Bridging the Gap:

An Ecological and Morphological Analysis on the California Margin

Expanding SPORE into the Infaunal Realm

By

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Realm

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Title of Study: Bridging the Gap: An Ecological and Morphological Analysis on the California Margin Expanding SPORE into the Infaunal Realm

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Abstract: Benthic foraminifera have been widely used by paleoceanography to assess changes in ocean conditions over geologic time. The distribution, abundance patterns, and morphological characteristics of modern benthic foraminifera can serve as modern analogs that allow interpretations within the paleo-realm. This study seeks to explore the ecological significance of pores in epifaunal and infaunal benthic foraminifera as a biological proxy for deep-sea paleo-oxygen. Expanding on the previous work of Rathburn et al., 2018, this study conducts an ecological analysis of four sites within the Southern California Bight. Finding appreciable amounts of shallow infaunal and epifaunal species commonly found at the boundary of oxic and dysoxic waters consistent with the TROX model. With bottom water oxygenation spanning 0.533ml/l to 1.274ml/l, this environment supported populations of *Bolivina spissa, Rosalina bradyi, Hoeglundina elegans*, along with many taxa from the *Reophax* and *Globobulimina* genera. Selecting the most abundant infaunal species, *B. spissa*, SPORE analysis was performed alongside living and dead populations of *Cibicidoides wuellerstorfi*. Similar trends to those published in Rathburn et al. (2018) in both species. Variations in SPORE between living and dead individuals varied only slightly, indicating that at least locally, dead individuals can reflect bottom water conditions in a similar way to living individuals. These findings suggest that the SPORE methodology is effective for studying both living and dead populations of *C. wuellerstorfi*. It was found that *B. spissa* show a similar, though less pronounced, inverse relationship to bottom water oxygenation consistent with *C. wuellerstorfi*, fitting expectations as a shallow infaunal species, much more tolerant to low oxygen conditions. Downcore, however, did not follow our expectations. SPORE values decrease with increasing depth within the sediment. Specific pore water geochemistry was not available for this study and could hold key insights into these observed trends. Further research is currently being conducted examining *B. spissa* both downcore and on average across a wider oxygen gradient. These works will continue to bolster the established *C. wuellerstorfi* data and begin to expand on these initial insights observed in this study.

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CHAPTER I

INTRODUCTION

Benthic foraminifera make up the most significant proportion of deep-sea biomass in the world (Thomas et al., 2007; Gooday et al., 1992; Jorissen et al., 1995) and due to their cosmopolitan distribution, high sensitivity to geochemical changes in their environment, and extensive geologic record, foraminifera are highly useful as indicators of both current and past bottom water conditions. They have historically been used as proxies for temperature, productivity, bathymetry, and oxygen concentration in both the bottom and pore-waters (Gooday, 2003). Current geochemical proxies, such as I/Ca ratios and $\delta^{13}C$, provide insights into the oxygen content of pore waters and the carbon flux to the seafloor that has been shown to vary with depth in the sediment (McCorkle et al., 1990) and may not accurately reflect the true bottom water conditions. Proxies involving microfossils typically include both epifaunal and infaunal taxa, which live at the sediment-water interface and within the upper 10 cm of sediments, respectively (Corliss, 1990). This, in addition to other variables, such as productivity in the ecosystem, makes it difficult to disentangle the actual influence of bottom water oxygen on extant foraminiferal taxa. A more precise, direct link between benthic foraminifera and bottom water oxygen levels could lead to a better understanding of the increasingly

deoxygenated, modern benthic ecosystem (Jaccard, 2011) and would enable a more accurate interpretation of the fossil record. The goal of this project was to examine the ecology of foraminifera collected at a variety of low-oxygen environments off the coast of San Diego and document any relationships between the ecology, sediment grain size, and bottom-water oxygenation to assess the commonly held paradigm that epifaunal foraminifera require a well oxygenated environment to thrive. Epibenthic foraminifera are typically found in locations with high oxygen levels and sufficient productivity (Jorissen, 1999). However, some can occasionally be found in areas with a much lower oxygen level than is typical (Venturelli et al., 2018; Burkett et al., 2016). This study examines the relationship between grain size, available oxygen, presence of epibenthic foraminifera species, and morphologic characteristics of foraminifera tests. We also expand on the work done by Rathburn et al. (2018) in analyzing a new proxy hypothesizing that pore size and abundance in the penultimate and antepenultimate chambers are inversely related to bottom water oxygen concentrations (called SPORE, Surface PORE percentage). The results of this study add more data to support an already very promising proxy and the prevalence of both extant and extinct foraminifera species allow these new findings to be applied to many different environments, both modern and past.

Background

Foraminifera

The efficacy of interpreting marine paleo-environments using fossilized benthic foraminifera relies heavily on an accurate interpretation of the factors that control the

habitat of modern, extant foraminifera. The habitat where benthic foraminifera are commonly found can be divided into two separate microhabitats: epifaunal and infaunal. An epifaunal microhabitat includes elevated substrates (where the foraminifera can be attached to substrates that rise above the sediment-water interface), the sediment surface itself, and within the first centimeter of sediment (Jorissen et al., 1992). Foraminifera are also found deeper within seafloor sediment. They are most commonly found in the upper 5 cm but can occasionally be found as deep as 20 cm (Corliss, 1985). The microhabitat from 1 cm to infinity is referred to as an infaunal microhabitat. The flux of organic matter to the seafloor and the amount of available oxygen in bottom waters are considered to be the primary controls on the regional distribution and abundances of foraminifera which can be seen in the common microhabitat distributions of species observed with depth in the sediment (Van Der Zwaan et al., 1999). Epibenthic foraminifera are thought to require a high amount of oxygen as well as high quality food (e.g., fresher phytodetritus, Jorissen et al., 1995). Thus, the presence of certain epibenthic foraminiferal species has been used as an indicator of high oxygen content, a high amount of productivity, or some combination of the two (e.g., Jorissen et al., 1995, Fig. 1).

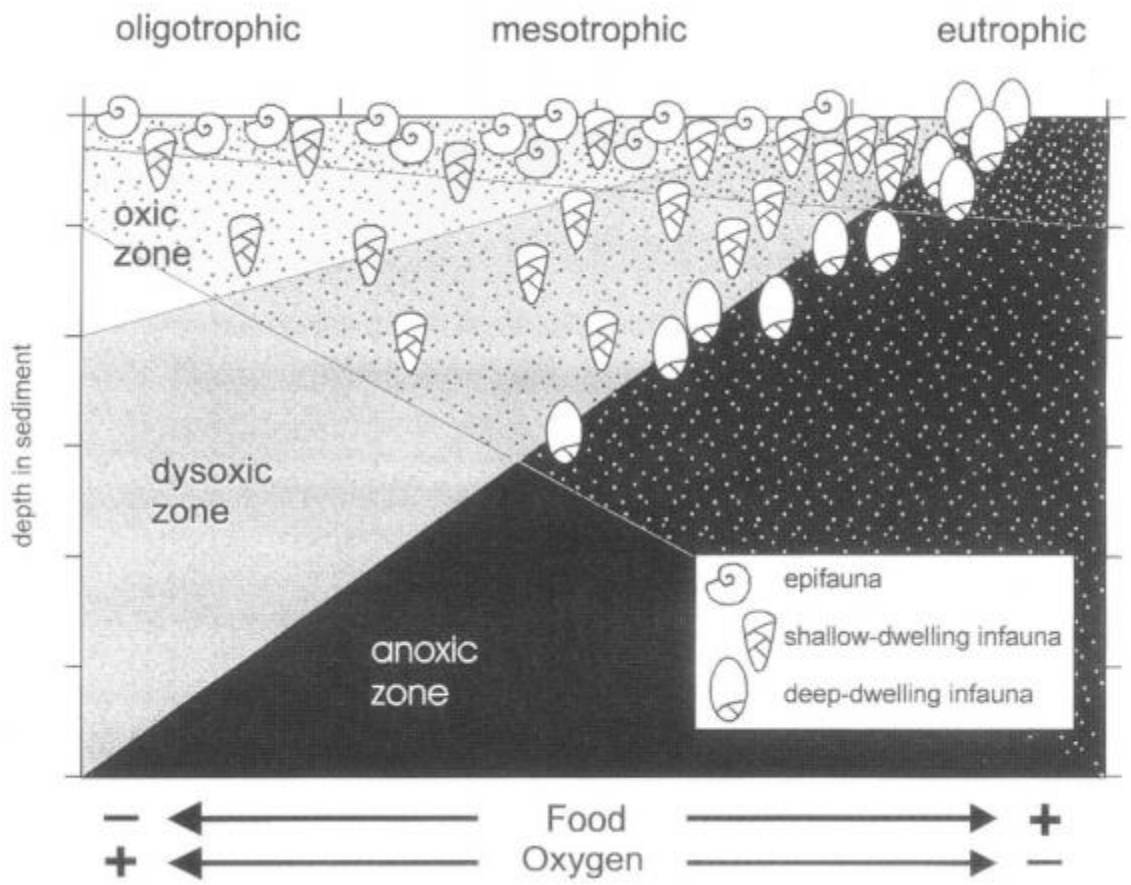


Fig 1 TROX-model (Jorissen, 1999) illustrates the microhabitat depth of epifaunal and infaunal taxa across different environments of variable food and oxygen.

It is important to determine exactly where these different microhabitats exist beyond the sediment-water interface. Jorissen et al. (1995) was one of the first studies to define microhabitats beyond just the upper centimeter of sediment by creating the TROX-model which is the microhabitat explained in terms of TRophic conditions and Oxygen concentrations. This study determined the average living depth (ALD) for a variety of foraminifera in their study area to quantify the vertical distribution within seafloor

sediments of the populations. Average living depth is defined as:

$$ALD_x = \sum_{i=1,x} \frac{n_i d_i}{N}$$

Where x is the depth of the deepest layer, ni is the number of foraminifera of the species in question in the ith sediment interval, di is the depth midpoint of the ith sediment interval, and N is the total number of individuals in all intervals.

Microhabitats and their Relationship to C and O2

It is commonly agreed that both oxygen and food quantity and quality strongly influence the foraminifera present in a microhabitat (Gooday, 1986). However, disentangling these two variables is very difficult as they are so highly interdependent. Oxygen is necessary in the metabolic processes involved in phytodetrital consumption thereby decreasing the oxygen available in the system when organic carbon is consumed. Therefore, differentiating which is the primary controlling factor determining the maximum depth at which foraminifera will be found, is still not clear (Jorissen et al., 1995). Strong correlations between benthic foraminifera and a single variable are only present under extreme conditions where a single variable is the limiting factor (Thomas, 2007). In oligotrophic systems, where there are higher oxygen levels and more scarce food resources, the food becomes the critical factor (far left of Fig. 1). Whereas when the system becomes more eutrophic, oxygen decreases as food increases and the lack of oxygen limits the system (Jorissen et al., 1995). Jorissen et al. (1995) demonstrated why there is a positive relationship between organic flux and the microhabitat depth in oligotrophic systems while that same relationship is negative in eutrophic systems. As the

benthic environment shifts from oligotrophic to more eutrophic (going from the far left to far right of Fig. 1), the infaunal microhabitat shallows and the percentage of infaunal foraminifera may increase. In oxygen-controlled systems though, the same microhabitat shallows as the less resistant epifaunal foraminifera begin to disappear from the system and the infaunal niche narrows, shifting up toward the sediment-water interface (the right side of Fig. 1). At what level oxygenation of the system becomes the primary limiting factor is still difficult to define because there are very few proxies to document only oxygenation. New geochemical proxies such as I/Ca and $\Delta\delta^{13}C_{epi\text{-}infauna}$ may only describe pore water oxygenation or global ocean oxygenation (Rathburn et al., 2018; Lu et al., 2020). While it is understood that oxygen is the limiting factor when there is little to none available as soon as there are oxic bottom water conditions, as well as some penetration beyond the sediment-water interface, other factors, such as the availability and quality of food, are likely to become the primary limiting factor (Murray, 2006).

Jorissen, (1999) went on to describe the shape of these microhabitats based on the vertical distribution of the species (Fig. 2). There were four vertical distribution patterns that were commonly found. The first type, Type A, exhibited a clear population maximum near the sediment-water interface and dropped off quickly after 1 cm (Fig. 2, far left). Taxa that exhibited a Type A distribution were termed epifaunal, or shallow infaunal, and while there was a sharp drop off in population numbers after 0.5 to 1 cm, these taxa are rare or entirely absent in the intervals below (Jorissen, 1999). Type B distributions show similar maximum densities through several successive layers of the upper sediment (Fig. 2, second from left). Taxa that typically show these patterns are considered shallow infaunal foraminifera. These distributions are more common in

shallow water, coarse grained systems and are relatively rare in deep-sea environments where there is greater variability in pore-water characteristics closer to the sediment-water interface (Jorissen, 1999). Type C profiles show one or more subsurface maxima in foraminiferal populations with low values near the sediment water interface (Fig. 2, second from right). These taxa tend to thrive in the low oxygenated, deeper sediments, the cause of which is still unclear (Jorissen, 1999). The final profile, Type D, exhibits one or more subsurface maxima along with a surface level maxima and again, are currently poorly understood (Fig. 2, far right).

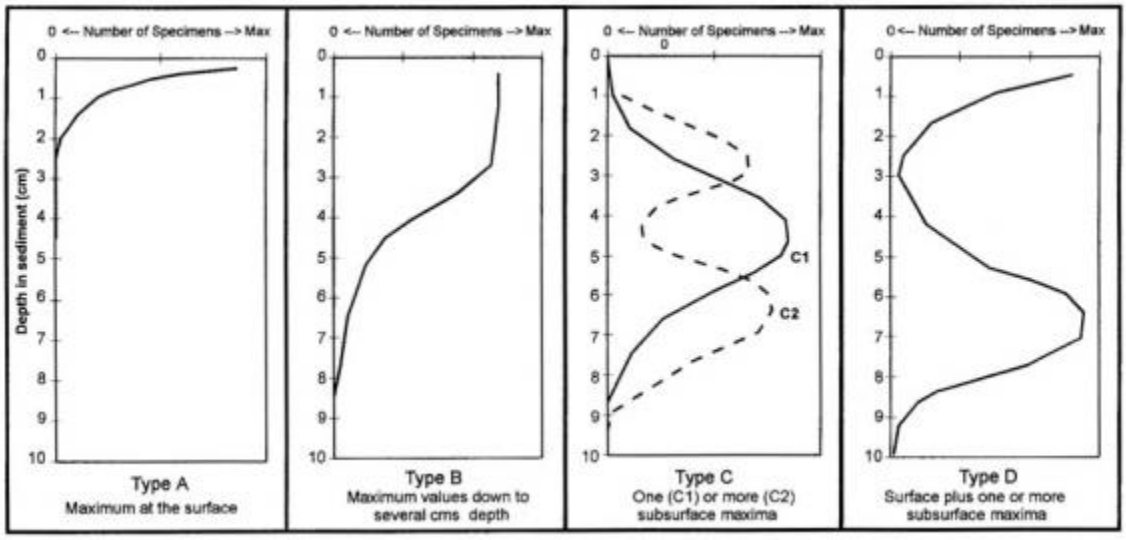


Fig 2 (Jorissen, 1999) Four quantitative vertical distribution types of benthic foraminifera. See above for details.

Foraminiferal Pores and O_2

With an increasingly deoxygenated benthic ecosystem, more sensitive proxies are needed to study the ancient deep ocean bottom water conditions. Understanding deoxygenation events of the past can better inform climate scientists about our current ecosystems and lead to better projections of future events. However, most current geochemical proxies

lack the sensitivity needed to accurately interpret bottom water oxygenation at the local level. I/Ca ratios and $\delta^{13}C$ are valuable redox proxies but interpretations of both are limited by complicated pore-water chemistry (Taylor et al., 2017). Traditional ecological studies that solely focus on microfossil assemblages may also not give an accurate picture of bottom water oxygenation. The focus on presence/absence data of various epifaunal taxa in these traditional studies limits their usefulness as epifaunal taxa, such as *Cibicidoides wuellerstorfi*, which have been found in environments with a wide range of bottom-water oxygenation (Venturelli et al., 2018). These studies often include infaunal taxa residing in pore waters with much different geochemistry than the bottom water only a few centimeters above (Jorissen, 2007). These indicator taxa also have a much more complicated relationship between the oxygenation of the system and the availability of the food, as described in the section above. This makes it difficult to isolate changes in oxygenation as the sole influence of any of these proxies.

New insights into benthic foraminifera and pores of their tests have led to the development of a proxy with the potential of describing bottom water oxygenation at the time of development of an individual's ultimate and penultimate test chambers. This proxy was developed by examining elevated epibenthic species of foraminifera, specifically *Cibicidoides wuellerstorfi*. Elevated epibenthic taxa are separated from standard epibenthics by their attachment to rocks and other substrates elevated above the sediment-water interface (Jorissen, 1995). There is much less risk that these species will be influenced by oxygen gradients within the upper layers of deep-sea sediments, given that they do not live on or within the sediments (Rathburn, 1994; Rathburn et al., 2018). Epifaunal foraminifera are typically the first to disappear as oxygen levels decrease

(Fig. 1; Jorissen, 1995). *Cibicidoides wuellerstorfi* was specifically selected due to its abundance in a variety of environments, including well-oxygenated systems and systems that have increasingly low amounts of oxygen (Burkett et al., 2016; 2020, Venturelli et al., 2018). Recent experimental substrate deployments have demonstrated that *C. wuellerstorfi* is capable of occupying environments with available oxygen as low as 0.04 ml/l (Burkett et al., 2016; Rathburn et. al., 2018; Lu et al., 2020).

