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Filling in the Spaces: Spatial Point Pattern Analysis of Sessile Ediacaran Taxa From
Nilpena Ediacara National Park, South Australia

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Geological Sciences

by

Phillip Charles Boan

June 2021

Thesis Committee:
Dr. Mary Droser, Chairperson
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The Thesis of Phillip Charles Boan is approved:

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University of California, Riverside

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Dedication

This manuscript is dedicated to the memory of Shirley Ann Boan and the other victims of the COVID-19 pandemic.

ABSTRACT OF THE THESIS

Filling in the Spaces: Spatial Point Pattern Analysis of Sessile Ediacaran Taxa From
Nilpena Ediacara National Park, South Australia

by

Phillip Charles Boan

Master of Science, Graduate Program in Geological Sciences
University of California, Riverside, June 2021
Dr. Mary Droser, Chairperson

The sharing of ecospace with organisms of the same or different species is one of the most fundamental properties of life. The excavation and conservation of nearly 40 bedding planes covered with *in situ* Ediacaran fossils at Nilpena Ediacara National Park in South Australia, allows for the application of spatial ecological techniques typically used on modern ecosystems to test hypotheses about spatial properties of Earth's oldest animal communities. Using a combination of photogrammetry and spatial point pattern analysis, the spatial relationships of the *sessile* taxa *Aspidella*, *Obamus*, and *Tribrachidium* in the context of body size and abundance is presented here. Two *Aspidella* dominated beds, a *Tribrachidium* dominated bed and one *Obamus* populated bed from two of the four fossiliferous facies at Nilpena were examined for this study. Results reveal that *Aspidella* and *Obamus* are distributed into segregated clusters, while

Tribrachidium more spatially homogenous. The *Aspidella* clusters are heavily influenced by the taxon's dominance on the beds and by environmental factors (surrounding taxa, taphonomy, etc.). Additionally, sized-based analysis reveals the potential for intraspecific competition amongst the *Aspidella*, while also fortifying a continuous reproduction hypothesis. *Obamus* show "hyper aggregation," which is potentially a result of dispersal limitation. Finally, *Tribrachidium* spatial results support a seasonal reproductive method and passive suspension feeding strategy.

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INTRODUCTION

The Ediacara Biota are a suite of multicellular soft-bodied organisms that comprise the first complex multicellular heterotrophic macroscopic life. These organisms diversified with a backdrop of rapidly changing environmental and climate conditions with ocean oxygen considerably lower than modern concentrations (Droser et al. 2017; Lyons et al. 2014). The Ediacara Biota are divided into three assemblages largely based on stratigraphic distribution and taxonomic composition: the Avalon Assemblage (579 – 559 Ma), the White Sea Assemblage (558 – 550 Ma), and the Nama Assemblage (549 – 541 Ma; Boag et al. 2016). The Avalon Assemblage includes a suite of taxa largely with fractal morphology. The White Sea Assemblage reflects a major increase in diversity and complexity of body plans including the advent of animals, the oldest bilaterian, evidence for the oldest sexual reproduction, and the rise of mobile taxa (Boag et al. 2016; Becker-Kerber et al. 2020; Droser et al. 2017; Evans et al. 2020; Rooney et al. 2020; Wang et al. 2020). The White Sea Assemblage primarily comprise sessile taxa that lived on atop or embedded in the laterally extensive microbial mats covering the Ediacaran seafloors (Droser et al. 2017). The Nama assemblage, while hosting the earliest evidence of skeletonization in macrofauna, is defined by a global loss in diversity and expansion of bathymetry for the Ediacara Biota (Boag et al. 2016; Evans et al. 2018; Rooney et al. 2020).

Several taxa from the Ediacara Biota are relatively well-constrained phylogenetically, such as the newly described *Ikaria wariotta* (Evans et al. 2020), but most remain enigmatic. Morphological studies of individual taxa are essential, but spatial

paleoecology potentially provides a distinctly different set of data that can be used to argue morphological studies and to test hypotheses about reproduction, life habits, and ecological strategies.

For most of the geologic record, community level spatial analysis is nearly impossible because of the lack of *in situ* fossils on extensive bedding planes. However, the exceptionally well-preserved White Sea Assemblage fossil communities excavated and housed at Nilpena Ediacara National Park, South Australia, provides a unique opportunity to collect spatial data using techniques traditionally reserved for modern ecology.

The spatial distribution of sessile organisms across the seafloor can be as simple as a few preserved individuals of the same species clustered together, to as complex as multiple species with hundreds of individuals clustering in complex configurations all sharing and competing for the same ecospace. In modern environments, maps of these complex patterns can be used to test hypotheses about spatial interactions (Atkinson et al. 2007; Chang and Marshell 2016; Carrer et al. 2018; Franklin and Santos 2010; Harms et al. 2000; He and Legendre 2002; Jacquemyn et al. 2007; Kenkel 1988; Law et al. 2009; Lin et al. 2011; Mitchell et al. 2020b; Schlicher et al. 2011; Watson et al. 2007; Wiegand et al. 2007; Zillio and He 2010). For example, intraspecific competition (spatial thinning) is a common spatial interaction that is tested for in modern ecosystems. This occurs when a species' spatial density decreases as their size increases, and is visible in both the spatial distribution and sizes of individuals (Atkinson et al. 2007; Carrer et al. 2018; Kenkel et al. 1988; Mitchell et al. 2020b Velázquez et al. 2016).

Most modern sessile organisms have spatial patterns so complex that they preclude effective visual interpretations. This is also true for the preserved communities at Nilpena. To resolve this problem, Spatial Point Pattern Analysis (SPPA), a statistical method heavily implemented in modern ecology, will be applied to the communities at Nilpena (Velázquez et al. 2016; Wiegand and Moloney 2004). Spatial analytical work has been done on some of the taxa preserved at Nilpena, but those methods implemented Nearest Neighbor Analysis. This form of spatial analytics simply does not take into account the entire aspect of a spatial pattern and can be hampered by irregularly shaped beds (Coutts et al. 2018; Evans et al. 2020; Hall et al. 2015; Dhungana and Mitchell 2021).

Given the lack of predation and bioturbation during the Ediacaran, one might assume that the distributions of dominant sessile organisms would differ from those of modern benthic ecosystems (Droser et al. 2017). However, large scale analyses of alpha and beta diversity suggest that, at least at the scale of tens of meters and kilometers, beta diversity was surprisingly similar to modern settings (Finnegan et al. 2019). Following on this large-scale pattern, this thesis tests the hypothesis that three taxa (*Aspidella*, *Obamus*, and *Tribrachidium*) share the basic spatial distributions that occur in modern ecosystems, and vary in complex spatial dynamics depending on preservation, ecology, and biology. Additionally, this work will test the interpretations of Mitchell et al. (2020a), that *Aspidella* from shallow water communities are spatially segregated and show signs of intraspecific competition. Finally, previously proposed hypotheses on *Tribrachidium*

reproductive and feeding methods will be tested by examining their spatial distributions (Hall et al. 2015; Rahman et al. 2015).

GEOLOGIC SETTING AND MATERIALS

Geologic Setting

The Ediacara Member of the Rawnsley Quartzite crops out in, and around the Flinders Ranges area of South Australia. It varies in thickness from 10 to 300m and consists mainly of siliciclastic, sandstone-dominated lithologies (Fig. 1; Droser et al. 2019; Gehling 2000; Tarhan et al. 2015b). The succession exposed at Nilpena Ediacara National Park is divided into four sandstone-dominated fossiliferous facies: Flat-Laminated to Linguoid-Rippled Sandstone Facies (FLLRS), Oscillation-Rippled Sandstone Facies (ORS), Planar-Laminated and Rip-Up Sandstone Facies (PLRUS), and Channelized Sandstone and Sand-Breccia Facies (CSSB; Droser et al. 2017a; Droser et al. 2019; Gehling and Droser 2013; Tarhan et al. 2017). This project will focus on beds excavated from the PLRUS and ORS facies. The PLRUS Facies consists of laterally continuous, planar-laminated, fine-grained sandstone beds and is interpreted to have been deposited under unidirectional flow (Droser et al. 2019). Fossils of this facies occur as external and internal hyporelief molds. The ORS Facies is characterized by sub-mm to centimeter thick, rippled, fine- to coarse-grained quartz sandstones interpreted to have been deposited under oscillatory and combined flow at and just below fairweather wave base (Droser et al. 2019). Fossils also occur as external and internal hyporelief molds in this facies. (Droser et al. 2019).

