despite being in two

different basins, revealed similarities between species present and tended to show lower successional zonations compared to the other localities. These Ohio locations were separated by the Findlay Arch, which was potentially breached allowing for species mixing between the Appalachian and southern Michigan Basins. Lithology and biogenic carbonate texture appear to have driven geospatial similarities among paleocommunities in the Middle Devonian.

Temporal patterns were harder to determine. Very few outcrops were sufficiently exposed to record changes in successional patterns at a single locality. The Besser Museum had the largest vertical outcrop, however the successional stage never changed, remaining in the domination zone. The best temporal pattern that can be discussed lies within the Michigan Basin, when sea level was slowly rising through several transgressive and regressive cycles, influencing reefal communities. Whitehouse Quarry exposes the Dundee Formation, representing the southern extent of the Michigan Basin, while Rockport and Alpena represent northern extents. The Dundee Limestone is older and successional models represent pioneer communities in the stabilization and subturbulent zones. Approximately two million years younger, the Rockport Formation (Rockport Quarry) exposes another pioneer community but in the colonization and quiet water successional zones in the northern extent of the Michigan Basin. Near Rockport, the still younger Alpena Formation at the Besser Museum shows a climax stage in the domination zone within turbulent waters. All three locations show unique and distinctive paleocommunities, which is why these three successional models should be used to describe bioherms. The models take into consideration numerous environmental factors, intrinsic species, and community variables that help describe several aspects of reefal buildup.

The second research question was addressed by identifying all successional zones and determining whether the zones were autogenically or allogenicly controlled. Walker and

Alberstadt (1975) suggested reefal communities are autogenically controlled, whereas Hoffman and Narkiewicz (1977) advocated for more allogenic controls. The Michigan Basin revealed the Dundee Formation (at Whitehouse Quarry) was a pioneer community in the stabilization zone in turbulent waters. Observations suggest both allogenic and autogenetic factors. Allogenic factors include evidence for storm activity in the area, lots of sediment between corals and stromatoporoids, lack of coral buildup, and presence of other organisms (brachiopods, gastropods, bivalves, etc.). Although there was a general lack of coral buildup, a few colonial corals grew directly on top of each other. At Whitehouse, autogenic controls include substrate stabilization, competition for space and nutrients between corals, and other organisms also occupying the habitat. The Rockport Formation (Rockport Quarry) revealed more allogenic factors were contributing to bioherm activity. The quiet water zone allowed pioneer communities to build up into the colonization zone. A large storm event toppled over several corals and stromatoporoids of all shapes and sizes, which resulted in the bioherm not reaching the next successional stage (diversification). The Alpena Formation exposed a true reef structure, truly autogenetic with little sediment associations and more competition for space. Alpena represents a climax community in the domination stage building into the turbulent zone.

The Illinois Basin (Falls of the Ohio, Bear Creek, and Champions Trace) exposes the Jeffersonville Limestone and all locations are characterized by a distinctive climax community within the diversification zone in the turbulent zone. These buildups show evidence of species competing for space, an autogenic factor, as well as evidence for storms in a moderate energy environment, suggesting both autogenic and allogenic controls. All coral units experienced different successional stages and showed evidence of intrinsic and extrinsic factors influencing the successional zone and buildup. Autogenic and allogenic factors need to be identified

separately from the successional stages in order to properly characterize reefal structures and controls.

Third, it was clear that environmental factors that differed among basins affected the buildups. Substrate lithology was found to be an important environmental variable dictating basinal communities in the ordination techniques (DCA and CCA). Biogenic carbonate texture also played a significant role in dictating biohermal activity according to CCA and cluster analyses. Other environmental factors such as open versus closed basin type, energy level, grain size, and substrate type were less important according to cluster and ordination techniques.

Fourth, no clear gradient was detected between more open versus closed basins. The Q-mode Jaccard cluster diagram revealed such a trend, but other analyses did not show basin type as a major environmental variable. In fact, CCA, which expresses the amount of variation among environmental factors, showed that the basin type was one of the lesser contributing factors. Lithology and biogenic carbonate texture dictate similarities (or differences) between buildups and locations, not open versus closed basin systems.

Lastly, successional patterns summarized environmental conditions, community compositions and biohermal activity. The successional models take into consideration some of the most important environmental factors. Lecompte (1970) used water turbulence and environmental energy to describe successional patterns. Walker and Alberstadt (1975) focused on environmental variables including autogenic versus allogenic successional types as well as species composition and diversity. Copper (1988) chose to focus on species and community factors by describing differences between pioneer and climax communities. Successional patterns describe important environmental parameters that dictate build up, but are not the only ecological variables that should be analyzed. Several other factors, including lithology, grain

size, and autogenic versus allogenic patterns, should always be observed and documented when studying reefal communities. The more environmental parameters reported, especially identifying lithology and allogenic/autogenic factors attributed to reef development, the better the units or bioherm communities under consideration can be described and compared. All reef and biohermal communities should be described by the successional models put forth by Lecompte (1970), Walker and Alberstadt (1975), and Copper (1988). The successional models should not be used separately, however, as the models are generalized and little knowledge is gained by using them individually. Applying all three models to bioherms allows one to fully explore ecological parameters used to document reef stages. In this study, the successional models effectively categorized biohermal activity in all three Paleozoic basins.

Future work regarding Paleozoic corals should include expanding localities across the Great Lakes region to provide better geospatial resolution during the Middle Devonian. Adding more localities will confirm trends between basins such as the mixing of fauna between the Appalachian and Michigan Basins. When did the faunas begin mixing? Did the species originate in the Appalachian or Michigan Basin? Is the Findlay Arch truly separating the basins during the Middle Devonian? The Kankakee Arch separates the Michigan Basin from the Illinois Basin and the Cincinnati Arch separates the Illinois from the Appalachian Basin. Is there evidence for species mixing during high sea levels between the Illinois and Michigan Basins or between the Illinois and Appalachian Basins? Ecological data pertaining to future studies should include additional environmental variables when available, such as nutrient levels, productivity, light, salinity, temperature and sedimentation rates in all three basins. More data gathered about the basins and fauna will allow workers to better characterize biohermal activity during the greenhouse interval in the Middle Devonian.

A major component of this study regarded differences in coral buildup depending on basin type (open versus closed). While a strong pattern differentiating these basin types was not observed here, collecting data from more localities within the Appalachian or Illinois Basins would help answer how corals are affected by open ocean conditions. Comparing buildups within the same basin would encompass differences attributed to influxes from the Rheic Sea. The Iowa Basin, another closed basin during the Middle Devonian, was not included in this study. Previous studies confirm biohermal activity within the Iowa Basin, which makes this an ideal basin to continue biohermal studies in North America. Identifying more locations in all four basins will add to the growing knowledge of Paleozoic biohermal communities.

Not only will more locations help us understand the distribution of coral complexes, but locating outcrops with larger vertical profiles will also add to the temporal scale of Devonian bioherms in North America. Temporal resolution was slim in this study due to the lack of vertical exposures in all seven locations. The Dundee (Whitehouse Quarry), Rockport (Rockport Quarry), and Alpena (Besser Museum) Formations revealed a trend towards higher successional stages in younger rocks, providing a slight temporal scale. Is this trend an inclination of reef development all across North America during this interval, or was it specific to the Michigan Basin? What extrinsic or intrinsic factors drive changes temporally in reef successions? Do successional models successfully characterize temporal patterns in bioherm or reefal structures? Future work should aim to answer these geospatial and temporal questions about reef successions.

CHAPTER VI. SUMMARY AND CONCLUSIONS

Despite the Middle Devonian being a time of great reef expansion, the ecology and evolution of small bioherm communities in epicontinental basins of North America have not been well documented. This study used a comparative approach to document biohermal activity and successional patterns in Middle Devonian formations of eastern North America. Field sampling and documentation of coral-stromatoporoid bioherms revealed geospatial and temporal patterns across the Appalachian, Michigan, and Illinois Basins.

Cluster analyses showed that biogenetic carbonate structure and basin type (open versus closed basin) influenced the community composition of these bioherms. Ordination techniques (detrended and canonical correspondence analyses) revealed the importance of lithology as the main driving factor explaining differences between buildups within and between basins. CCA agrees with the cluster analyses that biogenic carbonate texture is another driving factor associated with biohermal growth, while DCA claims substrate type is more important. Each documented bioherm was unique with respect to species composition, abundance and environmental controls. Both autogenic and allogenic factors were important, and differences in bioherm composition may have been affected by conditions in open versus closed basins. The results demonstrate similarities between the bioherms in the Appalachian and southern Michigan Basins, likely reflecting marine mixing across the Findlay Arch. Similarities were also strong between all three locations within the Illinois Basin. The northern Michigan Basin localities (Rockport and Alpena) were quite different compared to each other and the other localities. The data also support a temporal pattern within the Michigan Basin of lower successional stages in the Eifelian changing to higher successional stages by the Middle Givetian.

