Quantifying the Biotic Response to the Clarksville Phase of the Richmondian Invasion

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Abstract

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Quantifying the Biotic Response to the Clarksville Phase of the Richmondian Invasion

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Type Cincinnatian strata are among the best preserved Upper Ordovician deposits in the world and record a range of depositional environments as well as various biotic and abiotic changes, making them an ideal natural laboratory in which to study biotic and abiotic processes. The most substantial biotic change in the Type Cincinnatian Series is a biotic invasion known as the Richmondian Invasion. The first pulse of the Richmondian Invasion is referred to as the Clarksville Phase (Aucoin and Brett, 2016) and is the focal point of this study which quantifies the impact the Clarksville Phase had on the ecology and diversity of the fauna of the Cincinnati basin. A suite of methods were employed to quantify the invader impact including detrended correspondence analysis, cluster analysis, rarefaction, Simpson's index of dominance, guild analysis, and comparison of environmental preferences and tolerances through time. Results indicate the Clarksville Phase had numerous impacts on the fauna of the Cincinnati Sea including modification of occupied habitat, ecospace utilization, gradient structure, community structure, community composition, and biodiversity. Habitat occupation changed considerably following the introduction of the invaders with taxa shifting both their environmental tolerances and preferences. Ecospace utilization shifted as previously low diversity guilds were filled out with novel taxa. Faunal differentiation across the depth gradient increased with the introduction of the invaders. Generic richness increased within the basin, generic evenness decreased, and community composition became more complex. The results of

this study contribute to our understanding of the Richmondian Invasion and our general understanding of earth history as well as provide new insights about the potential long term ecological and biodiversity impacts of biotic invasions today.

Dedication

I dedicate this thesis to my family for giving me the gift of education and fostering in me a deep-seated love and appreciation for the natural world.

Acknowledgments

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Chapter 1: Introduction

During the Late Ordovician (Katian Stage), a broad area including what is now southwestern Ohio, northern Kentucky, and southeastern Indiana was inundated by a shallow epicontinental sea which developed in the distal Taconic foreland basin and is herein referred to as the Cincinnati Sea. The Cincinnati Sea hosted a diverse fauna of marine organisms which are now preserved as the abundant fossils of the Type Cincinnatian. In addition to being abundantly fossiliferous, the Type Cincinnatian preserves a range of depositional environments as well as a suite of biotic and abiotic environmental changes, making it an ideal natural laboratory in which to study an array of biotic and abiotic processes.

The most pronounced biotic change in the Type Cincinnatian was a regional biotic interchange known as the Richmondian Invasion which introduced a suite of invasive taxa into the Cincinnati Sea. Numerous studies of this biotic interchange have been conducted which examined the entire invasion interval (Holland and Patzkowsky, 2007; Patzkowsky and Holland, 2007; Malizia and Stigall, 2011; Brame and Stigall, 2014; Tyler and Leighton, 2011; and others) and general ecological and evolutionary patterns have been identified. Conversely, the individual pulses within the Richmondian Invasion have received comparatively little study (but see Schwalbach, 2017). In this study, I investigate ecological and diversity changes associated with the Clarksville Phase of the Richmondian Invasion specifically, which provides greater detail into a specific pulse of the Richmondian Invasion than any prior study. Studies of individual invasion pulses like the Clarksville Phase will help to answer unresolved questions about the Richmondian Invasion such as which regions of the seafloor were initially most impacted and how the incumbent taxa accommodated invaders—or not-- after each pulse of the invasion.

Understanding how the Clarksville Phase impacted the fauna of the Cincinnati Sea is not only important for furthering our understanding of the Richmondian Invasion and earth history in general but provides valuable insight which can be of use to modern conservation ecologists and conservation managers. Studies of modern biotic invasions generally employ data spanning at most a decade and often lack data preceding the arrival of invaders and use an uninvaded area believed to be similar as a surrogate. As a result, these studies cannot shed light on the long-term ecological consequences of biotic invasions and often struggle to determine how communities have changed since the arrival of invaders. As a result, many questions remain, including, but not limited to, whether there is an unpaid extinction debt from modern invasions, if biodiversity richness increases are transient or lasting, and how community structure is affected by biotic invasions, especially over longer timescales. Answering these questions is key to understanding how biotic invasions impact ecosystems and communities beyond human timescales. This study builds on previous studies of the Richmondian Invasion and helps to bridge the gap in knowledge between short term observations of modern invasions and long-term patterns in the fossil record by quantifying the impact the Clarksville Phase of the Richmondian Invasion had on the fauna of the Cincinnati Sea.

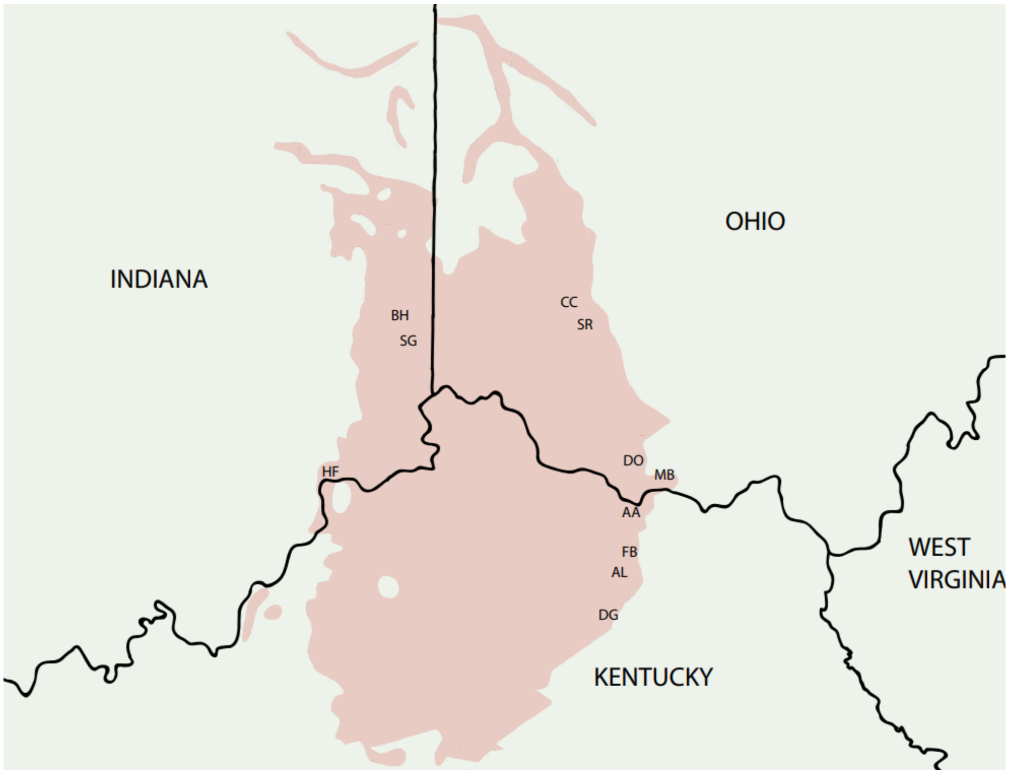
Chapter 2: Geologic Setting and Type Cincinnatian Invasions

Geologic Setting

The abundantly fossiliferous strata of the Type Cincinnatian Series were deposited during the Late Ordovician (Katian Stage) along a northward dipping mixed carbonate-siliciclastic ramp which was dominated by storm deposition (Figs. 1,11) (Tobin, 1982; Jennette & Pryor, 1993).

Figure 1

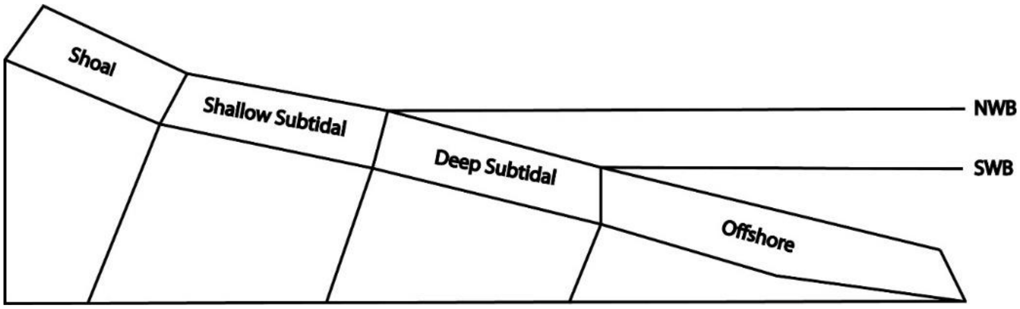
Ordovician outcrop belt is indicted by the pink shaded area. Sampling sites are indicated by the two-letter code which correspond to the codes in Table 1.



At the time of deposition, the Cincinnati Arch was located at approximately 20° S and the paleocontinent of Laurentia was rotated approximately 45° clockwise from its current position (Scotese & McKerrow, 1991). Because the Cincinnati Sea was in the distal part of the Taconic foreland basin sedimentation consisted primarily of fine grained siliciclastics shed from the Taconic Highlands and larger grains settled in the Queenston Delta to the east. Despite being dominated by fine grained siliciclastics Type Cincinnatian strata are punctuated by carbonate layers composed of calcium carbonate bioclasts which were concentrated through storm reworking and/or sediment starvation and subsequently lithified. These carbonate layers are particularly abundant in shallower environments where high wave energy hindered accumulation of fine grained siliciclastics. The Cincinnati Arch is now preserved as an eroded structural dome with outcrops exposed over a broad area comprising north-central Kentucky, southeastern Indiana, and southwestern Ohio (Fig. 1). Depositional environments preserving abundant fossils exposed along the Cincinnati Arch include shallow subtidal, deep subtidal, offshore, and to a lesser degree shoal and lagoon (Fig. 2) (Holland, 1993). Peritidal settings also occur but are sparsely fossiliferous (Holland, 1993).

Figure 2

Ramp model showing the depositional environments included in this study. NWB indicates normal wave base, and SWB indicates storm wave base.



This study focuses on the Waynesville Formation, which has been eroded away in the center of the Cincinnati Arch but is present around the edges of the dome. The Waynesville Formation is made up of four fourth order sequences, two of which (C5B and C5C) were sampled in this study (Figs. 3, 4). Each fourth order depositional sequence represents 200,000-500,000 years each (Aucoin and Brett, 2016; Schwalbach, 2017) and the entire Waynesville Formation represents approximately 1,000,000 years (Aucoin, 2021). Thus, the interval analyzed in this study represents no more than 400,000-500,000 years.

Figure 3

Sequence stratigraphic framework of Cincinnatian strata from Brett et al. (2020). This study focuses on the Waynesville Formation, Sequences C5B and C5C.

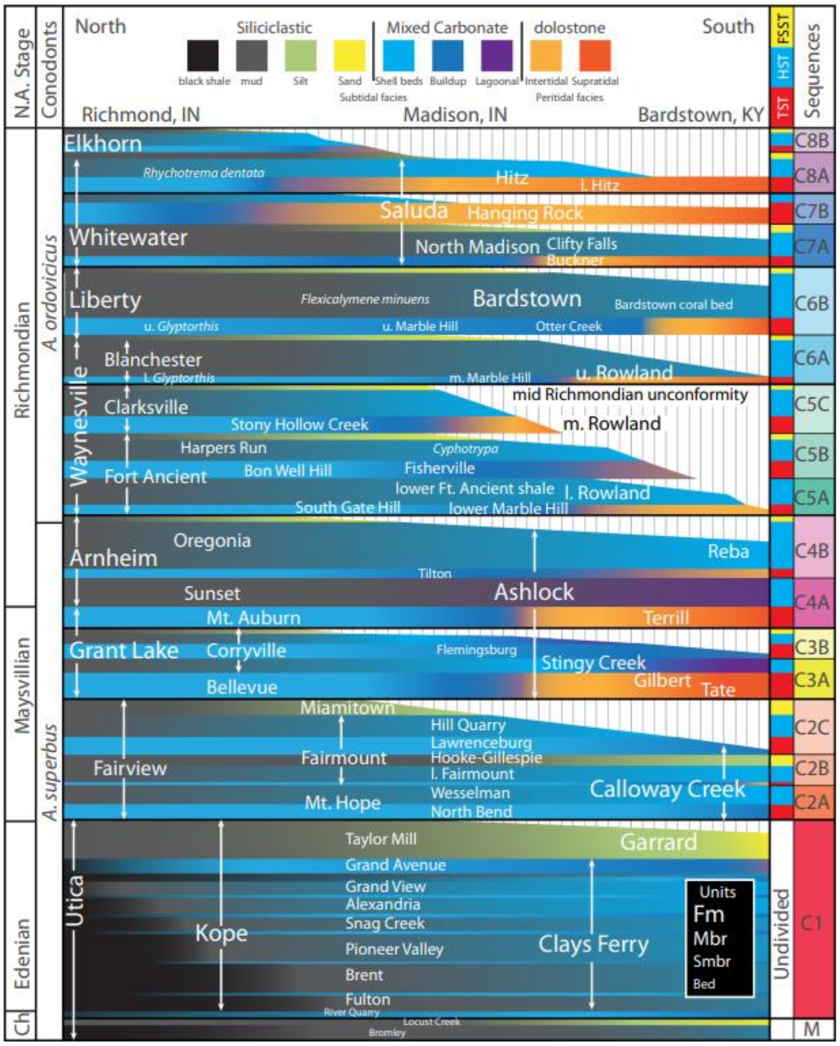
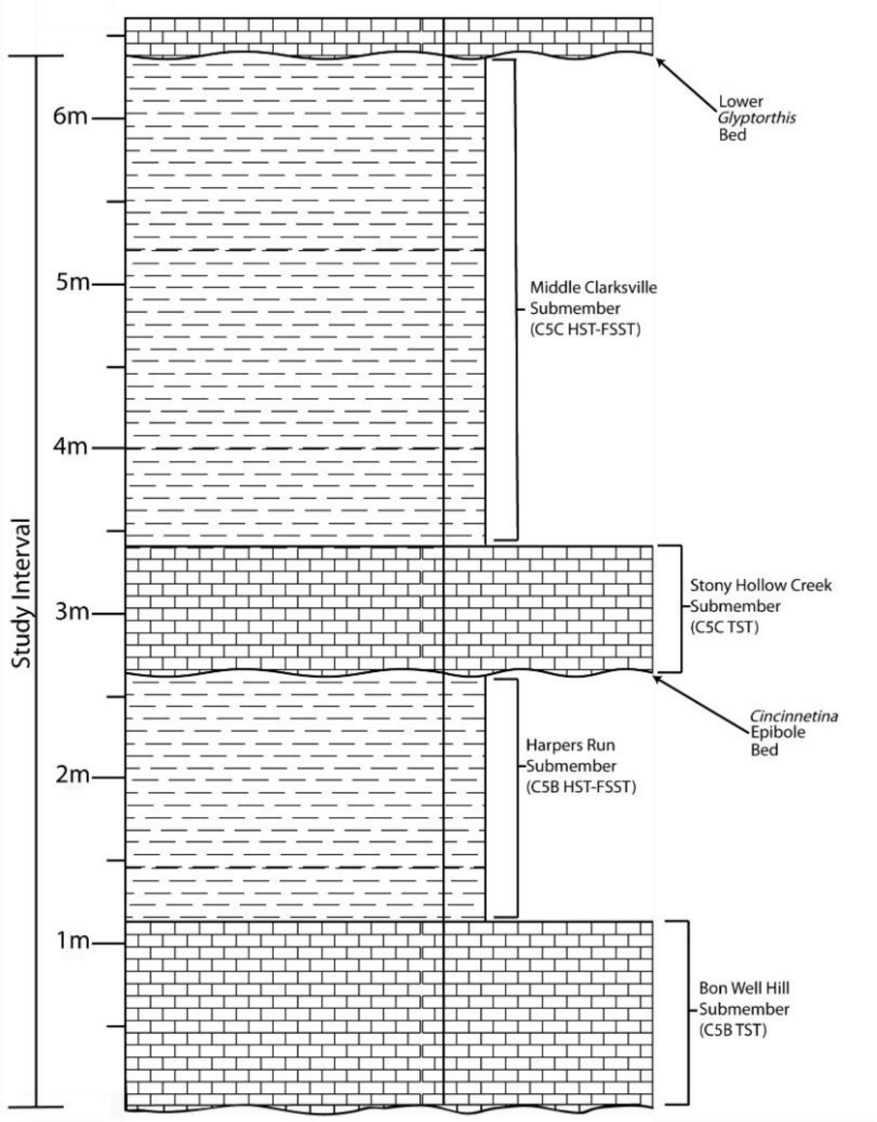


Figure 4

Idealized stratigraphic column of the study interval as it appears in the Waynesville Formation's type area in southwestern Ohio. Submembers and sequences follow Brett et al. (2020).



The base of the Waynesville Formation is the South Gate Hill Submember of the Fort Ancient Member. This submember represents the transgressive systems tract of the fourth order C5A sequence and is characterized by thickly bedded limestone in the northern part of the study area which thin to the south (Brett et al., 2020). This is overlain by the lower Fort Ancient Shale submember of the Fort Ancient Member. This submember represents the highstand to falling stage systems tract of the C5A sequence and is dominated by shale with thin carbonate layers in the northern part of the study area but grades into a rubbly carbonate facies in the south (Brett et al., 2020). This is overlain by the Bon Well Hill Submember of the Fort Ancient Member. This submember represents the transgressive systems tract of the C5B sequence (Brett et al., 2020). The Bon Well Hill Submember is expressed in the northern part of the study region as an approximately meter thick package of limestone layers which thin considerably to the south (Brett et al., 2020). This is overlain by the Harpers Run Submember of the Fort Ancient Member. This submember represents the highstand to falling stage systems tract of the C5B sequence. In the northern part of the study area the Harpers Run is dominated by shale but contains thin limestone beds, and is known for well-preserved trilobites and cephalopods, earning it the names "trilobite shale" (Frey, 1987) and "*Treptoceras duseri* shale" (Frey, 1989). In the southern portion of the study area the Harpers Run grades into a rubbly carbonate facies containing abundant *Cyphotrypa* (Schwalbach, 2017; Brett et al., 2020).

The Harpers Run Submember is overlain by the Stony Hollow Creek Submember of the Clarksville Member, which represents the transgressive systems tract of the C5C sequence. In the northern part of the study area this unit is expressed as an approximately meter thick package of limestone layers but thins to the south. In its type area in southwestern Ohio the base of this submember is marked by the *Cincinnetina meeki* epibole (Fig. 5) (Frey, 1996; Aucoin and Brett, 2016; Brett et al, 2020; and others).

Figure 5

The Cincinnetina meeki epibole bed as it is exposed at Caesars Creek State Park. This bed is dominated by shells of the orthid brachiopod Cincinnetina meeki. The strophomenid brachiopod Eochonetes clarksvillensis is also visible on the slab.

The Middle Clarksville Submember overlies the Stony Hollow Creek submember and represents the highstand to falling stage systems tract of the C5C sequence. In the northern part of the study area, this unit is dominated by shale with thin beds of limestone. In the southern portion of the study area, the unit thins, and the proportion of shale is reduced. The boundary between the Middle Clarksville Submember and the overlying Blanchester Member is marked by a bed containing the rare brachiopod *Glyptorthis insculpta* (Fig. 6) which has been termed the Lower *Glyptorthis* bed (Fig. 7)

(Aucoin and Brett, 2016; Brett et al., 2020). The Clarksville and Blanchester members are also separated by a major unconformity termed the Mid-Richmondian Unconformity (Brett et al., 2015).

Figure 6

Glyptorthis insculpta collected from the lower Glyptorthis bed at Caesars Creek State Park. Scale bar is 1 cm.

Figure 7

Lower Glyptorthis Bed as it is exposed at Caesars Creek State Park. Ian Forsythe's arm for scale. The dashed line indicates the boundary between sequences C5C and C6A, the boundary between the Clarksville and Blanchester Members of the Waynesville Formation, and the location of the Mid-Richmondian Unconformity.

Biotic Invasions in the Type Cincinnatian

The Richmondian Invasion was a biotic immigration event that introduced over 60 genera into the Cincinnati basin (Holland, 1997; Stigall, 2010). This was a multidirectional immigration event with invaders coming from several adjacent basins (Lam and Stigall, 2015; Aucoin and Brett, 2016). It has recently become apparent that the Richmondian Invasion occurred through a series of invasion pulses (Brett et al., 2020).

What was once believed to be the initial pulse was a series of isolated invasions (sensu Stigall, 2019) which occurred during the C4 sequence. This influx of invasive species disrupted the previously stable ecosystem, causing extinctions of native specialist taxa (Stigall, 2010) and resulting in a loss of faunal differentiation across the shelf (Holland and Patzkowsky, 2007). These isolated invasions are no longer considered a part of the Richmondian Invasion *sensu stricto* but still record the first appearance of some of the invaders that later become established in the basin (e.g., *Grewingkia canadensis* and *Leptaena richmondensis*) (Brett et al., 2020).