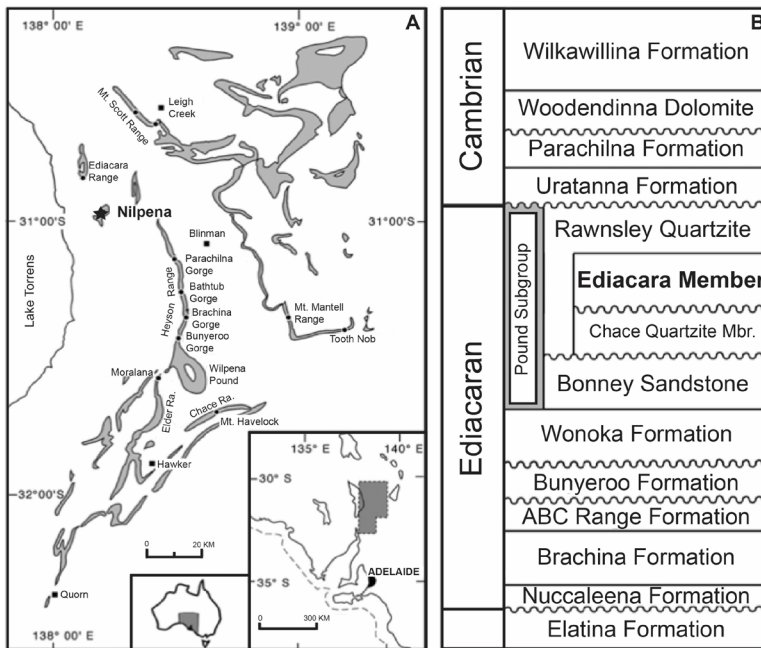


Figure 1. **A)** Distribution of the Pound Subgroup outcrops (grey) bearing the most prominent Ediacaran fossils horizons. Nilpena Ediacara National Park is marked by a black star. **B)** Stratigraphic locations of the Ediacara Member. Modified from Gehling and Droser (2009).

In the ORS facies, in particular, discrete beds can be sub-mm in thickness. These “shims” result from the widespread presence of organic surfaces covering the seafloor during the Ediacaran (Tarhan et al. 2017). These organic surfaces stabilized the upper surface of sediment and acted as a diagenetic separator preserving stacks of discrete beds of similar grain-size of various thickness. Thus, the beds are not amalgamated as they would typically be post-Ediacaran. Additionally, there is no evidence of erosion. The result of this is that not only is there a record the depositional event, which is standard, but also a record of the communities that developed and lived on the organic surface in between depositional events.

Shorter periods between storm events are recognized via less mat development; longer periods between events result in thicker mats with body fossils preserved (Tarhan et al. 2017). This ecologically mediated stratigraphic packaging makes Nilpena unique when compared to the rest of the shallow marine stratigraphic record, where large

proportions of time are missing due to erosional or depositional process (Patzkowsky and Holland 2012; Sadler 1981).

The fossils are preserved on the base of beds, it is necessary for the beds to be excavated, flipped, and reassembled to display entire bedding planes. It is important to note that the shapes and sizes of the beds examined are a function of geology, such as faults, logistics (the beds dip too deeply under the surface), and taphonomy (the bedding surface loses preservational integrity; Droser et al. 2019; Hall et al. 2015). Currently, Nilpena houses over 40 fossiliferous bedding planes from all four facies which range in size from 1 to 23 m².

Three taxa were chosen for this project due to their abundance on beds and size frequency distributions. Four beds were examined for this project, totaling 29.9 m² of fossilized seafloor from either the PLRUS or ORS facies (Table 1).

Table 1. Nilpena beds and taxa examined in this thesis.						
Bed	Area (m²)	Taxon	Number of Individual	Facies	Total Number of Genera per Bed	Taxon Size Ranges (diameter in cm)
TC-MM2	10.3	<i>Aspidella</i>	331	ORS	3	.4 - 14
STC-AB	3.4	<i>Aspidella</i>	249	ORS	4	.7 - 15
LV-FUN	10	<i>Obamus</i>	39	PLRUS	10	N/A
1T-T	6.2	<i>Tribrachidium</i>	114	ORS	9	.5 - 1.7



Figure 2. The three taxa examined in this thesis. All scales are 1 cm. **A)** The form genus *Aspidella*, which can range in size and morphology across facies and beds. **B)** *Obamus* embedded itself into the microbial mat and visually appears to be a spatially clustered taxon. **C)** *Tribrachidium* has been interpreted to have seasonal reproduction and feeding via passive filtering.

Aspidella

After *Funisia dorothea*, the second most common taxon excavated at Nilpena is *Aspidella* (Fig. 2A). Ranging in size from 1 to 50 cm in diameter, *Aspidella* is a circular form genus that is interpreted as the holdfast of frondose organisms that would have attached to the seafloor and protruded into the water column (Tarhan et al. 2015a). The right-skewed size-frequency distribution of the *Aspidella*, indicating a high infant mortality, has been tied to continuous reproduction (Tarhan et al. 2015a). At Nilpena, the fronds are commonly shredded or incomplete, but are generally considered to be all the same taxon and specifically *Arborea arborea* (LaFlamme et al. 2018). *Aspidella* is one of the most common Ediacara taxa, being found globally in all three assemblages and in a range of paleoenvironments/ paleobathymetries (Becker-Kerber et al. 2020; Bykova 2010; Hibbard et al. 2009; Inglez et al. 2019; Mitchell et al. 2020a; Moczyłowska and Meng 2016; Tarhan et al. 2015a; Weaver et al. 2008; Wilby et al. 2011; Zakrevskaya

2014). There are three major morphologies of *Aspidella*: Ringed, Radiating, and Puckered morphology, which do not correlate to size or assemblage (Tarhan et al. 2015a).

Aspidella are preserved in two modes: an internal mold taphomorph, and an external mold taphomorph (Tarhan et al. 2015a). On the beds examined here, the *Aspidella* are generally preserved as the internal mold taphomorph. In this mode of preservation, an *Aspidella* stalk was ripped off, likely during a storm event, and the hollow holdfast is infilled with sediment (Tarhan et al. 2015a). *Aspidella* at Nilpena are associated with densely packed felled *Funisia*, which are important for the *Aspidella* preservation, as the felled *Funisia* assist in stabilizing the hollow holdfast and preventing collapse (Surprenant et al. 2020; Tarhan et al. 2015a).

“Kissing *Aspidella*” is a relatively rare case when pairs of individuals not only share edges, but also share internal morphological features. This form of pairing has been considered to be a function of asexual fission or budding in the past; recent work however, argues that “Kissing *Apsidella*” are results of ingrowth-mediation deformation (Peterson et al. 2003; Tarhan et al. 2015a).

Obamus

Obamus coronatus is a circular organism that would have been partially embedded into the organic mats, and ranges in diameter from .5 to 2 cm (Dzaugis et al. 2018; Fig. 2B). Out of the three taxa examined here, *Obamus* uniquely occurs at Nilpena on four bedding surfaces (Dzaugis et al. 2018; Evans et al. 2020). These beds are either in

the ORS or PLRUS facies and are commonly associated with well-developed textured organic surface (TOS; Droser et al. 2019; Dzaugis et al. 2018; Surprenant et al. 2020).

Tribrachidium

Tribrachidium is an enigmatic triradial organism that occurs in both Australian and Russian White Sea Assemblage sites (Fig. 2C; Boag et al. 2016). They have a size range between .2 to 4 cm in diameter, are all generally circular, and occur on 10 beds at Nilpena (Droser et al. 2019; Hall et al. 2015; Rahman et al. 2015). Size-frequency distributions of *Tribrachidium* from Nilpena suggest that they lived in single-generation populations with seasonal reproduction (Hall et al. 2015). Nearest neighbor analysis on *Tribrachidium* beds at Nilpena reveal a random distribution and qualitatively “patchy” distribution, but no SPPA methods have been applied (Hall et al. 2015). While *Tribrachidium* are found in association with other taxa at Nilpena (*Coronacollina*, *Aspidella*, *Spriggina*, and *Dickinsonia*), it is not statistically associated with one specific taxa (Hall et al. 2015). *Tribrachidium* have also been hypothesized to be passive filter feeders, based on how the organisms’ shape affects water flow (Rahman et al. 2015). Due to their relative abundance at Nilpena, and hypothesized reproductive and feeding modes, *Tribrachidium* is an ideal candidate for spatial analysis.

METHODS

The project was divided into two main components: field collection and quantitative analysis.

Field Collection

The “seafloor snapshots” preserved at Nilpena are perfectly suited for spatial analysis (Droser et al. 2019). Using a combination of detailed bed logging and photogrammetry, it is possible for the fossil material at Nilpena to be preserved and examined in digital formats.