This research contributes to a better understanding of reefal development in eastern North America during the greenhouse interval of the Middle Devonian. Successional models used to describe bioherms have been shown to effectively characterize different components of reefal construction. An increased understanding of extrinsic and intrinsic factors that affect the buildup and construction of bioherms by corals and stromatoporoids was obtained. Future work can increase the number of localities from the three North American basins in order to improve spatial and temporal resolution, and add data from the Iowa Basin to further document bioherm activity in the Devonian of North America.

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APPENDIX A. ALPENA, MI PALEOZOIC CORAL FAUNA

Coral fossil species found around the northern extent of the Michigan Basin. Includes a combination of the Rockport and Alpena Formations. Faunal list was derived from studies by Grabau (1902), Stumm (1950, 1954, 1961, 1969), and Stumm and Tyler (1964).

<i>Alveolites goldfussi</i>	<i>Cylindrophyllum cf. aggregatum</i>
<i>Alveolites subramosus</i>	<i>Cylindrophyllum delicatulum</i>
<i>Antholites alpenensis</i>	<i>Cylindrophyllum grabaui</i>
<i>Antholites bridghami</i>	<i>Cylindrophyllum hindshawi</i>
<i>Atelophyllum magnum</i>	<i>Cylindrophyllum magnum</i>
<i>Atelophyllum subcylindricum</i>	<i>Cylindrophyllum panicum</i>
<i>Aulacophyllum alpenense</i>	<i>Cylindrophyllum petoskeyense</i>
<i>Aulacophyllum hemicrassatum</i>	<i>Cylindrophyllum phacelliforme</i>
<i>Aulacophyllum scyphus</i>	<i>Cylindrophyllum potterense</i>
<i>Aulocystis alectiformis</i>	<i>Depasophyllum adnetum</i>
<i>Aulocystis alectiformis dubia</i>	<i>Disphyllum compactum</i>
<i>Aulocystis alectiformis reptata</i>	<i>Drymopora erecta</i>
<i>Aulocystis alpenensis</i>	<i>Drymopora nobilis</i>
<i>Aulocystis commensalis</i>	<i>Eridophyllum archiaci</i>
<i>Aulocystis cooperi</i>	<i>Favosites (Emmonsia) alpenensis</i>
<i>Aulocystis crassimurata</i>	<i>Favosites (Emmonsia) radiata</i>
<i>Aulocystis fenestrata</i>	<i>Favosites alpenensis alpenensis</i>
<i>Aulocystis fenestrata problematica</i>	<i>Favosites alpenensis bellensis</i>
<i>Aulocystis hacksoni</i>	<i>Favosites alpenensis calveri</i>
<i>Aulocystis magnispina</i>	<i>Favosites alpenensis hindshawi</i>
<i>Aulocystis multicystosa</i>	<i>Favosites alpenensis kellyi</i>
<i>Aulocystis parva</i>	<i>Favosites alpenensis killiansensis</i>
<i>Aulocystis stummi</i>	<i>Favosites alpenensis peninsulae</i>
<i>Aulopora "serpens"</i>	<i>Favosites alpenensis tenuimuralis</i>
<i>Aulopora conferta</i>	<i>Favosites billingsi</i>
<i>Aulopora gregaria</i>	<i>Favosites clausus</i>
<i>Aulopora microbuccinata</i>	<i>Favosites digitatus</i>
<i>Bethanyphyllum bellense</i>	<i>Favosites mammillatus</i>
<i>Bethanyphyllum geniculatum</i>	<i>Favosites nitellus</i>
<i>Billingsastrea pauciseptata</i>	<i>Favosites placentus</i>
<i>Billingsastrea rockportensis</i>	<i>Favosites radiciformis</i>
<i>Billingsastrea romingeri</i>	<i>Favosites romingeri gilvisquamulata</i>
<i>Cladopora alpenensis</i>	<i>Favosites romingeri patella</i>
<i>Cylindrophyllum alpenense</i>	<i>Favosites romingeri romingeri</i>
<i>Cylindrophyllum amalgamatum</i>	<i>Favosites romingeri saetigera</i>
<i>Cylindrophyllum americanum</i>	<i>Favosites turbinatus</i>
<i>Cylindrophyllum americanum bellense</i>	<i>Favosites valentine</i>
<i>Cylindrophyllum americanum elongatum</i>	<i>Favosites warthini</i>

<i>Hallia vesiculata</i>	<i>Pachyphragma erectum</i>
<i>Heliophyllum ferronense</i>	<i>Platyaxum fischeri</i>
<i>Heliophyllum halli</i>	<i>Pleurodictyum (Procteria) cornu</i>
<i>Heliophyllum halli bellense</i>	<i>Pleurodictyum insigne</i>
<i>Heliophyllum halli potterense</i>	<i>Pleurodictyum wardi</i>
<i>Heliophyllum juvene</i>	<i>Spongophyllum alpenense</i>
<i>Heliophyllum rotatorium</i>	<i>Spongophyllum romingeri</i>
<i>Heliophyllum tenuiseptatum tentaculum</i>	<i>Stereolasma petoskeyense</i>
<i>Heliophyllum tenuiseptatum traversense</i>	<i>Striatopora cf. iowensis</i>
<i>Heterophrentis ferronensis</i>	<i>Striatopora linneana</i>
<i>Heterophrentis gregaria</i>	<i>Striatopora rugosa</i>
<i>Heterophrentis simplex alpenense</i>	<i>Synaptophyllum crassiseptatum</i>
<i>Hexagonaria alpenensis</i>	<i>Syringopora ehlersi</i>
<i>Hexagonaria anna</i>	<i>Tabulophyllum curtum</i>
<i>Hexagonaria attenuata</i>	<i>Tabulophyllum elongatum</i>
<i>Hexagonaria cristata</i>	<i>Tabulophyllum traversense</i>
<i>Hexagonaria fusiformis</i>	<i>Tortophyllum cysticum</i>
<i>Hexagonaria percarinata</i>	<i>Tortophyllum magnum</i>
<i>Hexagonaria potterensis</i>	<i>Trachypora alpenensis</i>
<i>Hexagonaria profunda</i>	<i>Trachypora alternans</i>
<i>Hexagonaria subcarinata</i>	<i>Trachypora dendroidea</i>
<i>Iowaphyllum alpenense</i>	<i>Trachypora elegantula</i>
<i>Lythophyllum alpenense</i>	<i>Trachypora lineata</i>
<i>Microcyclus alpenensis</i>	<i>Trachypora ornate</i>
<i>Naos ocatus</i>	<i>Trachypora perreticulata</i>
<i>Naos ponderosus</i>	<i>Trachypora proboscidalis</i>
<i>Pachyphragma concentricum</i>	<i>Trachypora reticulata</i>
<i>Pachyphragma cylindricum</i>	<i>Trachypora rockportensis</i>

APPENDIX B. WHITEHOUSE, OH PALEOZOIC CORAL FAUNA

Fossil list of coral species found in the southern extent of the Michigan Basin. This includes species from the Dundee Formation in Whitehouse Quarry. List was created using previous studies by Stauffer (1909), Bassett (1935), Stumm (1968), and Wright (2006).

<i>Bethanyphyllum robustum</i>	<i>Favosites sp.</i>
<i>Billingsastraea longicarinata</i>	<i>Heliophyllum bathycalyx</i>
<i>Cayugaea intermiteens</i>	<i>Heliophyllum microcarinatum</i>
<i>Cayugaea transitorius</i>	<i>Heterophrentis simplex</i>
<i>Cladopora reticulate</i>	<i>Hexagonaria anna</i>
<i>Cladopora roemeri</i>	<i>Hexagonaria stewartae</i>
<i>Cladopora sp.</i>	<i>Hexagonaria tabulata</i>
<i>Cladopora tela</i>	<i>Hexagonaria teruncata</i>
<i>Coleolus crenatocinctus</i>	<i>Idiostroma sp.</i>
<i>Coleolus sp.</i>	<i>Prismatophyllum davidsoni</i>
<i>Cylindrophyllum delicatulum</i>	<i>Stereolasma bethae</i>
<i>Cystiphyllodes americanum</i>	<i>Stromatopora nodulata</i>
<i>Cystiphyllum vesiculosum</i>	<i>Stromatopora ponderosa</i>
<i>Cythophyllum sp.</i>	<i>Syringopora sp.</i>
<i>Emmonsia polymorpha</i>	<i>Zaphrentis cornicula</i>
<i>Favosites (Emmonsia) emmonsi</i>	<i>Zaphrentis gigantea</i>
<i>Favosites hemisphericus</i>	<i>Zaphrentis perovalis</i>
<i>Favosites limitaris</i>	<i>Zaphrentis prolifica</i>
<i>Favosites nitellus</i>	<i>Zaphrentis simplex</i>

APPENDIX C. CLARKSVILLE, IN AND LOUISVILLE, KY PALEOZOIC CORAL

FAUNA

Faunal list of Middle Devonian Illinois Basin corals. This includes species from the Jeffersonville Formation near field sites near Falls of the Ohio State Park (IN), Fork Bear Creek and Champions Trace (KY). The list is a combination of the upper and lower coral zones, which was created using previous studies by Davis (1887), Greb et al. (1993), Hendricks et al. (2005), and Goldstein (2010).