The isolated invasions of the C4 were not the first failed invasions in the Cincinnatian series. They were preceded by a series of ephemeral invasions (sensu Stigall 2019) in the Kope Formation during which the invaders *Leptaena gibbosa, Cyathophylloides* cf. *C. burksae*, and *Holtedahlina millionensis* appear very briefly (Stigall and Fine, 2019; Harris et al., 2019; Brett et al., 2020). What is now considered to be the initial pulse of the Richmondian Invasion *sensu stricto* was termed the Clarksville Phase by Aucoin and Brett (2016). The Clarksville Phase was a coordinated invasion (sensu Stigall, 2019) that occurred during the C5 sequence of Brett et al. (2020) and introduced a suite of genera into the basin including brachiopods, bivalves, and bryozoans (Brett et al., 2020). The invaders which entered the basin during the Clarksville Phase were at least in part a tropical faunal, both *Eochonetes* and *Grewingkia* entered the Cincinnati Basin from what is now arctic Canada but was then located at equatorial latitudes (Foerste, 1905; Holland, 1997; Bauer and Stigall, 2014). The final pulse occurs during the C6 sequence in the uppermost Liberty Formation (Brett et al., 2020). This final phase was a coordinated invasion (sensu Stigall, 2019) and brought primarily mollusks and especially cephalopods into the Cincinnati basin which are abundant in the overlying Whitewater Formation (Brett et al., 2020). The Richmondian Invasion as a whole increased local generic richness within the Cincinnati basin despite initial faunal homogenization across the shelf (Holland and Patzkowsky, 2007), loss of endemicity (Stigall, 2010, 2019), and niche contraction (Brame and Stigall, 2014).

The Clarksville Phase of the Richmondian Invasion

The Clarksville Phase (*sensu* Aucoin and Brett, 2016) was the first successful pulse of the Richmondian Invasion (Brett et al., 2020). The Clarksville Phase occurred abruptly with the introduction of numerous genera of invaders in or just below the transgressive systems tract of the 4^{th} order C5C sequence which corresponds to the Stony Hollow Creek Submember of the Clarksville Member of the Waynesville Formation (Figs. 3,4). Identification of this interval in the field is simple in the Waynesville Formation's type area because the base of the Stony Hollow Creek Submember is marked by a packstone bundle containing abundant specimens of the small orthid *Cincinnetina meeki* (Aucoin, 2021), this layer is known as the "*Cincinnetina* Epibole" (Fig. 5). This invasion pulse introduced a suite of invaders into the Cincinnati Basin including but not limited to *Eochonetes clarksvillensis*, *Strophomena planumbona*, *Hiscobeccus capax*, *Leptaena richmondensis*, and *Grewingkia canadensis* (Brett et al., 2020). This rapid initial pulse of the Richmondian Invasion is the focal point of this study which aims to quantify the impact the Clarksville Phase had on the fauna of the Cincinnati Basin. In this study various hypotheses regarding the biotic impact of the Clarksville Phase are tested including how community structure, gradient structure, biodiversity, ecospace utilization, and stability of taxa's environmental parameters were impacted.

Chapter 3: Methods

Data Collection

To quantify how community structure changed across the Clarksville Phase of the Richmondian Invasion, paleocommunity parameters were reconstructed from faunal occurrence data collected from the stratigraphic levels before, during, and after the invasion pulse. In this study, a paleocommunity or community is defined as a generalized group of taxa which characterize a particular environment and may represent a segment of a biotic gradient and is synonymous with the biofacies of Brett et al. (2007).

Faunal occurrence data were collected from bedding planes using a 100 cm^2 quadrant. Data collection focused on obtaining census data from limestone layers rather than mudstone units because limestone units represent a time averaged faunal assemblage and have been shown to record a more complete census of alpha diversity in comparable Ordovician strata (Finnegan & Droser, 2008). There are two main depositional models for Cincinnatian limestones. The classical interpretation of these deposits termed the storm winnowing model and the more recently developed episodic starvation model (Dattilo et al., 2008). The storm winnowing model posits that Cincinnatian skeletal packstone and grainstone layers developed as shell lags through removal of mud during storm reworking. Conversely, the episodic starvation model suggests that shell beds developed as accumulation layers during periods of low sedimentation. Under the episodic starvation model, Cincinnatian shell beds are similar to the hiatal deposits of Kidwell (1991) but develop more rapidly and sediment starvation is less severe (Dattilo et al., 2008). Regardless of whether the deposition of Cincinnatian shell beds was the result of storm winnowing, episodic starvation, or a combination of both, these shell beds represent a time averaged faunal assemblage. When considered in tandem with the well-preserved community patchiness observed in Cincinnatian shell beds (ex. Frey, 1987), this suggests minimal transport of shelly remains (Dattilo et al., 2008). This indicates both that Cincinnatian limestones are faithful recorders of local habitats and that these limestones, like those of Finnegan and Droser (2008), will record a more complete census of alpha diversity than mudstones.

The primary data collected for this study are occurrences of macrofaunal invertebrate fossils exposed on bedding planes. Fossil occurrence data were collected from four submembers of the Waynesville Formation to provide coverage of the preinvasion, invasion, and post-invasion intervals. The preinvasion data were collected from the Bon Well Hill Submember, invasion data were collected from the Harpers Run and Stony Hollow Creek Submembers, and post-invasion data were collected from the Middle Clarksville Submember. Data were collected from 11 localities (Table 1) along a 187-kilometer northwest to southeast trending transect (Figs. 1, 8).

Limestone layers were either excavated and sampled in situ, excavated and returned to camp for sampling, or excavated and returned to the lab for sampling. When sampling was conducted the following elements were counted as individuals: Individual valves, or steinkerns of mollusks (e.g., gastropods, bivalves) over 50% complete, pygidia, cranidia, and hypostomes of trilobites, individual valves of brachiopods over 50% complete, solitary rugose corals, and each centimeter of coralline algae. Bryozoans were classified based on zoarium morphology using the classification scheme of Holland et al. (2001) and every 1 cm of length for thick ramose (>5mm), thin ramose(<5mm), encrusting, massive, and thin bifoliate (<5mm) bryozoan was counted as one individual.

Relative abundance of crinoid columnals was counted with 1-5 columnals counted as one individual, 6-10 columnals counted as two individuals, etc. The skeletal-element-to-individual ratio differ among the various taxa in order to produce the strongest data signal. For example, to impede a single taxon, such as bryozoans from dominating and obscuring the signal of the other taxa. The same correction factors apply to all parts of the study interval equally and should not hinder comparison between them (Finnegan & Droser, 2008).

Figure 8

Map of study area. Sampling sites are indicated by the blue pins and two letter codes which correspond to those in Table 1.

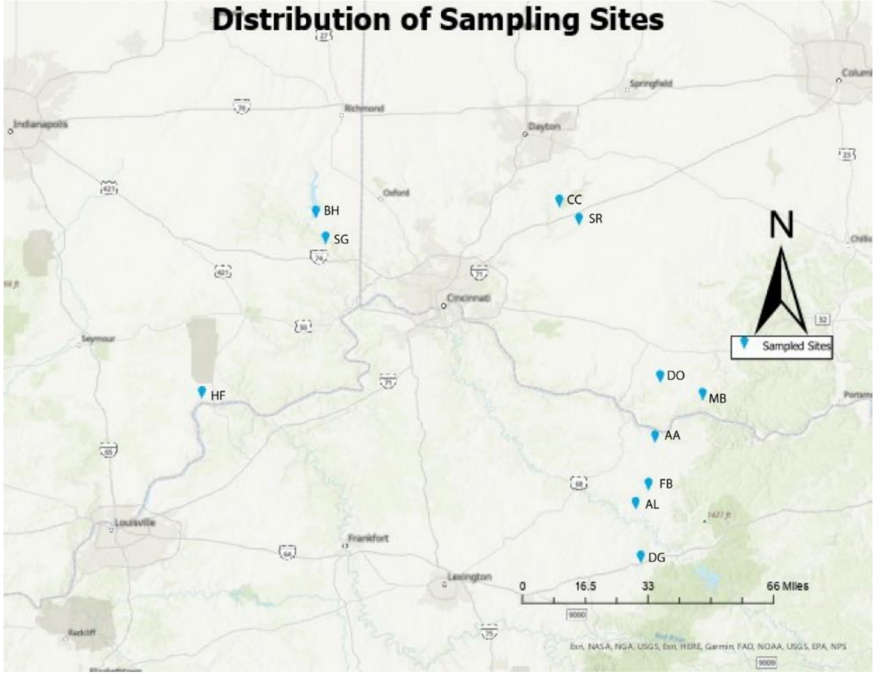


Table 1

Sampled localities

Locality	Latitude	Longitude	Submembers Sampled	Depositional Environment
AA-1449 (AA)	38.58	-83.70	Harpers Run, Stony Hollow Creek, Middle Clarksville	Deep Subtidal
Apricot Lane (AL)	38.33	-83.77	Bon Well Hill, Stony Hollow Creek, Middle Clarksville	Shallow Subtidal + Deep Subtidal
Flemingsburg 32-bypass (FB)	38.40	-83.72	Bon Well Hill, Harpers Run, Stony Hollow Creek	Shallow Subtidal
Moore's Branch (MB)	Private Property	Private Property	Middle Clarksville	Deep Subtidal
Stony Run Hollow (SR)	39.40	-83.98	Stony Hollow Creek, Middle Clarksville	Offshore
Dollar General (DG)	38.12	-83.75	Stony Hollow Creek, Middle Clarksville	Shoal
Bon Well Hill (BH)	39.43	-84.98	Bon Well Hill, Stony Hollow Creek	Offshore
South Gate Hill (SG)	39.33	-84.95	Bon Well Hill, Stony Hollow Creek	Offshore
Decatur Outcrop (DO)	38.81	-83.68	Bon Well Hill, Harpers Run, Stony Hollow Creek, Middle Clarksville	Deep Subtidal
Caesar's Creek (CC)	39.47	-84.06	Bon Well Hill, Stony Hollow Creek, Middle Clarksville	Offshore
Hoffman Falls (HF)	38.75	-85.42	Bon Well Hill, Harpers Run, Stony Hollow Creek	Offshore

Localities were selected to maximize exposure of the study interval and include the maximum coverage of depositional settings. Sites representing shoal, shallow subtidal, deep subtidal, and offshore environments were selected so that the impact of the invaders in different depositional settings could be quantified. Following the recommendation of Bulinski (2008), a minimum sample size of over 300 individuals was targeted for each outcrop. This was exceeded in the original sampling scheme for all outcrops except for AA where exposure was so limited the target sample size was not obtained. When bryozoan counts were later adjusted to account for differences in zoarium size the individual count was brought below this target threshold for some sites. Accessible limestone layers were identified in each submember and excavated for sampling (Fig. 9). In total, 84 individual beds were sampled with a cumulative sample area of 47.6m^2 (Appendix I). Sampled area for each bed was strongly controlled by exposure and accessibility of the layer and ranged from 100 cm^2 to 6300 cm^2 (Appendix I).

Figure 9

Limestone units being excavated from the Harpers Run, Stony Hollow Creek, and Middle Clarksville submembers at outcrop AA-1449.

Data Processing

Before analyses were conducted, the data were separated into four discrete taxon x sample matrices corresponding to the four sampled submembers. The counts for thick ramose, thin ramose, and thin bifoliate bryozoans were divided by 10 to capture differences in zoarium size between these forms and encrusting and massive morphologies. Once this was complete, all samples collected from the same site and layer were pooled to increase signal strength. Minimum number of individuals (MNI) was calculated for brachiopods, bivalves, and trilobites to ensure that the abundances of these taxa were not overestimated. This resulted in a final dataset of approximately 4,098 individuals of 36 taxa (approximately 11,759 individuals when all bryozoans are counted as 1 cm per individual) (Appendix I). Before these datasets could be analyzed, all samples containing only one taxon and all taxa occurring in only one sample were removed from each of the four datasets to prevent distortion during multivariate analyses (Holland and Patzkowsky, 2007). The full dataset was used without culling for calculating measures of biodiversity.

Two transformations were then performed on each dataset. Both of which were conducted in the vegan R package using the decostand function (Oksanen et al., 2020). The first transformation conducted was a percent transformation in which each value in a row is transformed to a percentage of the row total. This transformation was conducted to prevent multivariate analyses from being dominated by variations in sample size (McCune and Grace, 2002). The second transformation conducted was a maximum transformation. This transformation converts each value in a column to a percentage of the maximum value in that column. This transformation was conducted to give all the taxa the same weight in analyses (McCune and Grace, 2002).

Statistical Analyses

The first analysis conducted was detrended correspondence analysis (DCA), an ordination method. DCA was conducted to uncover the structure of the primary gradient, which is commonly water depth for ecological datasets collected from a marine environment (Holland et al., 2001). DCA was conducted in the R programming environment using the decorana function in the vegan R package with down weighting of rare taxa turned on (Oksanen et al., 2020). The Bray-Curtis dissimilarity index was used because it is an appropriate distance measure for analysis of multivariate ecological datasets (Beals, 1984). A second ordination method, nonmetric multidimensional scaling (NMDS), was conducted so the results could be compared to those obtained through DCA. NMDS was conducted in the R programming environment using the metaMDS function in the vegan r package (Oksanen et al., 2020) The number of dimensions was set to two and the maximum number of random starts was set to 50.

Q-mode and R-mode cluster analysis were then conducted to examine paleocommunity composition. The dissimilarity matrix for cluster analysis was calculated via the Bray-Curtis dissimilarity index using the vegdist function in the vegan R package (Oksanen et al, 2020). Cluster analysis was then conducted via Ward's agglomeration method using the agnes function in the cluster R package (Maechler et al., 2013). Two-way cluster analysis was then conducted so that the abundance of taxa within each paleocommunity could be visualized. The Bray-Curtis dissimilarity index and Ward's method were used. The two dendrograms that would be used were calculated using the hclust function in the vegan R package (Oksanen et al., 2020) and the heatmap was then produced using the heatmap function in the stats package (R Core Team, 2013).

Rarefied richness was also calculated for each of the four submembers at a subsample size of 300 individuals to test for changes in richness within the study interval while accounting for differences in sample size. Rarefied richness was calculated using the rarefy function in the vegan R package and rarefaction curves were plotted using the rarecurve function from the same package (Oksanen et al., 2020). Simpson's index of dominance was calculated for each of the four submembers to test for changes in evenness and dominance through the study interval. Simpson's index of dominance was calculated as the mean of 1000 bootstrap replicates using the diversity_boot function in the poppr R package (Kamvar et al., 2015).

An analysis of taxon's habitat preferences and tolerances throughout the study interval was conducted using the weighted averaging technique of Holland and Zaffos (2011). A detailed discussion of this method can be found in Holland and Zaffos (2011), but an overview is provided here. When DCA is conducted, axis one corresponds to the primary source of variation in the dataset which is commonly depth for marine ecological datasets (Holland et al., 2001). Because axis one corresponds to water depth, the axis one scores of sites and taxa can be used to estimate aspects of habitat occupation such as the preferred environment, environmental tolerance, and peak abundance of a taxon. The environmental tolerance of a taxon is calculated as the standard deviation of the DCA axis one scores for all samples in which the taxon occurs. The preferred environment of this taxon is the DCA axis one score of that taxon. These two parameters were calculated for each taxon in each of the fourth order systems tracts in the study interval (submembers). Through time comparison of taxon scores was conducted via Pearson's product moment correlation to assess temporal stability of habitat preferences. The calculations were conducted only for taxa with a peak abundance (probability of collecting that taxon in its preferred environment) of greater that 40% to ensure that the parameters were estimated as accurately as is possible with the current dataset. A positive correlation indicates conservation of environmental parameters, and a lack of correlation indicates restructuring of environmental parameters.

DCA axis one scores were then used to create a quantitative depth map of the study area (Fig. 11). All the data collected from each site was pooled and a single DCA axis one score for each site was calculated. Coordinates of sites and their associated DCA axis one scores were imported into ArcGIS Pro and a continuous raster layer of DCA scores was produced using the inverse distance weighting method of interpolation.

Finally, guild analysis was conducted to examine patterns of ecospace utilization through space and time. Guild analysis groups taxa into broad ecological niches regardless of taxonomy (Root, 1967). Guild membership was assigned using tier, food source, mobility, and habitat utilization based on a literature review. A modified version of the tiering scheme of Watkins (1991) was used in which low tier corresponds to 0-6 cm above the substrate, mid-tier corresponds to 6-10 cm above the substrate, and high tier corresponds to 10-25 cm above the substrate. The occurrences of taxa assigned to each guild were tabulated for each paleocommunity present in each of the four study intervals. The sampled taxa fall into a total of eight guilds (Table 2).

Table 2

Guild membership of sampled taxa based on tier, feeding style, and mobility.

Guild	**Lifestyle**	**Taxa**
Vagile active predator	Active predator	*Flexicalymene*, *Isotelus*
Low tier attached epifaunal passive suspension feeder	Suspension feeder	*Vinlandostrophia*, *Hebertella*, *Zygospira*, *Petrocrania*, massive bryozoan, encrusting bryozoan, *Modiolopsis*, Cornulites, *Caritodens*, *Ambonychia*, *Cincinnetina*, *Anomalodonta, Hiscobeccus, Holtedahlina*
Low tier unattached epifaunal passive suspension feeders	Suspension feeder	*Strophomena*, *Tetraphalerella*, *Eochonetes*, *Rafinesquina*, *Leptaena*, *Tentaculites*
Vagile epifaunal Grazer/browser	Grazer/browser	*Cyclonema*, *Liospira*, *Holopea*, *Paupospira*
Mid-tier Attached epifaunal suspension feeder	Suspension feeder	Thin ramose bryozoans, thick ramose bryozoans, thin bifoliate bryozoans, *Tetradium*
High tier attached epifaunal passive suspension feeder (dense fan)	Suspension feeder	*Glyptocrinus, Xenocrinus, Plicodendrocrinus*
High tier attached epifaunal passive suspension feeder (open fan)	Suspension feeder	*Cincinnaticrinus, Iocrinus*
Stationary epifaunal passive predator	Passive Predator	*Grewingkia*

The guild containing the most taxa is the low tier attached epifaunal passive suspension feeder guild (Table 2) which is made up of taxa that are attached to the substrate and filter feed 0-6 cm above the substrate. This guild contains the taxa *Vinlandostrophia* (Richards, 1972; Purcell and Stigall, 2021), *Hebertella* (Richards, 1972; Purcell and Stigall, 2021), *Zygospira* (Richards, 1972; Walker, 1972), *Petrocrania* (Richards, 1972), massive bryozoans (Watkins, 1991), encrusting bryozoans (Watkins, 1991), *Holtedahlina* (Richards, 1972), *Modiolopsis* (Pojeta, 1971), *Cornulites* (Watkins, 1991), *Caritodens* (Pojeta, 1971), *Ambonychia* (Pojeta, 1971), *Cincinnetina* (Richards, 1972; Purcell and Stigall, 2021), and *Anomalodonta* (Pojeta, 1971).

The next largest guild is the low tier unattached epifaunal passive suspension feeding guild (Table 2) which is made up of taxa that are free-living and filter feed 0-6 cm above the substrate. This guild which contains the taxa *Strophomena* (Richards, 1972; Walker, 1972; Alexander, 1975; Williams and Carlson, 2007; Plotnick et al., 2013; Purcell and Stigall, 2021), *Eochonetes* (Richards, 1972), *Tetraphalerella* (Lamont, 1934; Alexander, 1975; Williams and Carlson, 2007), *Rafinesquina* (Richards, 1972; Alexander, 1975; Williams and Carlson, 2007; Plotnick et al., 2013; Purcell and Stigall, 2021), *Leptaena* (Lamont, 1934; Richards, 1972; Purcell and Stigall, 2021), and *Tentaculites* (Lardeaux, 1969; Larsson, 1979).

The mid-tier attached epifaunal passive suspension feeder guild (Table 2) is made up of taxa that are attached to the substrate and filter feed 6-10 cm above the substrate. This guild contains thin ramose bryozoans, thick ramose bryozoans, thin bifoliate bryozoans (Watkins, 1991) and *Tetradium* (Walker, 1972). The mobile epifaunal grazer/browser guild also contains four taxa and includes *Cyclonema* (Wahlman, 1992), *Holopea* (Frey, 1987), *Liospira* (Frey, 1987), and *Paupospira* (Walker, 1972).

All the crinoids present in the dataset are a part of the high tier attached epifaunal passive suspension feeding guild which is made up of taxa which are attached to the substrate and filter feed 10-25 cm above the substrate. In addition to being epifaunally tiered passive suspension feeders, crinoids finely partition niches through differences in feeding ecology (Meyer, 1973; Ausich, 1980; Baumiller, 2008; Messing et al., 2017;

Cole and Wright, 2021; and many others). To incorporate differences in crinoid feeding ecology into the guild analysis, the high tier attached epifaunal passive suspension feeder guild is subdivided using higher taxonomic groups as a proxy for filtration fan guild membership (Kammer, 1985; Kammer and Ausich, 1987; Baumiller, 1993). In this framework, flexibles, disparids, cyathocrines, and some dendrocrines are considered open-fan forms, while other dendrocrines, poteriocrines, and camerates are considered dense-fan forms (Holterhoff, 1997). In this study, the dense fanned guild contains the taxa *Glyptocrinus, Xenocrinus, and Plicodendrocrinus* and the open fanned guild contains the taxa *Iocrinus* and *Cincinnaticrinus*.

The vagile active predator guild is made up entirely of trilobites and contains the taxa *Isotelus* (Fortney & Owens, 1999; Brandt et al, 1995) and *Flexicalymene* (Fortney & Owens, 1999).

The final guild is the stationary epifaunal passive predator guild which includes taxa that passively predate on other organisms above the substrate. This guild contains only one taxon, the solitary rugose coral *Grewingkia* (Elias, 1983; Neuman, 2003).