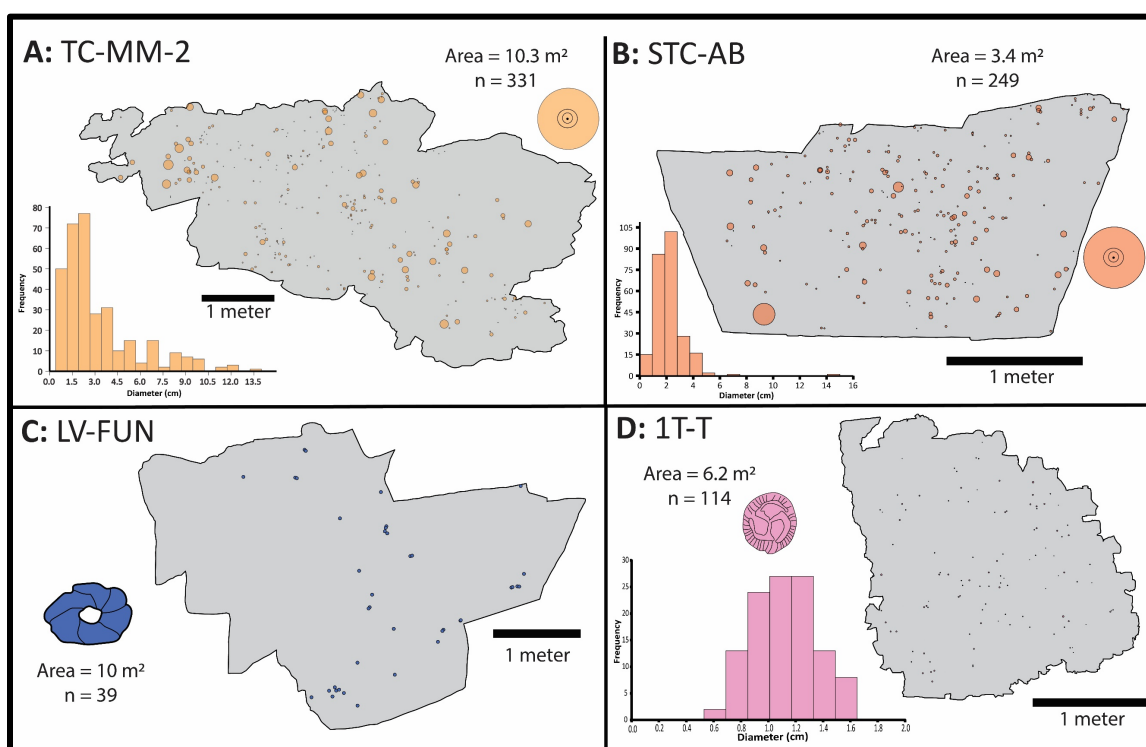


Figure 3. The four beds housed at Nilpena that are examined in this thesis. **A)** Bed TC-MM2 (ORS) is an *Aspidella*-dominated bed that is considered a mature community. **B)** Bed STC-AB (ORS) is an immature *Aspidella* community with only two individuals larger than 6 cm in diameter. **C)** Bed LV-FUN (PLRUS) is an ongoing excavation and preserves a highly diverse community of taxa. *Obamus* specimens on these beds were noted as being visually aggregated, thus making them an ideal subject for spatial analysis. Note that the sizes of the *Obamus* plotted here are not to scale. **D)** Bed 1T-T (ORS) is dominated by *Tribrachidium* which were determined to have a random distribution via nearest neighbor analysis (Hall et al. 2015).

The logging and measuring of individuals on each bed is the standard method of data collection at Nilpena (Droser et al. 2019). During logging, individual fossils are measured, described, and their locations on fossil beds are mapped using a bed specific

cm-scale coordinate system. Species that were not the focus of this project (such as the mobile taxon *Dickinsonia*) were also logged for completeness. The *Aspidella* on beds TC-MM2, and STC-AB were logged and measured on-site in July 2019 (Fig. 3A-B). Photogrammetry was also implemented, allowing for the creation of high resolution (sub-mm) 3D models. Both of these methods are important for completing any spatial analysis of the specimens, as their exact locations and sizes in relation to the bed border is vital.

The *Tribrachidium*-dominated bed 1T-T and the *Obamus*-populated bed LV-FUN were compiled using previously collected data (Fig. 3C-D). *Obamus* sizes were not measured due to their imbedded nature.

Statistical Analysis

Statistical methods were expanded from Mitchell (2015), (2019), and (2020a), which all focused on applying SPPA to Ediacaran communities, while adding methods proposed in Wiegand et al. (2016), Wiegand et al. (2004), and Wiegand and Moloney (2014).

Statistical analyses were conducted using *Programita* and the R package *Spatstat*, both of which are commonly used for SPPA (Baddeley et al. 2016; Wiegand and Moloney 2014). When mapped on a grid, the locations and sizes of *sessile* organisms in relation to one another can reveal interactions and life habits. To examine these interactions, SPPA has been implemented and can be used to quantifiably test relationships between specimens of the same or different species (Illian et al. 2008; Velázquez et al. 2016; Wiegand and Moloney 2014).

The distribution of marine sessile organisms reflects their biology and ecology (Chang and Marshall 2016). Additionally, in most sessile marine invertebrates, taxon size is correlated with age, with larger individuals being older. By combining this size-based assumption with the locations of individual taxa, reproductive methods (such as stolon and sexual reproduction) and life habits can be evaluated (Michell et al. 2015; Droser and Gehling 2008).

SPPA is divided into three major statistical components that allow for biological and ecological characteristics to be interpreted:

Summary Statistics

These statistical methods test how the existing pattern of points (or in this case fossilized organisms) are distributed in a given area. Specifically, they quantify the properties of a pattern using functions of distance (unmarked patterns) or size (marked patterns). Depending on the specific summary statistic used, one can assess how the current populations compare to possible spatial distributions observed in the modern (see Null Models' section). Since specific summary statistics examine different aspects of a pattern, multiple are required for a complete analysis to be conducted.

In *Programita* and *Spatstat*, summary statistics are depicted as lines going through, above, or below a simulation envelope, with the y-axis being function intensity. The higher a function value plotted along the y-axis, the stronger the spatial pattern, and vice versa (Dhungana and Mitchell 2021). For example, a common spatial pattern found in modern ecology is aggregation, or individuals being closer to one another than

predicted in a random pattern (see null models' section; Wiegand and Moloney 2014). Strong aggregation would be depicted as a high function value, while individuals being far apart (also known as segregation) would be visible as a low function value in relation to the simulation envelope.

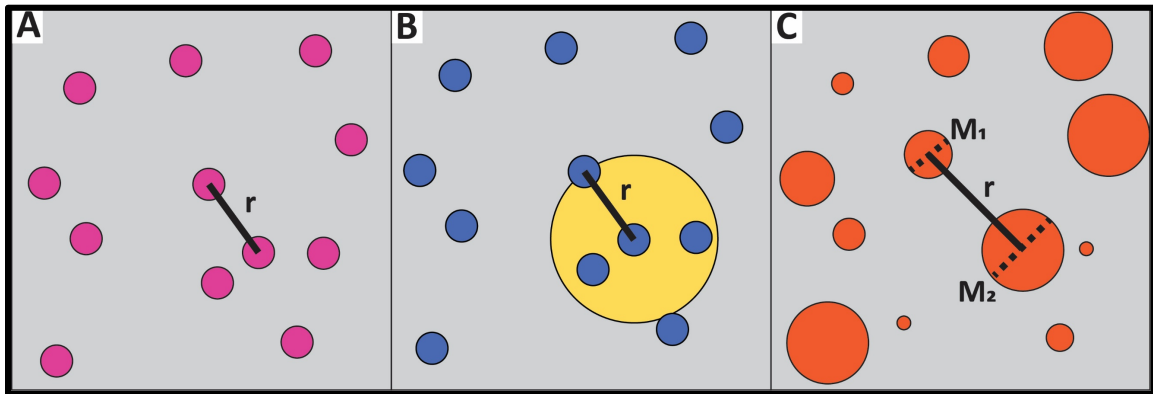


Figure 4. Simplified diagram of summary statistics used herein. **A)** The Pair Correlation Function (PCF) examines how many pairs of points are separated by a certain distance (r), and compares it to the total density of points within the study area (window). **B)** Examines the number of points within a circle with a radius of r . The circle will increase in size till statistical viability has been extinguished (r_{corr}). **C)** Examines the product of pairs of points (M_1M_2) separated by a certain distance (r). This value is then divided by the rest of the community resulting in a function value.

The primary summary statistic used in this thesis is the Pair-Correlation Function (PCF), which examines the probability of observing a pair of points in a pattern separated by a distance (r) and compares this value to the spatial average (density) of all points (Fig. 4A; Illian et al. 2008; Velázquez et al. 2016; Wiegand and Moloney 2014). In other words, it looks at how many pairs of fossils are separated by a certain distance, and compares it to the density of total fossils on the bed. PCF will continue to examine pairs at different distances until the range of correlation (r_{corr}) is reached, or the distance at which a correlation between points within a study area is no longer statistically relevant (Baddeley et al. 2016; Illian et al. 2008). While the PCF is the best suited for spatial

ecology, it is still a relatively new and underused method, with only 27% of SPPA ecological studies published before 2016 applying PCF (Velázquez et al. 2016).

The *L*-Function (LF) is far more common in published records, with nearly 75% of SPPA ecological studies before 2016 applying it (Fig. 4B; Velázquez et al. 2016). The LF examines the number of points within a circle with a radius of r , that increases in size until r_{corr} is reached. Basically, a central point is determined and the number of fossils within this increasing circle is compared to the total density of fossils on the bed.

The final summary statistical family used for this thesis is the Mark Correlation Function (MCF), which is specifically adapted for patterns which have quantitative data associated with the x,y coordinates, known as a mark (Fig. 4C; Wiegand and Moloney 2014). In this case, individual specimen sizes are the marks. MCF has two additional summary statistics within its classification: the *r*-Mark Correlation Function (*r*-MCF), and the Mark Variogram (MV). MCF examines all points separated by distance (r), determines the product of those pair's marks (size), then divides this value by the rest of the community in order to determine spatial and size associations at all distances to r_{corr} is reached (Velázquez et al. 2016; Wiegand and Moloney 2014). Similarly, *r*-MCF determines the mean value of both marked points separated by r , while MV is the squared difference of the two marked points (Wiegand and Moloney 2014). Due to its complexity, the MCF is seldom used in Ecology, with only 6% SPPA ecological studies using any form of marked analysis before 2016 (Velázquez et al. 2016).