<i>Acinophyllum mclareni</i>	<i>Chonostegites tabulates</i>
<i>Acinophyllum stokesi</i>	<i>Cladionophyllum cicatriciferum</i>
<i>Acrophyllum ellipticum</i>	<i>Cladopora acupicta</i>
<i>Acrophyllum oneidaense</i>	<i>Cladopora biferca</i>
<i>Aemuliophyllum exiguum</i>	<i>Cladopora gracilis</i>
<i>Aemuliophyllum exiguum elongatum</i>	<i>Cladopora labiosa</i>
<i>Alveolites asperus</i>	<i>Coleophyllum romingeri</i>
<i>Alveolites constans</i>	<i>Compressiphyllum davisana</i>
<i>Alveolites expatiatius</i>	<i>Craterophyllum latiradium</i>
<i>Alveolites minimus</i>	<i>Craterophyllum magnificum</i>
<i>Alveolites mordax</i>	<i>Cyanthocylindrium gemmatum</i>
<i>Alveolites squamosus</i>	<i>Cyanthocylindrium opulens</i>
<i>Alveolites winchellana</i>	<i>Cylindrophyllum gradatum</i>
<i>Amplexiphyllum cruciforme</i>	<i>Cystiphyllodes hispidum</i>
<i>Amplexiphyllum tenue</i>	<i>Cystiphyllodes infunibuliformis</i>
<i>Aulacophyllum mutabile</i>	<i>Cystiphyllodes limbatum</i>
<i>Aulacophyllum perlamellosum</i>	<i>Cystiphyllodes nanum</i>
<i>Aulacophyllum pinnatum</i>	<i>Cystiphyllodes plicatum</i>
<i>Aulacophyllum sulcatum</i>	<i>Cystiphyllodes pustulatum</i>
<i>Aulocystis fascicularis</i>	<i>Cystiphyllodes quadrangulare</i>
<i>Aulocystis incrustans</i>	<i>Cystiphyllodes tenuiradium</i>
<i>Aulocystis nobilis</i>	<i>Disphyllum synaptophylloides</i>
<i>Aulocystis procumbens</i>	<i>Enallophrentis duplicate</i>
<i>Aulopora culmula</i>	<i>Enallophrentis inflata</i>
<i>Aulopora edithana</i>	<i>Enallophrentis ovalis</i>
<i>Aulopora tubiporoides</i>	<i>Enallophrentis trisutura</i>
<i>Bethanyphyllum arctifossa</i>	<i>Enallophrentis? cyanthiformis</i>
<i>Bethanyphyllum pocillum</i>	<i>Eridophyllum apertum</i>
<i>Bethanyphyllum robustum</i>	<i>Eridophyllum coagulatum</i>
<i>Bethanyphyllum vesiculatum</i>	<i>Eridophyllum seriale</i>
<i>Blothrophyllum perplicatum</i>	<i>Favosites (Emmonsia) amplissimus</i>
<i>Blothrophyllum rominger</i>	<i>Favosites (Emmonsia) baculus</i>
<i>Blothrophyllum trisulcatum</i>	<i>Favosites (Emmonsia) convexus</i>
<i>Bractea arbor</i>	<i>Favosites (Emmonsia) cymosus</i>
<i>Bractea frutex</i>	<i>Favosites (Emmonsia) emmonsi</i>
<i>Bractea impedita</i>	<i>Favosites (Emmonsia) epidermatus</i>
<i>Breviphrentis nitida</i>	<i>Favosites (Emmonsia) ocellatus</i>
<i>Breviphrentis planima</i>	<i>Favosites (Emmonsia) radiceformis</i>
<i>Bucanophyllum ohioense</i>	<i>Favosites (Emmonsia) ramosa</i>
<i>Cayugaea subcylindrica</i>	<i>Favosites (Emmonsia) sp. nov.</i>

<i>Favosites (Emmonsia) tuberosus</i>	<i>Pleurodictyum (Procteria) papillosa</i>
<i>Favosites biloculi</i>	<i>Pleurodictyum (Procteria) spiculata</i>
<i>Favosites clelandi</i>	<i>Pleurodictyum cylindricum</i>
<i>Favosites hemisphericus (cornutiformis)</i>	<i>Pleurodictyum maximum</i>
<i>Favosites mundus</i>	<i>Prismatophyllum bella</i>
<i>Favosites patellatus</i>	<i>Prismatophyllum conjunctum</i>
<i>Favosites pirum</i>	<i>Prismatophyllum ovoideum</i>
<i>Favosites proximatus</i>	<i>Prismatophyllum prisma</i>
<i>Favosites quercus</i>	<i>Prismatophyllum truncate</i>
<i>Favosites ramulosus</i>	<i>Romingeria commutate</i>
<i>Favosites turbinatus</i>	<i>Romingeria fasculata</i>
<i>Heliophyllum agassizi</i>	<i>Romingeria umbellifera</i>
<i>Heliophyllum coalitum</i>	<i>Romingeria uva</i>
<i>Heliophyllum denticulatum</i>	<i>Scenophyllum conigerum</i>
<i>Heliophyllum incrassatum</i>	<i>Schlotheimophyllum typicum</i>
<i>Heliophyllum latericrescens</i>	<i>Siphonophrentis elongata</i>
<i>Heliophyllum pocillum</i>	<i>Siphonophrentis yandelli</i>
<i>Heliophyllum venatum</i>	<i>Skoliophyllum squamosum</i>
<i>Heliophyllum verticale</i>	<i>Stauromatidium trigemma</i>
<i>Heliophyllum yandelli</i>	<i>Stereolasma exile</i>
<i>Heterophrentis annulata</i>	<i>Stereolasma parvulum</i>
<i>Heterophrentis irregularis</i>	<i>Striatopora alba</i>
<i>Heterophrentis rafinesqui</i>	<i>Striatopora bellistriata</i>
<i>Homalophyllum fusiformis</i>	<i>Syringopora hisingeri</i>
<i>Homalophyllum herzeri</i>	<i>Syringopora perelegans</i>
<i>Homalophyllum ungulum</i>	<i>Tabulophyllum bellicinctum</i>
<i>Kionelasma coarticum</i>	<i>Tabulophyllum greeni</i>
<i>Kionelasma mammiferum</i>	<i>Tabulophyllum sinuosum</i>
<i>Lecfedites Canadensis</i>	<i>Tabulophyllum tripinnatum</i>
<i>Odontophyllum convergens</i>	<i>Thamnopora distans</i>
<i>Platyaxum foliatum</i>	<i>Thamnopora limitaris</i>
<i>Platyaxum orthosoleniskum</i>	<i>Thamnoptychia tuberculata</i>
<i>Platyaxum undosum</i>	<i>Trilophyllum terebrata</i>
<i>Pleurodictyum (Procteria) michelinoides</i>	<i>Zaphrentis Phrygia</i>

APPENDIX D. MARBLEHEAD, OH PALEOZOIC CORAL FAUNA

Faunal list of the northern extent of the Appalachian Basin near the Findlay Arch. This includes species from the Columbus Formation in Marblehead, OH. List was created using previous studies by Stewart (1955), Martin (2002), Feldman (1980), and Oliver (1976).

<i>Acinophyllum segregatum</i>	<i>Favosites hemispherica</i>
<i>Amplexiphyllum hamiltonae</i>	<i>Favosites hemisphericus</i>
<i>Aulopora sp.</i>	<i>Favosites maximus</i>
<i>Bethanyphyllum robustum</i>	<i>Favosites turbinatus</i>
<i>Blothrophyllum promissum</i>	<i>Favosites turbinatus</i>
<i>Breviphrentis yandelli</i>	<i>Heliophyllum halli</i>
<i>Calcisphaera robusta</i>	<i>Heliophyllum sp.</i>
<i>Ceratopora sp.</i>	<i>Heterophrentis prolifica</i>
<i>Cladopora pulchra</i>	<i>Heterophrentis prolifica</i>
<i>Cladopora robusta</i>	<i>Heterophrentis simplex</i>
<i>Cladopora tela</i>	<i>Heterophrentis sp.</i>
<i>Coenites roemeri</i>	<i>Hexagonaria prisma</i>
<i>Coenites sp.</i>	<i>Leptaena rhomboidalis</i>
<i>Cyathophyllum robustum</i>	<i>Pleurodictyum convexa</i>
<i>Cylindrophyllum elongatum</i>	<i>Prismatophyllum annum</i>
<i>Cystiphyllodes americanum</i>	<i>Prismatophyllum ovoideum</i>
<i>Cystiphyllodes americanus</i>	<i>Prismatophyllum prisma</i>
<i>Cystiphyllodes sulcatum</i>	<i>Prismatophyllum truncata</i>
<i>Cystiphyllum vesiculosum</i>	<i>Prismatophyllum whitfield</i>
<i>Cystodictya gilberti</i>	<i>Siphonophrentis gigantea</i>
<i>Diphyphyllum simcoensce</i>	<i>Siphonophrentis gigantean</i>
<i>Diphyphyllum strictum</i>	<i>Stromatopora ponderosa</i>
<i>Diphyphyllum verneuillanum</i>	<i>Synaptophyllum simcoense</i>
<i>Emmonsia emmonsi</i>	<i>Synaptophyllum sp.</i>
<i>Emmonsia polymorpha</i>	<i>Syringopora sp.</i>
<i>Eridophyllum seriale</i>	<i>Syringopora tabulata</i>
<i>Favosites basalticus</i>	<i>Zaphrentis cornicula</i>
<i>Favosites canadensis</i>	<i>Zaphrentis corniculum</i>
<i>Favosites emmonsi</i>	<i>Zaphrentis gigantea</i>
<i>Favosites goldfussi</i>	<i>Zaphrentis phyrigia</i>
<i>Favosites goldfussi</i>	<i>Zaphrentis prolifica</i>