The pores of calcareous foraminifera are important morphological features. The characteristics of these pores have served as an important diagnostic feature in several species (Lutze, 1986). The size and abundance of pores change between both species, and individuals within the species, in different environments (Rathburn et al., 2018). In the chambers of tests grown in oxygen-poor laboratory conditions, foraminifera have been found to develop larger pores with a greater relative pore to test surface area than foraminifera that were cultured in higher oxygen conditions (Moodley and Hess, 1992). Even though our understanding of the function of these pores is incomplete, it has more recently been shown that cell organelles involved in respiration, such as the mitochondria, were more abundant near pores in species that were especially low oxygen tolerant (Bernhard et al., 2010). These observations suggest a linkage between the pores of benthic foraminifera and the respiration of these organisms. Rathburn et al. (2018), demonstrated that pore area percentage in *Cibicidoides wuellerstorfi* is correlated with the bottom-water oxygenation of its environment. However, a down-core study of this proxy has yet to be established. In an environment with variable oxygen conditions, it could be possible to assess changes in bottom water oxygenation as reflected in the pore percentage of foraminifera through time (e.g., down-core). There are several factors that

could make interpreting the record difficult as epifaunal foraminifera, such as *Cibicidoides wuellerstorfi,* are the first species that are expected to disappear as available oxygen decreases (Jorissen et al., 1995). So, even though *Cibicidoides wuellerstorfi* can live in very low oxygen environments (Burkett et al., 2016; Venturelli et al., 2018), they are still not nearly as prevalent as many of the shallow infaunal foraminifera tolerant of lower oxygen conditions. It is for this reason that *C. wuellerstorfi* must be paired with a shallow infaunal species to enable continuous interpretation of bottom-water oxygenation even as *C. wuellerstorfi* disappears in increasingly deoxygenated environments. This study will focus on the shallow infaunal foraminifera *Hoeglundina elegans* and *Bolivina spissa* as potential species to be used in conjunction with *C. wuellerstorfi* in further developing this oxygen proxy connecting shallow infaunal foraminifera.

It has been shown by Glock et al. (2011) that the pore densities in *Bolivina spissa* reflect changes in bottom-water oxygenation in very anoxic conditions but as oxygen values increase, pore densities level out. It is also hypothesized that the pores reflect the intracellular nitrate levels in *B. spissa* (Glock et al., 2011), which could potentially convolute interpretations using this species. *Hoeglundina elegans*, however, has not been studied in this capacity. It typically has a Type B vertical distribution pattern and is present where pore-water geochemistry remains relatively stable in the upper few centimeters of sediment (Jorissen et al., 1995). Either *B. spissa* or *H. elegans* could allow us to link this pore density proxy where both *C. wuellerstorfi* and either of these species are present and their pores are potentially varying with oxygen concentrations to interpret down-core pore records. Furthermore, *H. elegans* has been proposed to be more of an epifaunal, rather than shallow infaunal species preferring to live on the surface of the

sediments (Venturelli et al., 2018). If this is the case, it may be expected to have less influence from pore-water chemical conditions and more consistency with bottom-water oxygenation.

Relationship to Grain Size

Foraminiferal microhabitats have traditionally been defined using the depth to which certain taxa penetrate below the sediment-water interface (Jorissen et al., 1999). Defining whether a certain species is epibenthic or shallow infaunal can be more straightforward when the bottom-water sediments include larger grain sizes where the epifaunals are clearly differentiated from infaunals as they are attached to the larger grained, and sometimes elevated substrates (Murray, 2001). The epibenthic fauna are typically only present in the first few millimeters of sediment in these cases. Below that, shallow infaunals and deep infaunals living in the sediment can typically be found. This easily identifiable boundary becomes less clear as moving to environments with soft-bottom substrates (Buzas et al., 1993). This boundary becomes even more difficult to discern in soft-bottom substrates as it is common practice to slice samples at 0-1 cm and then half centimeter intervals from there onward. This is due to the difficulty of separating and containing these muddy, unconsolidated sediments in half centimeter intervals at the top of collected cores.

It has been shown, based on high abundances and high diversity of benthic foraminifera in coarse grained sediments, that these environments are suitable for the success of these organisms (Schonfeld, 2002; Diz et al., 2004; Venturelli et al., 2018).

However, benthic foraminifera can be abundant in environments with higher proportions of fine grained sediments (Debernay et al., 2001). Suggesting that the grain size of the environment does not play as important a role in the abundance of benthic foraminifera as other more relevant factors, such as food availability or oxygen. However, it has been more recently found that epibenthic foraminifera, specifically *C. wuellerstorfi*, which typically prefer well oxygenated environments, can still be found in environments with nearly anoxic conditions (Burkett et al., 2016; 2020; Venturelli et al., 2018). It was found that there were elevated densities of epibenthic taxa in increasingly oxygen-poor habitats with coarser grained sediments (Venturelli et al., 2018). Similar discoveries were made when looking at the influence organic matter had on systems. Grain size was found to play a larger role in overall foraminiferal density and species richness than organic matter (Schonfeld, 2002; Chalet, 2009). However, Chalet (2009) found that there were elevated densities as well as higher species richness in areas with smaller grain sizes. These studies demonstrate that while the quantifiable effect that grain size has on foraminiferal abundances is unclear, grain size still plays a more important role in the distribution of epibenthic taxa than previously thought.

Geologic Setting

The Southern California Bight extends 462 miles from Point Conception in California south to Punta Colonet in Baja California, Mexico, and includes coastal southern California, the Channel Islands, and the local Pacific Ocean out to San Nicolas Island (Fig 2). The seafloor of this region is characterized by 13 basins that trend northwest-southeast and are separated by elevated ridges, sills, and islands that run parallel to both the basins and shoreline (Emory, 1960). The major surface current is the

California Current which runs south eastwards along the continental slope, while the California Countercurrent runs northwestwards along the shoreline. These opposing currents create eddies throughout the bight among the basins. Terrigenous sediments are prevalent in this system and are subject to seasonal runoff (Gorsline et al., 1984).

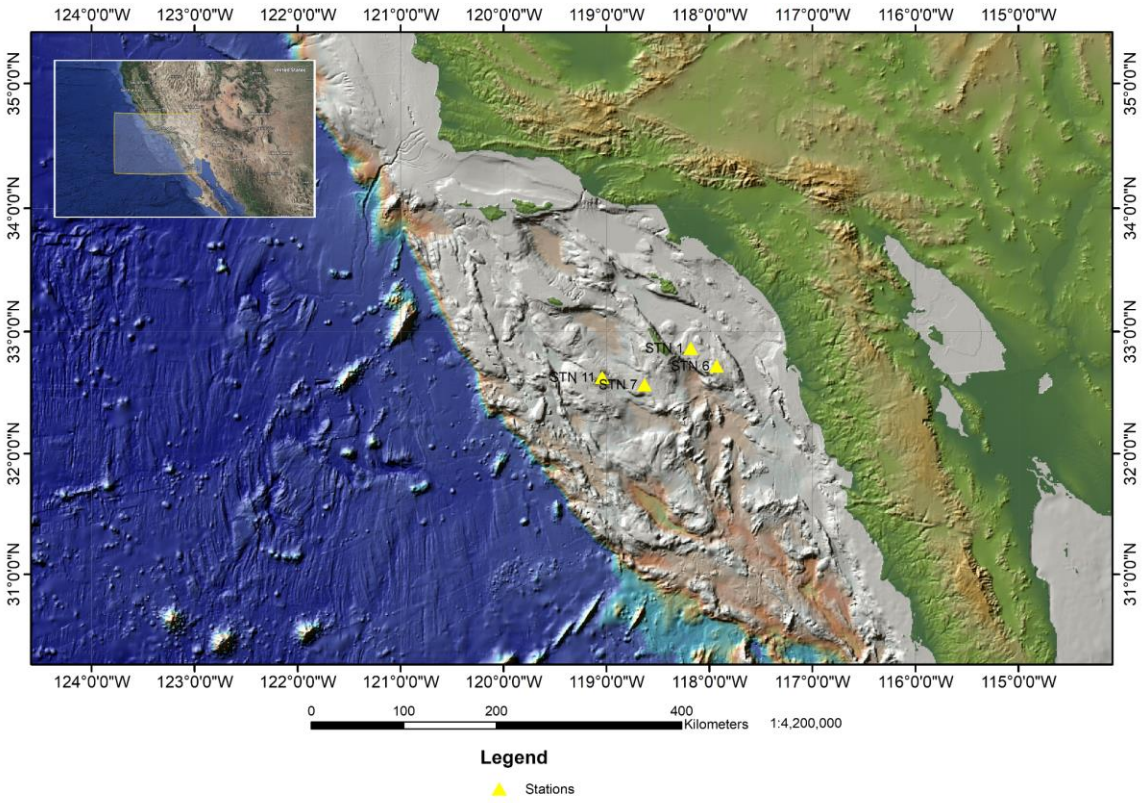


Fig 3 Map of the Southern California Bight with points to indicate core locations.

Objectives of this Thesis

Using materials from the coast of California, the following hypotheses were assessed:

1. Benthic foraminiferal ecology will vary with grain size, bottom-water oxygen, and water depth in ways that are consistent with explanation using the TROX model.
2. Average living depth calculations will show vertical distribution patterns consistent with those observed by Jorrison et al. (1999) and are likely to have been the results of subsurface geochemical gradients.
3. *C. wuellerstorfi* collected within the first three centimeters of samples will be used in SPORE analyses and these results will fill in gaps in our existing record of pore and oxygen data published in Rathburn et al. (2018).
4. Scanning Electron Microscope (SEM) images of shallow infaunal species will demonstrate significant pores, which can be utilized in the SPORE analyses and ultimately correlated with bottom water oxygen towards the development of a quantitative oxygen proxy. These specific hypotheses below will be tested:
    a. *Bolivina spissa* will have significant pores.
        i. B*olivina spissa* will have a variable number of pores in high and low oxygen locations.
    b. *Hoeglundina elegans* will have significant pores.

i. *Hoeglundina elegans* will have a variable number of pores in high and low oxygen locations.

CHAPTER II

ECOLOGIC ANALYSIS

Introduction

Oxygen availability plays a crucial role in marine ecosystems and biogeochemical processes, influencing oceanographic and biogeochemical conditions that can result in the formation of oxygen minimum zones (OMZs) in ocean margins. These zones are characterized by low oxygen concentrations, high organic carbon content, fine-grained sediments, and low bioturbation near the seafloor. Despite the limitation posed by oxygen-poor conditions, OMZs are home to many organisms, including benthic foraminifera, are sensitive to environmental changes and useful in studying deep-sea environments. Understanding the effects of oxygen-depleted environments on benthic ecosystems becomes increasingly crucial as climate change and eutrophication lead to the expansion of OMZs in terms of both size and distribution (e.g., Keeling & Garcia, 2002; Helly & Levin, 2004; Stramma et al., 2008; Meier et al., 2011).

Food availability is the second of two key factors that influence the distribution and abundance of benthic foraminifera. However, the relationship between oxygen and food availability is complex, as they are often inversely related, making it difficult to

determine which factor is more important for some species. Despite this complexity, it is well known that calcareous benthic foraminifera can thrive in oxygen-poor environments in the modern ocean (e.g. Venturelli et al., 2018). As a result, many studies have been conducted to investigate the relationship between benthic foraminifera and environmental parameters in low-oxygen conditions.

To infer the ecological preferences and environmental limitations of deep-sea foraminifera, researchers have analyzed distribution patterns of foraminiferal specimens collected from core tops (Murgese et al., 2005). For example, several studies have used foraminiferal species or groups of taxa to assess bottom water oxygen concentrations, with epifaunal taxa like *Cibicidoides* often considered as indicators of well-oxygenated environments (Kaiho 1991, 1994, 1999). Conversely, many infaunal taxa dominate oxygen-poor habitats and are considered indicators of low-oxygen environments. This is sometimes referred to as the Benthic Foraminiferal Oxygen Index (BFOI), which groups benthic foraminiferal species into oxygenic indicator categories based on their habitat preferences (Ref). In this index, epifaunal taxa like *Cibicidoides*, are regarded as oxic indicator species, while many infaunal taxa are considered indicators of low-oxygen environments.

Materials and Methods:

The *R/V Sally Ride* was used to collect ocean samples, including water column data and seafloor sediments, during Expedition SR1807 from June 1st to June 4th, 2018. Three different locations were selected around the Southern California Bight, on the edge of the oxygen minimum zone (OMZ) based on the oxygen content of the bottom waters: an

anoxic, dysoxic, and oxic environment. In this case, we will be following the definitions laid out in “Modern Foraminifera" (Sen Gupta, 2007) to describe oxygen conditions. Environments with O_2 values >1.0ml/l (44.658 µmol/l) will be considered oxic; O_2 values from 0.1 - 1.0ml/l (4.4658 - 44.568 µmol/l) will be considered dysoxic; O_2 values less than 0.10ml/l (4.4658 µmol/l) will be considered anoxic. An Ocean Instruments MC-800 Multicore was used to collect seafloor cores with an intact sediment-water interface from the stations shown on Figure 3. These cores were sectioned in a 1 cm interval from 0-1 cm, and in half centimeter intervals down to 3 cm (i.e. 1-1.5, 1.5-2, 2-2.5, 2.5-3). All cores were then frozen in a -80 degree Celsius freezer in order to preserve living tissue for later Rose Bengal staining and shipped to Oklahoma State University.

Conductivity, temperature, and depth (CTD) profiles of the water column were completed at all stations examined (Stations 1, 6, 7, and 12). Salinity and temperature values were extrapolated from the CTD reports of these 4 sites. Oxygen values were derived from an average of all cores collected at the site using a handheld oxygen probe.

Frozen samples were split in half, weighed, and submerged in 4% formalin and the Rose Bengal solution and left to sit for a minimum of 7 days with occasional stirring to ensure even distribution of the stain. Rose Bengal is a passive vital stain which adheres to tissues and is commonly used to differentiate living/recently living from dead individuals. Sediment volumes were then calculated using the volumetric procedures outlined in Rathburn and Corliss (1994) and standardized to 50 ccs based on sample volumes. These samples were then wet sieved with 63 µm and 150 µm wire sieves to separate the smaller and larger specimens. Individual samples were kept in the 4% formaldehyde and Rose Bengal solution, along with a sprinkle of borax as a buffer, in order to preserve the

stained tissues needed to separate the living individuals from the dead. Upon picking, the stained sediment was rinsed in reverse osmosis water, placed in a petri dish, and examined under a microscope. Rose Bengal stained foraminifera were then picked from the sediment with a fine paintbrush and organized on micropaleontological slides in order to identify and quantify specimens. About 10 ccs of frozen core material not examined for foraminifera were dried out in an oven at 350 °F for about an hour and then packaged and sent to the Baylor University Geology Department for average grain size analysis.

A Malvern 3000 Hydroseries Particle Size Analyzer with Hydro EV instrumentation was used to measure particle size for each sample. Samples were air dried, crushed, and sieved. Particle size is cut off at 1 mm through sieving. Malvern Instruments use low-power lasers as light-scattering sources. The Malvern Hydroseries offers 52 detectors on one lens and can measure a wide range of particle sizes without fractionation of the sample (Callesen et al., 2018). The laser particle analyzer measures particles less than 3500 µm. Particles were distributed by size category, including fine clay (<0.01 µm), medium clay (0.01-2 µm), coarse clay (2-3.9 µm), very fine silt (3.9-7.8 µm), fine silt (7.8-15.6 µm), medium silt (15.6-31 µm), coarse silt (31-62.5 µm), very fine sand (62.5-125 µm), fine sand (125-250 µm), medium sand (250-500 µm), coarse sand (500-1000 µm), very coarse sand (1000-2000 µm), and fine gravel (>2000 and <3500 µm).

Samples were measured twice with three runs and the results were averaged over the six runs. The resulting Particle Size Distribution PSD, the average of three runs, represents the 0-1 mm fraction of the sediment sample. The result is expressed in volume percent, which is equivalent to the weight percent assuming uniform specific density

Vertical distribution patterns were plotted downcore to examine the microhabitat preferences of the predominant taxa identified at examination sites. Species abundances were standardized to the number of individuals per 50 cc of sediment due to differences in available, sampleable material. Ecological results were based on the >150 μm counts of living individuals down to 3 cm sediment depth, with splits following standard ecological studies of a 0 - 1 cm split, and half cm splits down through the rest of the core being studied.

As a measure of diversity the Shannon-Wiener Index, which is reported as the H-value and defined and given by the function below, and Species Evenness (E) were determined for each site.

$$H=-\sum[(pi)\times\ln(pi)]$$

In this equation, pi = proportion of total sample represented by species i. This is determined by dividing the number of individuals of species i by total number of samples.

S = number of species, = species richness

$Hmax=\ln(S)$ = Maximum diversity possible

E = Evenness = H/Hmax

Results

Oxygen

Bottom water oxygen (BWO) values of sites examined for this study ranged from 0.533 ml/l to 1.274 ml/l. Three of the four sites examined for this study sit near the boundaries of oxic and dysoxic classifications. Sites 1 and 6, at 863 m and 617.9 m deep respectively, straddle that classification boundary at 0.9065 ml/l and 1.071 ml/l BWO. The highest BWO of at 1.274 ml/l was recorded at Station 7, just into the oxic range, and the lowest BWO of 0.533 ml/l was recorded at Station 12, well within the dysoxic classification.

The OMZ of the Southern California Bight has been reported to extend from water depths of 100 m to 900 m (McClatchie et al., 2010). For his study previously examined areas were targeted due to the high epifaunal populations reported throughout this OMZ.

Grain Size

Most samples ranged from the Silt to Sand range (3.9 to 2000 µm) with the exception of Station 1, which exhibited a coarse fraction of 1% fine gravel. Station 1 returned 26% silt, 72% sand, and 1% fine gravel. Station 6 had a distribution of 69% silt and 31% sand. Station 7 returned values of 14% silt and 86% sand. Station 12 had a distribution of 4% silt and 96% sand, making it, on average, the coarsest sample.

Standing Stock

The standing stocks of living (Rose Bengal stained) specimens were calculated for all sites as well as for each depth split (0 - 3 cm) individually. All 4 sites together averaged

1041.72 individuals/50cc (SD:370.88) of sediment. Station 6 has the highest standing stock of the four with 1450.71 individuals/50cc followed closely by Station 12 with 1370.13 individuals/50cc. Stations 7 and 1 had less than half at 713.12 individuals/50cc and 632.91 individuals/50cc. Maximum abundances of stained foraminifera of three of the four sites, Stations 6, 7, and 12, were all in the 0 - 1 cm sections of the collected cores and decreased with increasing depth within the sediment (Fig 5). Station 1 had two separate subsurface maxima at the 1 - 1.5cm interval and the 2 - 2.5cm interval. Station 12 exhibits a Type B microhabitat vertical distribution (Jorissen 1999), as described in Chapter 1, with a sharp decline in populations after the first few centimeters within the sediment. Station 7 exhibits closer to a type A distribution with foraminiferal populations falling off more consistently as you increase depth within the sediment. Station 6 exhibits a Type D distribution with surficial and subsurface maxima. Station 1 exhibits a Type C distribution with two separate subsurface maxima.