Null Models

The Summary Statistics only examine the existing distribution of fossils on the bed. In order to compare this to distributions found in modern ecosystems, and to test environmental or biological influences on the spatial patterns, a null model must be used. The null models are patterns that are expected when there is an absence of a particular ecological mechanism, such as reproduction or competition, thus acting as a null hypothesis (Velázquez et al. 2016; Wiegand and Moloney 2014). The summary statistics are then used to determine at what scales a pattern does not exist in the null model, or more simply at what scales a specific ecological mechanism is present (Velázquez et al. 2016).

Mathematically, a null model in SPPA is a standard parameter that determines the number of points within an area and reorients them into common spatial patterns to act as a control to observed distributions (Velázquez et al. 2016; Wiegand and Moloney 2014). For the Nilpena communities, the taxa were spatially reorganized 999 times (Monte Carlo simulations) within the bed area and then tested with each summary statistic. In univariate and bivariate null models (i.e., ones that use LF and PCF) the organisms' locations are reoriented, while marked null models (MCF, r-MCF, and MV) reorient size and do not move the organisms. From these 999 simulations, the 49 highest and 49 lowest summary statistic values were plotted creating simulation envelopes in *Programita* (See Confidence Test section for more details). When the summary statistic values for the taxon in question are graphed against this simulation envelope the null model will be confirmed or denied as either a positive or negative relationship at multiple

scales till r_{corr} is reached. A positive relationship has the summary statistic line going above the simulation envelope, while a negative relationship goes below. If the line is within the simulation envelope, the null model has been confirmed at that specific scale.

Six null models were used in this thesis:

Complete Spatial Randomness, also known as Homogenous Poisson, determines if a logged pattern is distributed randomly, aggregated, or segregated (Fig. 5A-C). Under aggregation, or clustering, individuals are spatially closer than average (positive relationship; Fig. 5B), while segregation is when organisms are spatially further apart than average (negative relationship; Fig. 5C). Aggregation is the standard spatial distribution in organisms living in modern ecosystems and is usually a result of either dispersal limitation and/or environmental factors (Carlson and Olson 1993; Carrer et al. 2018; Franklin and Santos 2010; He and Legendre 2002; Karlson et al. 1996; Lin et al. 2011).

The CSR null model is also suited to identify virtual aggregation. This spatial condition arises when the pattern shows signs of large-scale heterogeneity, or patches of points surrounded by large areas void of points (Velázquez et al. 2016; Watson et al. 2007; Wiegand and Moloney 2004; Wiegand and Moloney 2014). An example of this would be the tree line in a mountain range. When plotted, there would be a large area where trees could not live due to the elevation, and patches of aggregated tree growth in the valleys between peaks. For SPPA, this is depicted when the summary statistics (either PCF or LF) show aggregation at all scales, also known as global aggregation. For this

thesis, the LF will be used as the main identifier of Virtual aggregation. It is present if the LF shows aggregation at all spatial scales and shows a linear increase of aggregation value with increased distance.

In order to confirm the presence of virtual aggregation, the Heterogenous Poisson Null Model (HP) was implemented (Fig. 5D-F). Akin to CSR, the HP null model also tests for aggregation, segregation, or randomness. The key difference between the two null models is that CSR assumes the intensity (aka density) of the pattern is uniform throughout the area, while HP allows the intensity of the pattern to depend on location (Carrer et al. 2018; Schleicher et al. 2011; Velázquez et al. 2016; Wiegand et al. 2007; Wiegand and Moloney 2014). This changes the values of the simulation envelope, usually increasing/decreasing the highest and lowest values, thus increasing the general size of the simulation and affecting how the summary statistic line is interpreted. In an ecological sense, HP reveals a group of organisms' "true" spatial distribution without external variables possible affecting the interpretation.

The HP and CSR, while vital to exploring fundamental ecological questions, are limited by the fact they are unmarked univariate tests. In other words, these null models do not consider size or cohorts whilst analyzing the distribution. The final four analyses presented here examine the populations either as bivariate (two cohorts) or marked (size of individuals) populations. Pattern 1 fix, Pattern 2 CSR (PFPC) is a bivariate analysis ideally suited for examining two groups of individuals and determining if they are showing signs of attraction, repulsion, or independence (Wiegand and Moloney 2014). Under independence, the null hypothesis, two populations have no relation in their spatial

distributions (Fig. 5G). Repulsion is present if the two patterns are farther apart at short distances than expected under independence (negative relationship; Fig. 5I), while attraction is present if the two patterns are closer together than expected under independence (positive relationship; Fig. 5H). This test was only possible on the *Aspidella* populations, as they had a large enough size range to be divided into large and small cohorts (separated at 4.1 cm in diameter).

Finally, marked null models were used on the *Aspidella* and *Tribrachidium* beds. Marked Null Models (MNM) determine whether marked point placements are independent, mutually stimulating, or inhibiting to one another (Illian et al. 2008; Wiegand and Moloney 2014; Fig. 5J-L). Mutually stimulating is when individuals are larger in size when near each other (positive relationship; Fig. 5K), while inhibition is present when points are smaller in size when near each other (negative relationship; Fig. 5L). This differs when the MV summary statistic is used (Fig. 5M-O). For an MV-MNM with a positive relationship, the individuals are less similar in size than average at a given r (Fig. 5N); while negative relationships determine that individuals are more similar in size than average at a given scale (Fig. 5O). For marked analysis, an error of 2 cm overlap was allowed to compensate for the irregular shapes of *Aspidella*, particularly when “kissing.”

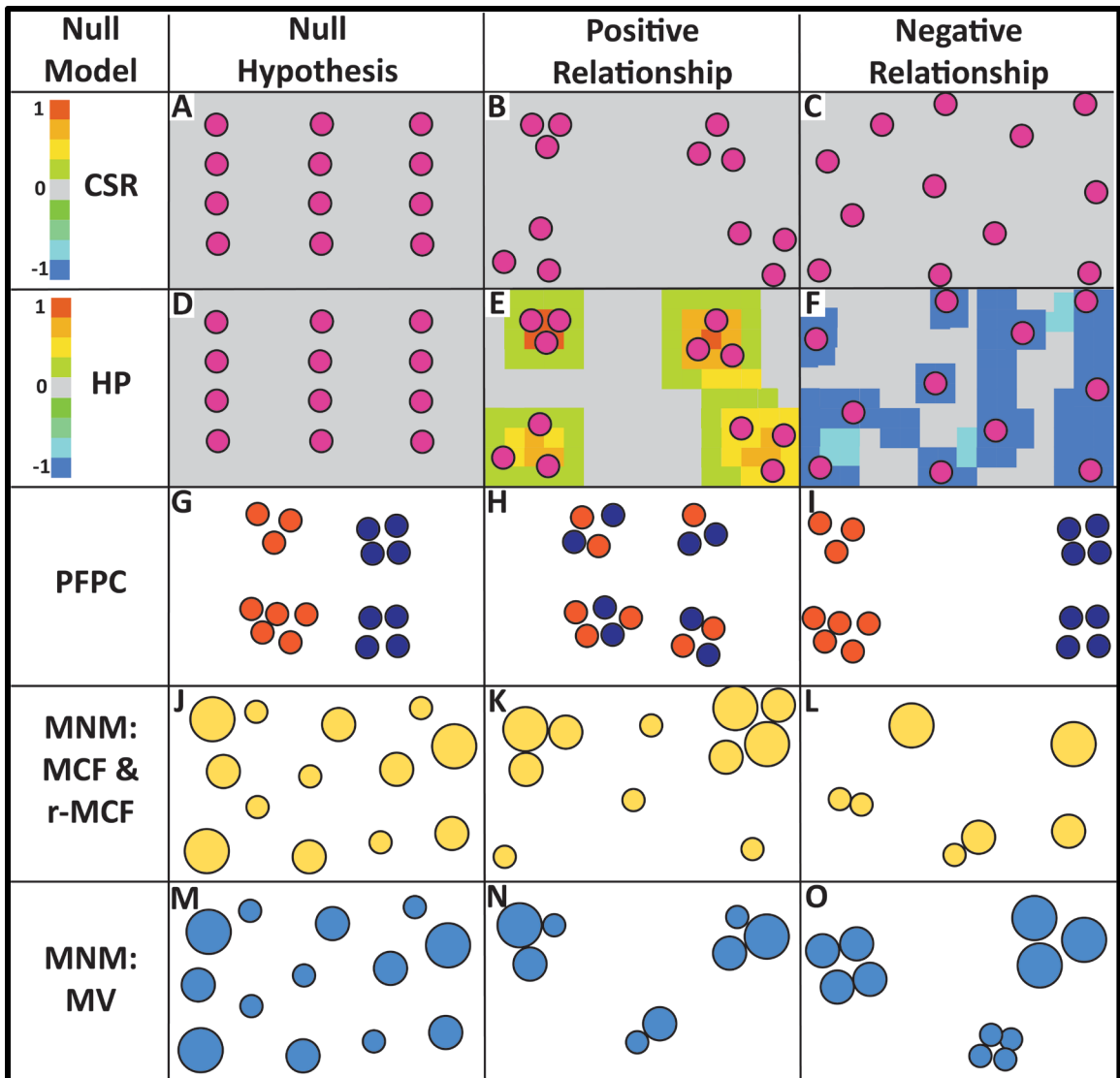


Figure 5. Simplified depictions of null models and some of the possible distribution present in sessile communities. For CSR and HP null models the colored bar indicates point intensity (density) with higher values being in red and lower in blue. Note for CSR intensity is uniform throughout the study area, while for HP tests it varies by location. **A)** Complete Spatial Randomness (CSR), or uniformity, is the control for the CSR null model. This distribution is very uncommon in modern ecology. **B)** Aggregation, or individuals being closer together than would be predicted in a random distribution, is the norm in modern terrestrial and marine ecosystems. **C)** Segregation is the inverse of aggregation, and is points being further apart than predicted in a random distribution. **D-F)** All three of these patterns are tested by the HP null model, which takes the density of the pattern into account when determining if the pattern is **D)** random, **E)** aggregated, or **F)** Segregated. **G-I)** Pattern 1 Fixed Pattern 2 CSR (PFPC) is a bivariate analysis where the individuals are divided into two groups and compared to each other spatially. These bivariate spatial distributions can be **G)** Independent **H)** Attraction (being closer at short distances), or **I)** Repulsion (being further apart at short distances). **J-O)** Marked null models determine if there is a relationship between individual size and location. When MCF or rMCF summary statistics are used individuals can either be distributed **J)** Independent of size, **K)** Mutually stimulating (larger when near each other), **L)** Inhibitions (smaller when near each other). If the MV summary statistic is used the distribution of a marked null model can be **M)** Independent of size, **N)** less similar in size when near each other, **O)** more similar in size when near each other.