APPENDIX E. PALEONTOLOGICAL ABUNDANCES BY QUADRAT

Abundances are divided into locations and quadrats: Besser Museum, Rockport Quarry, Whitehouse Quarry, Falls of Ohio State Park, Bear Creek, Champions Trace, and Marblehead Quarry. The quadrat data include species, code, type, area, cover percent, and total area coverage. The “code” refers to the Coral Point Count with Excel extensions (CPCe) two-three letter species codes: AM - *Acinophyllum mclarni*; ASG - *Acinophyllum segregatum*; AS - *Acinophyllum stokes*; BR - *Blothrophyllum romingeri*; CI - *Cladopora imbricata*; CT - *Cladopora tela*; CA - *Cystiphyllodes americanum*; CH - *Cystiphyllodes hispidum*; CYI - *Cystiphyllodes infundibuliformis*; CN - *Cystiphyllodes nanum*; ES - *Eridophyllum seriale*; FE - *Favosites (Emmonsia) emmonsi*; FEE - *Favosites (Emmonsia) epidermatus*; FER - *Favosites (Emmonsia) ramosa*; FET - *Favosites (Emmonsia) tuberosus*; FA - *Favosites alpenensis*; FB - *Favosites biloculi*; FD - *Favosites digitatus*; FH - *Favosites hemisphericus*; FL - *Favosites limitaris*; FM - *Favosites mammilatus*; FN - *Favosites nitellus*; FR - *Favosites ramulosus*; FT - *Favosites turbinatus*; HVN - *Heliophyllum venatum*; HV - *Heliophyllum verticale*; HI - *Heterophrentis irregularis*; HS - *Heterophrentis simplex*; HA - *Hexagonaria alpenensis*; HAA - *Hexagonaria anna*; PC - *Pleurodictyum cylindricum*; PLP - *Pleurodictyum planum*; PO - *Prismatophyllum ovoideum*; PP - *Prismatophyllum prisma*; SE - *Siphonophrentis elongata*; SY - *Siphonophrentis yandelli*; SB - *Striatopora bellistriata*; TL - *Thamnopora limitaris*; ZG - *Zaphrentis gigantea*; ZP - *Zaphrentis prolifica*; SS - *Stromatoporoid species*. The “type” refers to the order of corals to which the species belong: CR – Colonial Rugose; SR – Solitary Rugose; T – Tabulate; SS – *Stromatoporoid species*. “Area” is the quantified area abundances (cm²) provided by CPCe. The “total coral area coverage” is the sum of all the species areas to get a sense of coral versus sediment coverage. The individual species areas were then divided by the total quadrat area (10000 cm²) to get the “coverage”. The coverage was then multiplied by 100 to get the total percent (%) of area coverage.

MICHIGAN BASIN

Besser Museum Alpena, MI:

Quadrat 1: DSC_2883

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	1056.992	0.105699	10.56992
2	<i>Favosites alpenensis</i>	FA	T	55.4686	0.005547	0.554686
3	Stromatoporoid species	SS	S	1664.224	0.166422	16.64224
TOTAL CORAL AREA COVERAGE:				2776.685	0.277668	27.76685
TOTAL QUADRAT AREA:				10000		

Quadrat 2: DSC 2839

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	3903.519	0.390352	39.03519
2	<i>Favosites alpenensis</i>	FA	T	56.5515	0.005655	0.565515
3	Stromatoporoid species	SS	S	1238.68	0.123868	12.3868
TOTAL CORAL AREA COVERAGE:				5198.75	0.519875	51.9875
TOTAL QUADRAT AREA:				10000		

Quadrat 3: DSC_2827

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	4111.299	0.41113	41.11299
2	Stromatoporoid species	SS	S	726.3816	0.072638	7.263816
TOTAL CORAL AREA COVERAGE:				4837.681	0.483768	48.37681
TOTAL QUADRAT AREA:				10000		

Quadrat 4: DSC_2833

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	1193.605	0.35106	35.10603
TOTAL CORAL AREA COVERAGE:				1193.605	0.35106	35.10603
TOTAL IMAGE AREA:				3400		

Quadrat 5: DSC_2834

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	1904.743	0.544212	54.42123
2	Stromatoporoid species	SS	S	28.2577	0.008074	0.807363
TOTAL CORAL AREA COVERAGE:				1933.001	0.552286	55.22859
TOTAL QUADRAT AREA:				3500		

Quadrat 6: DSC 2861

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria alpenensis</i>	HA	CR	453.7439	0.137498	13.74982
2	Stromatoporoid species	SS	S	201.2233	0.060977	6.097676
TOTAL CORAL AREA COVERAGE:				654.9672	0.198475	19.84749
TOTAL QUADRAT AREA:				3300		

MICHIGAN BASIN

Rockport Quarry Alpena, MI:

RQ1 - Quadrat 1: DSC_2907

Area #	Species	Code	Type	Area cm ²	Cover cm ²	Percent
1	<i>Favosites digitatus</i>	FD	F	82.8588	0.138098	13.8098
TOTAL CORAL AREA COVERAGE				82.8588	0.138098	13.8098
TOTAL QUADRAT AREA:				600		

RQ2 - Quadrat 2: DSC_2910

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Cystiphyllodes americanum</i>	CA	SR	6.864	0.006864	0.6864
2	<i>Favosites digitatus</i>	FD	T	65.2549	0.0652549	6.52549
3	<i>Favosites mammilatus</i>	FM	T	76.2493	0.0762493	7.62493
4	<i>Siphonophrentis elongata</i>	SE	SR	9.7223	0.0097223	0.97223
5	Stromatoporoid species	SS	S	41.0615	0.0410615	4.10615
TOTAL CORAL AREA COVERAGE				199.152	0.199152	19.9152
TOTAL QUADRAT AREA:				1000		

RQ3 - Quadrat 3: DSC_2913

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Favosites digitatus</i>	FD	T	49.09	0.04909	4.909
2	Stromatoporoid species	SS	S	3.6526	0.0036526	0.36526
TOTAL CORAL AREA COVERAGE				52.7426	0.0527426	5.27426
TOTAL QUADRAT AREA:				1000		

RQ4 - Quadrat 4: DSC_2917

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Hexagonaria anna</i>	HAA	CR	611.4003	0.30570015	30.570015
2	<i>Favosites nitellus</i>	FN	T	28.4886	0.0142443	1.42443
TOTAL CORAL AREA COVERAGE				639.8889	0.31994445	31.994445
TOTAL QUADRAT AREA:				2000		

MICHIGAN BASIN

Whitehouse Quarry, OH:

WQ1 - Quadrat 1: DSC_2754

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Heterophrentis simplex</i>	HS	SR	92.259	0.0092259	0.92259
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	263.6052	0.02636052	2.636052
3	Other Fauna (worm tubes)	OF	OF	18.5197	0.00185197	0.185197
TOTAL CORAL AREA COVERAGE:				374.3839	0.03743839	3.743839
TOTAL QUADRAT AREA:				10000		

Continue Whitehouse Quarry, OH:
WQ2 - Quadrat 2: DSC_2754

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	210.1091	0.02101091	2.101091
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	21.5377	0.00215377	0.215377
3	<i>Favosites limitaris</i>	FL	T	196.2803	0.01962803	1.962803
4	<i>Hexagonaria anna</i>	HAA	CR	137.7974	0.01377974	1.377974
TOTAL CORAL AREA COVERAGE:				565.7245	0.05657245	5.657245
TOTAL QUADRAT AREA:				10000		

WQ3 - Quadrat 3: DSC_2763

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	51.7303	0.00517303	0.517303
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	357.6377	0.03576377	3.576377
3	<i>Hexagonaria anna</i>	HAA	CR	212.0499	0.02120499	2.120499
TOTAL CORAL AREA COVERAGE:				621.4179	0.06214179	6.214179
TOTAL QUADRAT AREA:				10000		

RQ4 - Quadrat 4: DSC_2769

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	57.7473	0.00577473	0.577473
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	680.0607	0.06800607	6.800607
3	<i>Cladopora tela</i>	CT	T	46.0478	0.00460478	0.460478
4	<i>Hexagonaria anna</i>	HAA	CR	193.8043	0.01938043	1.938043
TOTAL CORAL AREA COVERAGE:				977.6601	0.09776601	9.776601
TOTAL QUADRAT AREA:				10000		