Chapter 4: Results

Cluster Analysis and DCA

Bon Well Hill Submember: Paleocommunity Descriptions

Q-mode cluster analysis recovered three paleocommunities in the Bon Well Hill Submember (Fig. 10B). These are identified as the Thin Ramose Bryozoan-*Vinlandostrophia* Community, the *Cincinnetina*- *Tentaculites* community, and the *Cincinnetina*-Thin Ramose Bryozoan Community (Fig. 10B). The primarily shallow subtidal Thin Ramose Bryozoan-*Vinlandostrophia* community is dominated by thin ramose bryozoans and the orthid brachiopod *Vinlandostrophia* and is primarily present in the southern portion of the study area (Figs. 1, 8, 11). Additional contributors to this community include the orthid *Hebertella*, encrusting bryozoa, the monobathrid *Xenocrinus*, thin bifoliate bryozoa, thick ramose bryozoa, the disparid *Cincinnaticrinus*, the atrypid *Zygospira*, and the pterioid *Caritodens*. *Vinlandostrophia* and *Hebertella* are the largest and most robust brachiopods in the dataset.

The primarily deep subtidal to offshore *Cincinnetina*-*Tentaculites* Community is dominated by the orthid brachiopod *Cincinnetina* and the problematic genus *Tentaculites*. *Tentaculites* has probable molluscan affinities (Blind and Stürmer, 1977; Davis, 1998; Wittmer, 2007); but it has also been proposed that they are more closely related to brachiopods based on shell microstructure (Towe, 1978). This is the most diverse community and includes a mix of robust and delicate morphologies. Additional components of the *Cincinnetina-Tentaculites* community include thin ramose bryozoa, *Vinlandostrophia,* the small atrypid *Zygospira,* the phacopid trilobite *Flexicalymene,* encrusting bryozoans, the strophomenid *Rafinesquina*, the monobathrid *Xenocrinus*, the orthid brachiopod *Hebertella*, massive bryozoan, thin bifoliate bryozoan, the pterioid *Anomalodonta*, and the pterioid *Caritodens*.

The third community is the primarily offshore *Cincinnetina*-Thin Ramose Bryozoan Community, which is dominated by the orthid brachiopod *Cincinnetina* and thin ramose bryozoa. The crinoid *Cincinnaticrinus*, *Tentaculites,* and the small atrypid *Zygospira* are also common constituents. Notably, these taxa are characterized by small size or delicate morphologies. This deep-water community is primarily present in the northern portion of the study area (Figs. 1, 8, 11). Additional minor constituents of this community include the monobathrid *Xenocrinus*, the disparid *Iocrinus*, the orthid *Hebertella*, thin bifoliate bryozoan, thick ramose bryozoan, massive bryozoan, encrusting bryozoan, the orthid *Vinlandostrophia*, the strophomenid *Rafinesquina*, the pterioid *Anomalodonta*, and the phacopid *Flexicalymene*.

Figure 10

Cluster analysis and detrended correspondence analysis results. In the cluster analysis heat maps (B, D, F, H) the darker reds indicate higher abundance of a taxon and lighter reds indicate lower abundance.

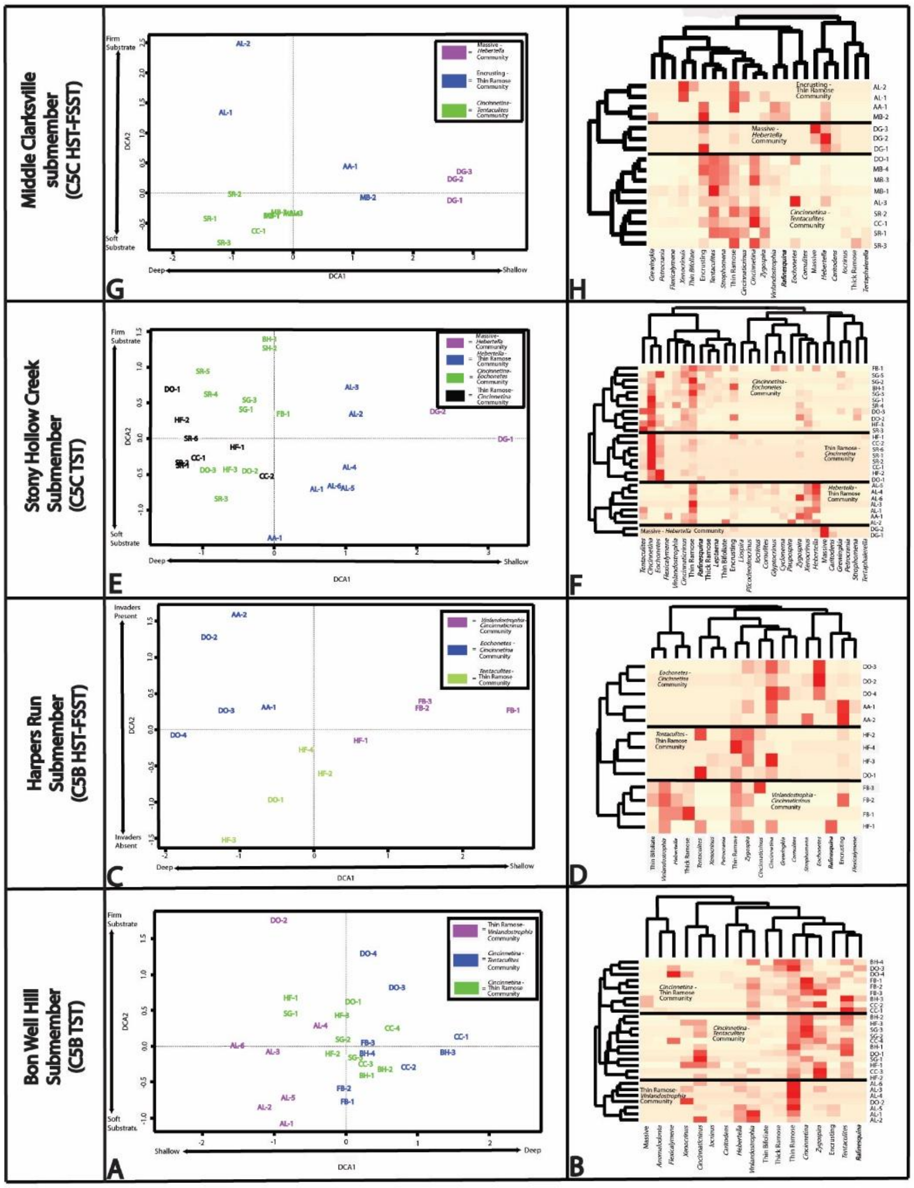
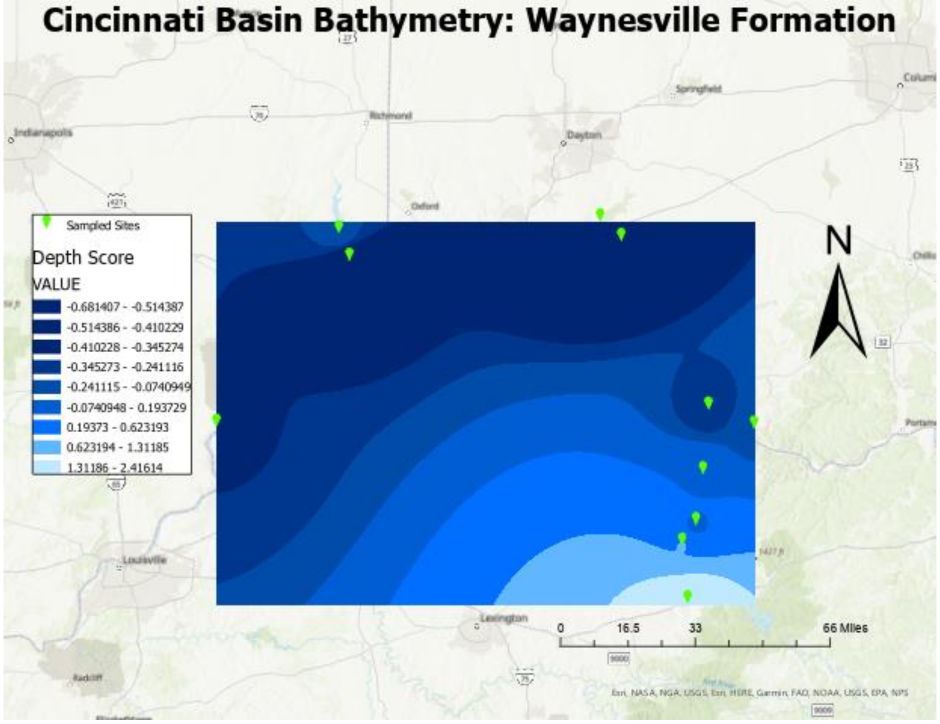


Figure 11

Bathymetric map of the Cincinnati Basin showing northward dip of ramp. Map was produced via inverse distance weighting. Dark blues correspond to deeper waters (lower DCA scores) and lighter blues correspond to shallower waters (higher DCA scores). Results reflect a classical understanding of Cincinnati Basin bathymetry as it has been interpreted based on lithology (deepening from south to north), further indicating the strength of the relationship between DCA axis one scores and water depth.



Bon Well Hill Submember: Paleocommunity Relationships

NMDS and DCA ordination analyses produced very similar results, and only the DCA ordinations are presented here (Fig. 10A). When the data are plotted in two-dimensional ecospace the Thin Ramose Bryozoan- *Vinlandostrophia* Community samples plot at low axis one scores and low axis two scores. The *Cincinnetina*- *Tentaculites* Community samples plot at moderate to high axis one scores and broadly across axis two. *Cincinnetina*- thin ramose bryozoan community samples plot at intermediate values on both axes one and two. Communities separate on axis one from the lower left corner to the upper right corner, but there is considerable overlap between samples of the *Cincinnetina*- *Tentaculites* and *Cincinnetina*- thin ramose bryozoan communities.

The gradational nature of the community structure in ecospace matches the general expectation from prior studies. The large bodied, robust organisms of the thin ramose-*Vinlandostrophia* community are typical of shallower water environments with wave influence (Holland, 1997), whereas the smaller-bodied, delicate taxa like *Cincinnetina* more commonly inhabit deeper settings with muddier substrates and less wave influence (Holland, 1997).

Harpers Run Submember: Paleocommunity Descriptions

Q-mode cluster analysis resolved three communities present in the Harpers Run Submember (Fig. 10D). These are identified as the *Vinlandostrophia – Cincinnaticrinus* Community, the *Eochonetes*- *Cincinnetina* Community, and the *Tentaculites*- Thin Ramose Bryozoan Community (Fig. 10D). The primarily shallow subtidal *Vinlandostrophia*- *Cincinnaticrinus* community is dominated by the orthid *Vinlandostrophia* and the heterocrinid *Cincinnaticrinus*. This community is dominated by robust morphologies (e.g., *Vinlandostrophia*) but more delicate morphologies are present at lower abundances. Additional constituents include thin ramose bryozoa, thin bifoliate bryozoa, thick ramose bryozoa, encrusting bryozoa, the problematic genus *Tentaculites,* the orthid *Cincinnetina*, the strophomenid *Rafinesquina, and* the small atrypid *Zygospira*.

The deep subtidal *Eochonetes*- *Cincinnetina* Community is dominated by the strophomenid brachiopod *Eochonetes* and the orthid brachiopod *Cincinnetina*. Additional constituents include stauriid Grewingkia, the disparid *Cincinnaticrinus*, thin ramose bryozoa, encrusting bryozoa, thin bifoliate bryozoa, the small atrypid *Zygospira*, the orthid *Vinlandostrophia*, the strophomenid *Rafinesquina*, the phacopid *Flexicalymene*, the strophomenid *Strophomena*, and the problematic genus *Cornulites*. This community is dominated by small delicate morphologies (e.g., *Eochonetes* and *Cincinnetina*) but contains more robust morphologies at low abundances (e.g., *Vinlandostrophia*). The *Eochonetes*- *Cincinnetina* Community is of particular interest because it captures the first abundant occurrence of the Clarksville invaders in the study interval (*Eochonetes*, *Grewingkia*, and *Strophomena*).

The primarily offshore *Tentaculites*- Thin Ramose Bryozoan Community is dominated by the problematic genus *Tentaculites* and thin ramose bryozoans. Additional constituents of this community include the disparid *Cincinnaticrinus*, the monobathrid *Xenocrinus*, the orthid *Cincinnetina*, and the small atrypid *Zygospira*. This deep-water community is mainly found in the northern portion of the study area and is dominated by small delicate morphologies (e.g., *Cincinnetina*, *Zygospira*) (Fig. 10D).

Harpers Run Submember: Paleocommunity Relationships

When the DCA results are plotted, the three communities separate clearly in two-dimensional ordination space (Fig. 10C). The *Vinlandostrophia*- *Cincinnaticrinus* community plots at high axis one scores and moderate axis two scores. The *Tentaculites*- Thin Ramose Bryozoan Community plots at low axis one and low axis two scores. The *Eochonetes*- *Cincinnetina* Community plots at low axis one scores and high axis two scores.

The gradational nature of the community structure in ecospace matches the general expectation from prior studies. The *Vinlandostrophia*- *Cincinnaticrinus* community contains large bodied, robust organisms (e.g., *Vinlandostrophia*) which are typical of shallower water environments with wave influence (Holland, 1997), whereas the smaller-bodied, delicate taxa like *Cincinnetina* and *Eochonetes* more commonly inhabit deeper settings with muddier substrates and less wave influence (Holland, 1997).

Stony Hollow Creek Submember: Paleocommunity Descriptions

Q-mode cluster analysis resolved four communities in the Stony Hollow Creek Submember (Fig. 10F). These are identified as the Massive Bryozoan- *Hebertella* Community, The *Hebertella*- Thin Ramose Community, the *Cincinnetina*- *Eochonetes* Community, and the *Cincinnetina*- Thin Ramose Community. The massive bryozoan-*Hebertella* community is restricted to near shore shoal settings and is dominated by large robust morphologies (e.g., *Hebertella*, massive bryozoans). Additional contributors to this community include thick ramose bryozoa, thin ramose bryozoa, encrusting bryozoa, the craniid *Petrocrania*, and the pterioid *Caritodens*. This shallow water community is restricted to the southernmost portion of the study area (Figs. 1, 8, 11).

The primarily shallow subtidal *Hebertella*- Thin Ramose Bryozoan Community is dominated by the orthid brachiopod *Hebertella* and thin ramose bryozoans. Additional contributors to this community include the cladid *Plicodendrocrinus*, the monobathrid *Glyptocrinus*, the disparid Cincinnaticrinus, the *monobathrid* Xenocrinus, the disparid *Iocrinus*, thin bifoliate bryozoa, thick ramose bryozoa, massive bryozoa, encrusting bryozoa, the atrypid *Zygospira*, the problematic genera *Tentaculites* and *Cornulites*, the phacopid *Flexicalymene*, the murchisoniinids *Liospira* and *Paupospira*, the euomphalinid *Cyclonema*, and the pterioid *Caritodens.* This community is dominated by large robust morphologies (e.g., *Hebertella*) but small delicate forms are also present at low abundances (e.g., *Zygospira*). Although the orthid *Hebertella* is a dominant component of both the Massive Bryozoan – *Hebertella* Community and the *Hebertella*- Thin Ramose Community, the former is far less diverse and lacks the small delicate morphologies (e.g., *Zygospira*) which are present at low abundance in the *Hebertella*- Thin Ramose Community.

The third community present in this submember is the deep subtidal to offshore *Cincinnetina*- Thin Ramose Bryozoan Community which is dominated by the orthid brachiopod *Cincinnetina* and thin ramose bryozoans. Additional contributors to this community include the monobathrid *Glyptocrinus*, the disparid *Cincinnaticrinus*, the monobathrid Xenocrinus, the orthid *Hebertella*, thin bifoliate bryozoa, thick ramose bryozoa, massive bryozoa, encrusting bryozoa, the problematic genus *Tentaculites*, the small atrypid *Zygospira*, the orthid *Vinlandostrophia*, the strophomenid *Rafinesquina*, stauriid *Grewingkia*, the craniid *Petrocrania*, the Strophomenid *Leptaena*, the phacopid *Flexicalymene*, the strophomenid *Strophomena*, the pterioid *Caritodens*, the strophomenid *Eochonetes*, the problematic genus *Cornulites*, the murchisoniinid *Paupospira*, euomphalinid *Cyclonema*, and the strophomenid *Tetraphalerella*. This community is found in the middle to northern portion of the study area (Figs. 1, 8, 11) and is dominated by small delicate morphologies (e.g., *Cincinnetina*) but contains large robust forms at low abundances (e.g., *Hebertella*).

The final community present is the primarily offshore *Cincinnetina*- *Eochonetes* community. The *Cincinnetina*- *Eochonetes* community is dominated by the orthid brachiopod *Cincinnetina* and the strophomenid brachiopod *Eochonetes*. Additional contributors to this community include thin ramose bryozoa, thin bifoliate bryozoa, thick ramose bryozoa, massive bryozoa, encrusting bryozoa, the orthid *Hebertella*, the monobathrid *Xenocrinus*, the disparid *Cincinnaticrinus*, the disparid *Iocrinus*, the strophomenid *Strophomena*, the problematic genus *Tentaculites*, the small atrypid *Zygospira*, the orthid *Vinlandostrophia*, the strophomenid *Rafinesquina*, the phacopid *Flexicalymene*, the murchisoniinid *Liospira*, and the strophomenid *Tetraphalerella*. This deep-water community is found in the northern portion of the study area (Figs. 1, 8, 11) and is dominated by small delicate morphologies (e.g., *Cincinnetina*, *Eochonetes*) with large robust forms present at low abundances (e.g., *Vinlandostrophia*, *Hebertella*). Although the orthid Cincinnetina is a dominant component of both the *Cincinnetina-Eochonetes* Community and the *Cincinnetina*- Thin Ramose community, the *Cincinnetina-Eochonetes* Community is the more diverse of the two.

Stony Hollow Creek Submember: Paleocommunity Relationships

The massive bryozoan -*Hebertella* community and *Hebertella*- thin ramose bryozoan community separate clearly from the other communities in two-dimensional space (Fig. 10E). However, there is considerable overlap between the *Cincinnetina-Eochonetes* community and Thin Ramose Bryozoan- *Cincinnetina* Community. The massive bryozoan -*Hebertella* community plots at high axis one scores and intermediate axis two scores. The *Hebertella*- thin ramose bryozoan community plots at intermediate axis one scores and a range of axis two scores. The *Cincinnetina- Eochonetes* community plots at low axis one scores and a range of axis two scores. The Thin Ramose Bryozoan-*Cincinnetina* community plots at low axis one scores and intermediate to high axis two scores.

The gradational nature of the community structure in ecospace matches the general expectation from prior studies. The large bodied, robust organisms of the massive bryozoan- *Hebertella* community (e.g., *Hebertella*) are typical of shallower water environments with wave influence (Holland, 1997), whereas the smaller-bodied, delicate taxa like *Cincinnetina* and *Eochonetes* more commonly inhabit deeper settings with muddier substrates and less wave influence (Holland, 1997).

Middle Clarksville Submember: Paleocommunity Descriptions

Q-mode cluster analysis resolved three communities present in the Middle Clarksville Submember (Fig. 10H). These are identified as the Massive Bryozoan-*Hebertella* Community, the Encrusting Bryozoan-Thin Ramose Bryozoan Community, and the *Cincinnetina*- *Tentaculites* Community. The massive bryozoan- *Hebertella* community is restricted to near shore shoal settings and is dominated by massive bryozoans and the orthid *Hebertella.* Additional contributors to this community include the pterioid *Caritodens*, the orthid *Vinlandostrophia*, encrusting bryozoa, thin bifoliate bryozoa, and thin ramose bryozoa. This shallow water community is restricted to the southernmost portion of the study area (Figs. 1,8,11) and is dominated by large robust morphologies (e.g., *Hebertella*).

The deep subtidal Encrusting Bryozoan- Thin Ramose Bryozoan community is dominated by encrusting bryozoans and thin ramose bryozoans. Additional contributors to this community include the orthid *Hebertella*, the orthid *Vinlandostrophia*, thin bifoliate bryozoa, the small atrypid *Zygospira*, the strophomenid *Rafinesquina*, the disparid *Cincinnaticrinus*, the monobathrid *Xenocrinus*, and the stauriid *Grewingkia*. This community contains a mix of large robust morphologies and small delicate morphologies with large robust morphologies being more abundant.

The final community present is the deep subtidal to offshore *Cincinnetina-Tentaculites* community which is dominated by the orthid *Cincinnetina* and the problematic genus *Tentaculites*. Additional contributors to this community include the disparid *Cincinnaticrinus*, the monobathrid *Xenocrinus*, the disparid *Iocrinus*, massive bryozoa, the phacopid *Flexicalymene*, the problematic genus *Cornulites*, encrusting bryozoa, thin ramose bryozoa, thick ramose bryozoa, thin bifoliate bryozoa, the small atrypid *Zygospira*, the orthid *Hebertella*, the orthid *Vinlandostrophia*, the stauriid *Grewingkia*, the strophomenid *Rafinesquina*, the craniid *Petrocrania*, the strophomenid *Strophomena*, the pterioid *Caritodens*, and the strophomenids *Eochonetes* and *Tetraphalerella*. This community is dominated by small delicate morphologies (e.g., *Cincinnetina*, *Tentaculites*) by large robust forms (e.g., *Hebertella, Vinlandostrophia*) are also present at low abundances.