Confidence Tests

The Analytical Global Envelope (AGE) was used to determine if a pattern fit a null model, which is depicted in the results as colored simulation envelopes. The AGE was chosen over the more popular pointwise simulation envelope (shown in results as dotted lines within AGE), which, as of 2016, was used in 93% of all SPPA publications due the test focusing on “local” significance levels, whilst calculating the simulation envelopes (Velázquez et al. 2016; Wiegand et al. 2016; Wiegand pers. comm.). AGE tests provide more precise information on point number (specimen number), size/shape of the window (fossil bed), and other aspects of the summary statistics lost during a simulation pointwise test (Wiegand et al. 2016).

Additionally, the Goodness-of-Fit (GoF) was also used in order to determine if patterns matched the null models. The GoF is represented as numerical values, similar to a p-value: A value of 0 indicates a complete rejection of the model, while 1.0 indicates a perfect fit (Mitchell et al. 2020a). In modern ecology, a value of .95 is often considered to be a statically significant match to a null model (Velázquez et al. 2016). However, it is vital to note that this test is only used in an auxiliary fashion and cannot override a visual inspection of the AGE plots (Wiegand and Moloney 2014).

RESULTS

This thesis focused on applying SPPA methods to three different taxa, distributed across four beds, and within two of the four fossiliferous facies (Table 1). Results show that taxa, while generally similar in distribution, vary in spatial complexity. Additionally,

distributions from the same taxon can vary depending on bed maturity, shape, and preservation conditions.

Aspidella

Over 550 *Aspidella* individuals on two beds were spatially analyzed using univariate, bivariate, and marked SPPA methods (Fig. 6-7). The first null model used for all communities examined here is the CSR, as it tests for the most basic spatial relationships and is foundational for HP analyses (Fig. 6B-C, 7B-C). Essentially, if a community matches the CSR null model (randomness) there is likely an error in data collection, because that pattern is very uncommon in nature. Results from the CSR test show that *Aspidella* are subject to strong virtual aggregation. This means some external factor present has “imprinted” itself, in a spatial sense, on the PCF/LFun resulting in “global aggregation” or clustering at all scales (Wiegand and Moloney 2014). This is confirmed using the HP test with the removal of “global aggregation” across both beds (Fig. 6D, 7D). HP also reveals the “true” *Aspidella* distribution to be segregated clusters of individuals, with a cluster radius of ~32-50 cm depending on bed.

The *Aspidella* were then tested using a bivariate analysis with individuals either being larger or smaller than 4.1 cm, with this value being deemed the most statistically viable for beds TC-MM2 and STC-AB (Wingard pers. comm.). When tested with the PFPC null model, *Aspidella* populations showed limited attraction with the exception of bed STC-AB, which was independent (Fig. 7E). When individuals from the large and small groups on bed TC-MM2 are within 4 to 24 cm, they are statically likely to be closer

together (Fig. 6E). This means on beds with mature *Aspidella* populations there is no spatial distribution that is size dependent, and the segregated clusters are mixed with individuals that range in size/maturity.

MNM tests on the *Aspidella* populations revealed small scale mutual attraction as measured by MCF and r-MCF but were independent of size when MV was applied (Fig. 6F-H, 7F-H). Mutual attraction, or individuals being larger in size when near each other, is visible on MCF results for both beds (Fig. 6F, 7F). While STC-AB results confirm this with the rMCF analysis, TC-MM2 r-MCF results are more ambiguous (Fig. 6G, 7G). However, the independence present on both beds for MV results means that *Aspidella* are, on average, independent of each other's size within their segregated clusters (Fig. 6H, 7H).

In order to test how different size groups are distributed, *Aspidella* were divided into 3 size-based cohorts (A:0-5.9 cm, B:5.9-11.4 cm, C: 11.4 < cm). Multiple size variations were examined ranging from three to six different cohorts; however, these cohort sizes were chosen as they allowed for MM-2 to have large enough n values in the C cohort. This configuration unfortunately only leaves one individual for B and C cohort on bed STC-AB; however, this was considered acceptable since a more mature community was necessary. Additionally, there is precedent for using three size groups when testing for univariate cohort-based distributions (Mitchell et al. 2015). In order to finalize the appropriate cohort variations, more beds dominated by *Aspidella* need to be logged and tested using SPPA (see Future Work).

Each cohort was tested against the CSR and HP null models. Because STC-AB only had one specimen in the larger cohorts (B and C) SPPA was only run on cohort A. For TC-MM2 the *Aspidella* larger than 5.9 cm in diameter are spatially random and those smaller than 5.9 cm are statistically more aggregated than the general population (Fig. 6I-K). In other words, smaller *Aspidella* will have larger short-scale PCF values than the general population.