Stations 1 and 12 were dominated by shallow infaunal species such as *Bolivina spissa, Reophax dentaliniformis,* and *Bulimina pupoides* while Stations 6 and 7 were dominated by epifaunal and transitional species such as *Hoeglundina elegans*, *Rosalina bradyi*, and *Uvigerina peregrina*. Stations 1, 6, and 7 all had ~75% calcareous taxa compared to agglutinated, while Station 12, which was heavily dominated by *B. spissa* (70%), was 97% calcareous taxa.

Vertical Distributions

Cores from all four sites were picked down to three centimeters depth to examine vertical distribution patterns and microhabitat preferences in the >150 μm size fraction. The top five most abundant taxa were plotted against depth within the sediment for each site (Fig 4).

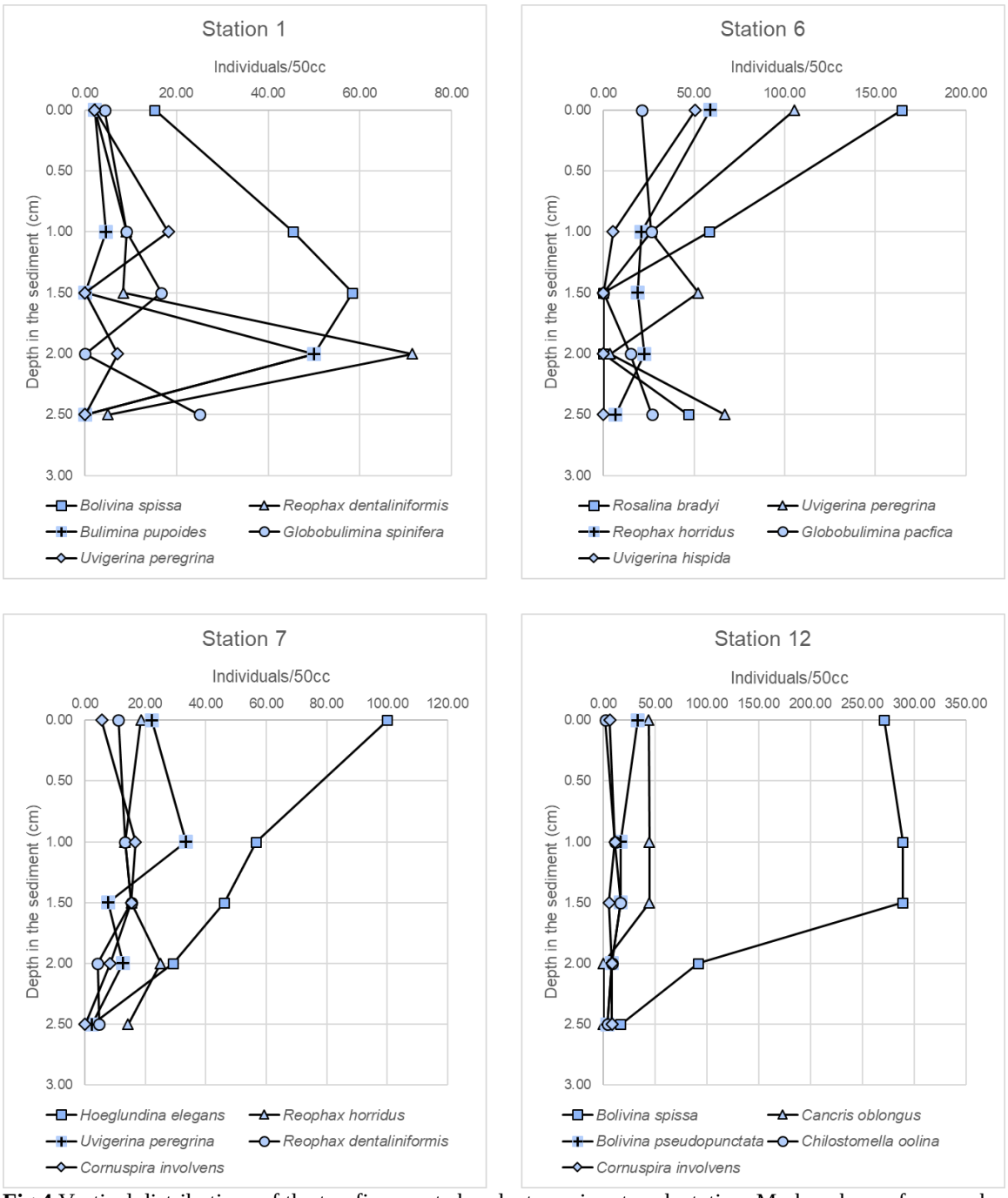


Fig 4 Vertical distributions of the top five most abundant species at each station. Marker shapes from each station represent the dominant taxa from each location rather than common taxa across sites. Marker points represent the upper half of a studied internal (i.e. the uppermost point represents the 0 - 1 cm interval, the next highest points represent the 1 - 1.5 cm interval, etc.).

Station 1, with a depth of 863 m, and comprised of 72% sand sized particles (62.5 - 2000 μm), was dominated by *Bolivina spissa, Reophax dentaliniformis, Bulimina pupoides, Globobulimina spinifera,* and *Uvigerina peregrina*. *B. spissa, R. dentaliniformis,* and *B. pupoides* all exhibited a Type C distribution pattern with low surficial abundances and one subsurface maxima. *B. spissa* had a maximum in the 1.5 - 2 cm interval while *R. dentaliniformis,* and *B. pupoides* both had maxima in the 2 - 2.5 cm interval. These three species had average living depths of 1.65 cm, 2.10 cm, and 2.10 cm respectively. *G. spinifera* and *U. peregrina* also both exhibited a Type C vertical distribution but had two subsurface maxima. Average living depths for these taxa were 2.02 cm and 1.45 cm respectively.

The five most abundant taxa at Station 6, at a depth of 617.9 m, and composed of 69% silt sized particles (3.6 - 62.5 μm), were *Rosalina bradyi, Uvigerina peregrina, Reophax horridus, Globobulimina pacifica,* and *Uvigerina hispida*. *R. bradyi* and *U. peregrina* both showed Type D distributions with maximum abundances at the sediment water interface, as well as one other local maxima further down core in the 2.5 - 3 cm section. *R. horridus* had a Type B distribution pattern with maximum abundances in the upper 2.5 cm of sediment before falling off in the 2.5 - 3 cm interval. *U. hispida* showed a Type A distribution pattern with maximum abundances in the upper 0 -1 cm split before decreasing quickly thereafter. *G. pacifica* doesn't fit neatly into any of the 4 Type distributions. It most closely resembles a Type C distribution with two separate maxima at the 1 - 1.5 cm interval and the 2.5 - 3 cm interval. Average living depths were 1.05 cm for *R. bradyi,* 1.45 cm for *U. peregrina,* 1.23 cm for *R. horridus,* 1.69 cm for *G. pacifica,* and 0.57 cm for *U. hispida*.

Station 7 had a depth of 1001 m and was composed of 86% sand. The five most abundant taxa were *Hoeglundina elegans, Reophax horridus, Uvigerina peregrina, Reophax dentaliniformis,* and *Cornuspira involvens*. At more than double any other individual taxa *H. elegans* exhibited a Type B distribution pattern with its maximum abundance at the sediment-water interface and only gradually decreasing moving downcore. *R. horridus* exhibited a Type D distribution pattern with maxima in the 0 - 1 cm interval and the 2 - 2.5 cm interval. *U. peregrina*, much like *G. pacifica* from Station 6 most closely resembled a Type C distribution pattern with two separate maxima at the 1 - 1.5 cm interval and the 2.5 - 3 cm interval. *R. dentaliniformis* and *C. involvens* exhibited a Type C distribution pattern with one subsurface maxima in the 1.5 - 2 cm and 1 - 1.5 cm intervals respectively. Average living depths were 1.17 cm for *H. elegans*, 1.72 cm for *R. horridus,* 1.29 cm for *U. peregrina,* 1.47 cm for *R. dentaliniformis,* 1.51 cm for *C. involvens*.

Station 12, with a depth of 328 m and composed of 96% silt, was dominated by *Bolivina spissa, Cancris oblongus, Bolivina pseudopunctata, Chilostomella oolina*, and *Cornuspira involvens*. *B. spissa* was by far the most abundant at this station with more individuals/50cc (956.94) than all other species combined (413.19). These taxa exhibited a very clear Type B distribution pattern with maximum abundances consistent down to 1.5 cm before falling off downcore. *C. oblongus* and *B. pseudopunctata* exhibited this same pattern but at much lower total abundances. Finally, *C. oolina* and *C. involvens* exhibited Type C1 and C2 distributions respectively. Average living depths were 1.31 cm for *B. spissa,* 1.17 cm for *C. oblongus,* 1.22 cm for *B. pseudopunctata,* 1.75 cm for *C. oolina, a*nd 1.73 cm for *C. involvens.*

Diversity

There were a total of 67 unique taxa identified across the four stations, 19 agglutinated species and 48 calcareous. Species richness was an average of 28 across all four stations with Station 6 having the highest species richness of 42 and Stations 1, 7, and 12 having 24, 25, and 21 respectively. Sites were not distributed very evenly with an average evenness value of 0.34. Stations 1, 6, and 7, had evenness values of 0.40, 0.41, and 0.37, respectively while Station 12 had a value of only 0.18 where *B. spissa* made up 70% of individuals at that site.

Shannon Diversity (H) was fairly consistent across the sites, outside of Station 12. Stations 1, 6, and 7 had diversity indices of 1.56, 2.97, and 2.42 respectively while Station 12 had a diversity index of 1.27.

Discussion

Results from this study can help improve our understanding of the ecology and habitats of benthic foraminifera and other organisms. The predicted expansion of oxygen deficient habitats due to global warming (Helly & Levin, 2004; Stramma et al., 2008; Meier et al., 2011, Falkowski et al. 2011, Jaccard et al., 2011) can be better understood by examining benthic environments that span these oxygen conditions. The stations studied here help provide information on these transitional zones as you move from oxic to dysoxic conditions. Three of the four sites are right at the delineation of the oxic and dysoxic boundaries with BWO values between 0.9 and 1.2 ml/l, while the fourth site sits within the dysoxic range at 0.5 ml/l. While replicate cores were not available and any

comparisons between other sites should be viewed with caution, these data provide useful clues to the benthic ecology in these zones.

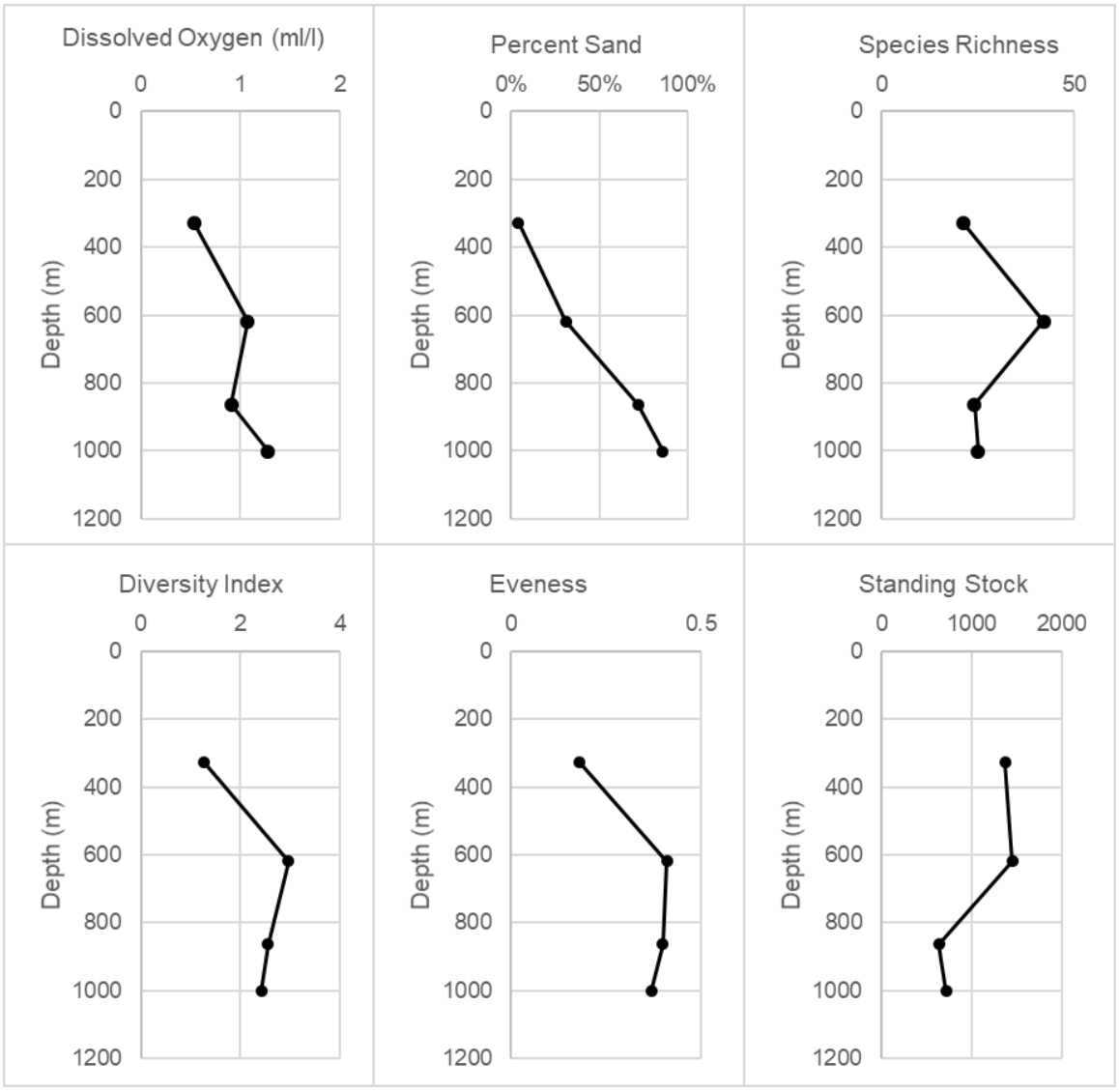


Fig 5 Dissolved oxygen, percent sand, species richness, foraminiferal diversity indices, evenness and standing stock abundances in relation to depth.

The populations of foraminifera in the surficial sediments were similar to other studies conducted in this area (Silva et al, 1996, Shepard et al., 2007, Venturelli et al., 2018). Total standing stock of studied sites generally decreased with depth (Fig 5) and showed

no correlation with BWO (Fig 6). However**,** there was an inverse correlation found between the grain size and the standing stock reported (Fig 7). Stations 6 and 12, with grain compositions being made of 69% and 96% silt, respectively, had standing stocks of around 1400 individuals/50cc while the remaining two stations, Stations 1 and 7, with grain sizes composed of 72% and 86% sand, reported standing stocks of about 700 individuals/50cc. While the high infaunal population counts at Station 12 could be attributed to *B. spissa* and plankton blooms, similarly to Station 1, as discussed above, the taxa present at Station 6 were the epifaunal and transitional infaunal species *R. bradyi, U, peregrina,* and *R. horridus*. So, this overall trend of increasing standing stock associated with a decrease in average grain size seems to be independent of the microhabitat preferences of the taxa present at each site.

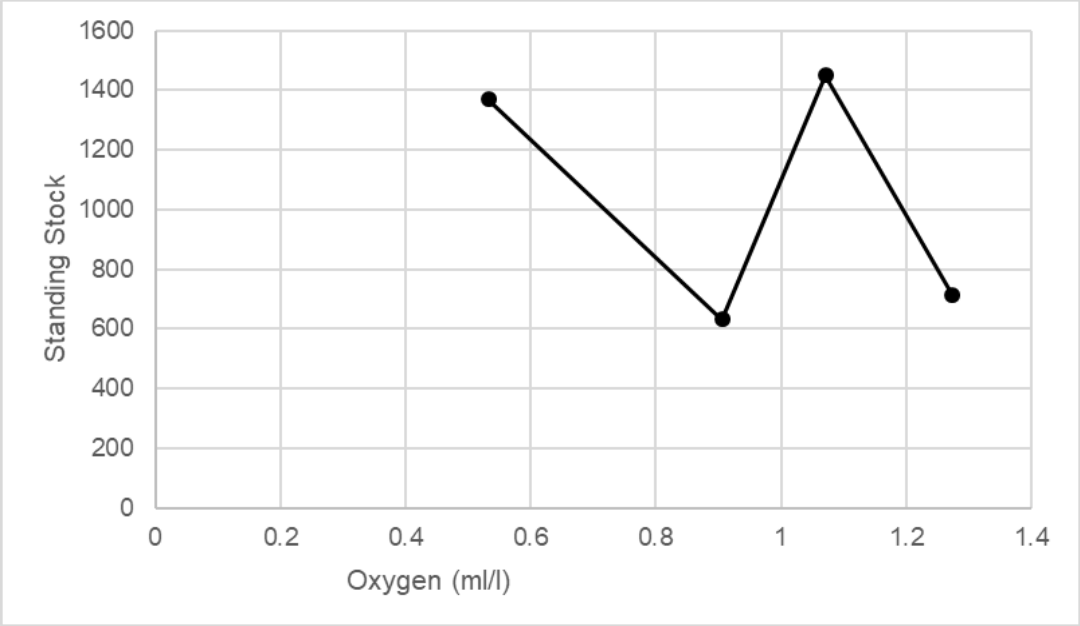


Fig 6 BWO oxygen values compared to overall standing stock abundances at each site.