Middle Clarksville Submember: Paleocommunity Relationships

The three communities plot in discrete regions of ecospace (Fig. 10G). The Massive Bryozoan- *Hebertella* community plots at high axis one scores and intermediate axis two scores. The Encrusting Bryozoan- Thin Ramose Bryozoan Community plots at a combination of high and low axis one scores and intermediate to high axis two scores. The *Cincinnetina- Tentaculites* community plots at low axis one scores and intermediate to low axis two scores. The gradational nature of the community structure in ecospace matches the general expectation from prior studies. The large bodied, robust organisms of the massive bryozoan- *Hebertella* community (e.g., *Hebertella*) are typical of shallower water environments with wave influence (Holland, 1997), whereas the smaller-bodied, delicate taxa like *Cincinnetina* and *Eochonetes* more commonly inhabit deeper settings with muddier substrates and less wave influence (Holland, 1997).

Guild Analysis: Changes in Ecospace Utilization

Bon Well Hill Submember

The primarily shallow subtidal Thin Ramose- *Vinlandostrophia* Community contains four guilds (Fig. 12). The most abundant guilds in this community are the low tier attached epifaunal passive suspension feeders (53%) and mid-tier attached epifaunal passive suspension feeders (42%). It is typical for low to mid-tier attached forms to be the primary components of communities developed above normal wave base (Fig. 12), although it should be noted that the low tier attached epifaunal passive suspension feeder guild is a substantial component of all communities regardless of depth (Fig. 12). Minor contributors to this community include the open-fan crinoids (3%) and the dense-fan crinoids (2%) (Fig. 12).

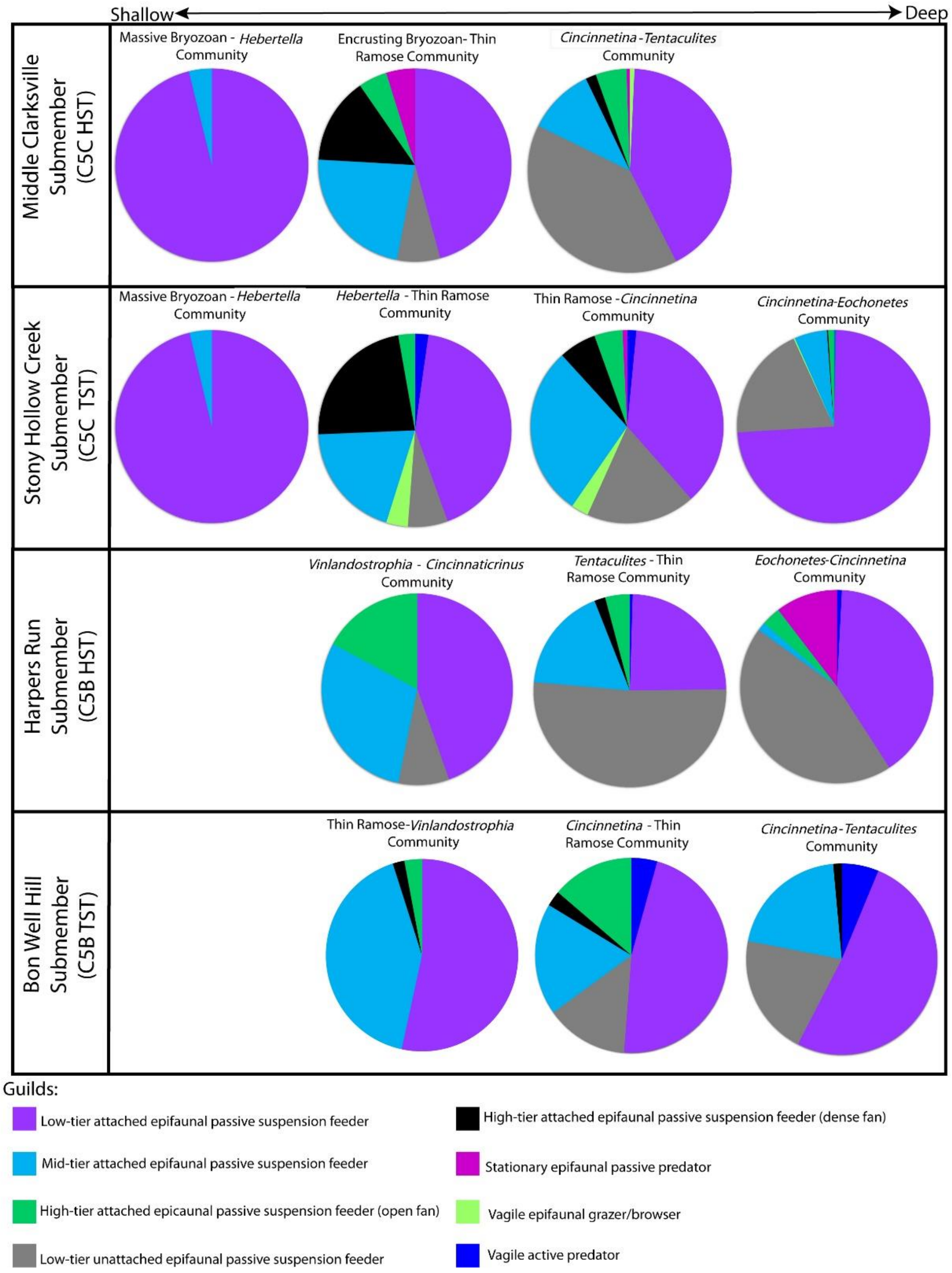
The primarily deep subtidal to offshore *Cincinnetina*- *Tentaculites* community contains five guilds (Fig. 12). Like in the previous community, the low tier attached epifaunal passive suspension feeders (51%) and mid-tier attached epifaunal passive suspension feeders (21%) are among the most abundant guilds. However, in this community the low tier unattached epifaunal passive suspension feeders (21%) also make a considerable contribution, as is common in deeper water communities (Fig. 12). Minor contributors to this community are the vagile active predators (6%) and the dense fan crinoids (1%).

The primarily offshore *Cincinnetina*-Thin Ramose Community contains six guilds (Fig. 12). Like the previous communities, the most abundant guilds of the *Cincinnetina*-

Thin Ramose Community are the low tier attached epifaunal passive suspension feeder guild (47%) and mid-tier attached epifaunal passive suspension feeders (19%) (Fig. 12). The low tier unattached epifaunal passive suspension feeder guild also makes a large contribution (14%), as is common in deeper water communities. However, its abundance is lower than is the previous community, due in part to a marked increase in the prevalence of open fanned crinoids (14%) (Fig. 12). Minor contributors to this community include the vagile active predators (4%) and dense fanned crinoids (2%) (Fig. 12).

Figure 12

Guild analysis of communities



Harpers Run Submember

The primarily shallow subtidal *Vinlandostrophia*- *Cincinnaticrinus* Community contains four guilds (Fig. 12). The most abundant guilds in this community are the low-tier attached epifaunal passive suspension feeders (45%) and mid-tier attached epifaunal passive suspension feeders (30%), which is typical of communities developed above normal wave base (Fig 12). The next most common guild in this community is the open fanned crinoids (17%). Minor contributors include the low tier unattached epifaunal passive suspension feeders (9%) which are typically absent in shallow water communities or present at low abundances (Fig. 12).

The primarily deep subtidal *Eochonetes*- *Cincinnetina* Community contains six guilds (Fig. 12). The most abundant guild present in this community is the low tier unattached epifaunal passive suspension feeders (44%) (Fig. 12). High abundance of this guild is typical for deeper water communities, especially those developed during highstand to falling stage systems tracts (Fig. 12). The next most abundant guild is the low tier attached epifaunal passive suspension feeders (40%) which are a common component of all communities (Fig. 12). The stationary epifaunal passive predator guild (10%) makes its first appearance in this community with the introduction of the stauriid *Grewingkia* (Fig. 12). Minor contributors to this community include open faned crinoids (3%), mid-tier attached epifaunal passive suspension feeders (1%), and vagile active predators (1%).

The primarily offshore *Tentaculites*–Thin Ramose Community contains six guilds (Fig. 12). The most abundant guild in this community is the low tier unattached epifaunal passive suspension feeder guild (52%), as is typically abundant in deeper water communities developed during highstand to falling stage systems tracts (Fig. 12). The next most abundant guilds are the low tier attached epifaunal passive suspension feeders (24%) and the mid-tier attached epifaunal passive suspension feeders (18%), both of which are ubiquitous despite generally being more abundant in shallower settings (Fig. 12). Minor contributors to this community include the open fanned crinoids (4%), dense fanned crinoids (2%), and vagile active predators (>1%).

Stony Hollow Creek Submember

The Massive Bryozoan- *Hebertella* Community contains two guilds, which is typical of communities restricted to near shore shoal settings (Fig. 12). Despite two guilds being present, the low tier attached epifaunal passive suspension feeders (96%) dominate the community whereas the mid-tier attached epifaunal passive suspension feeders (4%) are a very minor component (Fig. 12).

The primarily shallow subtidal *Hebertella*- Thin Ramose Community contains seven guilds (Fig. 12). The most abundant guild in this community is the low tier attached epifaunal passive suspension feeders (42%), which is typical of communities developed above normal wave base (Fig. 12). The second most abundant guild is the dense fanned crinoids (23%), this guild is generally most prevalent in the shallower southern portion of the study area (Fig. 12) and reaches its peak abundance in this community. The third most abundant guild is the mid-tier attached epifaunal passive suspension feeders (19%) which are typically a dominant component of communities developed above normal wave base (Fig. 12). Additional minor contributors are the low tier unattached epifaunal passive suspension feeders (7%), mobile epifaunal grazer/browsers (4%), open fanned crinoids (3%), and mobile active predators (1%).

The primarily deep subtidal to offshore Thin Ramose- *Cincinnetina* Community contains eight guilds (Fig. 12). The most abundant guilds in this community are the low tier attached epifaunal passive suspension feeders (37%) and mid-tier attached epifaunal passive suspension feeders (29%), both of which are ubiquitous regardless of water depth (Fig. 12). The next most common guild is the low tier unattached epifaunal passive suspension feeders (18%), which typically make up a considerable portion of deeper water communities (Fig. 12). Additional minor contributors to this community are the dense fanned crinoids (6%), open fanned crinoids (5%), mobile epifaunal grazers/browsers (3%), vagile active predators (1%), and stationary epifaunal passive predators (1%) (Fig. 12).

The primarily offshore *Cincinnetina-Eochonetes* Community contains five guilds (Fig. 12). The most common guild in this community is the low tier attached epifaunal passive suspension feeders (74%). While this guild is a large contributor to all communities (Fig. 12), it is generally not present at such high abundances in offshore settings. The abundance of this guild is anomalously high in this community due to the presence of the *Cincinnetina* epibole bed at the base of this submember which is dominated by the small orthid *Cincinnetina* (Fig. 12). The second most abundant guild is the low tier unattached epifaunal passive suspension feeders (19%), which is typical of deeper water communities (Fig. 12). Additional minor contributors to this community are the mid-tier attached epifaunal passive suspension feeders (6%), open fanned crinoids (1%), and vagile active predators (0.5%).

Middle Clarksville Submember

The Massive Bryozoan- *Hebertella* Community contains two guilds (Fig. 12), which is typical of communities restricted to near shore shoal settings. The low tier attached epifaunal passive suspension feeders (96%) dominates this community and the mid-tier attached epifaunal passive suspension feeders (4%) are only a minor contributor (Fig. 12).

The deep subtidal Encrusting Bryozoan- Thin Ramose Bryozoan Community contains six guilds (Fig. 12). The most abundant guilds in this community are the low tier attached epifaunal passive suspension feeders (46%) and mid-tier attached epifaunal passive suspension feeders (23%) which are generally more abundant in shallower settings despite being ubiquitous (Fig. 12). The next most abundant guild is the dense fan crinoids (14%). Additional minor contributors to this community are the low tier unattached epifaunal passive suspension feeders (7%), open fanned crinoids (5%), and stationary epifaunal passive predators (5%).

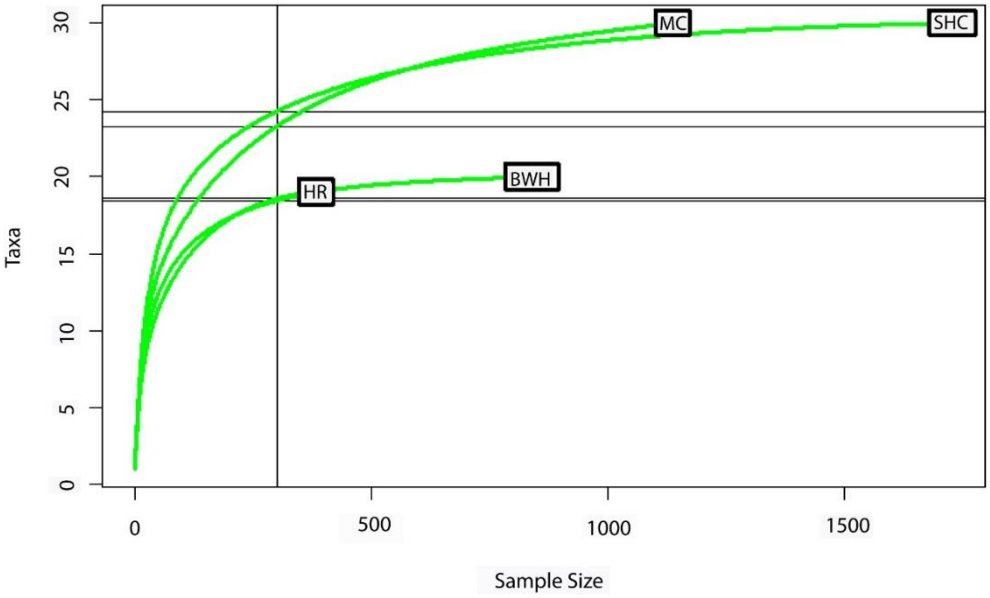
The deep subtidal to offshore *Cincinnetina-Tentaculites* Community contains seven guilds (Fig. 12). The most abundant guild in this community is the low tier attached epifaunal passive suspension feeders (42%) which are ubiquitous and a large contributor to all communities (Fig. 12). The next most abundant guild is the low tier unattached epifaunal passive suspension feeders (40%). High abundance of this guild is typical for deeper water communities, especially those developed during highstand to falling stage systems tracts (Fig. 12). The next most abundant guild is the mid-tier attached epifaunal passive suspension feeders (10%), which are typically less abundant in deeper water environments (Fig. 12). Additional minor contributors to this community are the open fanned crinoids (5%), dense fanned crinoids (2%), mobile active predators (1%), and stationary epifaunal passive predators (0.5%).

Biodiversity: Richness and Evenness

Biodiversity was assessed by calculating richness via rarefaction analysis (Fig. 13). Rarefied richness was calculated for each of the four submembers at a subsample size of 300 individuals. For the Bon Well Hill Submember, richness was estimated to be 18.43 genera with a standard error of 0.98, indicating 17.45-19.41 genera present. Richness of the Harpers Run Submember was estimated to be 18.56 genera with a standard error of 0.61, indicating 17.95-19.17 genera present. For the Stony Hollow Creek Submember, richness was estimated to be 24.24 genera with a standard error of 1.58, indicating 22.66-25.82 genera present. Richness of the Middle Clarksville Submember was estimated to be 23.36 genera with a standard error of 1.76, indicating 21.50-25.02 genera present. The richness values fall into two sets: the primarily pre-invasion Bon Well Hill and Harpers Run submembers have richness values that center on 17-19 genera, whereas the post-invasion Middle Clarksville and Stony Hollow Submembers are statistically more diverse with a richness of 21-25 genera.

Figure 13

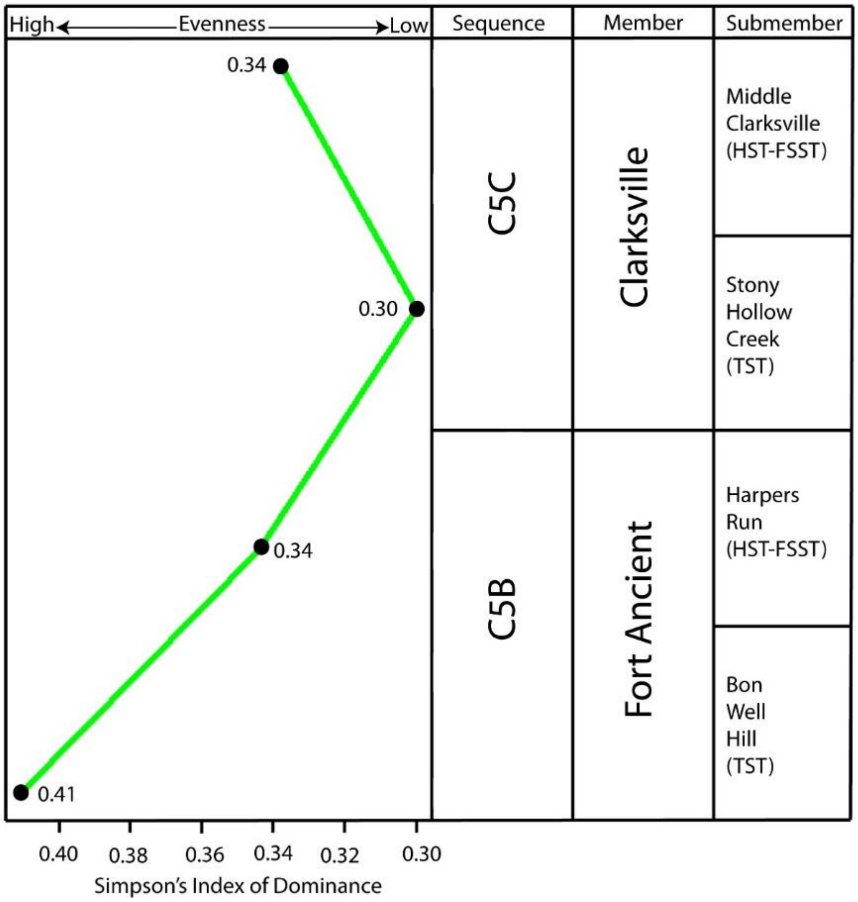
Rarefied richness for each submember calculated at a subsample size of 300 individuals.



Community structure was assessed via Simpson's index of dominance, in which values closer to 1.0 indicate a more even community structure. Evenness is relatively low in these communities (range from 0.41 to 0.30) (Fig. 14). Evenness decreased from Bon Well Hill Submember (E=0.41) to the Harpers Run Submember (E=0.34) to the Stony Hollow Creek Submember (E=0.30) before rebounding slightly in the Middle Clarksville Submember (E=0.34) (Fig. 14).

Figure 14

Simpson's index of dominance through the study interval.



Stability of Environmental Parameters

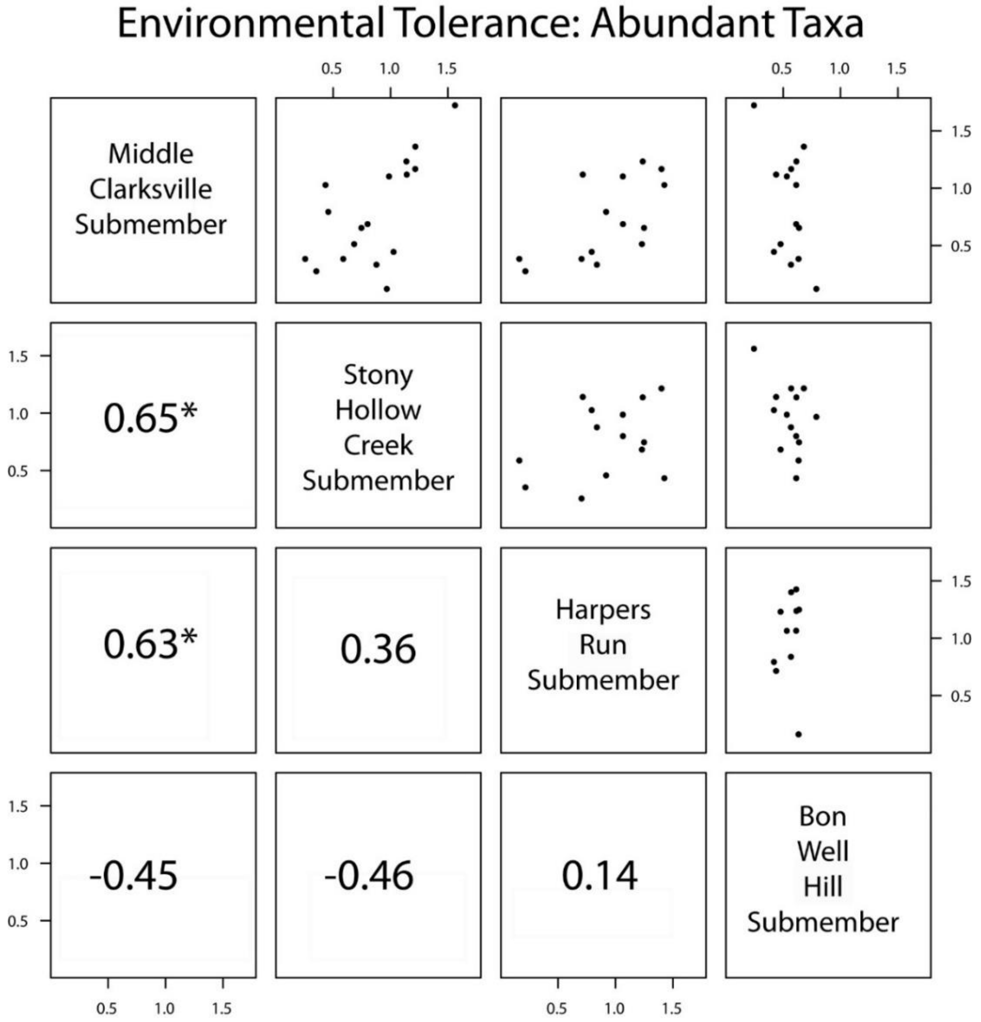
Environmental Tolerance

In general, conservation of habitat preferences increases from pre- to post-invasion. Although statistical significance is reported (Figs. 15, 16) the magnitude of the correlation is emphasized in interpretation rather than statistical significance because it is a direct measure of the strength of the correlation (Holland and Zaffos, 2011). Pearson's product moment correlation between the environmental tolerances of abundant taxa in the

Bon Well Hill and Harpers Run Submembers resulted is a correlation coefficient of 0.14 (Fig. 15). This weak correlation indicates that there is little evidence for conservatism of this parameter between these intervals. The correlation between the Harpers Run and Stony Hollow Creek resulted in a correlation coefficient of 0.36 (Fig. 15). This correlation is still weak but indicates that there is more evidence for conservatism of environmental tolerance than was observed between the previous intervals. The correlation between the Stony Hollow creek and Middle Clarksville resulted in a correlation coefficient of 0.65 (Fig. 15). This correlation is moderately strong and indicates that that there is stronger evidence for conservatism of environmental tolerance between these intervals than was observed between the previous intervals.