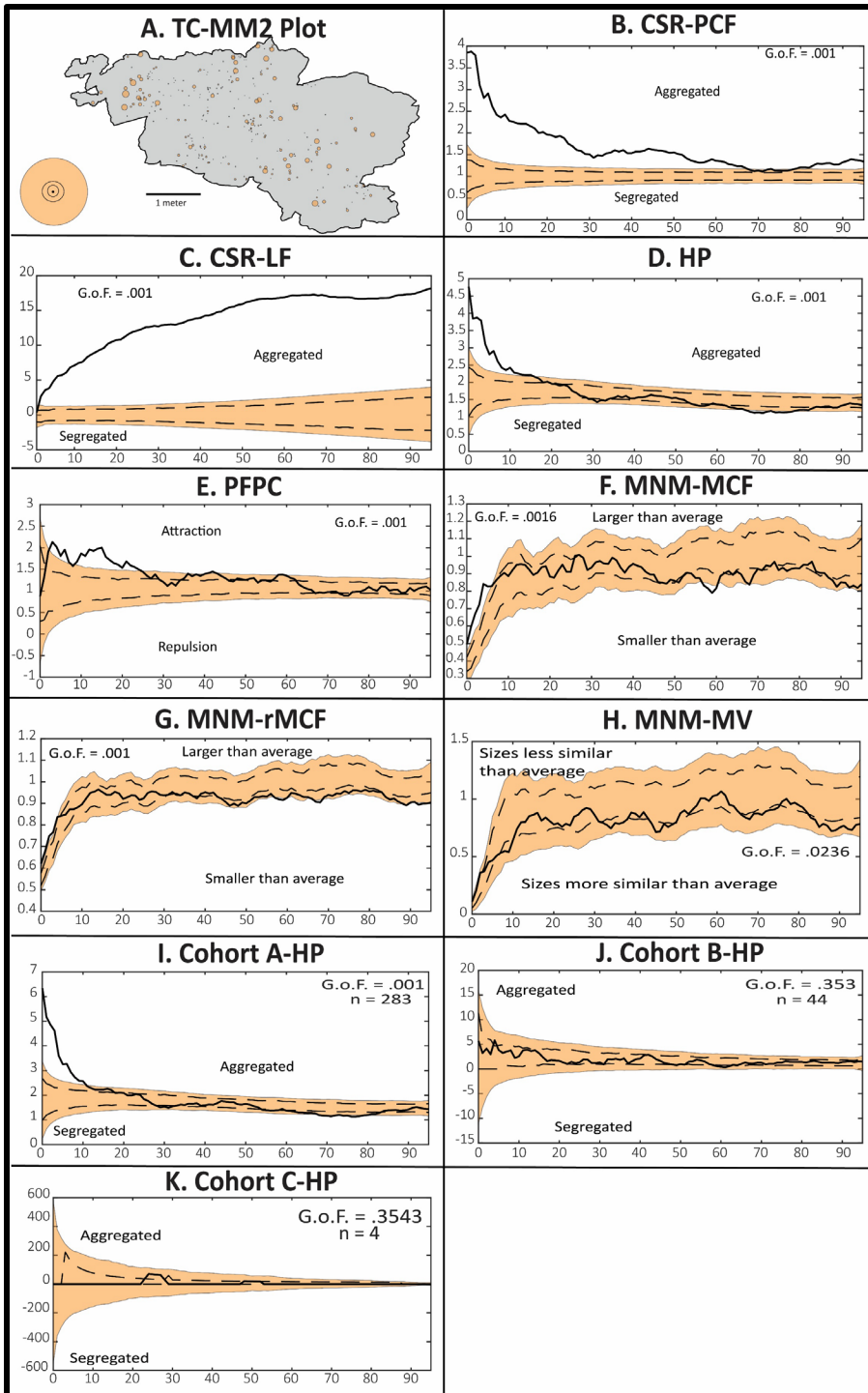


Figure 6. SPPA Results for the *Aspidella* on Bed TC-MM2. Orange envelope is the AGE, dotted lines are the pointwise simulation envelope, and black solid line is the summary statistic value for the *Aspidella* on TC-MM2. On all plots x-axis is distance (r), and y-axis is the summary function value. **A)** Location of the *Aspidella* on bed TC-MM2. **B)** CSR-PCF results show near global aggregation, or the *Aspidella* are aggregating at all statistically viable distances between pairs. **C)** CSR-LF additionally shows global aggregation. This is a good indicator that virtual aggregation is present. **D)** HP results show that *Aspidella* are aggregating till pairs are more than 16 cm apart, then they are randomly distributed, with the exception of small amounts of segregation between 67-78 cm. **E)** Between 2-25 cm small and large *Aspidella* are attracted to one another, while showing independence at all other scales. **F)** The *Aspidella* are larger than average when they are within 0-6 cm from one another, and when 56-60 cm apart they are smaller than average. The *Aspidella* are independent of size at the remaining spatial scales. **G)** rMCF results show that the *Aspidella* locations are generally independent of size. **H)** MV results confirm rMCF, showing the *Aspidella* size is independent of their location. **I)** For *Aspidella* with diameters smaller than 5.9 cm aggregation is slightly higher than general population when 0-11 cm apart. They are generally random at larger spatial scales, with a small amount of segregation between 70-80 cm. This matches the general *Aspidella* population on bed TC-MM2. **J)** *Aspidella* between 5.9-11.4 cm and **K)** 11.4 cm and larger in diameter are spatially random at all scales. This pattern of small taxa being clustered and larger ones being more spatially random is an indicator of spatial thinning.

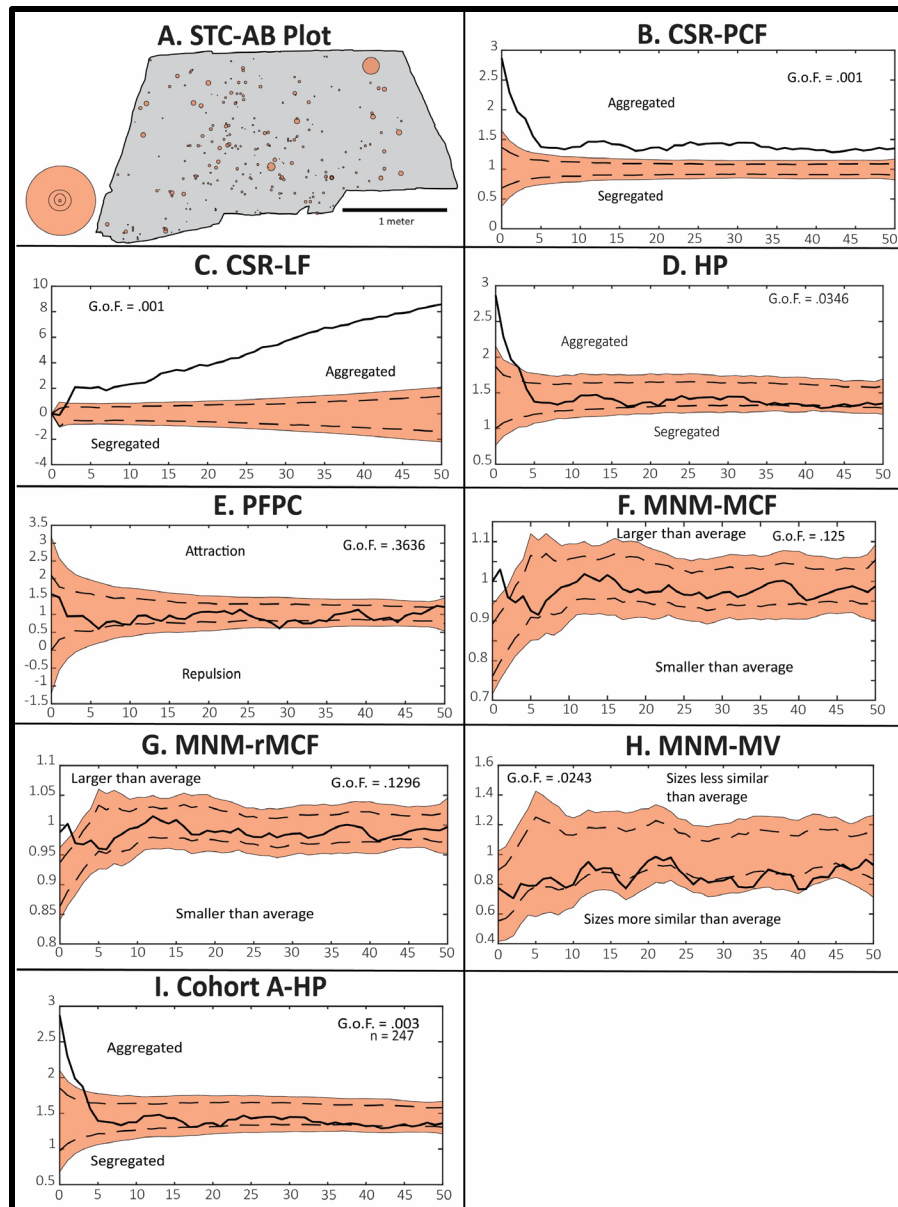


Figure 7. SPPA Results for the *Aspidella* on Bed STC-AB. Orange envelope is the AGE, dotted lines are the pointwise simulation envelope, and black solid line is the summary statistic value for the *Aspidella* on STC-AB. On all plots x-axis is distance (r), and y-axis is the summary function value. **A)** Location of the *Aspidella* on bed STC-AB. **B-C)** Both show global aggregation, indicating virtual aggregation is present in this *Aspidella* community. **D)** HP results confirm the presence of strong virtual aggregation, with “true distribution” being short scale aggregation when individuals are between 0-3 cm apart. **E)** When divided into two size based cohorts (split at 4.1 cm) the two patterns were determined to be independent of each other. Both **F)** MCF and **G)** rMCF show a positive relationship from 0-2 cm, with the remainder of the pattern being random. **H)** MV results show that *Aspidella* locations are independent of their locations. **I)** *Aspidella* smaller than 5.9 cm in diameter match the general population HP-PCF results exactly, which is due to them making up 99.2% of the total population.

Obamus

A community of 39 *Obamus* individuals from one bed in the PLRUS facies was examined using univariate SPPA methods (Fig. 8). Results from the CSR test reveal that *Obamus* is significantly more aggregated than *Aspidella* and *Tribrachidium*: 12 times more aggregated at scales less than 3 cm when PCF is applied (Fig. 8B). This means that *Obamus* are significantly more likely to be distributed in tightly packed clusters, than the other two taxa examined here. This strong level of aggregation would typically indicate virtual aggregation, or the environment producing pseudo-clustering within a study area. However, HP results confirm that there is no statistically significant virtual aggregation present, meaning this “hyper-aggregation” is the “true” *Obamus* distribution (Fig. 8D). These segregated clusters of *Obamus* are on average 6.35 cm in diameter. Such small cluster sizes likely explain why they have such a high aggregation value. Marked, bivariate, and cohort-based tests were not possible as no size data has been collected on the *Obamus* communities on LV-FUN.

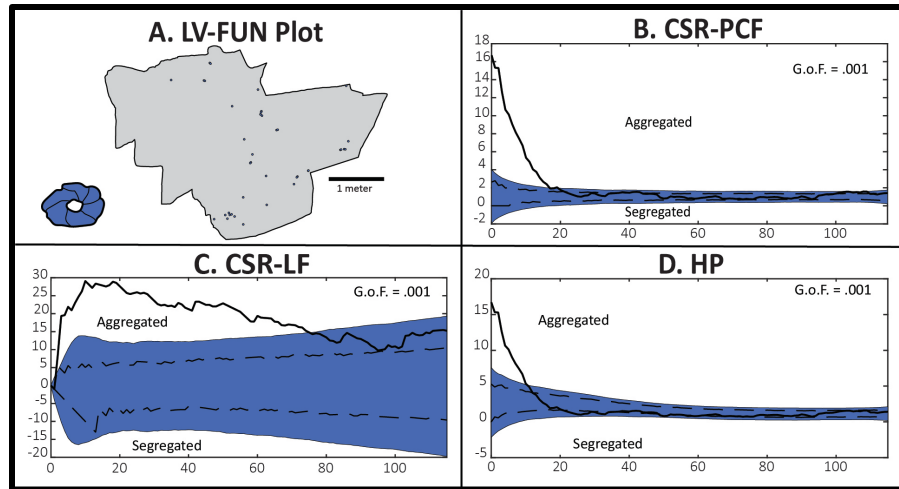


Figure 8. SPPA Results for the *Obamus* on Bed LV-FUN. Blue envelope is the AGE, dotted lines are the pointwise simulation envelope, and black solid line is the summary statistic value for the *Obamus* on LV-FUN. On all plots x-axis is distance (r), and y-axis is the summary function value. **A)** Location of the *Obamus* on bed LV-FUN. **B)** CSR-PCF results show *Obamus* is aggregated at decreasing values when separated by 0-16 cm. Note the aggregation value starts at 17, significantly higher than other taxa presented here. **C)** CSR-LF results do not show a linear increase of aggregation with distance, meaning virtual aggregation is not present in *Obamus* community. **D)** HP results confirm the true *Obamus* distribution to be segregated clusters of individuals that are hyper aggregated to each other.