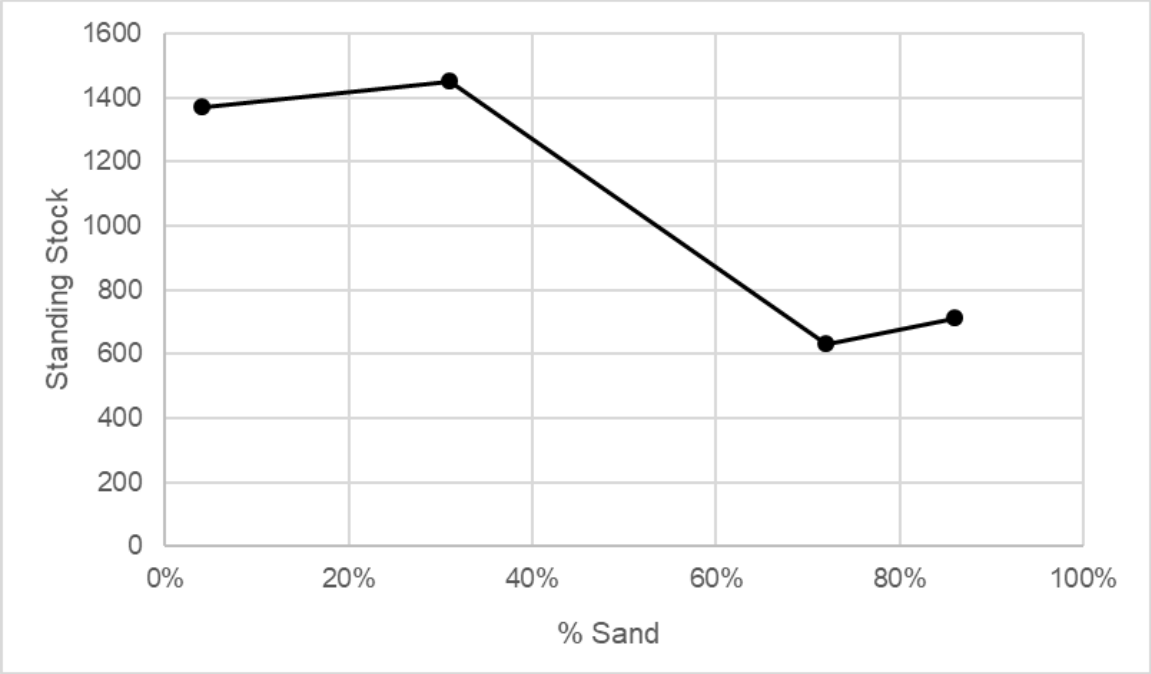


Fig 7 Standing stock abundances compared to grain sizes of each site.

Stations 6 and 12, however, differed in most other ecological aspects. Station 6, with a BWO of 1.071 ml/l, was dominated mostly by the epifaunal species *Rosalina bradyi* and the transitional species *Uvigerina peregrina*, with appreciable numbers of *Uvigerina hispida* which fill the same ecological niche as *U. peregrina*. When individual species from the *Globobulimina* genus are combined (referred to hereafter as *Globobuliminids*), they become one of the most abundant groups at this site. *Globobulimina pacifica, Globobulimina spinifera*, and *Globobulimina hoeglundi* are all present at fairly constant levels, decreasing only slightly as you move downcore. These *Globobuliminids* are typically identified as deep infaunal foraminifera present either only at very low oxygen levels or deep within the sediment. Their presence here, combined with the observation of a BWO of 1.071 ml/l and observations of the transitional species *U. peregrina* and *U.*

hispida is not typical. The typical organic-rich, oxygen-poor seafloor environments are characterized by fine-grained, soupy sediments and are usually dominated by these infaunal foraminifera such as the *Globobuliminids* that are adapted for reduced oxygen availability in pore waters **(**e.g. Bernhard, 1996, Jorissen et al., 2007). The presence of the deep infaunals preferred substrate could be the cause of a higher than expected deep infaunal population nearer to the sediment water interface.

Station 12, while having similar grain sizes to that of Station 6, was heavily dominated by infaunal foraminifera. *Bolivina spissa* and *Bolivina pseudopunctata* were among the top most abundant species present alongside *Chilostomella oolina* and *Cancris oblongus*, all infaunal taxa. With a BWO of 0.533 ml/l these are some of the expected taxa from these locations based on previous studies (Silva et al, 1996, Shepard et al., 2007, Venturelli et al., 2018). *Bolivina spissa* was the most abundant taxon at this site, present at higher numbers than all other taxa combined. The vertical distribution pattern is typical to that of other shallow infaunal species and *B. spissa* found at similar sites within the Southern California Bight. *Bolivina spissa* was present at every station and was thus chosen for subsequent analysis in Chapter 3. Station 12 had the overall lowest diversity, evenness and species richness due to the overwhelming abundance of *B. spissa*.

The taxa present at Station 1, composed of 72% sand sized particles and a BWO of 0.9065 ml/l, closely resembled that of Station 6 which had a similar BWO value of 1.071 ml/l. The ranked abundance of the taxa, however, did differ slightly, with *B. spissa* being the most prevalent, but to a lesser degree than Station 12. Epifaunal foraminifera such as *Rosalina bradyi* and *Hoeglundina elegans* were present in lower numbers while the shallow infaunals and transitional infaunals like the aforementioned *B. spissa* as well as

Chilostomella oolina, *Uvigerina peregrina*, and *Uvigerina hispida* made up the majority of the taxa present. Also much like Station 6, there was a substantial presence of the deep infaunal species *Globobulimina spinifera*. However, unlike Station 6, the average grain size of Station 1 was 72% sand. Previous studies regarding *B. spissa* suggests that this species preferentially ingest fresh phytodetritus, connecting these abundance patterns to phytoplankton blooms (Nomaki et al, 2006). This idea was supported in ecological studies of this area (Silva et al., 1996, Venturelli et al., 2018) and could explain this high population of this infaunal taxa in a non-typical environment.

Station 7, with BWO of 1.274 ml/l and composed of 86% sand, was dominated by the epifaunal species *Hoeglundina elegans*. This epifaunal species is typically indicative of oxic waters, which was the case here at Station 7. Transitional infaunal taxa such as *Uvigerina peregrina* were present here as well alongside members of the *Reophax* genus. Station 7 was also one of the two stations where living *Cibicidoides wuellerstorfi* were present. It has been suggested that epifaunal foraminifera such as *C. wuellerstorfi,* that can be commonly found attached to elevated substrates, may be present in higher numbers where average grain size is higher (Venturelli et al., 2018). Habitats with these coarser grains may allow *C. wuellerstorfi,* along with potentially many other epifaunal foraminifera, to more easily remain at their preferred habitat at or above the sediment water interface. However, the only other site at which living *C. wuellerstorfi* were present (Station 6) had a much smaller average grain size, being composed of only 31% sand sized particles and 69% silt, at nearly the same abundance/50cc sediment: 10.74 individuals/50cc at Station 7 compared to 15.13 individuals/50 cc at Station 6. This suggests that, while environmental conditions such as grain size can help predict trends of

an individual species, there are other limiting factors that influence whether or not a specific species will be present. As Station 1, with similar BWO and grain size to that of Station 7 (0.9065 ml/l and 72% sand vs 1.274ml/l and 86% sand) there were no living *C. wuellerstorfi* found at Station 1.

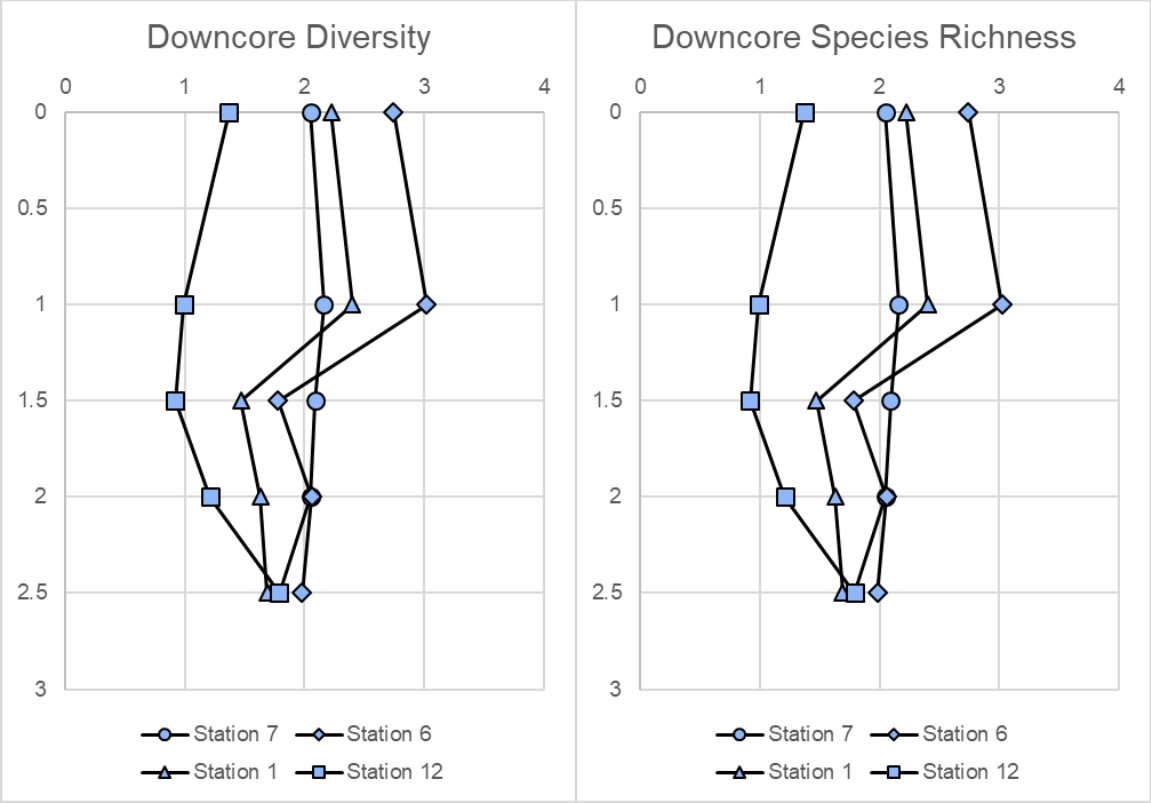


Fig 8 Diversity trends examined downcore. Marker points represent the upper half of a studied internal (i.e. the uppermost point represents the 0 - 1 cm interval, the next highest points represent the 1 - 1.5 cm interval, etc.).

Examining ecological trends downcore (Fig 8**)**, species richness and diversity followed expected trends, generally decreasing through the initial 2 cm of sediment before stabilizing thereafter. Station 12, however, showed a clear increase in diversity and species richness after that 2 cm mark. This could be due to a decrease in the impact of the bloom of *B. spissa* that dominates those upper 2 cm of sediment coupled with increased stability of the pore waters as you descend downcore.

Conclusions

Living (Rose Bengal stained) benthic foraminifera are abundant across our examination sites. Microhabitat preferences of epifaunal and infaunal taxa are consistent with the TROX model with the exception of the *Globobuliminids*. These were found in high numbers at Station 6, the lower limit of the "oxic" classification range. As suggested in previous studies (Venturelli et al. 2018), this could be due to the presence of the taxons more typical habitat with soupy, fine-grained sediments present at Station 6. However, the presence of epifaunal taxa within this same section indicates that other environmental parameters, such as BWO play important roles in the viability of different taxa within an environment. Future studies are being conducted observing these environmental parameters on a larger scale across a much larger portion of the Southern Californian Bight and how changes to these parameters over time influences the ecology and morphologies of benthic foraminifera in these environments.

CHAPTER III

SURFACE PORE MORPHOLOGY

Introduction

Paleoenvironmental and paleoceanographic studies can provide insights into ever-evolving modern ecosystems. By studying extant species in these modern environments, we aim to better understand both current and past deep sea environments. Current foraminiferal proxies examining bottom water oxygenation have begun to detail these bottom water conditions, but few currently exist and each has its own unique problems. It is common to use indicator species or presence/absence data of epifaunal and infaunal foraminifera as a proxy for both oxygen availability and productivity (Jorissen et al., 1999). This is what the TROX model attempts to explain. While this can give an adequate overview of an environment, it is unable to fully disentangle the influence of the availability of organic matter in the proxy. Thus this model cannot be used to elucidate any specific oxygen data from foraminifera. Kaiho (1991, 1994, 1999) created the Benthic Foraminiferal Oxygen Index (BFOI) in an attempt to quantify the relationship between the abundance of species that are adapted to low-oxygen conditions (e.g. *Bulimina* spp.) to those that require higher oxygen levels (e.g. *Cibicidoides* spp.). This,

however, fails to disentangle the influence of organic matter in the environment and is not consistent with current data from living populations. Kaiho (1991, 1994, 1999) suggested that *Cibicidoides* was only found in highly oxic environments consisting of greater than 2.0 ml/l oxygen. More recent studies, such as Venturelli et al. (2018) reported living *Cibicidoides* in environments consisting of less than 0.5 ml/l of oxygen suggesting some foraminiferal species can be tolerant of larger variations in oxygenation.

Rathburn et al. (2018) developed the Surface Pore Percentage proxy (SPORE), which attempts to describe the direct relationship between an individual foram and the oxygenation of the environment in which it calcified its test. This proxy was initially developed using *Cibicidoides wuellerstorfi*, an epifaunal foraminifera that can be found in environments with oxygen ranging from 1.78 µmoles/l - 267.948 µmoles/l, enabling them to describe this relationship between the surface pore percentage of an individuals penultimate and antepenultimate chambers and the oxygenation of the environment as those chambers calcified. Studies such as Kuhnt et al. (2013) have examined the relationship between pore density and other environmental factors in *Bolivina pacifica* however, they failed to address the fact that the pores of these *Bolivina* species vary in distribution. While some individuals have pores covering the entirety of a chamber, near uniformly, others only have pores along the sutures, or points of connection, between chambers. Their methodology can be biased based on the location of the chamber that is selected for analysis. This study aims to address these shortcomings and supplement the work of Rathburn et al. (2018) by analyzing additional *Cibicidoides wuellerstorfi* from oxygen environments not observed by Rathburn et al. (2018) and working toward

examining similarities and differences between epibenthic and infaunal foraminifera for application to the paleo-realm.

Study Area

Seafloor samples were collected using an Oceans Instrument multicore on the Sally Ride 1807 expedition in June of 2018 within the Southern California Bight. Sample sites were selected by analyzing seafloor oxygenation trends observed from previous cruises to the area. Areas were chosen in an effort to expand the dataset compiled by Rathburn et al. (2018), targeting locations that were expected to have seafloor oxygenation values that were absent in that original study, and where *C. wuellerstorfi* had been found in abundance in previous cruises (e.g., Venturelli et al., 2018). Cores analyzed in this study have oxygen values ranging from 23.80 µmoles/l to 56.89 µmoles/l. Collection depths varied from 328 m to 1001 m water depth (Fig 2).

Methodology

Specimens for this study were collected using R/V Sally Ride as outlined in Chapter 2. In an effort to further expand on the work done by Rathburn et al. (2018), both dead and living *C. wuellerstorfi* were picked from the preserved samples. This will allow us to begin the process of translating the SPORE procedure downcore, using dead individuals. After the completion of the ecological analysis of the study area, it was found that the most abundant infaunal species were *Hoeglundina elegans* and *Bolivina spissa*. In an

effort to initially connect the existing SPORE results published in Rathburn et al. (2018) to an infaunal species, only living infaunal individuals were examined in this study. Foraminiferal samples used in SPORE analyses were mounted on stubs, gold coated, and imaged with a Quanta 600 field emission gun at the Microscopy Facility at Oklahoma State University. SEM images revealed that *H. elegans* showed little to no signs of pores on their tests, making it impossible to perform the SPORE analysis procedures. Due to this, it was decided to proceed only with *B. spissa* and *C. wuellerstorfi* for subsequent processing and analysis.

Cibicidoides wuellerstorfi

Individuals were analyzed using the Chamber-Box SPORE method outlined in Willingham, (2014) and utilized in Rathburn et al. (2018). This involves the analysis of the penultimate (second to last) and antepenultimate (third to last) chambers of each specimen. These chambers are selected because they are typically the most well preserved, and youngest chambers at the time of collection. This will most closely reflect the environmental conditions at the time of collection. The ultimate – or final – chamber is not analyzed using this method due to the individuals commonly found with damaged ultimate chambers, especially in the fossil record. This method involves determining and quantifying the percentage of the test surface that is open (referred to as pore space), and the percentage that is the physical calcite test. In Willingham (2014), variations on the SPORE method were tested and compared to further improve and optimize the method. It was shown that, when analyzing one chamber of an individual *C. wuellerstorfi*, the pores tended to be evenly distributed. This enables the analysis of a sample box within the chamber rather than implementing the lengthier procedure of isolating the entire chamber

first. The largest rectangular box (referred to as “chamber-box”) that could be drawn within the chamber was selected and isolated using Photoshop. If an individual was slanted or uneven in any way during the SEM analysis, preference was given to the flattest area within the chamber for the chamber-box. This would minimize any error caused by a change in the apparent size of the pores. Once the chamber-boxes had been isolated, the colors were then inverted in Photoshop and made to be either entirely black or white using the curve functions within Photoshop. Because the pore space in the SEM images was typically completely black to begin with and was always much darker than the surrounding non-pore space, when the colors of the image are inverted, the pores become bright white with yellow and orange fringes. The non-pore space becomes entirely black, fully isolating all pores within the chamber-box. These altered images are then imported into ArcGIS in order to quantify the pore vs non-pore space. Using the *Iso Cluster Unsupervised Classification* Spatial Analyst tool within ArcGIS, the colors were further simplified into two categories: pore and non-pore pixels. These tools turned any pixels that were black into Color A, which were identified as non-pore pixels, and grouped all other colored pixels into Color B, which were identified as pore pixels. Then using the same Spatial Analyst tools, the number of pixels that were Color A and Color B were quantified, giving a final pore percentage for that individual chamber. After the SPORE analysis is performed on both the penultimate and antepenultimate chamber, the values are averaged to give the final SPORE value for that individual.

Bolivina spissa

Unlike *C. wuellerstorfi*, the pores of *B. spissa* are not typically evenly distributed across an entire chamber. Instead, the pores are generally clustered around the sutures of the

chambers. This would make the chamber-box selection method used for *C. wuellerstorfi* highly susceptible to user bias. So instead, analysis was performed using the entire chamber for both the penultimate and antepenultimate chambers of individuals. The subsequent process of isolating the chamber from the SEM stage, and exaggerating differences in color between pore and non-pore space was performed on *B. spissa* individuals using the same procedures mentioned above.

Results

A total of 34 individuals were SEM imaged for this study, 19 of which were *C. wuellerstorfi* (6 living and 13 dead at the time of collection), while 11 were *B. spissa* (all living), and 3 were *H. elegans* (also all living). Upon initial analysis of SEMs it was found that all 3 *H. elegans* individuals lacked visible pores. It was for this reason that further analysis was only performed on *C. wuellerstorfi* and *B. spissa*.