Figure 15

Comparison of the environmental tolerances of abundant taxa between submembers via Pearson's Product Moment Correlation. Correlations that are significant at an alpha level of 0.05 are marked with an asterisk. The box above the Bon Well Hill Submember label is a visualization of the correlation of environmental tolerance, the X-axis is the environmental tolerance during Bon Well Hill Time, and the Y-axis is environmental tolerance during Harpers Run Time. The box to the left of the Bon Well Hill Submember label is the magnitude of the correlation between Bon Well Hill and Harpers Run environmental tolerances. Note the increasing magnitude of the correlations through time which indicates increasing conservation of environmental tolerances through time.

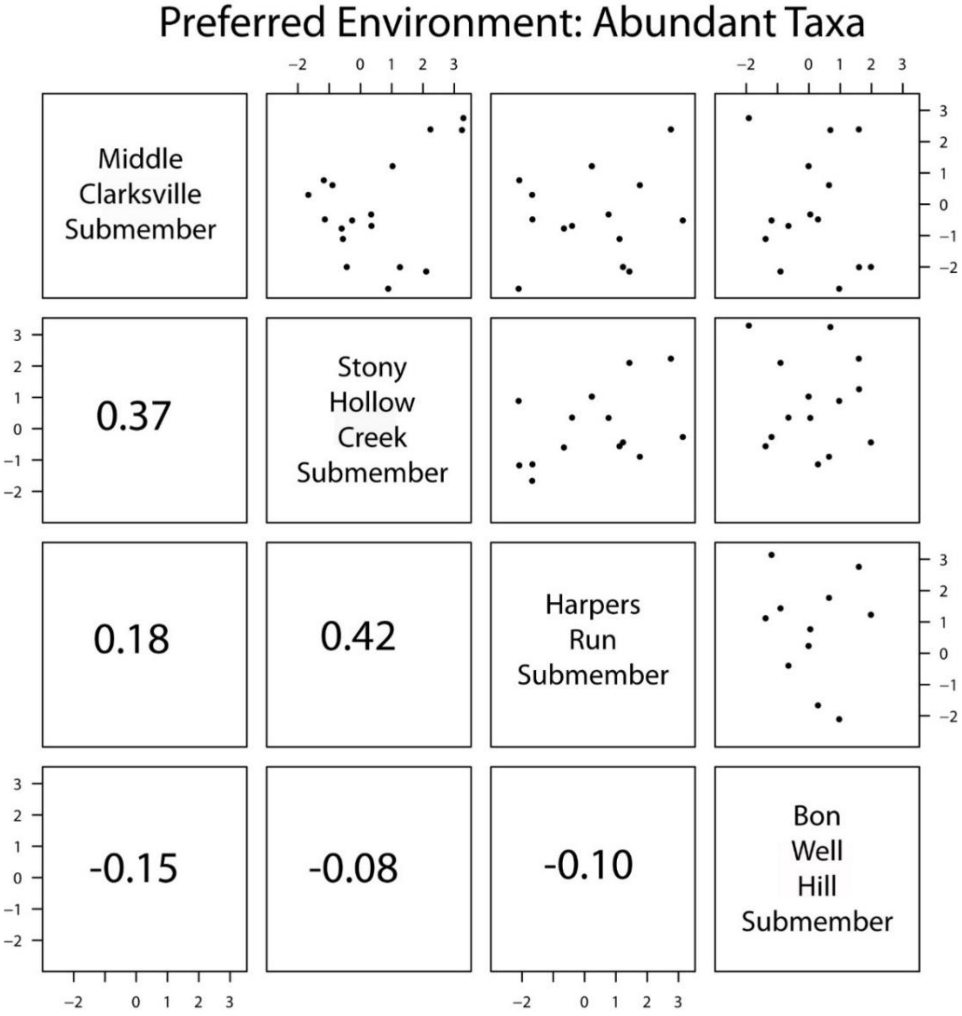


Preferred Environment

Taxa also increased their adherence to their previously preferred environment from pre- to post-invasion (Fig. 16). Pearson's product moment correlation between preferred environments of abundant taxa between the Bon Well Hill and Harpers Run Submembers resulted in a low correlation coefficient -0.10 (Fig. 16) indicating little evidence for conservation of this parameter. The correlation between the Harpers Run and Stony Hollow Creek Submembers resulted in a moderate correlation coefficient of 0.42 (Fig. 16) indicating increased evidence for conservation of this parameter. The correlation between the Stony Hollow Creek and Middle Clarksville Submembers resulted in a moderate correlation coefficient of 0.37 (Fig 16) indicating little change in the stability of this parameter.

Figure 16

Comparison of the preferred environment of abundant taxa between submembers via Pearson's Product Moment Correlation. Correlations that are significant at an alpha level of 0.05 are marked with an asterisk. The box above the Bon Well Hill Submember label is a visualization of the correlation of preferred environment, the X-axis is the preferred environment during Bon Well Hill Time, and the Y-axis is preferred environment during Harpers Run Time. The box to the left of the Bon Well Hill Submember label is the magnitude of the correlation between Bon Well Hill and Harpers Run preferred environment. Note the general increase in magnitude of the correlations through time which indicates increasing conservation of preferred environment through time.



Chapter 5: Discussion

The Arrival and Spread of Invaders

Changes in Communities

The fauna of the Cincinnati Basin is largely homogenous across the depth gradient during Bon Well Hill time (Fig. 10A). Minor differences exist among depositional environments in the pre-invasion Bon Well Hill Submember. For example, cluster analyses indicate that *Cincinnetina* comprise a large proportion of the fauna in deep subtidal and offshore environments, whereas *Hebertella* and *Vinlandostrophia* are dominant in shallow subtidal environments (Fig. 10B). However, differences in ecospace utilization are more pronounced between communities within the Bon Well Hill Submember (Fig. 12). The low tier unattached epifaunal passive suspension feeder guild is absent from the shallow subtidal Thin Ramose Bryozoan- *Vinlandostrophia* Community (Fig. 12) but is present in the deep subtidal to offshore *Cincinnetina-Tentaculites* and the *Cincinnetina*- Thin Ramose Bryozoan Communities (Fig. 12). Furthermore, the mid-tier attached epifaunal passive suspension feeder guild is sparse in the deep subtidal to offshore *Cincinnetina-Tentaculites* and *Cincinnetina*- Thin Ramose Bryozoan Communities when compared to the shallow subtidal Thin Ramose Bryozoan-*Vinlandostrophia* Community (Fig. 12).

Homogeneity across the Bon Well Hill Submember depth gradient is indicated by the broad overlap of communities along axis one of the DCA analysis (Fig. 10A). Gradient breakdown during this interval has been documented previously by Holland and Patzkowsky (2007). They attributed the faunal homogenization across the depth gradient to community reorganization and the breakdown of the depth gradient due to the series of isolated invasions (sensu Stigall, 2019) during the C4 sequence (Holland and Patzkowsky, 2007). Subsequent research further identified the loss of native specialist taxa (Stigall, 2010) during the C4 related to isolated invasions (sensu Stigall, 2019), which also contributed to loss of across shelf faunal differentiation. The observed differences in ecospace utilization between communities are attributed to variation in secondary environmental factors along the depth gradient. The absence of free-living taxa in the shallow subtidal Thin Ramose Bryozoan- *Vinlandostrophia* Community is due to the high energy conditions of the shallow subtidal zone hindering their establishment. Conversely, the normally quiet water conditions of the deep subtidal and offshore zones allowed free living forms to proliferate in the *Cincinnetina-Tentaculites* and *Cincinnetina*- Thin Ramose Bryozoan Communities. Higher abundance of the mid-tier attached epifaunal passive suspension feeder guild in the shallow subtidal Thin Ramose Bryozoan- *Vinlandostrophia* Community is attributed to high availability of suitable substrate in the shallow subtidal zone. Conversely, suitable substrate was restricted in the deep subtidal to offshore *Cincinnetina-Tentaculites* and *Cincinnetina*- Thin Ramose Bryozoan Communities which limited the guilds abundance.

Faunal and ecospace differentiation across the depth gradient are stronger in the overlying Harpers Run Submember as is readily apparent in both the DCA and guild analyses (Figs. 10A-D, 12). This is due to the introduction of the extrabasinal invaders *Eochonetes*, *Grewingkia*, and *Strophomena* in the uppermost beds of the Harpers Run in the deep subtidal facies. A single specimen of *Leptaena* was also detected at the shallow subtidal site FB during this interval. This observation is consistent with previous studies (e.g., Schwalbach, 2017; Brett et al., 2020) that indicate the mid-ramp depth was initially most impacted by the Clarksville Phase of the Richmondian Invasion. The arrival of the invaders is discernable in the DCA analysis (Fig. 10C). The *Eochonetes*- *Cincinnetina* community, which contains the newly arrived taxa, plots high on axis two while the *Tentaculites*-Thin Ramose community plots low. Relatedly, axis two manifests primarily at low axis one scores which correspond to deeper waters as this is where the invaders were initially abundant (Fig. 10C). Guild analysis of the Harpers Run communities indicates the deep subtidal to offshore *Eochonetes- Cincinnetina* and *Tentaculites*- Thin Ramose Bryozoan Communities differ from the primarily shallow subtidal *Vinlandostrophia- Cincinnaticrinus* in terms of the abundance of the low tier unattached epifaunal passive suspension feeding guild (Fig. 12). This guild is an important constituent of the *Eochonetes*- *Cincinnetina* and *Tentaculites*- Thin Ramose Bryozoan Communities but is comparatively sparse in the *Vinlandostrophia*- *Cincinnaticrinus* Community. Differences in the abundance of this guild between communities are attributed in part to differences in wave energy across the depth gradient but also to the introduction of the free-living invaders *Eochonetes* and *Strophomena* into deep subtidal settings at the top of the submember. Deeper water and shallower water communities also differ in the abundance of the mid-tier attached epifaunal passive suspension feeder guild which is highest in the *Vinlandostrophia- Cincinnaticrinus* Community due to high availability of suitable substrate in the shallow subtidal zone.

Ecospace utilization is notably different between the Harpers Run and Bon Well Hill Submembers (Fig. 12). Low tier unattached epifaunal passive suspension feeders are markedly more prevalent in all Harpers Run communities relative to Bon Well Hill communities. This is attributed primarily to the deeper waters of the highstand to falling stage systems tract allowing free-living forms to proliferate in areas where they were previously excluded or present at low abundances, and secondarily to the proliferation of free-living invaders in the deep subtidal zone. The onset of the Clarksville Phase also introduced the solitary rugose coral *Grewingkia*, which is responsible for the appearance of the stationary epifaunal passive predator guild in the Harpers Run Submember.

Faunal and ecospace differentiation across the depth gradient were strong in the overlying Stony Hollow Creek Submember as demonstrated by the DCA and guild analyses (Figs. 10E,12). The invaders *Eochonetes*, *Grewingkia*, and *Strophomena* expanded their geographic range during this interval and are present in deep subtidal and offshore environments. The invader *Leptaena* appears in offshore settings during the Stony Hollow Creek and is far more abundant at site FB, causing sample FB-1 to cluster with the Thin Ramose- *Cincinnetina* community despite being shallow subtidal. The spread of the invaders through the basin made deep water faunas more distinct from shallower faunas, resulting in clear geographic and ecological differentiation of communities across the depth gradient (Fig. 10E).

The Massive Bryozoan-*Hebertella* community present in shoal settings in the southern most portion of the study area (Figs. 1, 8, 11) was almost entirely low tier attached epifaunal passive suspension feeders and demonstrated the most limited use of ecospace due to the high energy conditions in which it occurred (Fig. 12). Down ramp (north) (Figs. 1, 8, 11) in the shallow subtidal zone the *Hebertella*- Thin Ramose Community dominated and ecospace utilization was more variable than in shoal settings (Fig. 12). Dense fanned crinoids were highly abundant in this community due to high feeding success in strong currents (Kammer, 1985). The deep subtidal to offshore Thin

Ramose- *Cincinnetina* Community is present primarily in the northern portion of the study area (Figs. 1, 8, 11) and differs from the shallower Massive Bryozoan-*Hebertella* and *Hebertella*- Thin Ramose Communities in that the low tier unattached epifaunal passive suspension feeder and mid-tier attached epifaunal passive suspension feeder guilds are more abundant. The increase in the prevalence of free-living taxa is due to the quiet waters in which this community occurs allowing them to proliferate.

Ecospace utilization is notably different between the Stony Hollow Creek and Harpers Run submembers in that low tier unattached epifaunal passive suspension feeders are markedly less prevalent in all Stony Hollow Creek communities relative to Harpers Run communities (Fig. 12). This is attributed to the shallower waters of the transgressive systems tract limiting the proliferation of free-living taxa during Stony Hollow Creek time. Some Stony Hollow Creek Communities demonstrated patterns of ecospace utilization that are divergent from general trends observed in other intervals. For example, the increase in the mid-tier attached epifaunal passive suspension feeders in the Thin Ramose- *Cincinnetina* Community is at odds with the general trend of decreased abundance of this guild in deeper waters observed in previous intervals (Fig. 12) and may be due to the introduction of invasive bryozoa into deeper water communities. However, serial thin sectioning of bryozoa across the depth gradient is required to test this hypothesis. The *Cincinnetina-Eochonetes* Community also differs from all other deep-water communities in the study interval in that it is dominated by the low tier attached epifaunal passive suspension feeder guild (Fig.12). *Cincinnetina* specimens comprise of over 68% of all specimens collected from this community, which denotes the presence of the *Cincinnetina meeki* epibole at the base of the submember (Fig. 4). *Cincinnetina* is a member of the low tier attached epifaunal passive suspension feeder guild (Table 2) and its anomalous abundance is responsible for the guild’s dominance in this community.

Faunal and ecospace differentiation across the depth gradient are again well developed in the Middle Clarksville Submember (Figs. 10G, 12). Patterns of ecospace utilization among communities in the Middle Clarksville are broadly like those in the underlying Stony Hollow Creek. The Massive Bryozoan- *Hebertella* Community found in shoal settings in the southern most portion of the study area (Figs. 1, 8, 11) is again almost entirely low tier attached epifaunal passive suspension feeders (Fig. 12). This highly limited use of ecospace is again attributed to the high physiological stress organisms are subject to in shoal environments. Moving down ramp (north) (Figs. 1, 8, 11) to the deep subtidal Encrusting Bryozoan- Thin Ramose Community, ecospace utilization again become more variable than in the shoal settings and the abundance of dense fanned crinoids increases (Fig. 12). The deep subtidal to offshore *Tentaculites*-Thin Ramose Community differs from shallower communities in the abundance of low tier unattached epifaunal passive suspension feeders which are far more abundant in deeper settings (Fig. 12). One marked difference in ecospace utilization between the communities of the Middle Clarksville and the Stony Hollow Creek is the increased abundance of the low tier unattached epifaunal passive suspension feeders observed in the Middle Clarksville (Fig. 12), which is attributed to the increased water depth associated with the highstand to falling stage systems tracts allowing such free-living forms to proliferate.

Eochonetes, *Strophomena*, and *Grewingkia* are all present in offshore environments during Middle Clarksville time and the same invaders are present in deep subtidal environments with the additions of *Leptaena* and *Hiscobeccus*. However, past studies indicate that *Hiscobeccus* initially arrives in the basin during the Stony Hollow Creek Submember (Aucoin and Brett, 2015; Brett et al., 2020), despite its non-detection during this interval in the present study.

Eochonetes, *Grewingkia*, and *Strophomena* as well as the native orthid *Cincinnetina* all appear for the first time at the Apricot Lane site during the Middle Clarksville interval. This site is interpreted as shallow subtidal during Bon Well Hill, Harpers Run, and Stony Hollow Creek time which raises the question of whether these taxa modified their niche parameters allowing for colonization of shallow subtidal environments or if the Apricot Lane site fell below normal wave base and this juxtaposition of deep and shallow water communities is due to habitat tracking (lateral migration of species or biofacies in response to shifting environments (Brett et al., 2007).

Niche evolution has been documented for both invaders and native taxa in past studies which analyzed the Richmondian Invasion as a whole (Malizia and Stigall, 2011; Brame and Stigall, 2014) and the results of these studies indicate that native and invasive taxa responded similarly and that both exhibited elevated levels of niche evolution in response to the invasion (Malizia and Stigall, 2011; Brame and Stigall, 2014). However, these studies indicate that taxa constricted their occupied niche to a subset of their initial ecological tolerances during the Richmondian Invasion rather than expanding their initial range of ecological tolerances, which suggests that niche evolution allowing for colonization of shallow subtidal settings is unlikely. Purcell and Stigall (2021) analyzed the entire Late Ordovician and found that the late Katian was characterized by niche stability which further suggests niche expansion is an unlikely scenario. Although the methods of analysis used here differ from the ecological niche modeling of the Malizia & Stigall (2011), Brame and Stigall (2014), and Purcell and Stigall (2021) studies, the analysis of the stability of environmental tolerances conducted in this study also suggests that that niche expansion is not likely to have occurred. The magnitude of the correlation between environmental tolerances for the Stony Hollow Creek – Middle Clarksville transition (Fig. 15) is the highest observed during the study interval which indicates that modification of environmental tolerances was at its lowest point during this transition.

Changes in lithology and faunal assemblage observed at Apricot Lane further suggest that habitat tracking in response to sea level rise and not niche evolution was responsible for the introduction of these taxa to this site. The Middle Clarksville Submember is poorly exposed at Apricot Lane, but excavated portions indicate an increase in the prevalence of shale compared to previous submembers which is indicative of deposition in a lower energy environment. Additionally, past studies have demonstrated that faunal assemblages are more sensitive indicators of changing environmental conditions than lithology (Holland et al., 2001) and there is a clear shift to a deeper water faunal assemblage during this interval. Taxa possessing small delicate morphologies such as *Cincinnetina* and *Eochonetes* are typically found in deep quiet water settings with little wave influence (Holland, 1997) and the arrival of these taxa at this site further suggests an increase in water depth. Furthermore, the observed vertical succession of fauna mirrors the lateral species gradient of the preceding submember which is known to be evidence of habitat tracking (Brett et al., 2007). When considered together, these lines of evidence indicate that the juxtaposition of shallow and deep-water communities observed between the Stony Hollow Creek and Middle Clarksville

Submembers represents typical vertical stacking of laterally adjacent facies and that taxa simply tracked their habitat up ramp. Therefore, Apricot Lane is classified as deep subtidal during Middle Clarksville time.

In summary, the Clarksville Phase of the Richmondian Invasion began when invaders were introduced to the Cincinnati basin at the top of the Harpers Run Submember, with the deep subtidal zone being most impacted. The introduction of the invaders increased faunal differentiation across the depth gradient and increased the prevalence of the low tier unattached epifaunal passive suspension feeder and stationary epifaunal passive predator guilds. Invaders then made their first abundant appearance in offshore environments during the Stony Hollow Creek Submember, which further increased faunal differentiation across the depth gradient. The invaders persisted in both offshore and deep subtidal environments in the post-invasion Middle Clarksville Submember and faunal differentiation across the depth gradient remained well developed.