Tribrachidium

Over 100 *Tribrachidium* individuals from one bed in the ORS facies were examined using univariate and marked SPPA methods (Fig. 9). *Tribrachidium*, while also aggregated at very short scales (less than 5 cm), are less affected by external factors. While virtual aggregation is revealed in the LF-CSR results, it is limited and likely due to the dominance of *Tribrachidium* over the bed surface since it is not confirmed according to either the PCF-CSR or HP results (Fig. 9B-D). This means that, much like *Obamus*, *Tribrachidium* distributions are consistent throughout a bed, which makes sense considering they dominate bed 1T-T. Marked results reveal *Tribrachidium* locations are independent of size (Fig. 9E-F). Finally, no bivariate or cohort analysis was possible due to their similarity in size across bed 1T-T.

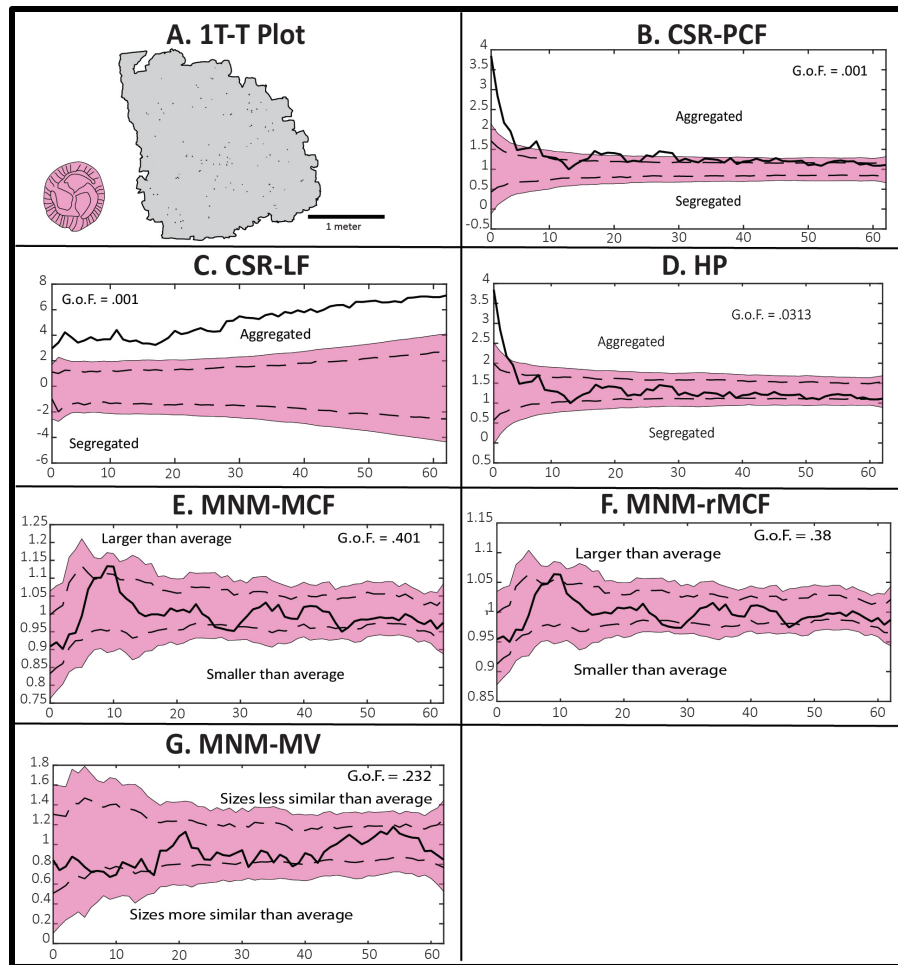


Figure 9. SPPA Results for the *Tribrachidium* on Bed 1T-T. Pink envelope is the AGE, dotted lines are the pointwise simulation envelope, and black solid line is the summary statistic value for the *Tribrachidium* on 1T-T. On all plots x-axis is distance (r), and y-axis is the summary function value. **A)** Locations of *Tribrachidium* on bed 1T-T. **B)** CSR-PCF show aggregation when *Tribrachidium* when separated by 0-5 cm **C)** CSR-LF shows global aggregation **D)** *Tribrachidium* are aggregated from 0-3 cm, but are random at all other spatial scales, implying a lack of major segregated clustering. All three marked results **E-G)** reveal that the *Tribrachidium* location is completely independent to their sizes.

DISCUSSION

Previous studies using SPPA on Ediacaran communities have generally focused on the older and bathymetrically deeper Avalon communities from Mistaken Point, Canada (Mitchell et al. 2015; 2019; 2020a). In regards to the taxa examined here, only four *Aspidella* communities had been examined using SPPA before this study, and out of

those, only one was from a comparable shallow water environment (Mitchell et al. 2019; 2020a). That community (excavated from the Onega Coast, White Sea, Russia) showed signs of spatial segregation, which is different from the Nilpena populations' aggregated results (Mitchell et al. 2020a).

Aggregation, not segregation, is the norm for organisms living in modern marine and terrestrial ecosystems, so it is unsurprising that all three taxa examined here showed some form of spatial aggregation (Carlson and Olson 1993; He and Legendre 2002; Lin et al. 2011). However, the beds still display univariate differences when it comes to intensity of aggregation and whether virtual aggregation is present. *Tribrachidium* and *Obamus* beds did not show virtual aggregation, while the distribution of *Aspidella* was heavily affected by it. This means that the *Aspidella* location is being impacted by an outside factor, which makes their distribution appear to be aggregated at all spatial scales for CSR tests.

In modern ecosystems environmental heterogeneity, such as a pond in a forest or poorly suited soil condition, is the cause of virtual aggregation (Velázquez et al. 2016; Wiegand and Moloney 2014). While microbial mats do range in maturity at Nilpena, *Aspidella* communities examined here lived on beds that are relatively homogeneous (Droser et al. 2019; Tarhan et al. 2017). The statistically significant spatial heterogeneity present in just the *Aspidella* communities is likely a result of taphonomic bias or surrounding taxa.

Taphonomy and interspecific relationships for Nilpena *Aspidella* both are reportedly associated with *Funisia* (Surprenant et al. 2020; Tarhan et al. 2015a). To preserve an *Aspidella*, the stalk needs to be ripped off, likely during one of the large storm events, and the hollow holdfast is infilled with soft sediment (Tarhan et al. 2015a). Collapse of this hollow holdfast does not occur due to the microbially bounded and *Funisia*-dominated TOS, which stabilize it (Tarhan et al. 2015a). In fact, the taphonomic relationship between *Aspidella* and *Funisia* at Nilpena has been described as inversed, with high quality *Aspidella* preservation being associated with poor *Funisia* preservation, and vice-versa (Surprenant et al. 2020). This is important in the sense that a lack of abundant *Funisia* on a specific part of a bed could result in the poor or total lack of preservation of *Aspidella*. Spatially, this would be visible as large “blank spots” on the bed maps where no *Aspidella* have been preserved but could have lived.

Bed TC-MM2 reveal that *Aspidella* with diameters smaller than 5.9 cm are aggregated, while the two larger cohorts (5.9-11.4 cm, >11.4 cm) were spatially random. Different aggregative patterns amongst cohorts have been interpreted in the past to be a function of intraspecific competition (spatial thinning; Franklin and Santos 2009). Spatial thinning occurs when organisms are dispersed into aggregated groups; as the juveniles begin to grow, they will compete for space, resulting in mortality (Kenkel 1988). Spatial thinning occurs among modern marine sessile organisms and, potentially, in other shallow water *Aspidella* communities from the Ediacaran (Fréchette et al. 2010; Mitchell et al. 2020a).

Certain marked results do show that *Aspidella* individuals, when very near each other, tend to be larger than average. This is likely the statistical expression of “Kissing *Aspidella*,” which, on the beds examined here, tend to occur with larger specimens. If spatial thinning is present, as *Aspidella* grow, two individuals would begin to encroach on each other’s space until one died. The “Kissing *Aspidella*” is a snapshot of this interaction. This also supports Tarhan et al. (2015) ingrowth-mediation deformation hypothesis instead of an asexual reproductive method for the cause of “Kissing *Aspidella*.” An asexual reproductive method for just the largest individuals would also not explain why *Aspidella* has such a large size variation even within a specific community.

Finally, bivariate analysis (PFPC) reveals that the locations of large *Aspidella* are attracted to the location of smaller ones on TC-MM2, a which has a mature *Aspidella* population. This means that within the segregated clusters the *Aspidella* were in mixed/multigenerational communities. This supports the continuous reproductive strategy currently proposed for *Aspidella*, as seasonal reproduction would result in segregated clusters of similar sized individuals. In summary, *Aspidella* are preserved as spatially segregated clusters of individuals that vary in size/maturity which confirms a continuous reproductive strategy and has implications for spatial thinning (Fig. 10A).