Cibicidoides wuellerstorfi

As discussed in Chapter 2, *C. wuellerstorfi* were only found in Stations 1, 6, and 7. Oxygen at these locations was 0.9065 mL/L, 1.071 mL/L, and 1.274 mL/L, respectively. These oxygenation values all sit in gaps in our existing SPORE datasets (Rathburn et al., 2018) and allow further refinement for future analysis. Two individuals from Station 1 were selected for SEM analysis, both dead at the time of collection. This station had the highest average SPORE value at 25.9% and the largest standard deviation as well at 16.51. 5 individuals from Station 6 were selected from Station 6; 2 living and 3 dead at the time of collection. The site average for Station 6 was 19.72%, with a standard deviation of 2.02. Station 7 had the largest amount of *C. wuellerstorfi* of all stations and

12 were selected for SEM analysis. Of those, 4 were living individuals and 8 were dead.

The site average SPORE was 10.27% with a standard deviation of 2.12.

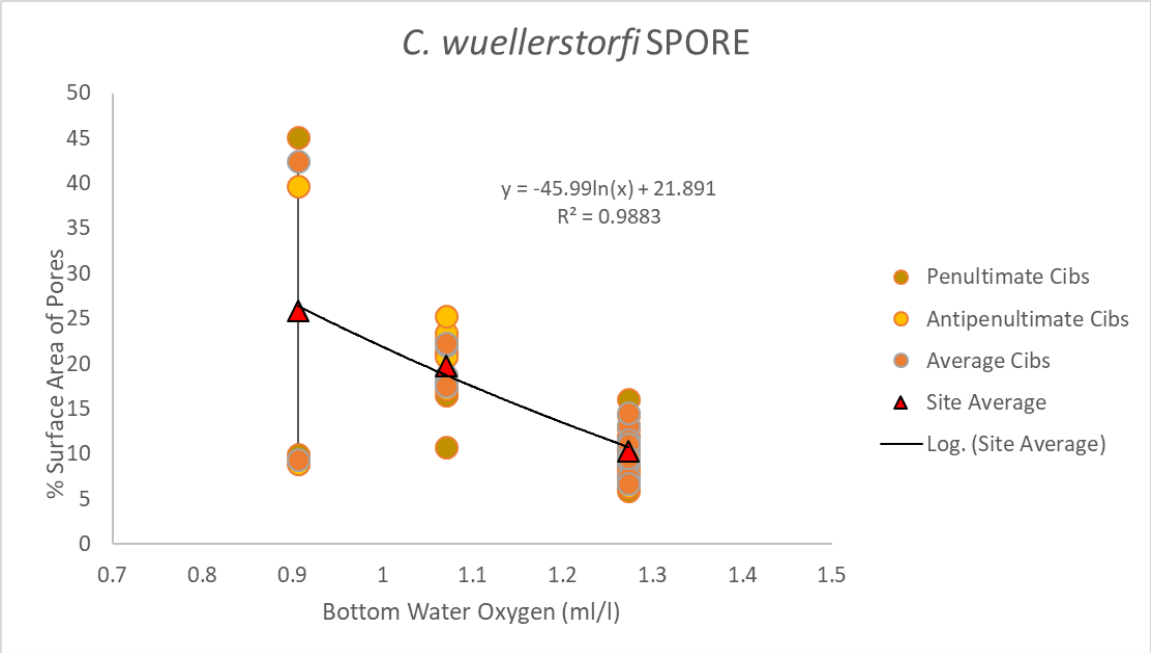


Fig 9 SPORE trends for *C. wuellerstorfi* from *SR1807* Stations 1, 6, and 7.

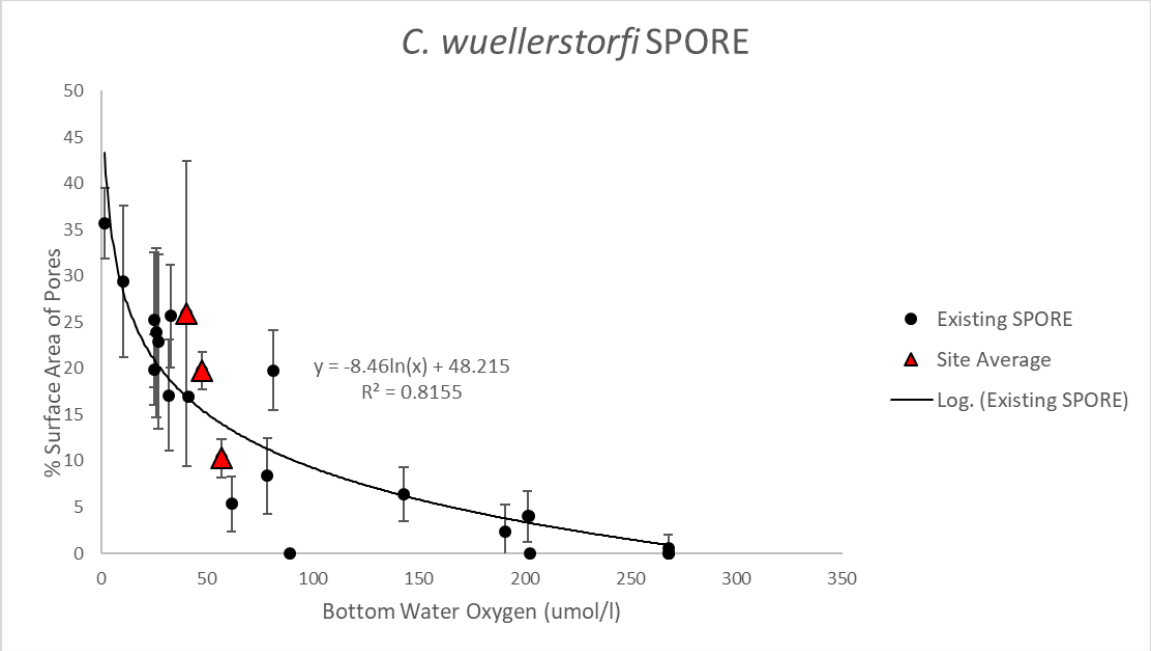


Fig 10 SPORE trends for *SR1807 C. wuellerstorfi* overlain on existing SPORE data.

Trends shown in Figures 9 and 10 follow previously established datasets showing the SPORE values decreasing as bottom water oxygenation increases. The range of SPORE values for Stations 6 and 7 have tighter spreads than that of existing datasets with standard deviations of 2.02 and 2.12 respectively. Station 1, however, has a much wider variance than that of the other stations examined in this and existing SPORE datasets which can be seen in Figure 10**.**

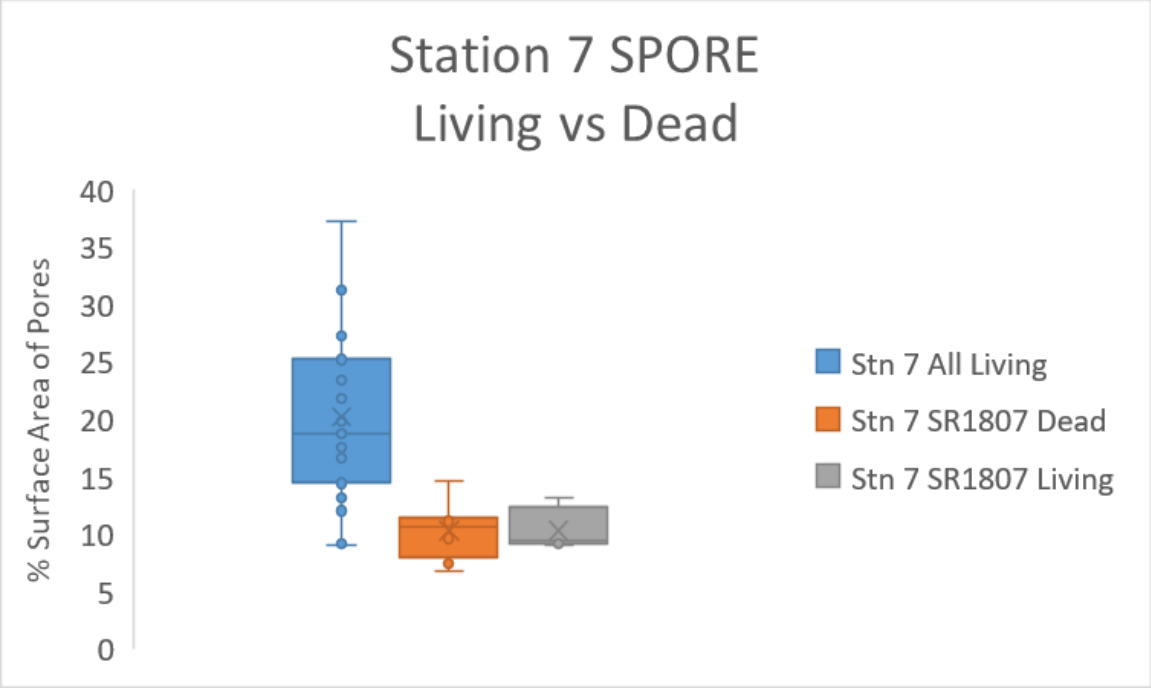


Fig 11 Comparison of living vs dead spreads at Station 7 across multiple cruises (blue) and new data from *SR1807* (orange and grey).

Station 7 was chosen for analysis of living vs dead SPORE due to the abundance of *C. wuellerstorfi*, living and dead, at this location utilizing data from this study, Rathburn et al. (2018), and Willingham (2014). Figure 11 shows the variation in SPORE from all living individuals collected from Station 7 from Willingham 2014 and Rathburn 2018 as well as the variation in SPORE from both living and dead samples collected at Station 7, specifically from cruise SR1807. SPORE from all living individuals, across all cruises,

had a much wider variance than both living and recently dead individuals from SR1807. These values ranged from 9.08% to 37.18% with a standard deviation of 7.14. However, bottom water oxygenation also varied between cruises. During cruise NH1108, bottom water oxygenation at Station 7 ranged from 0.562 ml/L to 0.608 ml/L. Oxygenation recorded on SR1807 was 1.275 ml/L. When examining only individuals from SR1807, the SPORE of the living population closely resembled that of the dead population (Fig 11).

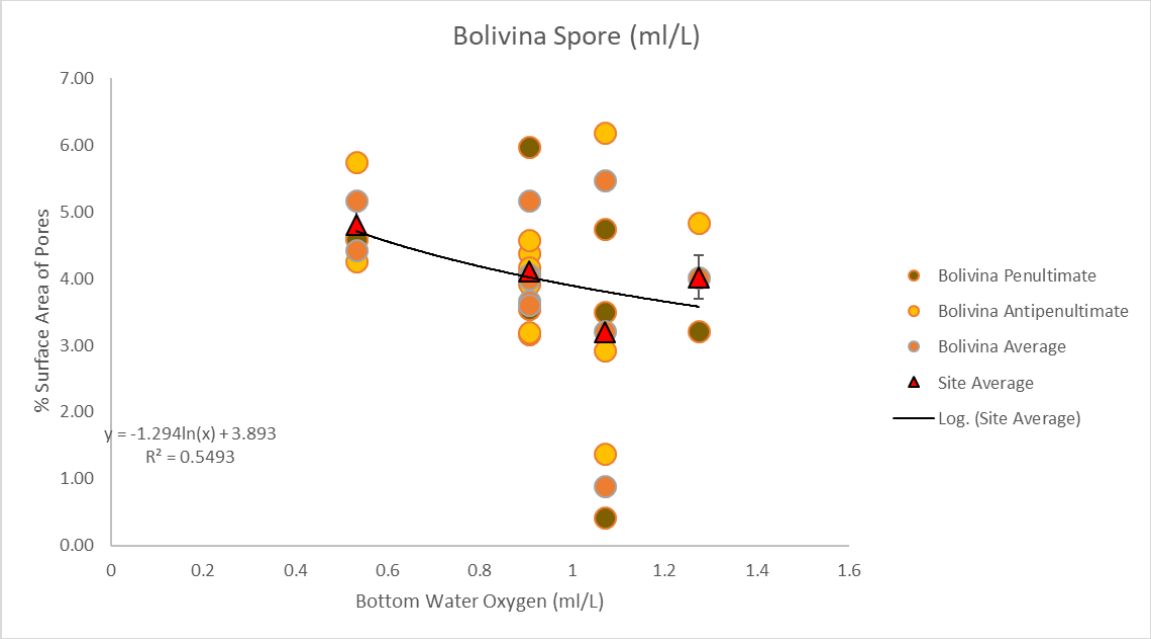


Fig 12 SPORE trends for *B. spissa* from *SR1807* Stations 1, 6, 7, and 12.

Bolivina spissa

Eleven living *B. spissa* were examined in this study, present at all 4 stations with bottom water oxygenation ranging from 0.533 ml/L to 1.274 ml/L. As mentioned above, the pores of *B. spissa* are not evenly distributed across the chamber**.** This meant that whole

chamber analysis would be required rather than the faster, more efficient chamber-box method. Pores were both more abundant and larger along the sutures connecting younger chambers to older chambers. Chambers were composed of more non-pore space than pore space along the uppermost portions of an individual chamber, in the direction of the aperture.

Bolivina SPORE values followed a similar general trend to that of *C. wuellerstorfi*. As oxygenation increased, SPORE values decreased. Starting with Station 12, with bottom water oxygenation of 0.533 ml/L there was an average SPORE value of 4.80% with a standard deviation of 0.37. Station 1 had an average SPORE value of 4.10% with a standard deviation of 0.56 and 0.9065 ml/L oxygen. The average SPORE of Station 6 was 4.34% with a standard deviation of 0.56 and 1.071 ml/L oxygen. Finally, Station 7 had only one individual undergo SEM analysis with a value of 4.02% and 1.274ml/L oxygen. SPORE downcore was also analyzed at Station 1. At Station 1, SPORE decreased as you moved downcore, dropping from 5.17% to 3.61%.

Discussion

Cibicidoides wuellerstorfi

One of the main objectives of this study was to add to the existing dataset compiled in Rathburn et al. (2018) and to continue to analyze SPORE trends in *C. wuellerstorfi*. The same negative correlation was observed in this study as was observed in Rathburn et al. (2018). The dorsal surface pores of epifaunal foraminiferal tests are believed to be used for gas acquisition (Leutenegger et al., 1979, Rathburn et al., 2018, Kuhnt et al., 2013), and our findings indicate that greater test pore surface area is necessary for respiration as

dissolved oxygen in bottom water decreases, shown in the logarithmic relationship between epifaunal pore surface area and ambient oxygen availability. We speculate that this relationship results from changes in metabolic requirements as ambient oxygen availability decreases.

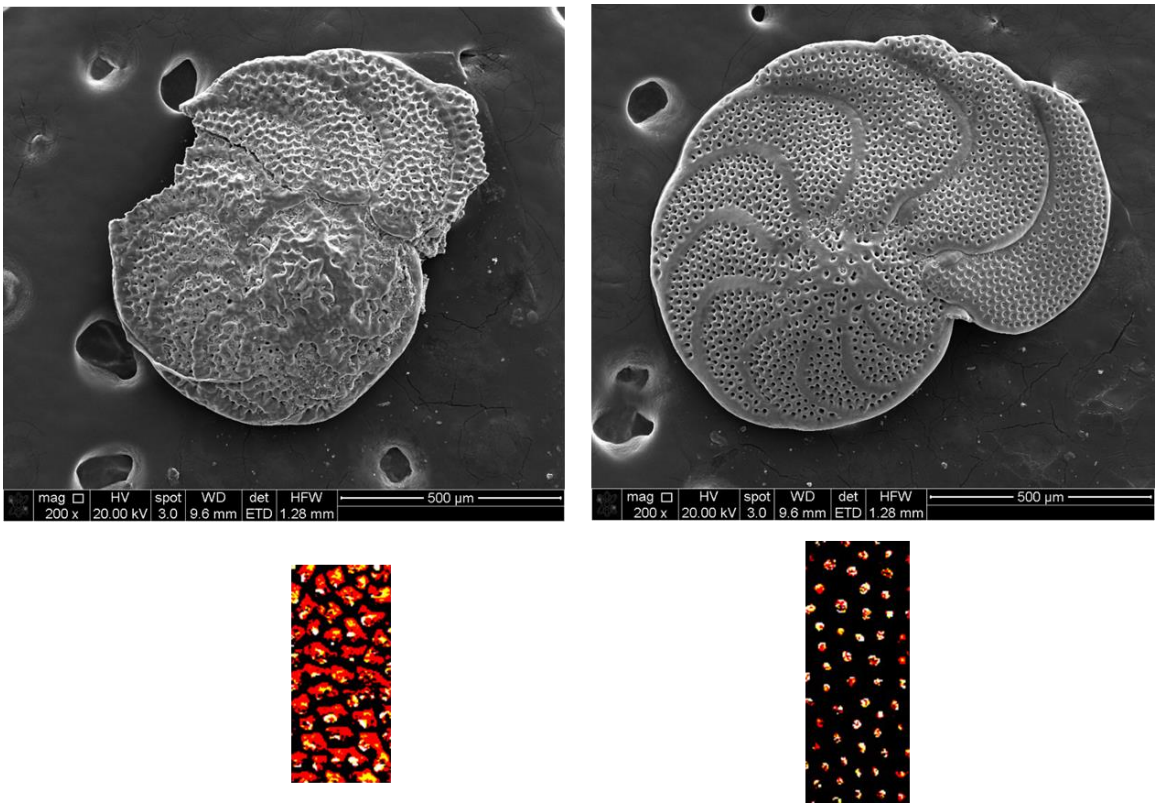


Fig 13 SEM images (above) and their associated, processed SPORE images (below). Individual 1B on the left. Individual 2B on the right.

With this being the first study to apply the SPORE methodology to both living and dead individuals, it provides initial insights into the effectiveness of this method as it is applied to the fossil record. The standard deviation for Stations 6 and 7 was only about 2% even when including both living and dead populations. Station 1 however, had a standard deviation of 16% when only two dead individuals were found at the site. These two individuals (Fig 13**)** difference becomes apparent after initial SEM analysis and is further

magnified after SPORE analysis. *C. wuellerstorfi* 1B (Fig 13**)** was larger and much less well defined pores than individual 2B. Examining the proloculus and the oldest chambers, as well as the sutures, it appears as if individual 1B has undergone heavy dissolution as compared to the cleaner 2B specimen. The individual pores and the delineations between pores of 1B have been obscured. This is reflected in the SPORE analysis (Fig 13**)** as the more typical spherical pores change into larger amorphous shapes, lacking clear boundaries. While this does begin to explain the large variation in SPORE values at a single site, it also suggests a need for further refinement of this method as it is applied downcore to dead individuals. Fossilized specimens are rarely in pristine condition, which led Rathburn et al. (2018) to select the average of the penultimate and antepenultimate chambers for analysis. The ultimate chamber is often damaged or entirely absent from individuals. These results, however, also demonstrate the importance of sample selection.