RQ5 - Quadrat 5: DSC_2772

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Zaphrentis prolifica</i>	ZP	SR	49.0051	0.00490051	0.490051
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	205.1167	0.02051167	2.051167
TOTAL CORAL AREA COVERAGE:				254.1218	0.02541218	2.541218
TOTAL QUADRAT AREA:				10000		

RQ6 - Quadrat 6: DSC_2773

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	672.7045	0.06727045	6.727045
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	365.2524	0.03652524	3.652524
3	<i>Zaphrentis gigantea</i>	ZG	SR	11.6548	0.00116548	0.116548
TOTAL CORAL AREA COVERAGE:				1049.6117	0.10496117	10.496117
TOTAL QUADRAT AREA:				10000		

ILLINOIS BASIN

Falls of the Ohio State Park, IN:

FO1 - Quadrat 1: DSC_2993

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Acinophyllum stokesi</i>	AS	CR	3786.771	0.3786771	37.86771
2	Stromatoporoid species	SS	S	1119.537	0.1119537	11.19537
TOTAL CORAL AREA COVERAGE:				4906.308	0.4906308	49.06308
TOTAL QUADRAT AREA:				10000		

FO2 - Quadrat 2: DSC_3015

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Heliophyllum venatum</i>	HVN	SR	24.8352	0.0024835	0.248352
2	Stromatoporoid species	SS	S	3879.044	0.3879044	38.790438
3	<i>Cladopora imbricata</i>	CI	T	8.7658	0.0008766	0.087658
4	<i>Favosites ramulosus</i>	FR	T	12.5321	0.0012532	0.125321
5	<i>Siphonophrentis elongata</i>	SE	SR	17.2087	0.0017209	0.172087
TOTAL CORAL AREA COVERAGE:				3942.386	0.3942386	39.423856
TOTAL QUADRAT AREA:				10000		

FO3 - Quadrat 3: DSC_3011

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Prismatophyllum prisma</i>	PP	CR	600.4374	0.0600437	6.004374
2	Stromatoporoid species	SS	S	2471.694	0.2471694	24.716944
3	<i>Favosites (Emmonsia) epidermatus</i>	FEE	T	73.4783	0.0073478	0.734783
4	<i>Favosites (Emmonsia) ramosa</i>	FER	T	281.3103	0.028131	2.813103
5	<i>Cystiphyllodes nanum</i>	CN	SR	48.909	0.0048909	0.48909
6	<i>Cladopora imbricata</i>	CI	T	395.5367	0.0395537	3.955367
7	<i>Thamnopora limitaris</i>	TL	T	712.6908	0.0712691	7.126908
8	<i>Siphonophrentis elongata</i>	SE	SR	37.7803	0.003778	0.377803
9	<i>Heterophrentis irregularis</i>	HI	SR	202.2691	0.0202269	2.022691
10	<i>Heliophyllum verticale</i>	HV	SR	18.9476	0.0018948	0.189476
11	<i>Favosites ramulosus</i>	FR	T	299.2827	0.0299283	2.992827
12	<i>Heliophyllum venatum</i>	HVN	SR	106.9876	0.0106988	1.069876
TOTAL CORAL AREA COVERAGE:				5249.324	0.5249324	52.493242
TOTAL QUADRAT AREA:				10000		

Continue Falls of Ohio State Park, IN

FO4 - Quadrat 4: DSC_2999

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Cystiphyllodes hispidum</i>	CH	SR	726.9003	0.07269	7.269003
2	<i>Cystiphyllodes nanum</i>	CN	SR	160.94	0.016094	1.6094
3	<i>Heterophrentis irregularis</i>	HI	SR	143.4851	0.0143485	1.434851
4	<i>Heliophyllum venatum</i>	HVN	SR	45.0472	0.0045047	0.450472
5	<i>Heliophyllum verticale</i>	HV	SR	53.6334	0.0053633	0.536334
6	<i>Siphonophrentis elongata</i>	SE	SR	150.0946	0.0150095	1.500946
7	<i>Favosites ramulosus</i>	FR	T	913.6527	0.0913653	9.136527
8	<i>Cladopora imbricata</i>	CI	T	670.0531	0.0670053	6.700531
9	<i>Striatopora bellistriata</i>	SB	T	899.2939	0.0899294	8.992939
10	<i>Thamnopora limitaris</i>	TL	T	740.7375	0.0740738	7.407375
11	<i>Favosites turbinatus</i>	FT	T	13.4553	0.0013455	0.134553
12	<i>Favosites (Emmonsia) ramosa</i>	FER	T	148.5847	0.0148585	1.485847
13	Stromatoporoid species	SS	S	576.4994	0.0576499	5.764994
TOTAL CORAL AREA COVERAGE:				5242.377	0.5242377	52.423772
TOTAL IMAGE AREA:				10000		

FO5 - Quadrat 5: DSC_3047

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	1380.59	0.138059	13.805901
2	<i>Favosites (Emmonsia) ramosa</i>	FER	T	172.1203	0.017212	1.721203
3	<i>Siphonophrentis elongata</i>	SE	SR	168.3683	0.0168368	1.683683
4	<i>Cystiphyllodes nanum</i>	CN	SR	49.202	0.0049202	0.49202
5	<i>Cystiphyllodes hispidum</i>	CH	SR	32.9651	0.0032965	0.329651
6	<i>Heterophrentis irregularis</i>	HI	SR	22.5462	0.0022546	0.225462
7	<i>Favosites ramulosus</i>	FR	T	66.0227	0.0066023	0.660227
8	<i>Cladopora imbricata</i>	CI	T	72.0011	0.0072001	0.720011
9	<i>Heliophyllum venatum</i>	HVN	SR	32.3252	0.0032325	0.323252
10	<i>Favosites (Emmonsia) epidermatus</i>	FEE	T	916.0494	0.0916049	9.160494
11	<i>Acinophyllum mclarni</i>	AM	CR	422.0035	0.0422004	4.220035
12	<i>Thamnopora limitaris</i>	TL	T	40.2355	0.0040236	0.402355
TOTAL CORAL AREA COVERAGE:				3374.429	0.3374429	33.744294
TOTAL QUADRAT AREA:				10000		

Continue Falls of Ohio State Park, IN

FO6 - Quadrat 6: DSC_3037

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	1139.888	0.0729237	7.2923737
2	<i>Prismatophyllum prisma</i>	PP	CR	121.7327	0.0077878	0.7787788
3	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	171.5846	0.010977	1.0977038
4	<i>Favosites turbinatus</i>	FT	T	32.0794	0.0020523	0.2052263
5	<i>Siphonophrentis elongata</i>	SE	SR	41.2406	0.0026383	0.2638346
6	<i>Heliophyllum venatum</i>	HVN	SR	80.5717	0.0051545	0.5154534
7	<i>Heterophrentis irregularis</i>	HI	SR	21.8811	0.0013998	0.1399832
8	<i>Cystiphyllodes nanum</i>	CN	SR	54.5337	0.0034888	0.3488766
9	<i>Cladopora imbricata</i>	CI	T	50.0341	0.0032009	0.3200906
TOTAL CORAL AREA COVERAGE:				1713.546	0.1096232	10.962321
TOTAL QUADRAT AREA:				15631.23		

FO7 - Quadrat 7: DSC_3033

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	818.0451	0.1658503	16.585032
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	99.477	0.0201679	2.016795
3	<i>Favosites (Emmonsia) ramosa</i>	FER	T	8.5057	0.0017244	0.1724444
4	<i>Heliophyllum verticale</i>	HV	SR	67.2808	0.0136405	1.3640498
5	<i>Prismatophyllum prisma</i>	PP	CR	22.624	0.0045868	0.4586786
6	<i>Pleurodictyum cylindricum</i>	PC	CR	338.7997	0.0686882	6.8688192
7	<i>Heliophyllum venatum</i>	HVN	SR	82.0955	0.016644	1.6644027
TOTAL CORAL AREA COVERAGE:				1436.828	0.2913022	29.130222
TOTAL QUADRAT AREA:				4932.43		

ILLINOIS BASIN**Bear Creek, KY:****BC1 - Quadrat 1: DSC_3087**

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Siphonophrentis elongata</i>	SE	SR	104.4768	0.0474003	4.7400299
2	<i>Favosites (Emmonsia) tuberosus</i>	FET	T	124.498	0.0564838	5.6483759
3	<i>Heliophyllum venatum</i>	HVN	SR	12.5685	0.0057022	0.5702229
4	<i>Cystiphyllodes nanum</i>	CN	SR	23.2	0.0105257	1.0525657
5	<i>Favosites (Emmonsia) epidermatus</i>	FEE	T	87.4806	0.0396893	3.9689257
6	<i>Favosites biloculi</i>	FB	T	88.4945	0.0401493	4.0149256
7	<i>Heterophrentis irregularis</i>	HI	SR	11.3835	0.0051646	0.5164604
8	<i>Cladopora imbricata</i>	CI	T	7.9602	0.0036115	0.361148
TOTAL CORAL AREA COVERAGE				460.0621	0.2087265	20.872654
TOTAL QUADRAT AREA:				2204.138		