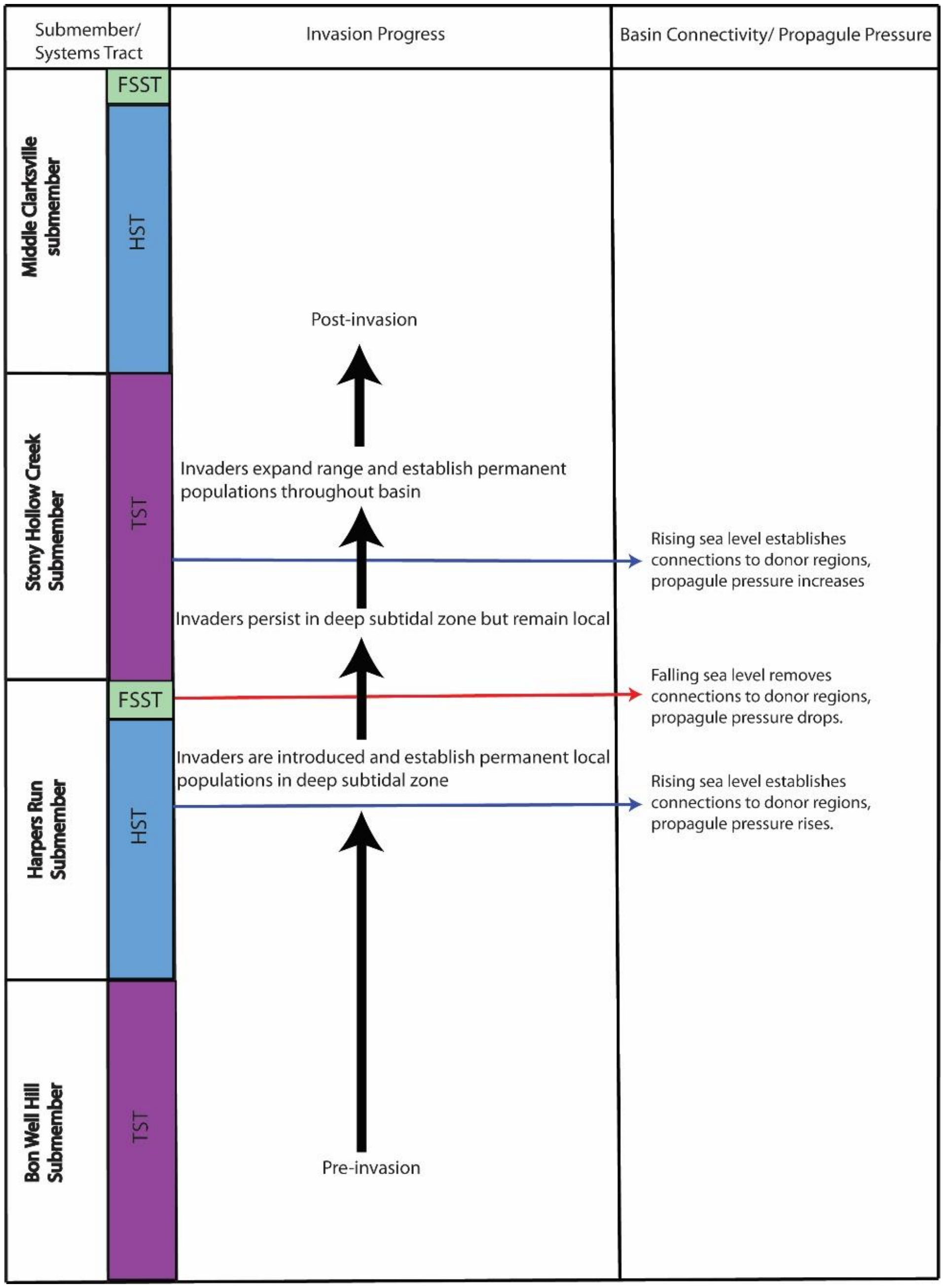
Process of Invasion and Community Change

A temporal lag was observed between the abundant appearance of invaders in deep subtidal environments and their spread to offshore settings. Similar patterns in which the geographic ranges of novel taxa are restricted for some time before they become widespread have been documented in studies of modern biotic invasions (Lockwood et al., 2013; Aiello-Lammens, 2020; and many others). The temporal lag observed in this study can be best understood by examining temporal variations in propagule pressure in response to fluctuations in sea level.

The initial occurrence of the invasive taxa within the deep subtidal of the Harpers Run Submember indicates that the pelagic larvae of the invading taxa initially settled in deep subtidal environments and established local populations at that time. The Harpers Run records the highstand to falling stage systems tract of the C5B sequence (Fig. 17) and corresponds to a period of warming and sea level rise which established connections to adjacent basins. The connections to the donor regions would have been severed during the falling stage systems tract of the C5B sequence (late Harpers Run Submember) following a period of cooling and sea level fall. This acted to reduce propagule pressure within the basin and restricted the further spread of invaders (Fig. 17). The connections to the donor regions were then reestablished during the transgressive systems tract of the C5C sequence (Stony Hollow Creek Submember) (Fig. 17) following a period of warming and sea level rise. The reestablishment of these connections increased propagule pressure and facilitated expanding geographic ranges, such that the invasive species expanded their geographic range beyond deep subtidal environments and established populations in other areas of the basin (Fig. 17).

Figure 17

Visualization of the propagule pressure hypothesis. Far right column indicates changes in propagule pressure and sea level, central column indicates invasion progress, left column indicates stratigraphic position



Aspects of the propagule pressure hypothesis can be tested if sea level fluctuations can be quantified. Although previous authors have documented sea level fluctuation during the Katian (Haq and Schutter, 2008; Elrick et al., 2013; Ghienne et al., 2014; Männik et al., 2021), the temporal scales of these studies are insufficient for application to the Clarksville Phase. Determining how parameters such as glacial ice volume, sea surface temperature, and sea level fluctuated on timescales applicable to the Clarksville phase requires isotopic data, some of which are available. A carbon isotopic excursion was identified in the Waynesville Formation by Bergström et al. (2010) and termed the Waynesville Isotopic Carbon Excursion (ICE). Aucoin (2021) recently determined that the Waynesville ICE is more complex than previous studies suggested and consists of three positive subpeaks. The first positive subpeak of the Waynesville ICE occurs in the Bon Well Hill Submember and is considered the main subpeak. This is followed by negative troughs in the Harpers Run and Stony Hollow Creek submembers. The second positive subpeak occurs at the Stony Hollow Creek to Middle Clarksville transition. After this, $\delta^{13}C_{carb}$ values remain steady halfway through the Middle Clarksville, at which point they dip toward more negative values. The final positive $\delta^{13}C_{carb}$ subpeak occurs in the overlying Blanchester member. In this work, Aucoin (2021) proposes the possibility that the positive $\delta^{13}C_{carb}$ subpeak in the Bon Well Hill and associated cooling (resulting from drawdown and burial of atmospheric CO_2) caused a minor drop in sea level followed by a period of warming and sea level rise which allowed for the initial introduction of the Clarksville invaders (Aucoin, 2021).

The carbon data are very compelling. However, to definitively determine how temperature and/or glacial ice volume fluctuated during Waynesville time and how that may have impacted the Clarksville Phase, high resolution $\delta^{18}O$ data are required. Although $\delta^{18}O$ data of sufficient resolution to develop a temperature curve for the

Waynesville Formation are not available, lower resolution $\delta^{18}O$ data are available for correlative sections in Estonia (Saunja Formation), Minnesota (Dubuque Formation), and Anticosti Island (Vauréal Formation). These correlative units support the interpretation of temperature fluctuation during this interval. Data from the Saunja Formation of Estonia (Kalijo et al., 2017) indicate that the highest point in the Saunja ICE (Waynesville ICE equivalent) corresponds to a positive $\delta^{18}O_{carb}$ excursion, although the variability of the $\delta^{18}O_{carb}$ data is larger than optimal due to diagenetic alteration. Männik et al. (2021) collected $\delta^{18}O_{phos}$ data from conodonts in the Saunja Formation and found that $\delta^{18}O$ values increase slowly but steadily through the formation, further supporting climatic cooling.

Data from Laurentia indicate a similar trend. Buggish et al. (2010) collected $\delta^{18}O_{phos}$ data from conodonts in the Dubuque Formation which suggested decreasing sea surface temperatures (Männik et al., 2021). The Dubuque Formation was later determined to be correlative to the rising limb of the Waynesville ICE using the conodont biostratigraphic framework employed by Bergström et al. (2010) (Männik et al., 2021). Männik et al. (2021) made this correlation based on the placement of the Dubuque Formation within Upper(?) *Amorphognathus superbus* conodont zone. This indicates that the Dubuque Formation corresponds to the upper Arnheim Formation and to the rising limb of the initial (Bon Well Hill) prong of the Waynesville ICE, which has been confirmed to begin with a general increase in $\delta\ ^{13}C_{carb}$ values in the upper Arnheim Formation which continue to rise until the initial subpeak in the Bon Well Hill Submember (Aucoin, 2021).

The detection of correlative positive $\delta^{18}O$ excursions in both Baltoscandian and Laurentian strata suggest a period of global cooling, potentially linked to the Taconic orogeny and increased silicate weathering, which may have been responsible for a glacioeustatic regression which produced the Mid-Richmondian Unconformity (Brett et al., 2015) and potentially correlative unconformities in the Slandrom Limestone and Saunja Formations of Sweden and Estonia (Aucoin, 2021). This possibility is further supported by recent evidence that icehouse conditions were not limited to the Hirnantian (Trotter et al., 2008; Finnegan et al., 2011; Rasmussen et al., 2016) and Quaternary scale ice sheets may have been in place as early as the Darriwilian (Rasmussen et al., 2016).

Additional data from Laurentia further suggest that glacioeustacy exerted strong controls on water depth in shelf settings during Waynesville time. Elrick et al. (2013) collected $\delta^{18}O_{phos}$ data from conodonts in the Vauréal Formation at Anticosti Island and observed variations consistent with glacioeustatic sea level fluctuation. Within the Vauréal Formation, they report 2-6m subtidal cycles believed to be 40-100 k.y. in duration within larger 400 k.y. glacioeustatic sequences. The stratigraphic framework they employed indicates that the upper Vauréal Formation is correlative to the lithostratigraphic Bull Fork Formation in the Cincinnati Arch. This lithostratigraphic formation is of little to no use in high resolution correlation as it is up to 200 feet thick (Peck, 1966) but it does contain the entire Waynesville Formation which indicates that the data collected by Elrick et al. (2013) support glacioeustatic sea level change during Waynesville time. Ghienne et al. (2014) also studied the Vauréal Formation at Anticosti Island and place it within the first of three glacial cycles they propose for the Late Ordovician.

However, despite considerable evidence for glaciation as well as temperature and sea level fluctuation during the study interval, none of the available data are of sufficient resolution to determine precisely how temperature and/or glacial ice volume varied during Waynesville time. High resolution chemostratigraphy will need to be applied in the Waynesville Formations type area to determine how sea level changed throughout the study interval and how that may have influenced propagule pressure and the spread of the Clarksville Invaders.

Changes in Biodiversity: Richness and Evenness

The Clarksville Phase of the Richmondian Invasion increased alpha diversity within the Cincinnati Basin (Fig. 13), with generic richness increasing approximately 10% - 30% from the preinvasion to post-invasion interval. This increase in alpha diversity occurred because native taxa were not driven to extinction following the introduction of the Clarksville invaders, resulting in an increase in the number of genera present in the basin. A pattern of increasing generic richness similar to that observed following the Clarksville Phase has been documented by past studies which looked at the entire Richmondian Invasion. One such study concluded that generic richness within the Cincinnati Basin was increased by nearly 40% following the Richmondian Invasion (Holland and Patzkowsky, 2007; Patzkowsky and Holland, 2007). This indicates that as much as 25%- 75% of the increase in alpha diversity observed following the Richmondian Invasion may be attributable to the Clarksville Phase.

However, not all biotic invasions in the Type Cincinnatian caused an increase in alpha diversity, some acted to reduce alpha diversity, and some caused fleeting increases with no long-term impact. The isolated invasions (sensu Stigall, 2019) of the C4 sequence caused the extinction of native specialist taxa (Stigall, 2010) and the invaders did not persist, each appearing in a single horizon and disappearing for the remainder of the sequence (Foerste, 1912; Patzkowsky and Holland, 2007). The extinction of native specialists and the subsequent disappearance of the invaders resulted in a net reduction of alpha diversity within the basin. The ephemeral invasions (sensu Stigall, 2019) of the C1 sequence did not cause any documented extinctions and the invaders persisted in the basin for only a brief interval, resulting in net zero change in alpha diversity (Stigall and Fine, 2019; Harris et al., 2019; Brett et al., 2020).

Although native taxa were not driven to extinction following the Clarksville Phase, they were not unaffected by the invaders. The Clarksville Phased induced competition for resources (space, food, etc.) between the novel and incumbent taxa and invaders became dominant components of deep-water communities (e.g., *Eochonetes*), resulting in a decrease in generic evenness within the basin (Fig. 14). The native fauna then progressively accommodated the Clarksville invaders through a combination of niche contraction and character displacement. This response acted to minimize niche overlap between incumbents and invaders and reduced competition between them, allowing for the moderate rebound in evenness observed in the post-invasion interval.

This interpretation is supported by past studies of the Richmondian Invasion which indicate competitive interactions were an important factor in Type Cincinnatian brachiopod assemblages (Tyler and Leighton, 2011), novel and incumbent taxa underwent character displacement due to competitive interactions (Tyler and Leighton, 2011), and niche evolution occurred in both novel and incumbent taxa following the invasion (Malizia and Stigall, 2011; Brame and Stigall, 2014). Competition between invaders and incumbents is also consistent with studies analyzing modern invasions which suggest that competition is the main mechanism of invader impact on the recipient biota when both novel and incumbent taxa occupy the same trophic level (Levine et al., 2003; Bradley et al., 2019). This interpretation gains support from ecological theory as well. Root (1967) states that interspecific competition has obvious deleterious effects and natural selection will favor divergence which reduces interspecific competition (character displacement minimizing niche overlap). However, despite being supported by empirical studies and ecological theory, ecological niche modeling and comparative morphometrics will need to be conducted at the submember level to test this hypothesis.

The competition induced fluctuations in evenness observed following the Clarksville Phase contrast with the results of past studies which analyzed the entire Richmondian Invasion and found that evenness changed little between time intervals (Patzkowsky and Holland, 2007). The stratigraphic framework employed in the previous study consisted of third order depositional sequences representing approximately one million years each (Patzkowsky and Holland, 2007), making the temporal duration of their study interval approximately 4,000,000 years. The stratigraphic framework employed in this study consists of fourth order depositional sequences representing 200,000-500,000 years each (Aucoin and Brett, 2016; Schwalbach, 2017). Considering the Waynesville Formation in its entirety represents approximately 1,000,000 years (Aucoin, 2021), the interval considered in this study represents at most 400,000-500,000 years. The contrasting results of the present study and that of Patzkowsky and Holland (2007) are attributed to the large difference in temporal resolution between studies, with the changes in evenness observed in this study being indiscernible at coarser temporal scales.

Stability of Habitat Preferences

Environmental Tolerance and Preferred Environment

The stability of taxa's environmental tolerance generally increased through time. Between the Bon Well Hill and Harper's Run Submembers shifts in environmental tolerances were recovered among abundant taxa (Fig. 15). This modification of environmental tolerance was induced by the introduction and establishment of invaders into deep subtidal environments at the top of the Harpers Run. Previous studies which analyzed the entire Richmondian Invasion via ecological niche modeling (Malizia and Stigall, 2011; Brame and Stigall, 2014) have recovered similar patterns in which the arrival of invaders induced elevated rates of niche evolution. The transition from the Harpers Run to Stony Hollow Creek Submember indicates that restructuring of environmental tolerances continued but was not as substantial as it was between the pre-invasion and invasion intervals (Fig.15), indicating that community accommodation of invaders was ongoing but beginning to decrease during this transition. The transition from the Stony Hollow Creek to Middle Clarksville Submember records considerable evidence for conservation of environmental tolerances between these intervals (Fig 15). This pattern of initially intense then progressively decreasing amounts of restructuring of environmental tolerances is indicative of ongoing community accommodation of the invaders via niche evolution.

The stability of taxa's preferred environment showed a similar pattern to environmental tolerance and generally increased through time following the invasion

(Fig. 16). There is marked restructuring between the Bon Well Hill and Harpers Run which is again due to modification of taxa's preferred environment as communities accommodated the invaders (Fig. 16). There is also considerable restructuring between the Harpers Run and Stony Hollow Creek although less than between the previous intervals (Fig.16). The decrease in restructuring is due to progressively more complete community accommodation of invaders. The amount of restructuring between the Stony Hollow Creek and Middle Clarksville is comparable to that between the Harpers Run and Stony Hollow Creek (Fig. 16). This is sensible considering an appreciable amount of time had elapsed since establishment of the connection to the donor basins and restructuring of taxa's preferred environment in response to the biotic and abiotic changes that accompanied the increase in basin connectivity was largely complete.

Studies of modern invasions have documented similar patterns in which alteration of the habitat occupied by native taxa acts as a mechanism for accommodating invaders. For example, Spanier and Galil (1991) documented shifts in the depth occupied by native Mediterranean red mullet and hake following the introduction of the goldband goatfish and brushtooth lizardfish. Furthermore, Borden et al. (2021) documented an increase in the range of habitats occupied by native green anoles in response to the presence of invasive brown anoles. Together, studies of modern invasions, past studies of the Richmondian Invasion, and this study of the Clarksville Phase suggest that alteration of the habitat occupied by native taxa is a common mechanism by which novel taxa are accommodated.

Implications for Modern Invasions

The Clarksville Phase has important implications for the study of modern biotic invasions as it contributes to answering questions regarding what factors influence invader success as well as how biodiversity and community structure change following biotic invasions.

Ecological theory predicts that incumbent taxa should most strongly inhibit invaders from their own guild (Root, 1967; MacArthur and Levins, 1967; Fargione et al., 2003). This prediction has not been empirically tested for animals and studies of plants have yielded mixed results with some supporting this prediction (Ordonez et al., 2010) and some indicating guild membership plays a limited role (Price and Pärtel, 2013). The Clarksville Phase provides an opportunity to test this prediction for animal invasions and patterns of invader establishment and proliferation following the Clarksville Phase support this notion. The invaders that became most abundant following the Clarksville Phase were brachiopods in the low tier unattached epifaunal passive suspension feeder guild (*Strophomena*, *Eochonetes, Leptaena, Tetraphalerella*) and corals in the stationary epifaunal passive predator guild (*Grewingkia*). Conversely, brachiopod invaders from the low tier attached epifaunal passive suspension feeder guild (*Hiscobeccus*, *Holtedahlina*) remained comparatively rare. During the pre-invasion interval the low tier unattached epifaunal passive suspension feeder guild was represented by only two taxa (*Rafinesquina* and *Tentaculites*) and the stationary epifaunal passive predator guild was represented only by the colonial rugosan *Cyathophylloides* (Brett et al., 2020) (not detected in this study). Conversely, the low tier attached epifaunal suspension feeder guild was represented by eleven taxa in the pre-invasion interval. In summary, the invaders which were initially most successful occupied ecospace that was underutilized by the pre-invasion community; whereas those that were initially less successful occupied ecospace that was heavily utilized by the preinvasion community. This suggests that patterns of ecospace utilization in pre-invasion communities played a role in determining the initial success and abundance of invaders.

Data from modern species invasions indicate that alpha diversity often increases following regional scale biotic invasions (Sax and Gaines, 2003; Briggs, 2007) and that despite the vast number of biotic invasions documented in modern systems there are very few instances in which extinctions of native species can be attributed to competition from novel species (Davis, 2003). For example, over 250 species have been introduced to the Mediterranean Sea from the Red Sea, but only one extinction has been documented (Por, 1978). The result is a considerable increase in species richness in the Mediterranean Sea (Por, 1978). However, questions remain such as whether these increases are transient and if there is an extinction debt that is yet to be paid (Sax and Gaines, 2003). In the case of the Clarksville Phase, the increase in alpha diversity was not transient and no native taxa were lost following the invasion, indicating a lack of extinction debt. The lack of extinction following the Clarksville Phase is attributed to the loss of native specialists in the C4 sequence (Stigall, 2010), which are most vulnerable to competition from invaders (Rhode and Lieberman, 2004; Colles et al., 2009; Stigall, 2012; Morris et al., 2021; and many others) and the low trophic level of the Clarksville invaders. It has been observed in modern systems that extinctions of native taxa occur most frequently following the introduction of novel predators and pathogens (Davis, 2003) and that invaders at higher trophic levels have the strongest effects on native communities (Moyle and Light, 1996;

Howeth et al., 2015). Had the Clarksville invaders occupied a higher trophic level, or the Cincinnati basin hosted many specialist taxa at the time of the invasion, extinction of native taxa would have been more probable.

Studies of recent biotic invasions have also documented breakdown of preinvasion community structure following the introduction of novel taxa and as a result invasive species are considered a threat to ecosystem function worldwide (Sanders et al., 2003). However, these studies have been conducted over short intervals (less than a decade) and questions remain regarding how community structure changes on longer timescales. Following their introduction, the Clarksville invaders competed with the incumbent taxa for resources (food, space, etc.) and became dominant taxa in deeper water communities. As a result of these competitive interactions, generic evenness within the basin decreased. Communities accommodated the invaders over time through niche evolution and a modest rebound in generic evenness occurred in the post-invasion interval as niche overlap was minimized. However, pre-invasion levels of evenness were not attained again during the study interval and invaders remained abundant. These findings indicate that even those biotic invasions that do not result in extinctions can have impacts on community structure which persist far beyond human timescales.

In summary, the Clarksville Phase of the Richmondian Invasion indicates that biotic invasions where invader taxa occupy a low trophic level, and the recipient system contains few ecological specialists result in lasting increases in alpha diversity. Furthermore, such invasions are unlikely to cause extinction of native taxa, impacts on community structure are not transient and can last far beyond human timescales, and invaders may be more likely to proliferate if they occupy ecospace that is underutilized by the recipient biota. These findings have important implications for the allocation of conservation resources and long-term conservation planning. They suggest that biotic invasions where the recipient region contains many ecological specialists and/or the invaders include novel predators or pathogens should be prioritized to mitigate extinction, invaders that occupy ecospace underutilized by the recipient biota may be more likely to proliferate rapidly and may need to be assigned higher priority for extirpation, and the impacts of invaders on community structure can last far beyond human timescales and intervention is required if a return to near pre-invasion community structure is desired.