In this study, we examined the populations of *C. wuellerstorfi*, both living and dead, across all cruises from Station 7, where a larger sample size was found. We were able to compare the populations using the SPORE methodology, as shown in Figure 11. The significant range of SPORE values obtained from all living data can be attributed to the variation of local oxygenation levels at this site. Samples used to establish the SPORE methodology were initially obtained by targeting different bathymetric locations along an oxygen transect off the coast of San Diego, predicting different oxygenation conditions at each site which were verified through CTD profiles of the water column. While the same location was sampled in the summer months of multiple years, bottom water oxygenation may have varied as the intensity of the OMZ at the location may vary temporally and

spatially. Bottom-water oxygenation values recorded at Station 7 during the different cruises ranged from 0.562 ml/L to 1.274 ml/L. However, when we compared living and dead populations of one core, we found much less variation in the SPORE values. Around 10% variance compared to the 30% variation observed in all living populations. The same variation of 10% was also observed in the dead population, indicating that at least locally, dead individuals can reflect bottom water conditions in a similar way to living individuals. Taken together, these findings suggest that the SPORE methodology is effective for studying both living and dead populations of *C. wuellerstorfi*. Furthermore, our results underscore the importance of taking into account local variations in oxygenation when using this methodology, especially when comparing populations across different cruises or sampling locations.

Bolivina spissa

The presence of *C. wuellerstorfi*, similar to many epifaunal species, can be connected to a well oxygenated bottom water environment. Even though it has been shown that *C. wuellerstorfi* can survive in locations with much lower oxygen than previously expected (Venturelli et al., 2018; Burkett et al., 2016), this species becomes increasingly rare as oxygenation drops resulting in these species not always being present in the environment. This makes the application of the SPORE method to fossil assemblages particularly challenging when consistent *C. wuellerstorfi* populations are not expected in abundance in oxygen-poor environments. As epibenthic populations decrease in low oxygen environments, it becomes necessary to conduct SPORE analysis of species present. To this end, part of the goal of this thesis was to examine similarities and differences between epibenthic and infaunal populations so when applied to the paleo record both

microhabitats could be assessed and combined for a total bottom water oxygenation reconstruction.

It has been shown that in very low oxygen conditions, some foraminifera are capable of nitrate respiration (Koho, 2011; Piña-Ochoa et al.,, 2010; Risgaard-Petersen et al., 2006) leading to an interpretation that nitrate availability, rather than oxygen, can be correlated to pore abundances of some infaunal species (Glock et al., 2011). Pore abundances of infaunal species have also been correlated to bottom water oxygen availability (Kuhnt et al., 2013). Despite any debate and uncertainty as to the function and mechanism of use of the pores of infaunal foraminifera, it is important to ascertain if these pore percentages change at a consistent rate with *C. wuellerstorfi* and other epibenthics which would enable the proxy to be utilized regardless of what species are present in the paleo-record.

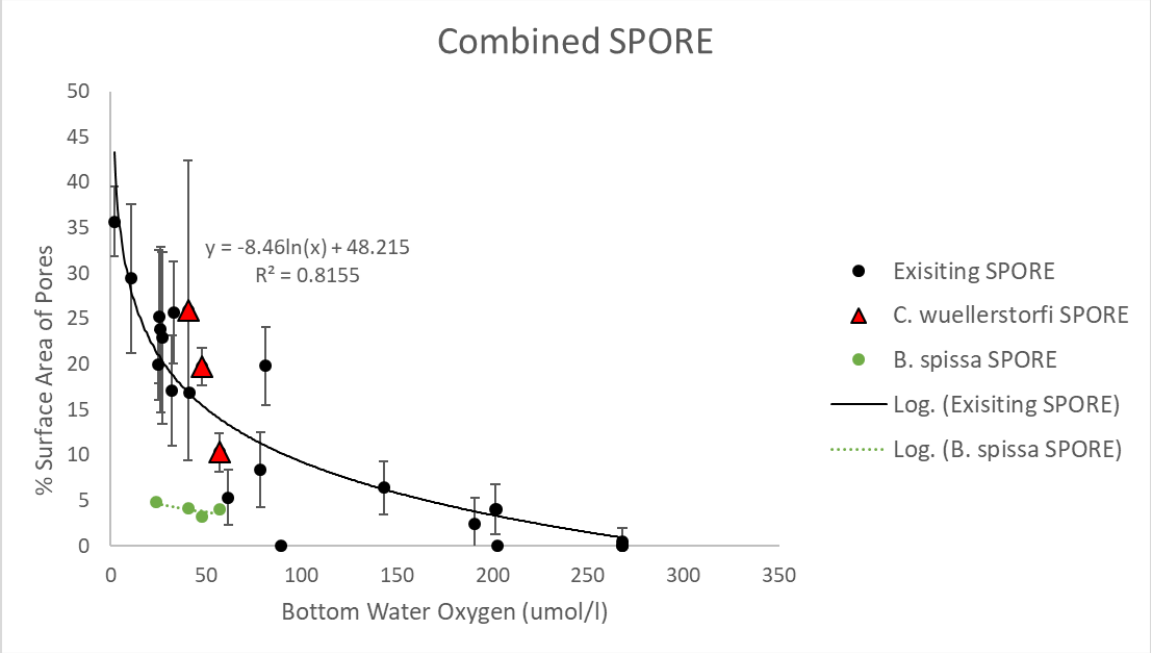


Fig 14 All SPORE data to date. *C. wuellerstorfi* indicated with black dots (exisiting data) and red triangles (newly added data). *B. spissa* indicated with green dots.

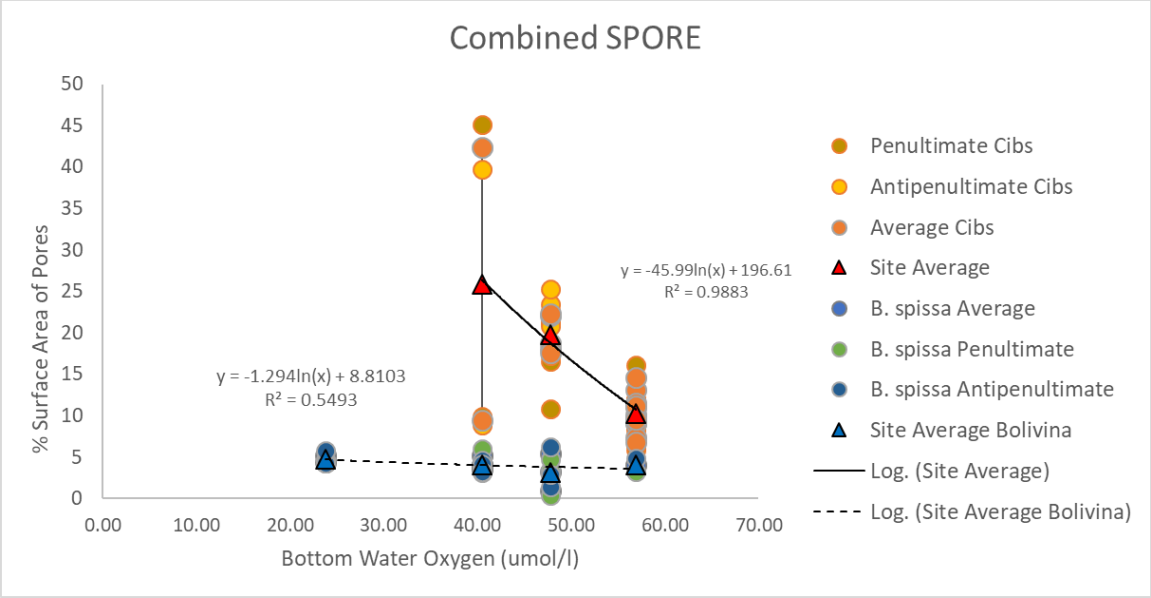


Fig 15 Combined SPORE of all specimens collected for this study.

Initial comparisons between *B. spissa* show a similar inverse relationship to bottom water oxygenation consistent with *C. wuellerstorfi.* The decreasing trend in SPORE values is less pronounced in *B. spissa* than that of *C. wuellerstorfi* and is also consistently lower (Fig 14 & 15). This fits with the expectation of *B. spissa* as a shallow infaunal species, much more tolerant to low oxygen conditions. Because this species does not require as much oxygen to thrive it therefore requires fewer pores to facilitate the transfer of oxygen.

Going downcore, however, *B. spissa* SPORE values do not reflect our expectation and understanding of the SPORE proxy. In both *C. wuellerstorfi* and *B. spissa* that inverse relationship is present when examining site averages (Fig 16). However, at Station 1, as you move down in the sediment, from 0 - 3 cm, *B. spissa* SPORE decreases from approximately 5% to 3.5%. Typically, oxygenation decreases as depth in the sediment increases. In the absence of more detailed pore water oxygenation values, this commonly observed depletion of porewater oxygen is what we base our expectations on (e.g. Cai et

al., 1996) We do not know for sure what is happening geochemically in the porewaters of this Station 1 core at the time of collection and further examination into these relationships are currently being done.

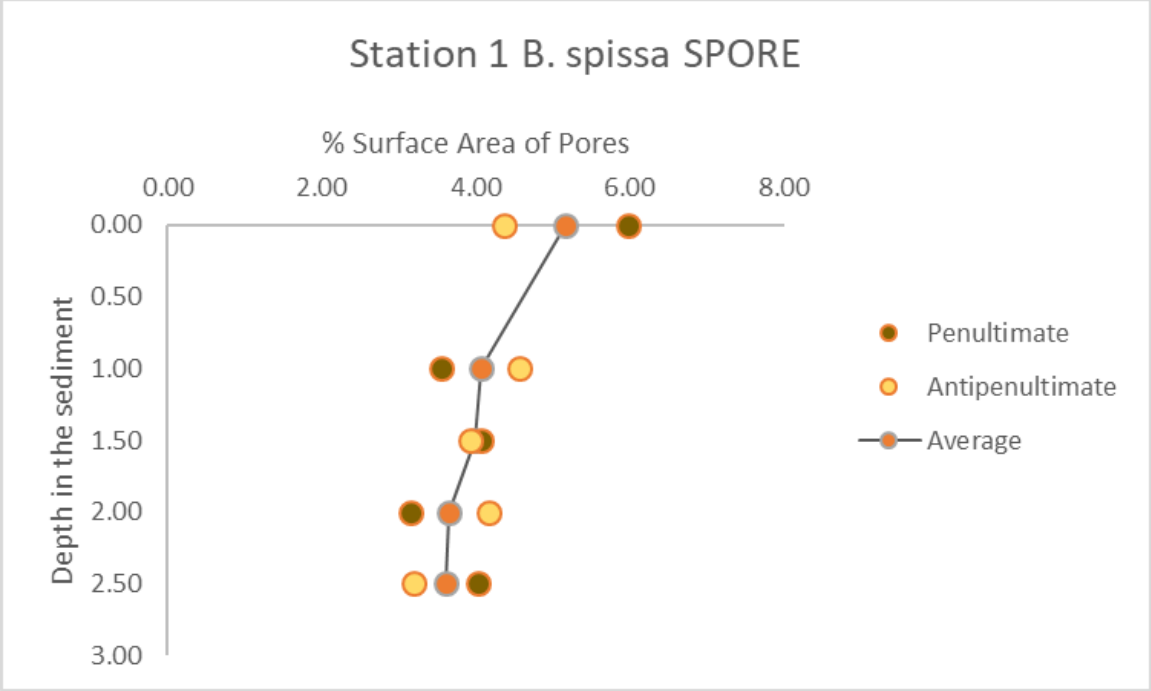


Fig 16 Downcore SPORE values for *B. spissa* at Station 1. Marker points represent the upper half of a studied internal (i.e. the uppermost point represents the 0 - 1 cm interval, the next highest points represent the 1 - 1.5 cm interval, etc.).

Further research is needed to better illustrate the relationship between *B. spissa* and the morphological response to oxygen variations. More robust site averages, including a larger number of individuals per site would enable more accurate analysis of these relationships. It could begin to show similar trends and difficulties as brought up above with *C. wuellerstorfi*. Variations between living and dead individuals have yet to be studied as well.

Conclusions

This study aimed to add to existing datasets examining surface pore percentage (SPORE) trends of *Cibicidoides wuellerstorfi.* Despite sampling at previously sampled locations where high populations *C. wuellerstorfi* had been recorded, there were only six living individuals collected that were suitable for SEM and SPORE analysis. Due to these lower than expected abundances an initial analysis between the SPORE of living and dead individuals was also performed. Similar trends to that of previously published studies were found in collected living samples. A negative correlation between epifaunal pore surface area and ambient oxygen availability, indicating that greater pore surface area is necessary for respiration when dissolved oxygen in bottom water decreases. These data have been added to the larger available dataset and fit well within expected values, further validating interpretations made in previous studies. The variance in SPORE values shown between living and dead individuals highlights the need for further refinement of the methodology as it is applied to the fossil record.

This is the first study that to expand SPORE to taxa beyond *C. wuellerstorfi*. The most abundant taxa found were the epifaunal species *Hoegulndina elegans* and the infaunal species *Bolivina spissa* with the primary goal of examining these two taxa using the SPORE methodology looking for if there were any relationships similar to that of *C. wuellerstorfi* SPORE and BWO. It was found that *B. spissa* show a similar, though less pronounced, inverse relationship to bottom water oxygenation consistent with *C. wuellerstorfi*, fitting expectations as a shallow infaunal species, much more tolerant to low oxygen conditions. Downcore, however, did not follow our expectations. SPORE values decrease with increasing depth within the sediment. Specific pore water

geochemistry was not available for this study and could hold key insights into these observed trends.

CHAPTER IV

OVERALL CONCLUSIONS

Expanding on the previous work of Rathburn et al., 2018, this study conducts an ecological analysis of four sites within the Southern California Bight. Finding appreciable amounts of shallow infaunal and epifaunal species commonly found at the boundary of oxic and dysoxic waters consistent with the TROX model. With bottom water oxygenation spanning 0.533ml/l to 1.274ml/l, this environment supported populations of *Bolivina spissa, Rosalina bradyi, Hoeglundina elegans,* along with many taxa from the *Reophax* and *Globobulimina* genera. The taxa present were consistent with interpretations made using the TROX model outside of a select few species, namely the Globobuliminds. We suggest that these deep infaunal foraminfera are present in higher oxygen environments due to the presence of smaller average grain sizes that are more consistent with their typical distribution throughout anoxic waters. Selecting the most abundant infaunal species, *B. spissa,* SPORE analysis was performed alongside living and dead populations of *Cibicidoides wuellerstorfi*. Similar trends to those published in Rathburn et al. (2018) in both species. Variations in SPORE between living and dead individuals varied only slightly, indicating that dead individuals can reflect local bottom water conditions in a similar way to living individuals. These findings suggest that the

SPORE methodology is effective for studying both living and dead populations of *C. wuellerstorfi*. It was found that *B. spissa* show a similar, though less pronounced, inverse relationship to bottom water oxygenation consistent with *C. wuellerstorfi*. This fits expectations as *B. spissa*, a shallow infaunal species, is much more tolerant to low oxygen conditions. Downcore, SPORE values decrease with increasing depth within the sediment, against our expectations. Further research is currently being conducted examining *B. spissa* both downcore and on average across a wider oxygen gradient as more specific pore water geochemical data are needed to clarify the relationships between SPORE and an individual's surrounding environment. These works will continue to bolster the established *C. wuellerstorfi* data and begin to expand on these initial insights observed in this study.

REFERENCES

Bernhard J.M., Bowser S.S., Goldstein S., (2010). An ectobiont-bearing foraminiferan, Bolivina pacifica, that inhabits microxic pore waters: cell-biological and paleoceanographic insights. Environmental Microbiology, vol 12: 2107–2119.

Bernhard, J. M. and Alve, E. (1996). Survival, ATP pool, and ultrastructural characterization of benthic foraminifera from Drammensfjord (Norway): response to anoxia. Marine Micropaleontology, vol. 28: 5-17.

Burkett, A. M., Rathburn, A. E., Pérez, M. E., Martin, J. & Levin, L. A., (2016). Colonization of over a thousand Cibicidoides wuellerstorfi (foraminifera; Schwager, 1866) on artificial substrates in seep and adjacent off-seep locations in dysoxic, deep-sea environments. Deep-Sea Research, vol 117: 39–50.

Burkett, A.., Rathburn A., Pratt R. B., Holzmann, M., (2020). Insights into the ecology of epibenthic calcareous foraminifera from a colonization study at 4000 m (Station M) in the NE Pacific Ocean. Deep Sea Research Part II, vol 173.

Buzas, M. A., Culver, S. J., and Jorissen, F. J., (1993). A statistical evaluation of the microhabitats of living (stained) infaunal benthic foraminifera: Marine Micropaleontology, vol 20: 311–320.

Chalet E. A., Bout.Roumazeillers, V., Riboulleau, A., Trentesaux, A., (2009). Sediment (grain size and clay mineralogy) and organic matter quality control on living benthic foraminifera. Journal of Micropaleontology, vol. 52: 75-84.

Corliss, B. H., (1985). Microhabitats of Benthic Foraminifera within deep-sea sediments: Nature, vol. 314: 435-438.

Corliss, B. H. & Emerson, S., (1990). Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep-Sea, vol. 37: 381–400.

Debernay, J.P., Tsakiridis, E., Soulard, R., Grossel, H., (2001). Factors determining the distribution of foraminiferal assemblages inPort Joinville Harbour (Ile d'Yeu, France_: the influence of pollution. Marine Micropaleontology, vol. 43, 75-118.

Diz, P., Frances, G., Costas, S., Alejo, I., (2004). Distribution of benthic foraminifera in coarse sediment, Ria de Vigo, NW Iberian margin. Journal of Foraminiferal Research, vol. 34, 258-275.

Douglas, R. G., and Woodruff, F., (1981). Deep-sea benthic foraminifera. In: Emiliana, C., ed., The Sea, vol. 7: 1233-1327.