BC2 - Quadrat 2: DSC_3130

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	Stromatoporoid species	SS	S	930.9653	0.1874546	18.745455
2	<i>Favosites turbinatus</i>	FT	T	76.0083	0.0153047	1.5304654
3	<i>Cladopora imbricata</i>	CI	T	17.0304	0.0034292	0.3429157
4	<i>Cystiphyllodes infundibuliformis</i>	CYI	SR	91.155	0.0183545	1.8354519
5	<i>Siphonophrentis elongata</i>	SE	SR	141.335	0.0284585	2.8458514
6	<i>Heliophyllum verticale</i>	HV	SR	159.849	0.0321864	3.2186402
7	<i>Heliophyllum venatum</i>	HVN	SR	9.7801	0.0019693	0.1969272
8	<i>Favosites ramulosus</i>	FR	T	20.7493	0.004178	0.4177976
TOTAL CORAL AREA COVERAGE				1446.872	0.291335	29.133505
TOTAL QUADRAT AREA:				4966.352		

ILLINOIS BASIN

Champions Trace, KY:

CT1 - Quadrat 1: DSC_3175

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Favosites biloculi</i>	FB	T	1365.194	0.1365194	13.65194
2	<i>Pleurodictyum cylindricum</i>	PC	CR	485.8151	0.0485815	4.858151
3	<i>Pleurodictyum planum</i>	PLP	CR	491.5702	0.049157	4.915702
4	<i>Siphonophrentis elongata</i>	SE	SR	160.1366	0.0160137	1.601366
5	<i>Heliophyllum verticle</i>	HV	SR	165.2794	0.0165279	1.652794
6	<i>Heliophyllum venatum</i>	HVN	SR	61.6128	0.0061613	0.616128
7	<i>Favosites turbinatus</i>	FT	T	59.0954	0.0059095	0.590954
TOTAL CORAL AREA COVERAGE				2788.704	0.2788704	27.887035
TOTAL QUADRAT AREA:				10000		

CT2 - Quadrat 2: DSC_3186

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Heterophrentis irregularis</i>	HI	SR	83.7947	0.0083795	0.837947
2	<i>Pleurodictyum planum</i>	PLP	CR	1505.686	0.1505686	15.05686
3	<i>Favosites turbinatus</i>	FT	T	728.1515	0.0728152	7.281515
4	<i>Heliophyllum verticle</i>	HV	SR	287.9006	0.0287901	2.879006
5	<i>Heliophyllum venatum</i>	HVN	SR	464.8275	0.0464828	4.648275
6	<i>Siphonophrentis yandelli</i>	SY	SR	91.612	0.0091612	0.91612
7	<i>Blothrophyllum romingeri</i>	BR	SR	52.2834	0.0052283	0.522834
TOTAL CORAL AREA COVERAGE				3214.256	0.3214256	32.142557
TOTAL QUADRAT AREA:				10000		

CT3 - Quadrat 3: DSC_3197

Area #	Species	Code	Type	Area cm ²	Cover	Percent
1	<i>Favosites biloculi</i>	FB	T	176.4917	0.0352983	3.529834
2	<i>Favosites turbinatus</i>	FT	T	80.8568	0.0161714	1.617136
3	<i>Favosites (Emmonsia) epidermatus</i>	FEE	T	187.2627	0.0374525	3.745254
4	<i>Stromatoporoid species</i>	SS	S	75.9607	0.0151921	1.519214
5	<i>Heliophyllum verticle</i>	HV	SR	143.4675	0.0286935	2.86935
6	<i>Heliophyllum venatum</i>	HVN	SR	30.4637	0.0060927	0.609274
7	<i>Siphonophrentis yandelli</i>	SY	SR	26.1885	0.0052377	0.52377
8	<i>Blothrophyllum romingeri</i>	BR	SR	27.3404	0.0054681	0.546808
TOTAL CORAL AREA COVERAGE				748.032	0.1496064	14.96064
TOTAL QUADRAT AREA:				5000		

APPALACHIAN BASIN**Marblehead Lafarge Quarry, OH:****Quadrat 1: DSC_3175**

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	506.7007	0.0506701	5.067007
2	<i>Zaphrentis gigantea</i>	ZG	SR	37.5305	0.0037531	0.375305
3	<i>Acinophyllum segregatum</i>	ASG	CR	347.1337	0.0347134	3.471337
TOTAL CORAL AREA COVERAGE:				891.365	0.089136	8.913649
TOTAL QUADRAT AREA:				10000		

Quadrat 2: DSC_3181

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Eridophyllum seriale</i>	ES	CR	2591.948	0.2591948	25.919476
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	1615.712	0.1615712	16.157119
3	<i>Prismatophyllum ovoideum</i>	PO	CR	167.8844	0.0167884	1.678844
4	Stromatoporoid species	SS	S	57.3874	0.0057387	0.573874
TOTAL CORAL AREA COVERAGE:				4432.93	0.443293	44.32931
TOTAL QUADRAT AREA:				10000		

Quadrat 3: DSC_3188

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Eridophyllum seriale</i>	ES	CR	2459.224	0.2459224	24.59224
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	291.071	0.0291071	2.91071
3	<i>Zaphrentis gigantea</i>	ZG	SR	10.7998	0.00108	0.107998
4	<i>Prismatophyllum ovoideum</i>	PO	CR	523.7065	0.0523707	5.237065
TOTAL CORAL AREA COVERAGE:				3284.8	0.32848	32.84801
TOTAL QUADRAT AREA:				10000		

Quadrat 4: DSC_3200

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Prismatophyllum ovoideum</i>	PO	CR	478.2615	0.0478262	4.782615
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	402.5813	0.0402581	4.025813
3	<i>Eridophyllum seriale</i>	ES	CR	942.509	0.0942509	9.42509
4	<i>Favosites turbinatus</i>	FT	T	17.5286	0.0017529	0.175286
TOTAL CORAL AREA COVERAGE:				1840.88	0.184088	18.4088
TOTAL QUADRAT AREA:				10000		

Continue Marblehead Quarry, OH

Quadrat 5: DSC_3220

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	170.8999	0.01709	1.708999
2	<i>Prismatophyllum ovoideum</i>	PO	CR	373.1114	0.0373111	3.731114
3	<i>Zaphrentis gigantea</i>	ZG	SR	94.807	0.0094807	0.94807
4	<i>Eridophyllum seriale</i>	ES	CR	4111.81	0.411181	41.1181
TOTAL CORAL AREA COVERAGE:				4750.63	0.475063	47.50628
TOTAL QUADRAT AREA:				10000		

Quadrat 6: DSC_3211

Area #	Species	Code	Type	Area	Cover	Percent
1	<i>Favosites hemisphericus</i>	FH	T	401.641	0.0401641	4.01641
2	<i>Favosites (Emmonsia) emmonsi</i>	FE	T	182.5297	0.018253	1.825297
3	<i>Zaphrentis prolifica</i>	ZP	SR	5.7903	0.000579	0.057903
4	<i>Zaphrentis gigantea</i>	ZG	SR	6.0881	0.0006088	0.060881
5	<i>Heliophyllum verticle</i>	HV	SR	91.1891	0.0091189	0.911891
6	<i>Favosites turbinatus</i>	FT	T	12.5637	0.0012564	0.125637
7	<i>Prismatophyllum ovoideum</i>	PO	CR	374.497	0.0374497	3.74497
8	Stromatoporoid species	SS	S	81.3363	0.0081336	0.813363
TOTAL CORAL AREA COVERAGE:				1155.64	0.115564	11.55635
TOTAL QUADRAT AREA:				10000		

APPENDIX F. BUILDUP DATA AND SEDIMENT ASSOCIATION

Observations of buildup data include contacts between coral-on-coral growth; coral-on-stromatoporoid (strom); strom-on-strom; or strom-on-coral. The interactions between the organisms were observed by documenting whether sediment was between growths or not. “NO SED” refers to no sediment between buildups and direct organismal interactions. On the other hand, “SED” identifies sediment between individual colonies and less competition. Appendix F1 includes the total amount of coral and stromatoporoid interactions. Appendix F2 divides the observed interactions between locations and includes all individual quadrats.