Chapter 6: Conclusions

Conclusions

The Clarksville Phase of the Richmondian Invasion impacted the fauna of the Cincinnati Basin in various ways including measurable changes in biodiversity, community structure, ecospace utilization, gradient structure, and the environmental preferences/tolerances of taxa. It also serves as a case study for analyzing the long-term impacts of biotic invasions and has important implications for management of modern biotic invasions

1. The Clarksville Phase introduced numerous invaders into the Cincinnati basin from adjacent basins, increasing generic richness within the basin by at least 25% and potentially as much as 75%. This increase in richness was not transient, with generic richness remaining elevated in the post-invasion interval. This increase in richness occurred because native taxa were not driven to extinction following the invasion, which increased the number of genera present in the basin. The lack of extinction is attributed to the loss of native specialists in the earlier C4 sequence and to the low trophic level of the invaders.
2. Community structure was altered by the Clarksville Phase, with generic evenness decreasing throughout the invasion interval due to competition between novel and incumbent taxa. Communities then progressively accommodated the invaders through niche evolution which minimized niche overlap between novel and incumbent taxa and allowed for a moderate rebounding toward pre-invasion evenness levels in the post-invasion interval.

However, evenness never again reached pre-invasion levels during the study interval which demonstrates that changes to community structure caused by biotic invasions can persist far beyond human timescales.

3. Ecospace utilization varied both spatially and temporally throughout the study interval. The prevalence of low tier unattached epifaunal passive suspension feeders and stationary epifaunal passive predators increased following the Clarksville Phase. However, not all observed variations in ecospace utilization could be attributed to the invasion. Low tier unattached epifaunal suspension feeders are more prominent components of communities during highstand to falling stage systems tracts than in transgressive systems tracts due to the increase in water depths. Ecospace utilization also varied along the onshore-offshore gradient. Ecospace utilization was very limited in shoal settings which were dominated by low tier epifaunal passive suspension feeders. In shallow subtidal environments ecospace utilization was more variable with low and mid-tier epifaunal passive suspension feeders being dominant. In deep subtidal and offshore settings, low and mid-tier attached epifaunal passive suspension feeders still make up large portions of communities but low tier unattached epifaunal passive suspension feeders increase in abundance in these deeper water settings.
4. Faunal differentiation across the depth gradient increased following the Clarksville Phase, with invasion and post invasion communities demonstrating clearer separation along DCA axis one than pre-invasion communities. This increase in faunal differentiation across the depth gradient

is attributed to the higher prevalence of invaders in deeper environments making shallow water and deep-water communities more distinct than in the pre-invasion interval.

5. The environmental preferences and tolerances of taxa were modified following the introduction of the Clarksville invaders. Modification of both parameters was most intense following the initial introduction of the invaders and then slowed as community accommodation of invaders became progressively more complete. Modification of occupied habitat following the introduction of invaders has been documented by past studies of the Richmondian Invasion and studies of modern biotic invasions. Suggesting that the pattern of increased restructuring of occupied habitat observed following the Clarksville Phase may be a common mechanism through which incumbent taxa accommodate invaders.
6. Clarksville type biotic invasions in which the recipient region contains few ecological specialists, and the invaders occupy a low trophic level are unlikely to cause extinction of incumbent taxa. Therefore, biotic invasions in which the recipient region contains many ecological specialists and/or the invaders include novel predators and pathogens should be prioritized for intervention by managers.
7. The invaders that were initially most successful following the Clarksville Phase (low tier unattached epifaunal passive suspension feeders and stationary epifaunal passive predators) occupied ecospace that was underutilized by the pre-invasion community. Conversely, those that were initially less successful

occupied ecospace which was heavily utilized by the preinvasion community (low tier attached epifaunal passive suspension feeders). This suggests that patterns of ecospace utilization in pre-invasion communities played a role in determining the initial success and abundance of invaders. This pattern indicates that invaders which occupy ecospace that is unutilized or underutilized by the recipient biota may establish and proliferate more rapidly and should be priority targets for eradication.

Recommendations for Future Work

1. The detection of taxa within the study interval by previous authors (e.g., *Streptelasma rusticum* (Aucoin and Brett, 2016), *Cyathophylloides stellata* (Brett et al., 2020) and their non-detection in this study exemplifies the need for future studies to explicitly model sampling as a part of data collection procedures to ensure all taxa present are detected. Incorporating occupancy modeling as a part of sampling procedures in future studies of the Clarksville Phase is recommended as a solution to this issue. Such an approach will allow for sampling probabilities to be determined for each taxon and an appropriate number of samples to be collected to ensure 95% confidence that the rarest taxon in the dataset has been detected given that it is truly present.
2. High resolution isotopic oxygen data from the Waynesville Formation are required to constrain how fluctuations in temperature and glacial ice volume may have impacted sea level and by extension the Clarksville Phase of the Richmondian Invasion. A bed-by-bed study in which $\delta^{18}O_{phos}$ data are collected from conodont elements, $\delta^{18}O_{Carb}$ data are collected from the

secondary layer fibers of brachiopods, and $\delta^{18}O_{Carb}$ data are collected from bulk carbonate is recommended. Apatite from conodont elements and calcite from the secondary later fibers of brachiopods have been posited to be more faithful recorders of environmental conditions than bulk carbonate due to lower potential for diagenetic alteration. Collecting data from all three of these sources will allow for high confidence in recovered patterns and will allow for a direct test of the degree to which diagenesis has altered the isotopic composition of Type Cincinnatian carbonates.

3. Future studies should sample additional sites on the western side of the Cincinnati Arch should be conducted to further test the fidelity of these patterns, expand studies of the Clarksville Phase to other parts of the Cincinnati Arch, and improve the resolution of bathymetric maps of the Cincinnati Basin.

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Appendix I: Raw Data

Raw species occurrence data collected from field work. The first two letters of the sample code indicate the site and correspond to the two letter abbreviations in Table 1. The letters after the dash indicate Submember (BWH= Bon Well Hill, HR= Harpers Run, SH= Stony Hollow Creek, and MC= Middle Clarksville). The number indicates relative stratigraphic position of the sample within the Submember with (1) being the stratigraphically lowest sample collected from that Submember at that site. Note that the *Strophomena* specimens from site AA are *Strophomena concordensis* and not the invader *Strophomena planumbona*.

	HF-BWH2	**HF-HR4**	**HF-HR1**	**HF-BWH3**	**CC-SH1**	**CC-SH2**	**CC-MC1**	**CC-BWH1**
Sample Area cm^2	100	100	400	300	1200	300	1200	400
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	1	0	0	2	0	1	14	0
Xenocrinus	0	0	0	2	0	0	2	0
Iocrinus	0	0	0	0	0	1	0	0
Hebertella	0.5	0	0	0	0	0	0	0
Cincinnetina	0	0	1	4	143	19	104.5	0
Thin Ramose	19.687	40.271	8.893	23.557	110.029	51.52	151.213	12.094
Thin Bifoliate	0	0	2.017	0	16.547	3.979	8.48	0.904
Tentaculites	1	0	1	3	19	1	42	9
Zygospira	3.5	2	1	0	2.5	1	21.5	0.5
Thick Ramose	1.965	0	0	0	21.824	0.865	7.185	0
Vinlandostrophia	0	0	1	0.5	0.5	0	0	1
Rafinesquina	0	0	1.5	0	2	1	0	3.5
Grewingkia	0	0	0	0	0	0	1	0
Encrusting	0	0	0	0	0	0.71	25.56	0.46
Petrocrania	0	0	0	0	0	0	2	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0	0	0	0	0.5	22	0
Anomalodonta	0	0	0	0	0	0	0	0.5
Flexicalymene	0	0	0	0	4	0	6	0
Massive	0	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	1	0
Eochonetes	0	0	0	0	11.5	4	0	0
Liospira	0	0	0	0	0	1	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	1	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	CC-BWH2	**CC-BWH3**	**CC-BWH4**	**SR-SH1**	**SR-SH2**	**SR-SH3**	**SR-SH5**	**SR-SH4**
Sample Area cm^2	200	100	500	400	600	200	200	100
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	0	0	0	0	2	2	0
Xenocrinus	0	0	1	0	0	1	0	0
Iocrinus	0	0	1	0	0	0	0	0
Hebertella	0	0	0	0	0	0	0	0
Cincinnetina	3	0.5	11	41.5	116	4	1	2
Thin Ramose	28.951	17.534	165.104	23.144	16.198	20.25	14.035	9.738
Thin Bifoliate	2.963	0	1.928	0	10.878	0	0	0
Tentaculites	4	1	16	3	8	10	0	0
Zygospira	8.5	4.5	16	6	0.5	1	0	0.5
Thick Ramose	0	0	0	0	0	2.31	8.951	0.944
Vinlandostrophia	3.5	1	2.5	0	0	1.5	0.5	1
Rafinesquina	0	0	1.5	0	0	0	0	0
Grewingkia	0	0	0	0	0	0	1	0
Encrusting	0	0	2.728	0	0	0	0	0
Petrocrania	0	0	8	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0	0	0	0	0	0	0
Anomalodonta	0	0	0.5	0	0	0	0	0
Flexicalymene	0	0	36	0	0	4	0	0
Massive	2.689	0	1.594	0	3	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	14.5	17.5	0	3.5	0.5
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	SR-MC2	**SR-MC3**	**DG-MC1**	**MB-MC1**	**MB-MC3**	**MB-MC2**	**MB-MC4**	**AL-BWH2**
Sample Area cm^2	1000	200	100	400	1700	100	300	400
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	15	0	0	1	4	0	0	1
Xenocrinus	1	0	0	3	3	0	0	0
Iocrinus	2	0	0	0	0	0	0	0
Hebertella	0	0	1.5	1	3	1	0.5	0.5
Cincinnetina	35.5	5	0	3.5	31.5	0	4	0
Thin Ramose	316.13	48.796	0.208	26.5363	79.776	1.546	17.574	2.847
Thin Bifoliate	13.443	0	0	2.027	13.132	0.72	2.992	0
Tentaculites	30	0	0	34	25	0	5	0
Zygospira	4.5	1	0	0	6.5	0.5	1	0
Thick Ramose	1.93	20.396	0	0	0	0	0	0
Vinlandostrophia	0	0	0	1.5	7.5	1	0.5	1
Rafinesquina	0	0	0	0	3	1	0.5	0
Grewingkia	1	0	0	1	0	1	0	0
Encrusting	1.667	0.69	2.603	2.634	13.195	3.591	5.783	0
Petrocrania	0.5	0	0	1.5	0	0	0	0
Leptaena	0	0	0	0	2.5	0	0	0
Strophomena	3	0	0	7.5	21.5	0	4.5	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	1	0	0	0
Massive	1.22	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	1	0	0	0.5	0	0	0
Liospira	1	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0.5	0	0	0
Holopea	0	0	0	0	1	0	0	0
Caritodens	0	0	0.5	0.5	0.5	0	0	0
Cornulites	0	0	0	0	1	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0.5	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	AL-BWH3	**AL-BWH4**	**AL-BWH6**	**AL-SH2**	**AL-SH3**	**AL-MC1**	**AL-MC2**	**FB-BWH2**
Sample Area cm^2	100	100	100	100	100	100	100	200
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	0	1	1	0	1	0	0
Xenocrinus	1	0	0	1	0	2	1	0
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	1	0	0.5	1.5	0.5	0	0	0.5
Cincinnetina	0	0	0	0	0	0	0	3.5
Thin Ramose	41.2	43.988	36.74	14.9	12.93	18.39	6.736	11.34
Thin Bifoliate	0	0.0262	0	18.75	0	0	3.69	3.39
Tentaculites	0	0	0	0	0	0	0	0
Zygospira	1	0	0	0	0	0.5	0	1.5
Thick Ramose	0	2.598	0	0	0	0	0	3.55
Vinlandostrophia	0.5	0.5	0	0	0	0	0	2
Rafinesquina	0	0	0	0	0	0	0	0
Grewingkia	0	0	0	0	0	0	0	0
Encrusting	0	0	0	0	0	0	0	0.99
Petrocrania	0	0	0	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0	0	0	0	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	0	0	0	0
Massive	0	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	0	0	0	0	0
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0.5	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	3	2	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	FB-BWH3	**FB-HR1**	**FB-HR2**	**FB-HR3**	**DO-BWH1**	**DO-BWH2**	**DO-BWH3**	**DO-BWH4**
Sample Area cm^2	200	100	100	400	100	100	300	800
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	0	0	5	1	0	0	0
Xenocrinus	0	0	0	0	0	1	0	3
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0	0.5	0.5	0.5	0	0	0	0
Cincinnetina	2.5	0	0	0	0	0	0.5	0.5
Thin Ramose	6.97	2.49	6.97	30.663	4.602	8.885	27.502	29.041
Thin Bifoliate	3.601	0	4.96	9.52	0.994	0.536	6.987	3.155
Tentaculites	0	0	0	0	1	0	0	3
Zygospira	3.5	0	0.5	0.5	0	0	0	1
Thick Ramose	8.38	9.73	2.21	8.604	1.352	0	12.886	18.584
Vinlandostrophia	1	0.5	1	3	0	0	0	0
Rafinesquina	0	0	0	0	0	0	1	0
Grewingkia	0	0	0	0	0	0	0	0
Encrusting	0	0	0.962	0.509	0	0	0	0
Petrocrania	0	0	0	0	0	0	0	0
Leptaena	0	0	0	0.5	0	0	0	0
Strophomena	0	0	0	0	0	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	0	0	2	13
Massive	0	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	0	0	0	0	0
Liospira	0	0	0	0	0	0	0	4
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0.5
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	DO-HR1	**DO-HR2**	**DO-HR3**	**DO-HR4**	**DO-SH1**	**DO-SH2**	**DO-SH3**	**DO-MC1**
Sample Area cm^2	900	400	600	400	300	200	300	900
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	8	1	3	0	0	2	2	5
Xenocrinus	3	0	0	0	0	1	1	2
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0	0	0	0	0	0	0	1
Cincinnetina	24.5	4.5	15.5	13.5	2.5	3	5.5	24
Thin Ramose	284.768	6.35	3.8271	0.864	0	11.796	10.819	62.341
Thin Bifoliate	0	0	0	0.744	0	1.239	0.454	8.404
Tentaculites	107	0	0	0	0	0	5	30
Zygospira	1.5	0	6	0.5	0	2.5	1	5.5
Thick Ramose	12.332	0	0	0	0	0	0	0
Vinlandostrophia	0	0.5	0	0	0	0	0	0
Rafinesquina	0	0	0	0.5	1	0	0.5	0
Grewingkia	0	0	4	9	0	0	1	0
Encrusting	0.544	0.694	0.534	0	0	2.829	0	24.618
Petrocrania	0.5	0	0	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	1.5	0	0.5	0	1.5	1.5	24
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	1	0	0	0	0	0	0	0
Massive	4.512	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	1	0
Eochonetes	0	19.5	20.5	9	4.5	1	0	18.5
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0.5	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0.5	0	0	0	0	0	0	0
Cornulites	1	0	0	1	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	3.5
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0.5	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0.5	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	AA-SH1	AA-HR2	AA-HR1	AA-MC1	SR-MC1	SR-SH6	HF-BWH1	HF-HR2
Sample Area cm^2	200	100	100	100	300	100	200	100
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	2	0	0	0	4	1	2	1
Xenocrinus	5	0	0	0	0	0	2	0
Iocrinus	0	0	0	0	1	0	1	0
Hebertella	0	0	0	0.5	0	0	0.5	0
Cincinnetina	0	1.5	5	0	0	8	0.5	0
Thin Ramose	26.68	2.931	3.065	16.935	59.577	14.836	8.222	37.84
Thin Bifoliate	0	0	0	0	0	0	0.937	0
Tentaculites	2	0	0	0	7	0	1	5
Zygospira	6	0	2	0	5.5	0	2	4
Thick Ramose	0	0	0	0	1.344	0	1.322	0
Vinlandostrophia	0	0	0	1	0	0	0	0
Rafinesquina	0	0	1	0.5	0	0	0	0
Grewingkia	0	0	0	0	0	0	0	0
Encrusting	0.751	4.032	6.812	1.412	0	0	0	0.86
Petrocrania	0	0	0	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	2.5	0	0	6.5	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	5	0	1	0	0	0	0	0
Massive	0	0	0	0	0	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	0	0	2.5	0	0
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	1	0	0	0	0
Cyclonema	1	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	1	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	HF-HR3	**HF-SH1**	**HF-SH3**	**HF-SH2**	**BW-BWH1**	**BW-SH1**	**BW-BWH2**	**BW-BWH3**
Sample Area cm^2	100	300	200	100	100	1500	1200	500
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	1	2	1	1	1	0	0
Xenocrinus	1	1	3	0	0	0	0	0
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0	1	0.5	0	0	0	0	0
Cincinnetina	8	23	8.5	2.5	1	13	28.5	1
Thin Ramose	6.09	11.39	24.97	3.75	34.37	151.192	179.821	37.899
Thin Bifoliate	0	0	0	0	0	25.502	0	0
Tentaculites	0	0	5	0	3	0	24	11
Zygospira	4.5	0	0	0	0.5	1	8.5	0.5
Thick Ramose	0	0	0.118	0	2.2	25.028	16.747	0
Vinlandostrophia	0	0	1	0	0	4	16.5	2.5
Rafinesquina	0	0	0	0	0	12	5.5	2.5
Grewingkia	0	0	0	0	0	3	0	0
Encrusting	0.58	9.79	0.2	0.4	1.36	20.57	4.465	0
Petrocrania	0.5	0	0	0	0	1.5	0	0
Leptaena	0	0	0	0	0	1.5	0	0
Strophomena	0	0.5	0	0	0	0	0	0
Anomalodonta	0	0	0	0	0	0.5	0	0
Flexicalymene	0	0	0	0	0	0	4	0
Massive	0	0	0	0	0	0	0	2.776
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	3.5	3	5.5	0	0	0	0
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	2	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	1.5	0	0	0	0

	BW-BWH4	**DG-SH1**	**DG-SH2**	**DG-MC2**	**DG-MC3**	**SG-BWH1**	**SG-BWH2**	**SG-BWH3**
Sample Area cm^2	500	400	2200	700	1800	600	600	900
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	0	0	0	0	41	12	13
Xenocrinus	0	0	0	0	0	5	1	2
Iocrinus	0	0	0	0	0	3	1	0
Hebertella	0.5	0.5	17	14.5	17	0	0	0
Cincinnetina	2.5	0	0	0	0	18.5	29.5	47.5
Thin Ramose	78.744	1.563	53.07	14.927	29.6	50.95	174.992	228.655
Thin Bifoliate	0	5.351	0	0	9.231	0	5.959	0
Tentaculites	4	0	0	0	0	1	0	10
Zygospira	0	0	0	0	0	1.5	11	12.5
Thick Ramose	68.407	0	4.147	0	0	0	0	1.88
Vinlandostrophia	5.5	0	0	0	1	0	0	0
Rafinesquina	1	0	0	0	0	0	1	1
Grewingkia	0	0	0	0	0	0	0	0
Encrusting	0.96	0	10.96	1.736	20.806	0	0.632	3.906
Petrocrania	0	0	0.5	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0	0	0	0	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	0	0	0	0
Massive	0	15.782	115.06	3.82	64.4898	0	0	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	0	0	0	0	0
Liospira	0	0	0	0	0	0	0	0
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	3	3	1	5.5	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	14.192	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	SG-SH1	SG-SH2	SG-SH3	AL-MC3	AL-BWH1	AL-BWH5	AL-SH1	AL-SH4
Sample Area cm^2	600	500	1500	1700	2000	400	1100	500
Plicodendrocrinus	0	0	0	0	0	0	0	2
Glyptocrinus	0	0	0	3	0	0	6	4
Cincinnaticrinus	2	3	6	1	0	1	1	0
Xenocrinus	1	0	2	5	0	0	28	10
Iocrinus	0	0	0	0	0	0	0	1
Hebertella	0	0	0	16	9	5	29.5	18.5
Cincinnetina	30.5	3	21.5	10.5	0	0	0	0
	134.53	127.70	331.10	168.7	141.97	116.4	329.83	118.4
Thin Ramose	4	6	6	9	9	9	4	4
Thin Bifoliate	5.8785	0	9.495	0	0	3.05	0	0
Tentaculites	0	1	1	14	0	0	22	0
Zygospira	0.5	0	3.5	1.5	0.5	1	10	1
Thick Ramose	7.942	7.38	13.885	8.73	16.24	9.95	3.29	6
Vinlandostrophia	0.5	1.5	6.5	1.5	24.5	1.5	0	0
Rafinesquina	0.5	0	5.5	0	0	0	0	0
Grewingkia	0	0	0	2	0	0	0	0
Encrusting	2.848	1.138	6.417	13.97	3.87	2.02	2.21	6.29
Petrocrania	0	0.5	0	0	0	0	0	0
Leptaena	2.5	1	2.5	0	0	0	0	0
Strophomena	0	0	0	10	0	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	1	0	4	3	0	0	2	0
Massive	0	0	0	0	0	0	1.23	0
Isotelus	0	0	0	0	0	0	0	0
Eochonetes	0	0	0	65	0	0	0	0
Liospira	0	0	0	0	0	0	1	1
Modiolopsis	0	0	0	0	0	0	0	0
Holopea	0	0	0	0	0	0	0	0
Caritodens	0	0	0	1.5	1.5	0	0.5	0.5
Cornulites	0	0	0	3	0	0	0	2
Hiscobeccus	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	4	1
Cyclonema	0	0	0	0	0	0	2	0
Tetraphalerella	0	0	0	0	0	0	0	0
Tetradium	0	0	0	0	0	0	0	0
Ambonychia	0	0	0	0	0	0	0	0
Holtedahlina	0	0	0	0	0	0	0	0

	AL-SH5	**AL-SH6**	**FB-BWH1**	**FB-SH1**
Sample Area cm^2	500	700	1400	6300
Plicodendrocrinus	3	3	0	0
Glyptocrinus	3	1	0	31
Cincinnaticrinus	0	1	0	30
Xenocrinus	9	7	0	1
Iocrinus	3	1	0	0
Hebertella	19	18	1	27.5
Cincinnetina	0	0	28.5	0
Thin Ramose	82.69	84.85	50.87	618.224
Thin Bifoliate	0	0	6.495	30.666
Tentaculites	0	0	0	0
Zygospira	1.5	28	3	21
Thick Ramose	1.17	0.66	3.42	275.39
Vinlandostrophia	0	0	9	5
Rafinesquina	0	0	3.5	32.5
Grewingkia	0	0	0	0
Encrusting	2.84	3.02	9.779	24.504
Petrocrania	0	0	0	0
Leptaena	0	0	0	28
Strophomena	0	0	0	0
Anomalodonta	0	0	0	0
Flexicalymene	2	0	0	4
Massive	1.77	0	0	1.62
Isotelus	0	0	0	0
Eochonetes	0	0	0	0
Liospira	1	0	0	0
Modiolopsis	0	0	0	0
Holopea	0	0	0	0
Caritodens	0	0	1	5.5
Cornulites	0	0	0	1
Hiscobeccus	0	0	0	0
Paupospira	0	0	0	1
Cyclonema	0	0	0	18
Tetraphalerella	0	0	0	0
Tetradium	0	0	0	0
Ambonychia	0	0	0	0
Holtedahlina	0	0	0	0

Appendix II: Bon Well Hill Submember Data

Final dataset from Bon Well Hill Submember after processing as described in the Methods. The first two letters of the sample code indicate the site and correspond to the two letter site codes in Table 1. The second two letters (BW) indicate the sample is from the Bon Well Hill Submember. The number indicates relative stratigraphic position of the sample within the Submember with (1) being the stratigraphically lowest sample collected from the Bon Well Hill Submember at that site. The final letter indicates depositional environment (O= offshore, D= deep subtidal, S= shallow subtidal, s= shoal).