Emery, K. O., (1960). The Sea off Southern California, a Modern Habitat of Petroleum. Oakland, CA: University of California.

Glock, N., Eisenhauer, A., Milker, Y., Liebetrau, V., Schönfeld, J., Mallon, J., Sommer, J., Hensen, C., (2011). ENVIRONMENTAL INFLUENCES ON THE PORE DENSITY OF BOLIVINA SPISSA. Journal of Foraminiferal Research, vol. 4: 22–32.

Goldstein, S., (1999). Foraminifera: A biological overview. In "Modern Foraminifera" (B.K. Sen Gupta, ed.), pp. 37-55. Kluwer Academic Publishers, London.

Gooday A.J., (1986). Meiofaunal foraminiferans from the bathyal Porcupine Seabight (north-east Atlantic): size structure, standing stock, taxonomic composition, species diversity, and vertical distribution in the sediment. Deep Sea Research Part A. Oceanographic Research Papers, vol. 33: 1345 - 1375.

Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., (1992). The role of benthic foraminifera in deep-sea food webs and carbon cycling. In: Rowe, G.T., Pariente, V. (Eds.), Deep-sea Food Chains and the Global Carbon Cycle. Kluwer Academic Publishers, The Nether-lands, p 63–91.

Gorsline, D., Kolpack, R., Karl, H., Drake, D., Thornton, S., Schwalbach, J., et al. (1984). Studies of fine-grained sediment transport processes and products in the California Continental Borderland. Geological Soc. Lond. Special Public, vol. 15: 395–415.

Harmann R.A. (1964) Distribution of foraminifera in the Santa Barbara basin, California. Micropaleontology, vol. 10: 81–96.

Helly, J. J., & Levin, L. A. (2004). Global distribution of naturally occurring marine hypoxia on continental margins. Deep Sea Research Part I: Oceanographic Research Papers, 51(9), 1159-1168.

Hunt, A.S., Corliss, B.H., (1993). The distribution of living (stained) benthic foraminifera from the Canadian Arctic Archipelago. Mar. Micropaleontology. vol. 20: 321–345.

Jaccard, S. L. & Galbraith, E. D., (2011). Large climate-driven changes of oceanic oxygen concentration during the last deglaciation. Nature Geoscience, vol 5: 51–156.

Jorissen, F. J., Barmawidjaja, D. M., Puskaric, S., and Van Der Zwaan, G.J., (1992). Vertical Distribution of benthic foraminifera in the northern Adriatic Sea; the relation with the organic flux: Marine Micropaleontology, vol. 19: 1-2.

Jorissen, F.J., De Stigter, H.C., Widmark, J.G.V., (1995). A conceptual model explaining benthic foraminiferal microhabitats. Mar. Micropaleontology. vol. 26 (1–4): 3–15.

Jorissen, F. (1999). Benthic foraminiferal microhabitats below the sediment-water interface. In "Modern Foraminifera" (B.K. Sen Gupta, ed.), pp. 161-179. Kluwer Academic Publishers, London.

Jorissen, F., Fontanier, C., Thomas, E., (2007). Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. In: "Proxies in late Cenozoic paleoceanography" (C. Hillaire-Marcel and A. de Cernal, ed). pp 862 Elsevier.

Kaiho, K. (1991). Global changes of Paleogene aerobic/anaerobic benthic foraminifera and deep-sea circulation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 83, 65–85.

Kaiho, K. (1994). Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. Geology 22, 719–722.

Kaiho, K. (1999). Evolution in the test size of deep-sea benthic foraminifera during the past 120 my. Mar. Micropaleontol. 37, 53–65.

Keeling, R. F., & Garcia, H. E. (2002). The change in oceanic O2 inventory associated with recent global warming. Proceedings of the National Academy of Sciences, 99(12), 7848-7853.

Koho, C. & Pina-Ochoa, E. (2012). Benthic Foraminifera: inhbaitants of low oxygen environments. In Anoxia, A. V. Altenbach, J. M. Bernhard, and J. Seckbach, eds. (Springer), 251–285.

Kuhnt, T., Friedrich, O., Schiemdl, G., Milker, Y., Mackensen, A., and Luckge, A. (2013). Relationship between pore density in benthic foraminifera and bottom-water oxygen content. Deep-sea Research I, vol. 76: 85-95.

Leutenegger, S., & Hansen, H. J. (1979). Ultrastructural and radiotracer studies of pore function in foraminifera. Marine biology, 54, 11-16.

Levin, L. A., Gage, J. D., Martin, C., & Lamont, P. A. (2000). Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. Deep Sea Research Part II: Topical Studies in Oceanography,47(1), 189-226.

Levin, L. A. (2003). Oxygen minimum zone benthos: Adaptation and community response to hypoxia. Oceanography and Marine Biology: An Annual Review, vol. 41: 1-45.

Lu, W., Riackaby, R., Hoogakker, B., Rathburn, A., Burkett, A., Dickson, A., Martinez-Mendez, G., Hillenbrand, C., Zhou, X., Thomas, E., Lu, Z (2020). I/Ca in epifaunal benthic foraminifera: A semi-quantitative proxy for bottom water oxygen in a multi-proxy compilation for glacial ocean deoxygenation. Earth and Planetary Science Letters, vol 533.

Lutze, G.F., (1986). Uvigerina species of the eastern North Atlantic. In: van der Zwaan, G.J., Jorissen, F.J., Verhallen, P., von Daniels, C.H. (eds.) Atlantic-European Oligocene to recent Uvigerina: Utrecht Micropaleontological Bulletins, vol. 35: 21-46.

McCorkle, C. D., Keigwin, L. D., Corliss, B. H., and Emerson, S. R. (1990). The influence of microhabitats on the carbon isotopic composition of deep-sea benthic foraminifera. Paleoceanography, vol. 5: 161-185.

Meier, H. M., Andersson, H. C., Eilola, K., Gustafsson, B. G., Kuznetsov, I., Müller-Karulis, B., ... & Savchuk, O. P. (2011). Hypoxia in future climates: A model ensemble study for the Baltic Sea. Geophysical Research Letters,38(24).

Moodley, L. & Hess, C., (1992). Tolerance of infaunal benthic foraminifera for low and high oxygen concentrations. Biol. Bulletin, vol. 183: 94–98.

Murgese, D. S., & De Deckker, P. (2005). The distribution of deep-sea benthic foraminifera in core tops from the eastern Indian Ocean. Marine Micropaleontology, 56(1-2), 25-49.

Murray, J.W., (2001). The niche of benthic foraminifera, critical thresholds and proxies. Marine Micropaleontology, vol. 41 1-2:. 1-7.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., & Kitazato, H. (2005). Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments. Limnology and Oceanography,50(1), 134- 146.

Piña-Ochoa, E., Hogslund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., Schweizer, M., Jorissen,F., Rysgaard, S., Risgaard-Petersen, N. (2010).

Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida. PNAS, vol. 107: 1148-1153.

Rathburn. A. E. et al., (2018). A New biological proxy for deep-sea paleo-oxygen: Pores of epifaunal benthic foraminifera: Scientific Reports. Article 9456

Rathburn, A. E. & Corliss, B. H. (1994) The ecology of deep-sea benthic foraminifera from the Sulu Sea. Paleoceanography, vol. 9: 87–150.

Risgaard-Petersen, N., Langezaal, A. M., Ingvardsen, S., Schmid, M. C., Jetten, M. S. M., Op den Camp, H. J. M., Derksen, J. W. M., Pina-Ochoa, E., Eriksson, S. P., Nielsen, L. P., Revsbech, N. P., Cedhagen, T., van der Zwaan, G. J. (2006). Evidence for complete denitrification in a benthic foraminifer. Nature, vol. 443: 93-96.

Schönfeld, J., (2002). A new benthic foraminiferal proxy for near-bottom current velocities in the Gulf of Cadiz, northeastern Atlantic Ocean. Deep Sea Research Part I: Oceanographic Research Papers, vol. 49: 1853-1875.

Sen Gupta, B., K., K., (2007). Modern Foraminifera. Springer Netherlands.

Shepherd, A. S., Rathburn, A. E., & Pérez, M. E. (2007). Living foraminiferal assemblages from the Southern California margin: a comparison of the> 150, 63–150, and> 63 μm fractions. Marine Micropaleontology, 65(1), 54-77.

Silva, K. A., Corliss, B. H., Rathburn, A. E., & Thunell, R. C. (1996). Seasonality of living benthic foraminifera from the San Pedro Basin, California Borderland. The Journal of Foraminiferal Research, 26(1), 71-93.

Snider, L.J., Burnett, B.R., Hessler, R.R., (1984). The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep-Sea Research, vol. 31: 1225–1249.

Stramma, L., Johnson, G. C., Sprintall, J., & Mohrholz, V. (2008). Expanding oxygen-minimum zones in the tropical oceans. science, 320(5876), 655-658.

Taylor, M. A., Hendy, I. L. & Chappaz A., (2017).Assessing oxygen depletion in the Northeastern Pacific Ocean during the last deglaciation using I/Ca ratios from multiple benthic foraminiferal species. Paleoceanography, vol. 32: 746–762

Thomas, E., (2007). Cenozoic mass extinctions in the deep sea: What perturbs the largest habitat on Earth?, In: “Large Ecosystem Perturbations: Cause and Consequences: Geological Society of America Special Paper, Volume 242” (Monechi, S., Coccino, R., and Rampino, M.R., eds) pp. 1-23.

Willingham, J. (2014). The ecology and morphology of deep-sea benthic foraminifera: The Australian Margin and epifaunal pore characteristics (Doctoral dissertation, Indiana State University).

Van der Zwaan, G.J., Duijnstee, I.A.P., den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoen, T.J., (1999). Benthic foraminifers: proxies or problems? A review of paleoecological concepts. Earth Science Reviews, vol. 46: 213–236.

Venturelli, R., Rathburn, A., Burkett, A., Ziebis, W., (2018). Epifaunal Foraminifera in an Infaunal World: Insights Into the Influence of Heterogeneity on the Benthic Ecology of Oxygen-Poor, Deep-Sea Habitats. Frontiers in Marine Science, vol. 5: 344.

APPENDICES

APPENDIX A: Foraminiferal Abundance

Core	Station 1	Station 6	Station 7	Station 12
Latitude	32° 52.002	32° 43.301	32° 33.997	32° 37.660
Longitude	118° 10.997	117° 55.898	118° 37.847	119° 02.583
Dissolved Oxygen (mL/L)	0.9065	1.071	1.274	0.533
Dissolved Oxygen (µmol/L)	40.482	47.826	56.894	23.803
Depth	863	617.9	1001	328
Average Grain Size	72% Sand	69% Silt	86% Sand	96% Silt
Species				
Ammodiscus tenuis	0.00	30.61	0.00	0.00
Angulogerina carinata	0.00	0.00	0.00	4.17
Bolivina alata	0.00	47.04	0.00	0.00
Bolivina sp	0.00	4.22	0.00	0.00
Bolivina pacifica	0.00	31.37	25.00	0.00
Bolivina pseudopunctata	0.00	0.00	19.11	79.17
Bolivina spathulata	0.00	0.00	0.00	2.08
Bolivina spissa	169.01	28.55	18.72	956.94
Bulimina marginata	0.00	0.00	6.02	0.00
Bulimina pupoides	56.72	45.08	0.00	0.00
Cancris oblongus	0.00	3.75	0.00	132.64
Cassidulina carinata	0.00	5.30	0.00	9.72
Chilostomella oolina	22.14	22.58	3.33	42.36
Cibicidoides wuellerstorfi	0.00	15.13	10.74	0.00
Cornuspira involvens	5.00	0.00	45.94	39.58
Cyclammina sp	0.00	9.52	2.38	4.17
Deflated sphere	4.55	5.30	0.00	2.08
Eggerelloides sp A	9.55	30.61	0.00	0.00
Eggerelloides sp B	5.00	0.00	0.00	0.00
Eggerelloides sp C	0.00	4.75	0.00	0.00
Ehrenbergina trigona	0.00	16.88	3.85	4.17
Eratidus foliaceus	0.00	4.22	0.00	0.00
Fissurina sp	0.00	5.30	0.00	0.00
Frondicularia sp	0.00	0.00	0.00	2.08

Globigerina eggeri	6.52	0.00	0.00	6.25
Globobulimina hoeglundi	0.00	5.30	0.00	0.00
Globobulimina pacfica	0.00	89.37	0.00	8.33
Globobulimina spinifera	55.11	53.11	0.00	0.00
Globocassidulina subglobosa	15.84	42.82	7.41	32.64
Haplophragmoides canariensis	0.00	0.00	0.00	5.56
Haplophragmoides sp	22.20	43.88	0.00	0.00
Hoeglundina elegans	6.72	13.19	234.37	0.00
Laticarinina pauperata	0.00	0.00	8.52	0.00
Martinottiella communis	0.00	13.74	0.00	0.00
Milliolid sp	0.00	13.74	0.00	0.00
Mutated Reophax sp A	0.00	0.00	9.03	0.00
Mutated Unknown	0.00	0.00	1.85	0.00
Nonionella glabra	0.00	0.00	1.85	0.00
Oridosalis umbonatus	0.00	0.00	30.60	0.00
Pullenia subcarinata	0.00	0.00	4.17	0.00
Pyrgo murrhina	0.00	4.22	0.00	0.00
Pyrgo sp A	0.00	8.44	0.00	0.00
Pyrgo sp B	0.00	4.22	0.00	0.00
Pyrgo williamsoni	0.00	4.22	0.00	0.00
Quinqueloculina laevigata	15.61	0.00	0.00	0.00
Reophax dentaliniformis	96.03	25.41	48.76	2.08
Reophax hispidula	5.00	0.00	0.00	0.00
Reophax horridus	8.33	128.49	86.52	0.00
Reophax pilulifer	0.00	0.00	25.19	6.25
Reophax scorpiurus	0.00	0.00	0.00	18.06
Rosalina bradyi	21.74	269.67	0.00	0.00
Sphere C	0.00	4.22	0.00	0.00
Sphere D	0.00	4.22	0.00	0.00
Spiral A	0.00	0.00	15.19	0.00
Spiral B	0.00	9.52	11.86	0.00
Spiroloculina tenuiseptata	0.00	0.00	10.88	0.00
Thurammina sp	0.00	30.61	0.00	0.00
Trochammina sp	0.00	13.74	0.00	0.00
Unidentified Agglutinate 1	13.64	0.00	0.00	0.00
Unidentified agglutinate juvenile	4.55	0.00	0.00	0.00
Unidentified juvenile	32.48	24.25	3.70	9.72
Uvigerina hispida	17.98	55.93	0.00	0.00
Uvigerina peregrina	27.50	254.94	78.13	0.00
Valvulinera glabra	7.14	0.00	0.00	0.00
Valvulineria minuta	0.00	5.30	0.00	0.00
Valvulineria oblongata	4.55	17.95	0.00	0.00
Valvulineria rugosa	0.00	0.00	0.00	2.08

Core/Split	Station 1: 0 - 1 cm	Station 1: 1 - 1.5 cm	Station 1: 1.5 - 2 cm
Species			
Ammodiscus tenuis	0.00	0.00	0.00
Angulogerina carinata	0.00	0.00	0.00
Bolivina alata	0.00	0.00	0.00
Bolivina sp	0.00	0.00	0.00
Bolivina pacifica	0.00	0.00	0.00
Bolivina pseudopunctata	0.00	0.00	0.00
Bolivina spathulata	0.00	0.00	0.00
Bolivina spissa	15.22	45.45	58.33
Bulimina marginata	0.00	0.00	0.00
Bulimina pupoides	2.17	4.55	0.00
Cancris oblongus	0.00	0.00	0.00
Cassidulina carinata	0.00	0.00	0.00
Chilostomella oolina	0.00	0.00	0.00
Cibicidoides wuellerstorfi	0.00	0.00	0.00
Cornuspira involvens	0.00	0.00	0.00
Cyclammina sp	0.00	0.00	0.00
Deflated sphere	0.00	4.55	0.00
Eggerelloides sp A	0.00	4.55	0.00
Eggerelloides sp B	0.00	0.00	0.00
Eggerelloides sp C	0.00	0.00	0.00
Ehrenbergina trigona	0.00	0.00	0.00
Eratidus foliaceus	0.00	0.00	0.00
Fissurina sp	0.00	0.00	0.00
Frondicularia sp	0.00	0.00	0.00
Globigerina eggeri	6.52	0.00	0.00
Globobulimina hoeglundi	0.00	0.00	0.00
Globobulimina pacfica	0.00	0.00	0.00
Globobulimina spinifera	4.35	9.09	16.67
Globocassidulina subglobosa	8.70	0.00	0.00
Haplophragmoides canariensis	0.00	0.00	0.00
Haplophragmoides sp	2.17	4.55	8.33
Hoeglundina elegans	2.17	4.55	0.00
Laticarinina pauperata	0.00	0.00	0.00
Martinottiella communis	0.00	0.00	0.00
Milliolid sp	0.00	0.00	0.00
Mutated Reophax sp A	0.00	0.00	0.00
Mutated Unknown	0.00	0.00	0.00
Nonionella glabra	0.00	0.00	0.00

Oridosalis umbonatus	0.00	0.00	0.00
Pullenia subcarinata	0.00	0.00	0.00
Pyrgo murrhina	0.00	0.00	0.00
Pyrgo sp A	0.00	0.00	0.00
Pyrgo sp B	0.00	0.00	0.00
Pyrgo williamsoni	0.00	0.00	0.00
Quinqueloculina laevigata	6.52	9.09	0.00
Reophax dentaliniformis	2.17	9.09	8.33
Reophax hispidula	0.00	0.00	0.00
Reophax horridus	0.00	0.00	8.33
Reophax pilulifer	0.00	0.00	0.00
Reophax scorpiurus	0.00	0.00	0.00
Rosalina bradyi	21.74	0.00	0.00
Sphere C	0.00	0.00	0.00
Sphere D	0.00	0.00	0.00
Spiral A	0.00	0.00	0.00
Spiral B	0.00	0.00	0.00
Spiroloculina tenuiseptata	0.00	0.00	0.00
Thurammina sp	0.00	0.00	0.00
Trochammina sp	0.00	0.00	0.00
Unidentified Agglutinate 1	0.00	13.64	0.00
Unidentified agglutinate juvenile	0.00	4.55	0.00
Unidentified juvenile	2.17	13.64	16.67
Uvigerina hispida	4.35	13.64	0.00
Uvigerina peregrina	2.17	18.18	0.00
Valvulinera glabra	0.00	0.00	0.00
Valvulineria minuta	0.00	0.00	0.00
Valvulineria oblongata	0.00	4.55	0.00
Valvulineria rugosa	0.00	0.00	0.00