**Appendix F1 –
MICHIGAN BASIN
Besser Museum, MI:**

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	49	9	11	1
NO SED	75	11	10	6
	124	20	21	7

Rockport Quarry, MI:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	7	3	1	3
NO SED	7	2	2	4
	14	5	3	7

Whitehouse Quarry, OH:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	21	3	0	2
NO SED	3	3	2	1
	24	6	2	3

APPALACHIAN BASIN

Marblehead Lafarge Quarry, OH:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	66	3	0	0
NO SED	29	0	0	0
	95	3	0	0

ILLINOIS BASIN

Falls of the Ohio State Park, IN:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	24	12	10	13
NO SED	34	21	15	10
	58	33	25	23

Bear Creek, KY:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	11	0	0	0
NO SED	15	1	0	0
	26	1	0	0

Champions Trace, KY:

Interaction	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
SED	61	1	0	0
NO SED	54	1	3	0
	115	2	3	0

Appendix F2
MICHIGAN BASIN
Besser Museum, MI:

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	5	1	2	0
Q1 NO SED	6	2	1	0
Q2 SED	6	1	2	0
Q2 NO SED	13	6	5	5
Q3 SED	23	5	5	1
Q3 NO SED	18	3	4	1
Q4 SED	3	0	0	0
Q4 NO SED	32	0	0	0
Q5 SED	12	2	2	0
Q5 NO SED	6	0	0	0
	124	20	21	7

Rockport Quarry, MI:

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	1	0	0	0
Q1 NO SED	0	0	0	0
Q2 SED	2	0	0	0
Q2 NO SED	3	0	0	0
Q3 SED	0	0	0	0
Q3 NO SED	0	0	0	0
Q4 SED	3	0	0	0
Q4 NO SED	4	0	0	0
Q5 SED	1	0	0	0
Q5 NO SED	0	0	0	0
Q6 SED	0	1	0	2
Q6 NO SED	0	1	0	1
Q7 SED	0	2	1	1
Q7 NO SED	0	1	2	3
	14	5	3	7

Whitehouse Quarry, OH:

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	7	0	0	0
Q1 NO SED	1	0	0	0
Q2 SED	2	2	0	2
Q2 NO SED	0	0	1	0
Q3 SED	3	1	0	0
Q3 NO SED	0	1	0	0
Q4 SED	8	0	0	0
Q4 NO SED	0	0	0	0
Q5 SED	1	0	0	0
Q5 NO SED	1	0	0	0
Q6 SED	0	0	0	0
Q6 NO SED	1	2	1	1
	24	6	2	3

APPALACHIAN BASIN**Marblehead Lafarge Quarry, OH:**

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	12	0	0	0
Q1 NO SED	6	0	0	0
Q2 SED	10	1	0	0
Q2 NO SED	7	0	0	0
Q3 SED	8	0	0	0
Q3 NO SED	6	0	0	0
Q4 SED	11	0	0	0
Q4 NO SED	3	0	0	0
Q5 SED	17	0	0	0
Q5 NO SED	5	0	0	0
Q6 SED	8	2	0	0
Q6 NO SED	2	0	0	0
	95	3	0	0

ILLINOIS BASIN**Falls of the Ohio State Park, IN:**

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	0	0	0	0
Q1 NO SED	0	2	2	0
Q2 SED	0	0	0	1
Q2 NO SED	0	8	0	3
Q3 SED	0	0	0	0
Q3 NO SED	0	2	3	2
Q4 SED	0	0	0	0
Q4 NO SED	15	0	3	0
Q5 SED	0	0	0	0
Q5 NO SED	12	5	6	1
Q6 SED	15	6	7	6
Q6 NOSED	3	4	1	0
Q7 SED	9	6	3	6
Q7 NO SED	4	0	0	4
	58	33	25	23

Bear Creek, KY:

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	4	0	0	0
Q1 NO SED	3	0	0	0
Q2 SED	7	0	0	0
Q2 NO SED	12	1	0	0
	26	1	0	0

Champions Trace, KY:

Quadrat #	Coral on Coral	Coral on Strom	Strom on Coral	Strom on Strom
Q1 SED	26	0	0	0
Q1 NO SED	13	0	0	0
Q2 SED	23	0	0	0
Q2 NO SED	19	0	0	0
Q3 SED	12	1	0	0
Q3 NO SED	22	1	3	0
	115	2	3	0

APPENDIX G. PAST ABUNDANCE DATA MATRIX BY QUADRAT

The species, species code, species type, and abundances are listed by locality and quadrat. Locations include Besser Museum, Rockport Quarry, Whitehouse Quarry, Falls of Ohio State Park, Bear Creek, Champions Trace, and Marblehead Quarry. The “code” refers to the CPCe two-three letter species codes: AM - *Acinophyllum mclarni*; ASG - *Acinophyllum segregatum*; AS - *Acinophyllum stokes*; BR - *Blothrophyllum romingeri*; CI - *Cladopora imbricata*; CT - *Cladopora tela*; CA - *Cystiphyllodes americanum*; CH - *Cystiphyllodes hispidum*; CYI - *Cystiphyllodes infundibuliformis*; CN - *Cystiphyllodes nanum*; ES - *Eridophyllum seriale*; FE - *Favosites (Emmonsia) emmonsi*; FEE - *Favosites (Emmonsia) epidermatus*; FER - *Favosites (Emmonsia) ramosa*; FET - *Favosites (Emmonsia) tuberosus*; FA - *Favosites alpenensis*; FB - *Favosites biloculi*; FD - *Favosites digitatus*; FH - *Favosites hemisphericus*; FL - *Favosites limitaris*; FM - *Favosites mammilatus*; FN - *Favosites nitellus*; FR - *Favosites ramulosus*; FT - *Favosites turbinatus*; HVN - *Heliophyllum venatum*; HV - *Heliophyllum verticale*; HI - *Heterophrentis irregularis*; HS - *Heterophrentis simplex*; HA - *Hexagonaria alpenensis*; HAA - *Hexagonaria anna*; PC - *Pleurodictyum cylindricum*; PLP - *Pleurodictyum planum*; PO - *Prismatophyllum ovoideum*; PP - *Prismatophyllum prisma*; SE - *Siphonophrentis elongata*; SY - *Siphonophrentis yandelli*; SB - *Striatopora bellistriata*; TL - *Thamnopora limitaris*; ZG - *Zaphrentis gigantea*; ZP - *Zaphrentis prolifica*; SS - *Stromatoporoid* species. The “type” refers to the order of corals to which the species belong: CR – Colonial Rugose; SR – Solitary Rugose; T – Tabulate; SS – *Stromatoporoid* species.

Species			Marblehead Quarry						Whitehouse Quarry					
% Abundance by Quadrat/Locality	Type	Code	MQ1	MQ2	MQ3	MQ4	MQ5	MQ6	WQ1	WQ2	WQ3	WQ4	WQ5	WQ6
<i>Acinophyllum mclarni</i>	CR	AM	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acinophyllum segregatum</i>	CR	ASG	3.471	0	0	0	0	0	0	0	0	0	0	0
<i>Acinophyllum stokesi</i>	CR	AS	0	0	0	0	0	0	0	0	0	0	0	0
<i>Blothrophyllum romingeri</i>	SR	BR	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladopora imbricata</i>	T	CI	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cladopora tela</i>	T	CT	0	0	0	0	0	0	0	0	0	0.46	0	0
<i>Cystiphyllodes americanum</i>	SR	CA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes hispidum</i>	SR	CH	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes infundibuliformis</i>	SR	CYI	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes nanum</i>	SR	CN	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eridophyllum seriale</i>	CR	ES	0	25.919	24.592	9.425	41.118	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) emmonsi</i>	T	FE	5.067	16.157	2.911	4.026	1.709	1.825	2.636	0.215	3.576	6.801	2.051	3.653
<i>Favosites (Emmonsia) epidermatus</i>	T	FEE	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) ramose</i>	T	FER	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) tuberosus</i>	T	FET	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites alpenensis</i>	T	FA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites biloculi</i>	T	FB	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites digitatus</i>	T	FD	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites hemisphericus</i>	T	FH	0	0	0	0	0	4.016	0	0	0	0	0	0
<i>Favosites limitaris</i>	T	FL	0	0	0	0	0	0	0	1.963	0	0	0	0
<i>Favosites mammillatus</i>	T	FM	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites nitellus</i>	T	FN	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites ramulosus</i>	T	FR	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites turbinatus</i>	T	FT	0	0	0	0.175	0	0.126	0	0	0	0	0	0
<i>Heliophyllum venatum</i>	SR	HVN	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heliophyllum verticale</i>	SR	HV	0	0	0	0	0	0.912	0	0	0	0	0	0
<i>Heterophrentis irregularis</i>	SR	HI	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heterophrentis simplex</i>	SR	HS	0	0	0	0	0	0	0.923	0	0	0	0	0
<i>Hexagonaria alpenensis</i>	CR	HA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hexagonaria anna</i>	CR	HAA	0	0	0	0	0	0	0	1.378	2.12	1.938	0	0
<i>Pleurodictyum cylindricum</i>	CR	PC	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleurodictyum planum</i>	CR	PLP	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prismatophyllum ovoideum</i>	CR	PO	0	1.679	5.237	4.783	3.731	3.745	0	0	0	0	0	0
<i>Prismatophyllum prisma</i>	CR	PP	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphonophrentis elongata</i>	SR	SE	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphonophrentis yandelli</i>	SR	SY	0	0	0	0	0	0	0	0	0	0	0	0
<i>Striatopora bellistriata</i>	T	SB	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thamnopora limitaris</i>	T	TL	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zaphrentis gigantea</i>	SR	ZG	0.375	0	0.108	0	0.948	0.061	0	0	0	0	0	0.117
<i>Zaphrentis prolifica</i>	SR	ZP	0	0	0	0	0	0.058	0	0	0	0	0.49	0
Stromatoporoid species	SS	SS	0	0.574	0	0	0	0.813	0	2.101	0.517	0.577	0	6.727