	HFBW2O	**HFBW3O**	**CCBW1O**	**CCBW2O**	**CCBW3O**	**CCBW4O**	**ALBW2S**	**ALBW3S**
Cincinnaticrinus	1	2	0	0	0	0	1	0
Xenocrinus	0	2	0	0	0	1	0	1
Iocrinus	0	0	0	0	0	1	0	0
Hebertella	0.5	0	0	0	0	0	0.5	1
Cincinnetina	0	4	0	3	0.5	11	0	0
Thin Ramose	1.9687	2.3557	1.2094	2.8951	1.7534	16.5104	0.2847	4.12
Thin Bifoliate	0	0	0.0904	0.2963	0	0.1928	0	0
Tentaculites	1	3	9	4	1	16	0	0
Zygospira	3.5	0	0.5	8.5	4.5	16	0	1
Thick Ramose	0.1965	0	0	0	0	0	0	0
Vinlandostrophia	0	0.5	1	3.5	1	2.5	1	0.5
Rafinesquina	0	0	3.5	0	0	1.5	0	0
Encrusting	0	0	0.46	0	0	2.728	0	0
Anomalodonta	0	0	0.5	0	0	0.5	0	0
Flexicalymene	0	0	0	0	0	19	0	0
Massive	0	0	0	2.689	0	1.594	0	0
Caritodens	0	0	0	0	0	0	0	0

	ALBW4S	**ALBW6S**	**FBBW2S**	**FBBW3S**	**DOBW1D**	**DOBW2D**	**DOBW3D**	**DOBW4D**
Cincinnaticrinus	0	1	0	0	1	0	0	0
Xenocrinus	0	0	0	0	0	1	0	3
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0	0.5	0.5	0	0	0	0	0
Cincinnetina	0	0	3.5	2.5	0	0	0.5	0.5
Thin Ramose	4.3988	3.674	1.134	0.697	0.4602	0.8885	2.7502	2.9041
Thin Bifoliate	0.00262	0	0.339	0.3601	0.0994	0.0536	0.6987	0.3155
Tentaculites	0	0	0	0	1	0	0	3
Zygospira	0	0	1.5	3.5	0	0	0	1
Thick Ramose	0.2598	0	0.355	0.838	0.1352	0	1.2886	1.8584
Vinlandostrophia	0.5	0	2	1	0	0	0	0
Rafinesquina	0	0	0	0	0	0	1	0
Encrusting	0	0	0.99	0	0	0	0	0
Anomalodonta	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	0	0	1	12
Massive	0	0	0	0	0	0	0	0
Caritodens	0	0.5	0	0	0	0	0	0.5

	HFBW1O	**BWBW1O**	**BWBW2O**	**BWBW3O**	**BWBW4O**
Cincinnaticrinus	2	1	0	0	0
Xenocrinus	2	0	0	0	0
Iocrinus	1	0	0	0	0
Hebertella	0.5	0	0	0	0.5
Cincinnetina	0.5	1	28.5	1	2.5
Thin Ramose	0.8222	3.437	17.9821	3.7899	7.8744
Thin Bifoliate	0.0937	0	0	0	0
Tentaculites	1	3	24	11	4
Zygospira	2	0.5	8.5	0.5	0
Thick Ramose	0.1322	0.22	1.6747	0	6.8407
Vinlandostrophia	0	0	16.5	2.5	5.5
Rafinesquina	0	0	5.5	2.5	1
Encrusting	0	1.36	4.465	0	0.96
Anomalodonta	0	0	0	0	0
Flexicalymene	0	0	3	0	0
Massive	0	0	0	2.776	0
Caritodens	0	0	0	0	0

	SGBW1O	**SGBW2O**	**SGBW3O**	**ALBW1S**	**ALBW5S**	**FBBW1S**
Cincinnaticrinus	41	12	13	0	1	0
Xenocrinus	5	1	2	0	0	0
Iocrinus	3	1	0	0	0	0
Hebertella	0	0	0	9	5	1
Cincinnetina	18.5	29.5	47.5	0	0	28.5
Thin Ramose	5.095	17.4992	22.8655	14.1979	11.649	5.087
Thin Bifoliate	0	0.5959	0	0	0.305	0.6495
Tentaculites	1	0	10	0	0	0
Zygospira	1.5	11	12.5	0.5	1	3
Thick Ramose	0	0	0.188	1.624	0.995	0.342
Vinlandostrophia	0	0	0	24.5	1.5	9
Rafinesquina	0	1	1	0	0	3.5
Encrusting	0	0.632	3.906	3.87	2.02	9.779
Anomalodonta	0	0	0	0	0	0
Flexicalymene	0	0	0	0	0	0
Massive	0	0	0	0	0	0
Caritodens	0	0	0	1.5	0	1

Appendix III: Harpers Run Submember Data

Final dataset from Harpers Run Submember after processing as described in the Methods. The first two letters of the sample code indicate the site and correspond to the two letter site codes in Table 1. The second two letters (HR) indicate the sample is from the Harpers Run Submember. The number indicates relative stratigraphic position of the sample within the Submember with (1) being the stratigraphically lowest sample collected from the Harpers Run Submember at that site. The final letter indicates depositional environment (O= offshore, D= deep subtidal, S= shallow subtidal, s= shoal).

	HFHR4 O	**HFHR1 O**	**FBHR1S**	**FBHR2S**	**FBHR3S**	**DOHR1 D**	**DOHR2 D**
Cincinnaticrinus	0	0	0	0	5	8	1
Xenocrinus	0	0	0	0	0	3	0
Hebertella	0	0	0.5	0.5	0.5	0	0
Cincinnetina	0	1	0	0	0	24.5	4.5
Thin Ramose	4.0271	0.8893	0.249	0.697	3.0663	28.4768	0.635
Thin Bifoliate	0	0.2017	0	0.496	0.952	0	0
Tentaculites	0	1	0	0	0	107	0
Zygospira	2	1	0	0.5	0.5	1.5	0
Thick Ramose	0	0	0.973	0.221	0.8604	1.2332	0
Vinlandostrophia	0	1	0.5	1	3	0	0.5
Rafinesquina	0	1.5	0	0	0	0	0
Grewingkia	0	0	0	0	0	0	0
Encrusting	0	0	0	0.962	0.509	0.544	0.694
Petrocrania	0	0	0	0	0	0.5	0
Strophomena	0	0	0	0	0	0	1.5
Flexicalymene	0	0	0	0	0	1	0
Eochonetes	0	0	0	0	0	0	19.5
Cornulites	0	0	0	0	0	1	0

	DOHR3D	**DOHR4D**	**AAHR2D**	**AAHR1D**	**HFHR2O**	**HFHR3O**
Cincinnaticrinus	3	0	0	0	1	0
Xenocrinus	0	0	0	0	0	1
Hebertella	0	0	0	0	0	0
Cincinnetina	15.5	13.5	1.5	5	0	8
Thin Ramose	0.38271	0.0864	0.2931	0.3065	3.784	0.609
Thin Bifoliate	0	0.0744	0	0	0	0
Tentaculites	0	0	0	0	5	0
Zygospira	6	0.5	0	2	4	4.5
Thick Ramose	0	0	0	0	0	0
Vinlandostrophia	0	0	0	0	0	0
Rafinesquina	0	0.5	0	1	0	0
Grewingkia	4	9	0	0	0	0
Encrusting	0.534	0	4.032	6.812	0.86	0.58
Petrocrania	0	0	0	0	0	0.5
Strophomena	0	0.5	2.5	0	0	0
Flexicalymene	0	0	0	1	0	0
Eochonetes	20.5	9	0	0	0	0
Cornulites	0	1	0	0	0	0

Appendix IV: Stony Hollow Creek Submember Data

Final dataset from Stony Hollow Creek Submember after processing as described in the Methods. The first two letters of the sample code indicate the site and correspond to the two letter site codes in Table 1. The second two letters (SH) indicate the sample is from the Stony Hollow Creek Submember. The number indicates relative stratigraphic position of the sample within the Submember with (1) being the stratigraphically lowest sample collected from the Stony Hollow Creek Submember at that site. The final letter indicates depositional environment (O= offshore, D= deep subtidal, S= shallow subtidal, s= shoal).

	CCSH1O	**CCSH2O**	**SRSH1O**	**SRSH2O**	**SRSH3O**	**SRSH5O**	**SRSH4O**	**ALSH2S**
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	1	0	0	2	2	0	1
Xenocrinus	0	0	0	0	1	0	0	1
Iocrinus	0	1	0	0	0	0	0	0
Hebertella	0	0	0	0	0	0	0	1.5
Cincinnetina	143	19	41.5	116	4	1	2	0
Thin Ramose	11.0029	5.152	2.3144	1.6198	2.025	1.4035	0.9738	1.49
Thin Bifoliate	1.6547	0.3979	0	1.0878	0	0	0	1.875
Tentaculites	19	1	3	8	10	0	0	0
Zygospira	2.5	1	6	0.5	1	0	0.5	0
Thick Ramose	2.1824	0.0865	0	0	0.231	0.8951	0.0944	0
Vinlandostrophia	0.5	0	0	0	1.5	0.5	1	0
Rafinesquina	2	1	0	0	0	0	0	0
Grewingkia	0	0	0	0	0	1	0	0
Encrusting	0	0.71	0	0	0	0	0	0
Petrocrania	0	0	0	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0.5	0	0	0	0	0	0
Flexicalymene	2	0	0	0	2	0	0	0
Massive	0	0	0	3	0	0	0	0
Eochonetes	11.5	4	14.5	17.5	0	3.5	0.5	0
Liospira	0	1	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	2
Cyclonema	0	0	0	0	0	0	0	0
Tetraphalerella	0	0	0	0	0	0	0	0

	ALSH3S	**DOSH1D**	**DOSH2D**	**DOSH3D**	**AASH1D**	**SRSH6O**	**HFSH1O**	**HFSH3O**
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	0
Cincinnaticrinus	0	0	2	2	2	1	1	2
Xenocrinus	0	0	1	1	5	0	1	3
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0.5	0	0	0	0	0	1	0.5
Cincinnetina	0	2.5	3	5.5	0	8	23	8.5
Thin Ramose	1.293	0	1.1796	1.0819	2.668	1.4836	1.139	2.497
Thin Bifoliate	0	0	0.1239	0.0454	0	0	0	0
Tentaculites	0	0	0	5	2	0	0	5
Zygospira	0	0	2.5	1	6	0	0	0
Thick Ramose	0	0	0	0	0	0	0	0.0118
Vinlandostrophia	0	0	0	0	0	0	0	1
Rafinesquina	0	1	0	0.5	0	0	0	0
Grewingkia	0	0	0	1	0	0	0	0
Encrusting	0	0	2.829	0	0.751	0	9.79	0.2
Petrocrania	0	0	0	0	0	0	0	0
Leptaena	0	0	0	0	0	0	0	0
Strophomena	0	0	1.5	1.5	0	0	0.5	0
Flexicalymene	0	0	0	0	4	0	0	0
Massive	0	0	0	0	0	0	0	0
Eochonetes	0	4.5	1	0	0	2.5	3.5	3
Liospira	0	0	0	0	0	0	0	0
Caritodens	0	0	0	0	0	0	0	0
Cornulites	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	0
Cyclonema	0	0	0	0	1	0	0	0
Tetraphalerella	0	0	0	0.5	0	0	2	0

	HFSH2O	BWSH1O	DGSH1s	DGSH2s	SGSH1O	SGSH2O	SGSH3O	ALSH1S
Plicodendrocrinus	0	0	0	0	0	0	0	0
Glyptocrinus	0	0	0	0	0	0	0	6
Cincinnaticrinus	1	1	0	0	2	3	6	1
Xenocrinus	0	0	0	0	1	0	2	28
Iocrinus	0	0	0	0	0	0	0	0
Hebertella	0	0	0.5	14.5	0	0	0	29.5
Cincinnetina	2.5	13	0	2.5	30.5	3	21.5	0
Thin Ramose	0.375	15.1192	0.1563	5.307	13.4534	12.7706	33.1106	32.9834
Thin Bifoliate	0	2.5502	0.5351	0	0.58785	0	0.9495	0
Tentaculites	0	0	0	0	0	1	1	22
Zygospira	0	1	0	0	0.5	0	3.5	10
Thick Ramose	0	2.5028	0	0.4147	0.7942	0.738	1.3885	0.329
Vinlandostrophia	0	4	0	0	0.5	1.5	6.5	0
Rafinesquina	0	12	0	0	0.5	0	5.5	0
Grewingkia	0	3	0	0	0	0	0	0
Encrusting	0.4	20.57	0	10.96	2.848	1.138	6.417	2.21
Petrocrania	0	1.5	0	0.5	0	0.5	0	0
Leptaena	0	1.5	0	0	2.5	1	2.5	0
Strophomena	0	0	0	0	0	0	0	0
Flexicalymene	0	0	0	0	1	0	3	2
Massive	0	0	15.782	115.06	0	0	0	1.23
Eochonetes	5.5	0	0	0	0	0	0	0
Liospira	0	0	0	0	0	0	0	1
Caritodens	0	0	3	3	0	0	0	0.5
Cornulites	0	0	0	0	0	0	0	0
Paupospira	0	0	0	0	0	0	0	4
Cyclonema	0	0	0	0	0	0	0	2
Tetraphalerella	0	0	0	0	0	0	0	0

	ALSH4S	**ALSH5S**	**ALSH6S**	**FBSH1S**
Plicodendrocrinus	2	3	3	0
Glyptocrinus	4	3	1	31
Cincinnaticrinus	0	0	1	30
Xenocrinus	10	9	7	1
Iocrinus	1	3	1	0
Hebertella	18.5	19	18	27.5
Cincinnetina	0	0	0	0
Thin Ramose	11.844	8.269	8.485	61.8224
Thin Bifoliate	0	0	0	3.0666
Tentaculites	0	0	0	0
Zygospira	1	1.5	28	21
Thick Ramose	0.6	0.117	0.066	27.539
Vinlandostrophia	0	0	0	5
Rafinesquina	0	0	0	32.5
Grewingkia	0	0	0	0
Encrusting	6.29	2.84	3.02	24.504
Petrocrania	0	0	0	0
Leptaena	0	0	0	28
Strophomena	0	0	0	0
Flexicalymene	0	2	0	3
Massive	0	1.77	0	1.62
Eochonetes	0	0	0	0
Liospira	1	1	0	0
Caritodens	0.5	0	0	5.5
Cornulites	2	0	0	1
Paupospira	1	0	0	1
Cyclonema	0	0	0	18
Tetraphalerella	0	0	0	0

Appendix V: Middle Clarksville Submember Data

Final dataset from Middle Clarksville Submember after processing as described in the Methods. The first two letters of the sample code indicate the site and correspond to the two letter site codes in Table 1. The second two letters (MC) indicate the sample is from the Middle Clarksville Submember. The number indicates relative stratigraphic position of the sample within the Submember with (1) being the stratigraphically lowest sample collected from the Middle Clarksville Submember at that site. The final letter indicates depositional environment (O= offshore, D= deep subtidal, S= shallow subtidal, s= shoal).

	CCMC1O	**SRMC2O**	**SRMC3O**	**DGMC1s**	**MBMC1D**	**MBMC3D**	**MBMC2D**
Cincinnaticrinus	14	15	0	0	1	4	0
Xenocrinus	2	1	0	0	3	3	0
Iocrinus	0	2	0	0	0	0	0
Hebertella	0	0	0	1.5	1	3	1
Cincinnetina	104.5	35.5	5	0	3.5	31.5	0
Thin Ramose	15.1213	31.613	4.8796	0.0208	2.65363	7.9776	0.1546
Thin Bifoliate	0.848	1.3443	0	0	0.2027	1.3132	0.072
Tentaculites	42	30	0	0	34	25	0
Zygospira	21.5	4.5	1	0	0	6.5	0.5
Thick Ramose	0.7185	0.193	2.0396	0	0	0	0
Vinlandostrophia	0	0	0	0	1.5	7.5	1
Rafinesquina	0	0	0	0	0	3	1
Grewingkia	1	1	0	0	1	0	1
Encrusting	25.56	1.667	0.69	2.603	2.634	13.195	3.591
Petrocrania	2	0.5	0	0	1.5	0	0
Strophomena	22	3	0	0	7.5	21.5	0
Flexicalymene	3	0	0	0	0	1	0
Massive	0	1.22	0	0	0	0	0
Eochonetes	0	0	1	0	0	0.5	0
Caritodens	0	0	0	0.5	0.5	0.5	0
Cornulites	0	0	0	0	0	1	0
Tetraphalerella	0	0	0.5	0	0	0	0

	MBMC4D	ALMC1D	ALMC2D	DOMC1D	AAMC1D
Cincinnaticrinus	0	1	0	5	0
Xenocrinus	0	2	1	2	0
Iocrinus	0	0	0	0	0
Hebertella	0.5	0	0	1	0.5
Cincinnetina	4	0	0	24	0
Thin Ramose	1.7574	1.839	0.6736	6.2341	1.6935
Thin Bifoliate	0.2992	0	0.369	0.8404	0
Tentaculites	5	0	0	30	0
Zygospira	1	0.5	0	5.5	0
Thick Ramose	0	0	0	0	0
Vinlandostrophia	0.5	0	0	0	1
Rafinesquina	0.5	0	0	0	0.5
Grewingkia	0	0	0	0	0
Encrusting	5.783	0	0	24.618	1.412
Petrocrania	0	0	0	0	0
Strophomena	4.5	0	0	24	0
Flexicalymene	0	0	0	0	0
Massive	0	0	0	0	0
Eochonetes	0	0	0	18.5	0
Caritodens	0	0	0	0	0
Cornulites	0	0	0	0	0
Tetraphalerella	0	0	0	0	0

	SRMC1O	**DGMC2s**	**DGMC3s**	**ALMC3D**
Cincinnaticrinus	4	0	0	1
Xenocrinus	0	0	0	5
Iocrinus	1	0	0	0
Hebertella	0	14.5	17	16
Cincinnetina	0	0	0	10.5
Thin Ramose	5.9577	1.4927	2.96	16.879
Thin Bifoliate	0	0	0.9231	0
Tentaculites	7	0	0	14
Zygospira	5.5	0	0	1.5
Thick Ramose	0.1344	0	0	0.873
Vinlandostrophia	0	0	1	1.5
Rafinesquina	0	0	0	0
Grewingkia	0	0	0	2
Encrusting	0	1.736	20.806	13.97
Petrocrania	0	0	0	0
Strophomena	6.5	0	0	10
Flexicalymene	0	0	0	3
Massive	0	3.82	64.4898	0
Eochonetes	0	0	0	65
Caritodens	0	1	5.5	1.5
Cornulites	0	0	0	3
Tetraphalerella	1	0	0	0