Obamus on LV-FUN show such high aggregation values within their spatially segregated clusters that the term hyper-aggregation is necessary (Fig.10B). With this level of aggregation present in the *Obamus* community, the first step is to determine if this is a result of an external factor or a dispersal limitation. The HP null model revealed

no external factors, such as environmental or taphonomic heterogeneity, affecting the *Obamus* distribution. It is important to reiterate that aggregation in modern marine sessile invertebrate communities, in a broad and simplified sense, is a function of either environmental factors and/or dispersal limitation (Carlson and Olson 1993; Carrer et al. 2018; Franklin and Santos 2010; He and Legendre 2002; Karlson et al. 1996; Lin et al. 2011). Since *Obamus* has no detectable external factors affecting its distribution, the intense aggregation is likely a function of dispersal limitation. Highly aggregated marine invertebrates in modern ecosystems have been associated with rapidly settling and spatially selective larval stages in order to secure “preferred substrate” (Carlson and Olson 1993; Manríquez and Castilla 2007). However, *Obamus* is a recently discovered taxon and additional work is required before reproductive interpretations can be solidified.

While *Tribrachidium* are aggregated at very short scales, they do not display the segregated clusters observed in *Aspidella* and *Obamus* communities. This limited aggregation only occurs when pairs of *Tribrachidium* are separated by 0-3 cm, which is within the size range of the average individual on the bed. This pattern is more consistent with *Tribrachidium* individuals that are only slightly closer than average on a surface, with the majority of the pattern showing “general randomness” (Fig. 10C). This is a similar distribution to the juvenile *Aspidella* community on bed STC-AB, which also shows general randomness. The *Tribrachidium* and the STC-AB *Aspidella* dominate their respective bed surfaces and are relatively uniform in body size. This “general randomness” is likely a function of dispersal, while more mature communities show *Aspidella* to be reproducing continuously and competing with one another as they grow,

explaining the differences between mature and immature communities, *Tribrachidium* requires exploration.

The current consensus is that *Tribrachidium* reproduced seasonally, thus living in single generational groups (Hall et al. 2015). The general randomness found could be a function of a cohort establishing itself on a relatively profitable substrate. As *Tribrachidium* is considered to be an ecological generalist, living at a range of depths, it is likely that they were able to establish dominance over a relatively free surface (Hall et al. 2015; Rahman et al. 2015).

In order to test if the general randomness was a function of reproduction, and if the population was a single cohort, marked SPPA methods were used. Results showed that the *Tribrachidium* locations on 1T-T are completely independent of their size. Size-independence among *Tribrachidium* on bed 1T-T supports Hall et al. (2015) argument that *Tribrachidium* reproduced via seasonal/opportunistic sexual reproduction. If they had continuous reproduction there would be size variance visible in the pattern, as shown on the *Aspidella* bed TC-MM2.

Finally, highly aggregated *Tribrachidium* would likely affect their ability to feed if the Rahman et al. (2015) hypothesis of passive suspension feeding is true. If highly aggregated, like *Aspidella* or *Obamus*, *Tribrachidium* in the center of clusters would be less likely to gain nutrients, as exterior individuals would affect current/nutrient distribution. This would also result in a pattern of large *Tribrachidium* being relatively closer to small ones, with the larger individuals impeding the smaller. However, our

finding of a general randomness in distribution and independence of size supports the passive suspension feeding hypothesis. When distributed in a generally random pattern, the *Tribrachidium* were able to have a higher chance of securing nutrients via currents as an individual's neighbor would be less likely to directly compete.

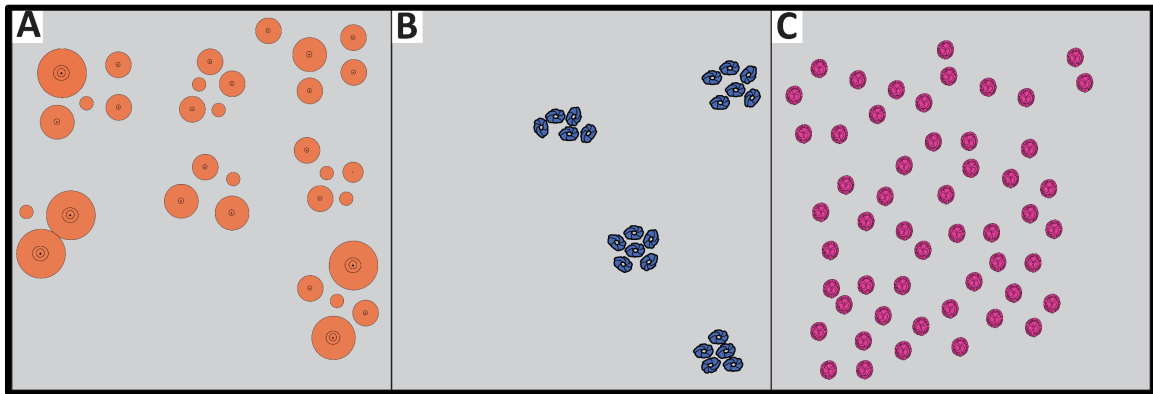


Figure 10. Simplified distribution of *Aspidella*, *Obamus*, and *Tribrachidium* populations. **A)** *Aspidella*, when able to mature, are distributed in multi-generational segregated cohorts. In more mature populations there are also examples of larger *Aspidella* being closer together as they continue to grow and compete spatially. **B)** *Obamus* populations are in hyper-aggregated groups that are segregated from each other. **C)** *Tribrachidium* are generally random, with certain individuals closer or further away than a true uniform distribution. This general randomness confirms preexisting hypotheses on their seasonal reproduction and filter feeding.

FUTURE WORK

In order to expand on and test the work presented in this thesis, future work is required to increase the number of beds, taxa, and facies examined at Nilpena. Completion of the logging and measuring of *Aspidella* on bed WS-MAB (PLURS facies) is the most pressing work required. Analysis of the beds after the statistical analysis and data collection of *Aspidella* on WS-MAB was hampered as a result of the COVID-19 pandemic. In particular, WS-MAB, which has a large variation of individual sizes (2-17 cm), is vital for determining more biologically relevant *Aspidella* cohort sizes. Additionally, this bed will allow for *Aspidella* SPPA to be tested in different facies. The

Obamus community on Nilpena’s flagship bed, TB-ARB, needs to be logged and tested in order to determine if the hyper-aggregation on LV-FUN is not an outlier.

Tribrachidium communities on WS-TBEW need to be measured and SPPA analysis needs to be conducted. Finally, beds dominated by different taxa and multiple taxa need to be examined to determine how spatial variability changed by taxon, bed, and facies at Nilpena (Table 2).

Table 2. Proposed Nilpena beds and taxa to be examined using SPPA.				
Bed	Area (m²)	Taxa being examined	Facies	Total Number of Genera per Bed
1T-F	23.4	<i>Aspidella, Coronacollina, Parvancorina, Rugoconites</i>	ORS	14
1T-LS	1.4	<i>Aspidella, Coronacollina</i>	ORS	7
1T-NA	4.1	<i>Aspidella, Rugoconites</i>	ORS	12
SE-Rugo	3.7	<i>Rugoconites</i>	ORS	7
STC-I	15.4	<i>Aspidella, Rugoconites</i>	ORS	7
STC-ARB	8.6	<i>Obamus</i>	ORS	11
TB-Duck	4.9	<i>Funisia</i>	ORS	4
TC-MM3	19.7	<i>Aspidella, Intridges, Tribrachidium, Rugoconites</i>	ORS	3
TC-MM4	20	<i>Aspidella</i>	ORS	6
TC-MM5	10.4	<i>Aspidella, Intridges</i>	ORS	8
WS-MAB	3.3	<i>Aspidella</i>	PLRUS	3
WS-Parv	7.5	<i>Parvancorina</i>	PLRUS	9
WS-Sub	3.9	<i>Coronacollina</i>	PLRUS	10
WS-TBEW	3.5	<i>Tribrachidium</i>	PLRUS	8

CONCLUSIONS

Results presented here demonstrate that certain Ediacara taxa are distributed in similar spatial patterns as modern marine invertebrates. *Aspidella*, *Obamus*, and *Tribrachidium* populations all showed some form of spatial aggregation, however each

taxon and community varied depending on preservation, ecology, and biology. *Aspidella* are spatially limited by an external factor, likely related to taphonomic bias, and are preserved as spatially segregated clusters of individuals that vary in size/maturity. *Aspidella* also show signs of intraspecific competition/spatial thinning, with smaller individuals being aggregated and larger ones being more spatially random. *Obamus* populations are hyper-aggregated, not as a function of external factors (taphonomy, environmental heterogeneity, competition), but as a result of their reproductive method. Finally, *Tribrachidium* are less aggregated than any other taxa examined here to the point that they can be considered randomly distributed. This is a result of their dominance over bed surfaces, cohort style reproductive method, and lack of statistically significant spatial thinning. These results show that SPPA is a viable technique for analyzing the spatial distributions of taxa excavated and housed at Nilpena. However, it is imprudent to assess the biological and ecological traits of an entire taxon the distributions of a few select communities. Further work is required at Nilpena in order to more rigorously assess the true spatial dynamics of these early animals.

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