Species			Besser Museum						Rockport Quarry			
% Abundance by Quadrat/Locality	Type	Code	BM1	BM2	BM3	BM4	BM5	BM6	RQ1	RQ2	RQ3	RQ4
<i>Acinophyllum mclarni</i>	CR	AM	0	0	0	0	0	0	0	0	0	0
<i>Acinophyllum segregatum</i>	CR	ASG	0	0	0	0	0	0	0	0	0	0
<i>Acinophyllum stokesi</i>	CR	AS	0	0	0	0	0	0	0	0	0	0
<i>Blothrophyllum romingeri</i>	SR	BR	0	0	0	0	0	0	0	0	0	0
<i>Cladopora imbricata</i>	T	CI	0	0	0	0	0	0	0	0	0	0
<i>Cladopora tela</i>	T	CT	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes americanum</i>	SR	CA	0	0	0	0	0	0	0	0.686	0	0
<i>Cystiphyllodes hispidum</i>	SR	CH	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes infundibuliformis</i>	SR	CYI	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes nanum</i>	SR	CN	0	0	0	0	0	0	0	0	0	0
<i>Eridophyllum seriale</i>	CR	ES	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) emmonsi</i>	T	FE	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) epidermatus</i>	T	FEE	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) ramose</i>	T	FER	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) tuberosus</i>	T	FET	0	0	0	0	0	0	0	0	0	0
<i>Favosites alpenensis</i>	T	FA	0.555	0.566	0	0	0	0	0	0	0	0
<i>Favosites biloculi</i>	T	FB	0	0	0	0	0	0	0	0	0	0
<i>Favosites digitatus</i>	T	FD	0	0	0	0	0	0	13.81	6.525	4.909	0
<i>Favosites hemisphericus</i>	T	FH	0	0	0	0	0	0	0	0	0	0
<i>Favosites limitaris</i>	T	FL	0	0	0	0	0	0	0	0	0	0
<i>Favosites mammilatus</i>	T	FM	0	0	0	0	0	0	0	7.625	0	0
<i>Favosites nitellus</i>	T	FN	0	0	0	0	0	0	0	0	0	1.424
<i>Favosites ramulosus</i>	T	FR	0	0	0	0	0	0	0	0	0	0
<i>Favosites turbinatus</i>	T	FT	0	0	0	0	0	0	0	0	0	0
<i>Heliophyllum venatum</i>	SR	HVN	0	0	0	0	0	0	0	0	0	0
<i>Heliophyllum verticale</i>	SR	HV	0	0	0	0	0	0	0	0	0	0
<i>Heterophrentis irregularis</i>	SR	HI	0	0	0	0	0	0	0	0	0	0
<i>Heterophrentis simplex</i>	SR	HS	0	0	0	0	0	0	0	0	0	0
<i>Hexagonaria alpenensis</i>	CR	HA	10.57	39.035	41.113	35.106	54.421	13.7498	0	0	0	0
<i>Hexagonaria anna</i>	CR	HAA	0	0	0	0	0	0	0	0	0	30.57
<i>Pleurodictyum cylindricum</i>	CR	PC	0	0	0	0	0	0	0	0	0	0
<i>Pleurodictyum planum</i>	CR	PLP	0	0	0	0	0	0	0	0	0	0
<i>Prismatophyllum ovoideum</i>	CR	PO	0	0	0	0	0	0	0	0	0	0
<i>Prismatophyllum prisma</i>	CR	PP	0	0	0	0	0	0	0	0	0	0
<i>Siphonophrentis elongata</i>	SR	SE	0	0	0	0	0	0	0	0.972	0	0
<i>Siphonophrentis yandelli</i>	SR	SY	0	0	0	0	0	0	0	0	0	0
<i>Striatopora bellistriata</i>	T	SB	0	0	0	0	0	0	0	0	0	0
<i>Thamnopora limitaris</i>	T	TL	0	0	0	0	0	0	0	0	0	0
<i>Zaphrentis gigantea</i>	SR	ZG	0	0	0	0	0	0	0	0	0	0
<i>Zaphrentis prolifica</i>	SR	ZP	0	0	0	0	0	0	0	0	0	0
Stromatoporoid species	SS	SS	16.642	12.387	7.264	0	0.807	6.0977	0	4.106	0.365	0

Species			Falls of the Ohio State Park							Bear Creek		Champions Trace		
% Abundance by Quadrat/Locality	Type	Code	FO1	FO2	FO3	FO4	FO5	FO6	FO7	BC1	BC2	CT1	CT2	CT3
<i>Acinophyllum mclarni</i>	CR	AM	0	0	0	0	4.22	0	0	0	0	0	0	0
<i>Acinophyllum segregatum</i>	CR	ASG	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acinophyllum stokesi</i>	CR	AS	37.868	0	0	0	0	0	0	0	0	0	0	0
<i>Blothrophyllum romingeri</i>	SR	BR	0	0	0	0	0	0	0	0	0	0	0.523	0.547
<i>Cladopora imbricata</i>	T	CI	0	0.088	3.955	6.7	0.72	0.32	0	0.361	0.343	0	0	0
<i>Cladopora tela</i>	T	CT	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes americanum</i>	SR	CA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cystiphyllodes hispidum</i>	SR	CH	0	0	0	7.269	0.33	0	0	0	0	0	0	0
<i>Cystiphyllodes infundibuliformis</i>	SR	CYI	0	0	0	0	0	0	0	0	1.835	0	0	0
<i>Cystiphyllodes nanum</i>	SR	CN	0	0	0.489	1.609	0.492	0.349	0	1.053	0	0	0	0
<i>Eridophyllum seriale</i>	CR	ES	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites (Emmonsia) emmonsi</i>	T	FE	0	0	0	0	0	1.098	2.017	0	0	0	0	0
<i>Favosites (Emmonsia) epidermatus</i>	T	FEE	0	0	0.735	0	9.16	0	0	3.969	0	0	0	3.745
<i>Favosites (Emmonsia) ramose</i>	T	FER	0	0	2.813	1.486	1.721	0	0.172	0	0	0	0	0
<i>Favosites (Emmonsia) tuberosus</i>	T	FET	0	0	0	0	0	0	0	5.648	0	0	0	0
<i>Favosites alpenensis</i>	T	FA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites biloculi</i>	T	FB	0	0	0	0	0	0	0	4.015	0	13.652	0	3.53
<i>Favosites digitatus</i>	T	FD	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites hemisphericus</i>	T	FH	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites limitaris</i>	T	FL	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites mammilatus</i>	T	FM	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites nitellus</i>	T	FN	0	0	0	0	0	0	0	0	0	0	0	0
<i>Favosites ramulosus</i>	T	FR	0	0.125	2.993	9.137	0.66	0	0	0	0.418	0	0	0
<i>Favosites turbinatus</i>	T	FT	0	0	0	0.134	0	0.205	0	0	1.53	0.591	7.282	1.617
<i>Heliophyllum venatum</i>	SR	HVN	0	0.248	1.07	0.45	0.3232	0.515	1.664	0.57	0.197	0.616	4.648	0.609
<i>Heliophyllum verticale</i>	SR	HV	0	0	0.189	0.536	0	0	1.364	0	3.219	1.653	2.879	2.869
<i>Heterophrentis irregularis</i>	SR	HI	0	0	2.023	1.435	0.225	0.14	0	0.516	0	0	0.838	0
<i>Heterophrentis simplex</i>	SR	HS	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hexagonaria alpenensis</i>	CR	HA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hexagonaria anna</i>	CR	HAA	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleurodictyum cylindricum</i>	CR	PC	0	0	0	0	0	0	6.869	0	0	4.858	0	0
<i>Pleurodictyum planum</i>	CR	PLP	0	0	0	0	0	0	0	0	0	4.916	15.057	0
<i>Prismatophyllum ovoideum</i>	CR	PO	0	0	0	0	0	0	0	0	0	0	0	0
<i>Prismatophyllum prisma</i>	CR	PP	0	0	6.004	0	0	0.779	0.459	0	0	0	0	0
<i>Siphonophrentis elongata</i>	SR	SE	0	0.172	0.378	1.501	1.684	0.263	0	4.74	2.846	1.601	0	0
<i>Siphonophrentis yandelli</i>	SR	SY	0	0	0	0	0	0	0	0	0	0	0.916	0.524
<i>Striatopora bellistriata</i>	T	SB	0	0	0	8.993	0	0	0	0	0	0	0	0
<i>Thamnopora limitaris</i>	T	TL	0	0	7.127	7.407	0.4025	0	0	0	0	0	0	0
<i>Zaphrentis gigantea</i>	SR	ZG	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zaphrentis prolifica</i>	SR	ZP	0	0	0	0	0	0	0	0	0	0	0	0
Stromatoporoid species	SS	SS	11.195	38.79	24.717	5.765	13.806	7.292	16.585	0	18.745	0	0	1.519