Core/Split	Station 1: 2 - 2.5 cm	Station 1: 2.5 - 3 cm	Average Living Depth (cm)
Species			
Ammodiscus tenuis	0.00	0.00	
Angulogerina carinata	0.00	0.00	
Bolivina alata	0.00	0.00	
Bolivina sp	0.00	0.00	
Bolivina pacifica	0.00	0.00	
Bolivina pseudopunctata	0.00	0.00	
Bolivina spathulata	0.00	0.00	
Bolivina spissa	50.00	0.00	1.65
Bulimina marginata	0.00	0.00	
Bulimina pupoides	50.00	0.00	2.10
Cancris oblongus	0.00	0.00	
Cassidulina carinata	0.00	0.00	

Chilostomella oolina	7.14	15.00	2.59
Cibicidoides wuellerstorfi	0.00	0.00	
Cornuspira involvens	0.00	5.00	2.75
Cyclammina sp	0.00	0.00	
Deflated sphere	0.00	0.00	1.25
Eggerelloides sp A	0.00	5.00	2.04
Eggerelloides sp B	0.00	5.00	2.75
Eggerelloides sp C	0.00	0.00	
Ehrenbergina trigona	0.00	0.00	
Eratidus foliaceus	0.00	0.00	
Fissurina sp	0.00	0.00	
Frondicularia sp	0.00	0.00	
Globigerina eggeri	0.00	0.00	0.50
Globobulimina hoeglundi	0.00	0.00	
Globobulimina pacfica	0.00	0.00	
Globobulimina spinifera	0.00	25.00	2.02
Globocassidulina subglobosa	7.14	0.00	1.29
Haplophragmoides canariensis	0.00	0.00	
Haplophragmoides sp	7.14	0.00	1.69
Hoeglundina elegans	0.00	0.00	1.01
Laticarinina pauperata	0.00	0.00	
Martinottiella communis	0.00	0.00	
Milliolid sp	0.00	0.00	
Mutated Reophax sp A	0.00	0.00	
Mutated Unknown	0.00	0.00	
Nonionella glabra	0.00	0.00	
Oridosalis umbonatus	0.00	0.00	
Pullenia subcarinata	0.00	0.00	
Pyrgo murrhina	0.00	0.00	
Pyrgo sp A	0.00	0.00	
Pyrgo sp B	0.00	0.00	
Pyrgo williamsoni	0.00	0.00	
Quinqueloculina laevigata	0.00	0.00	0.94
Reophax dentaliniformis	71.43	5.00	2.10
Reophax hispidula	0.00	5.00	2.75
Reophax horridus	0.00	0.00	1.75
Reophax pilulifer	0.00	0.00	
Reophax scorpiurus	0.00	0.00	
Rosalina bradyi	0.00	0.00	0.50
Sphere C	0.00	0.00	
Sphere D	0.00	0.00	
Spiral A	0.00	0.00	
Spiral B	0.00	0.00	
Spiroloculina tenuiseptata	0.00	0.00	
Thurammina sp	0.00	0.00	
Trochammina sp	0.00	0.00	
Unidentified Agglutinate 1	0.00	0.00	1.25

Unidentified agglutinate juvenile	0.00	0.00	1.25
Unidentified juvenile	0.00	0.00	1.46
Uvigerina hispida	0.00	0.00	1.07
Uvigerina peregrina	7.14	0.00	1.45
Valvulinera glabra	7.14	0.00	2.25
Valvulineria minuta	0.00	0.00	
Valvulineria oblongata	0.00	0.00	1.25
Valvulineria rugosa	0.00	0.00	

Core/Split	Station 6: 0 - 1 cm	Station 6: 1 - 1.5 cm	Station 6: 1.5 - 2 cm
Species			
Ammodiscus tenuis	25.32	5.30	0.00
Angulogerina carinata	0.00	0.00	0.00
Bolivina alata	21.10	21.19	4.75
Bolivina sp	4.22	0.00	0.00
Bolivina pacifica	4.22	15.89	0.00
Bolivina pseudopunctata	0.00	0.00	0.00
Bolivina spathulata	0.00	0.00	0.00
Bolivina spissa	0.00	10.59	0.00
Bulimina marginata	0.00	0.00	0.00
Bulimina pupoides	21.10	10.59	0.00
Cancris oblongus	0.00	0.00	0.00
Cassidulina carinata	0.00	5.30	0.00
Chilostomella oolina	0.00	15.89	0.00
Cibicidoides wuellerstorfi	8.44	0.00	0.00
Cornuspira involvens	0.00	0.00	0.00
Cyclammina sp	4.22	5.30	0.00
Deflated sphere	0.00	5.30	0.00
Eggerelloides sp A	25.32	5.30	0.00
Eggerelloides sp B	0.00	0.00	0.00
Eggerelloides sp C	0.00	0.00	4.75
Ehrenbergina trigona	16.88	0.00	0.00
Eratidus foliaceus	4.22	0.00	0.00
Fissurina sp	0.00	5.30	0.00
Frondicularia sp	0.00	0.00	0.00
Globigerina eggeri	0.00	0.00	0.00
Globobulimina hoeglundi	0.00	5.30	0.00
Globobulimina pacfica	21.10	26.48	0.00
Globobulimina spinifera	12.66	5.30	14.26
Globocassidulina subglobosa	16.88	21.19	4.75
Haplophragmoides canariensis	0.00	0.00	0.00
Haplophragmoides sp	8.44	21.19	14.26
Hoeglundina elegans	8.44	0.00	4.75
Laticarinina pauperata	0.00	0.00	0.00

Martinottiella communis	8.44	5.30	0.00
Milliolid sp	8.44	5.30	0.00
Mutated Reophax sp A	0.00	0.00	0.00
Mutated Unknown	0.00	0.00	0.00
Nonionella glabra	0.00	0.00	0.00
Oridosalis umbonatus	0.00	0.00	0.00
Pullenia subcarinata	0.00	0.00	0.00
Pyrgo murrhina	4.22	0.00	0.00
Pyrgo sp A	8.44	0.00	0.00
Pyrgo sp B	4.22	0.00	0.00
Pyrgo williamsoni	4.22	0.00	0.00
Quinqueloculina laevigata	0.00	0.00	0.00
Reophax dentaliniformis	4.22	21.19	0.00
Reophax hispidula	0.00	0.00	0.00
Reophax horridus	59.07	21.19	19.01
Reophax pilulifer	0.00	0.00	0.00
Reophax scorpiurus	0.00	0.00	0.00
Rosalina bradyi	164.56	58.26	0.00
Sphere C	4.22	0.00	0.00
Sphere D	4.22	0.00	0.00
Spiral A	0.00	0.00	0.00
Spiral B	4.22	5.30	0.00
Spiroloculina tenuiseptata	0.00	0.00	0.00
Thurammina sp	25.32	5.30	0.00
Trochammina sp	8.44	5.30	0.00
Unidentified Agglutinate 1	0.00	0.00	0.00
Unidentified agglutinate juvenile	0.00	0.00	0.00
Unidentified juvenile	0.00	5.30	4.75
Uvigerina hispida	50.63	5.30	0.00
Uvigerina peregrina	105.49	26.48	52.28
Valvulinera glabra	0.00	0.00	0.00
Valvulineria minuta	0.00	5.30	0.00
Valvulineria oblongata	0.00	0.00	0.00
Valvulineria rugosa	0.00	0.00	0.00

Core/Split	Station 6: 2 - 2.5 cm	Station 6: 2.5 - 3 cm	Average Living Depth (cm)
Species			
Ammodiscus tenuis	0.00	0.00	0.63
Angulogerina carinata	0.00	0.00	
Bolivina alata	0.00	0.00	0.96
Bolivina sp	0.00	0.00	0.50
Bolivina pacifica	11.26	0.00	1.51
Bolivina pseudopunctata	0.00	0.00	
Bolivina spathulata	0.00	0.00	

Bolivina spissa	11.26	6.69	2.00
Bulimina marginata	0.00	0.00	
Bulimina pupoides	0.00	13.39	1.34
Cancris oblongus	3.75	0.00	2.25
Cassidulina carinata	0.00	0.00	1.25
Chilostomella oolina	0.00	6.69	1.69
Cibicidoides wuellerstorfi	0.00	6.69	1.49
Cornuspira involvens	0.00	0.00	
Cyclammina sp	0.00	0.00	0.92
Deflated sphere	0.00	0.00	1.25
Eggerelloides sp A	0.00	0.00	0.63
Eggerelloides sp B	0.00	0.00	
Eggerelloides sp C	0.00	0.00	1.75
Ehrenbergina trigona	0.00	0.00	0.50
Eratidus foliaceus	0.00	0.00	0.50
Fissurina sp	0.00	0.00	1.25
Frondicularia sp	0.00	0.00	
Globigerina eggeri	0.00	0.00	
Globobulimina hoeglundi	0.00	0.00	1.25
Globobulimina pacfica	15.02	26.77	1.69
Globobulimina spinifera	7.51	13.39	1.72
Globocassidulina subglobosa	0.00	0.00	1.01
Haplophragmoides canariensis	0.00	0.00	
Haplophragmoides sp	0.00	0.00	1.27
Hoeglundina elegans	0.00	0.00	0.95
Laticarinina pauperata	0.00	0.00	
Martinottiella communis	0.00	0.00	0.79
Milliolid sp	0.00	0.00	0.79
Mutated Reophax sp A	0.00	0.00	
Mutated Unknown	0.00	0.00	
Nonionella glabra	0.00	0.00	
Oridosalis umbonatus	0.00	0.00	
Pullenia subcarinata	0.00	0.00	
Pyrgo murrhina	0.00	0.00	0.50
Pyrgo sp A	0.00	0.00	0.50
Pyrgo sp B	0.00	0.00	0.50
Pyrgo williamsoni	0.00	0.00	0.50
Quinqueloculina laevigata	0.00	0.00	
Reophax dentaliniformis	0.00	0.00	1.13
Reophax hispidula	0.00	0.00	
Reophax horridus	22.52	6.69	1.23
Reophax pilulifer	0.00	0.00	
Reophax scorpiurus	0.00	0.00	
Rosalina bradyi	0.00	46.85	1.05
Sphere C	0.00	0.00	0.50
Sphere D	0.00	0.00	0.50
Spiral A	0.00	0.00	
Spiral B	0.00	0.00	0.92

Spiroloculina tenuiseptata	0.00	0.00	
Thurammina sp	0.00	0.00	0.63
Trochammina sp	0.00	0.00	0.79
Unidentified Agglutinate 1	0.00	0.00	
Unidentified agglutinate juvenile	0.00	0.00	
Unidentified juvenile	7.51	6.69	2.07
Uvigerina hispida	0.00	0.00	0.57
Uvigerina peregrina	3.75	66.93	1.45
Valvulinera glabra	0.00	0.00	
Valvulineria minuta	0.00	0.00	1.25
Valvulineria oblongata	11.26	6.69	2.44
Valvulineria rugosa	0.00	0.00	

Core/Split	Station 7: 0 - 1 cm	Station 7: 1 - 1.5 cm	Station 7: 1.5 - 2 cm
Species			
Ammodiscus tenuis	0.00	0.00	0.00
Angulogerina carinata	0.00	0.00	0.00
Bolivina alata	0.00	0.00	0.00
Bolivina sp	0.00	0.00	0.00
Bolivina pacifica	0.00	0.00	0.00
Bolivina pseudopunctata	1.85	0.00	0.00
Bolivina spathulata	0.00	0.00	0.00
Bolivina spissa	0.00	3.33	15.38
Bulimina marginata	1.85	0.00	0.00
Bulimina pupoides	0.00	0.00	0.00
Cancris oblongus	0.00	0.00	0.00
Cassidulina carinata	0.00	0.00	0.00
Chilostomella oolina	0.00	3.33	0.00
Cibicidoides wuellerstorfi	7.41	3.33	0.00
Cornuspira involvens	5.56	16.67	15.38
Cyclammina sp	0.00	0.00	0.00
Deflated sphere	0.00	0.00	0.00
Eggerelloides sp A	0.00	0.00	0.00
Eggerelloides sp B	0.00	0.00	0.00
Eggerelloides sp C	0.00	0.00	0.00
Ehrenbergina trigona	0.00	0.00	3.85
Eratidus foliaceus	0.00	0.00	0.00
Fissurina sp	0.00	0.00	0.00
Frondicularia sp	0.00	0.00	0.00
Globigerina eggeri	0.00	0.00	0.00
Globobulimina hoeglundi	0.00	0.00	0.00
Globobulimina pacfica	0.00	0.00	0.00
Globobulimina spinifera	0.00	0.00	0.00
Globocassidulina subglobosa	7.41	0.00	0.00

Haplophragmoides canariensis	0.00	0.00	0.00
Haplophragmoides sp	0.00	0.00	0.00
Hoeglundina elegans	100.00	56.67	46.15
Laticarinina pauperata	1.85	6.67	0.00
Martinottiella communis	0.00	0.00	0.00
Milliolid sp	0.00	0.00	0.00
Mutated Reophax sp A	1.85	3.33	3.85
Mutated Unknown	1.85	0.00	0.00
Nonionella glabra	1.85	0.00	0.00
Oridosalis umbonatus	14.81	3.33	7.69
Pullenia subcarinata	0.00	0.00	0.00
Pyrgo murrhina	0.00	0.00	0.00
Pyrgo sp A	0.00	0.00	0.00
Pyrgo sp B	0.00	0.00	0.00
Pyrgo williamsoni	0.00	0.00	0.00
Quinqueloculina laevigata	0.00	0.00	0.00
Reophax dentaliniformis	11.11	13.33	15.38
Reophax hispidula	0.00	0.00	0.00
Reophax horridus	18.52	13.33	15.38
Reophax pilulifer	18.52	6.67	0.00
Reophax scorpiurus	0.00	0.00	0.00
Rosalina bradyi	0.00	0.00	0.00
Sphere C	0.00	0.00	0.00
Sphere D	0.00	0.00	0.00
Spiral A	1.85	13.33	0.00
Spiral B	0.00	0.00	7.69
Spiroloculina tenuiseptata	3.70	3.33	3.85
Thurammina sp	0.00	0.00	0.00
Trochammina sp	0.00	0.00	0.00
Unidentified Agglutinate 1	0.00	0.00	0.00
Unidentified agglutinate juvenile	0.00	0.00	0.00
Unidentified juvenile	3.70	0.00	0.00
Uvigerina hispida	0.00	0.00	0.00
Uvigerina peregrina	22.22	33.33	7.69
Valvulinera glabra	0.00	0.00	0.00
Valvulineria minuta	0.00	0.00	0.00
Valvulineria oblongata	0.00	0.00	0.00
Valvulineria rugosa	0.00	0.00	0.00

Core/Split	Station 7: 2 - 2.5 cm	Station 7: 2.5 - 3 cm	Average Living Depth (cm)

Species			
Ammodiscus tenuis	0.00	0.00	
Angulogerina carinata	0.00	0.00	
Bolivina alata	0.00	0.00	
Bolivina sp	0.00	0.00	
Bolivina pacifica	8.33	16.67	2.58
Bolivina pseudopunctata	12.50	4.76	2.21
Bolivina spathulata	0.00	0.00	
Bolivina spissa	0.00	0.00	1.66
Bulimina marginata	4.17	0.00	1.71
Bulimina pupoides	0.00	0.00	
Cancris oblongus	0.00	0.00	
Cassidulina carinata	0.00	0.00	
Chilostomella oolina	0.00	0.00	1.25
Cibicidoides wuellerstorfi	0.00	0.00	0.73
Cornuspira involvens	8.33	0.00	1.51
Cyclammina sp	0.00	2.38	2.75
Deflated sphere	0.00	0.00	
Eggerelloides sp A	0.00	0.00	
Eggerelloides sp B	0.00	0.00	
Eggerelloides sp C	0.00	0.00	
Ehrenbergina trigona	0.00	0.00	1.75
Eratidus foliaceus	0.00	0.00	
Fissurina sp	0.00	0.00	
Frondicularia sp	0.00	0.00	
Globigerina eggeri	0.00	0.00	
Globobulimina hoeglundi	0.00	0.00	
Globobulimina pacfica	0.00	0.00	
Globobulimina spinifera	0.00	0.00	
Globocassidulina subglobosa	0.00	0.00	0.50
Haplophragmoides canariensis	0.00	0.00	
Haplophragmoides sp	0.00	0.00	
Hoeglundina elegans	29.17	2.38	1.17
Laticarinina pauperata	0.00	0.00	1.09
Martinottiella communis	0.00	0.00	
Milliolid sp	0.00	0.00	
Mutated Reophax sp A	0.00	0.00	1.31
Mutated Unknown	0.00	0.00	0.50
Nonionella glabra	0.00	0.00	0.50
Oridosalis umbonatus	0.00	4.76	1.25
Pullenia subcarinata	4.17	0.00	2.25
Pyrgo murrhina	0.00	0.00	
Pyrgo sp A	0.00	0.00	
Pyrgo sp B	0.00	0.00	
Pyrgo williamsoni	0.00	0.00	
Quinqueloculina laevigata	0.00	0.00	
Reophax dentaliniformis	4.17	4.76	1.47
Reophax hispidula	0.00	0.00	

Reophax horridus	25.00	14.29	1.72
Reophax pilulifer	0.00	0.00	0.70
Reophax scorpiurus	0.00	0.00	
Rosalina bradyi	0.00	0.00	
Sphere C	0.00	0.00	
Sphere D	0.00	0.00	
Spiral A	0.00	0.00	1.16
Spiral B	4.17	0.00	1.93
Spiroloculina tenuiseptata	0.00	0.00	1.17
Thurammina sp	0.00	0.00	
Trochammina sp	0.00	0.00	
Unidentified Agglutinate 1	0.00	0.00	
Unidentified agglutinate juvenile	0.00	0.00	
Unidentified juvenile	0.00	0.00	0.50
Uvigerina hispida	0.00	0.00	
Uvigerina peregrina	12.50	2.38	1.29
Valvulinera glabra	0.00	0.00	
Valvulineria minuta	0.00	0.00	
Valvulineria oblongata	0.00	0.00	
Valvulineria rugosa	0.00	0.00	

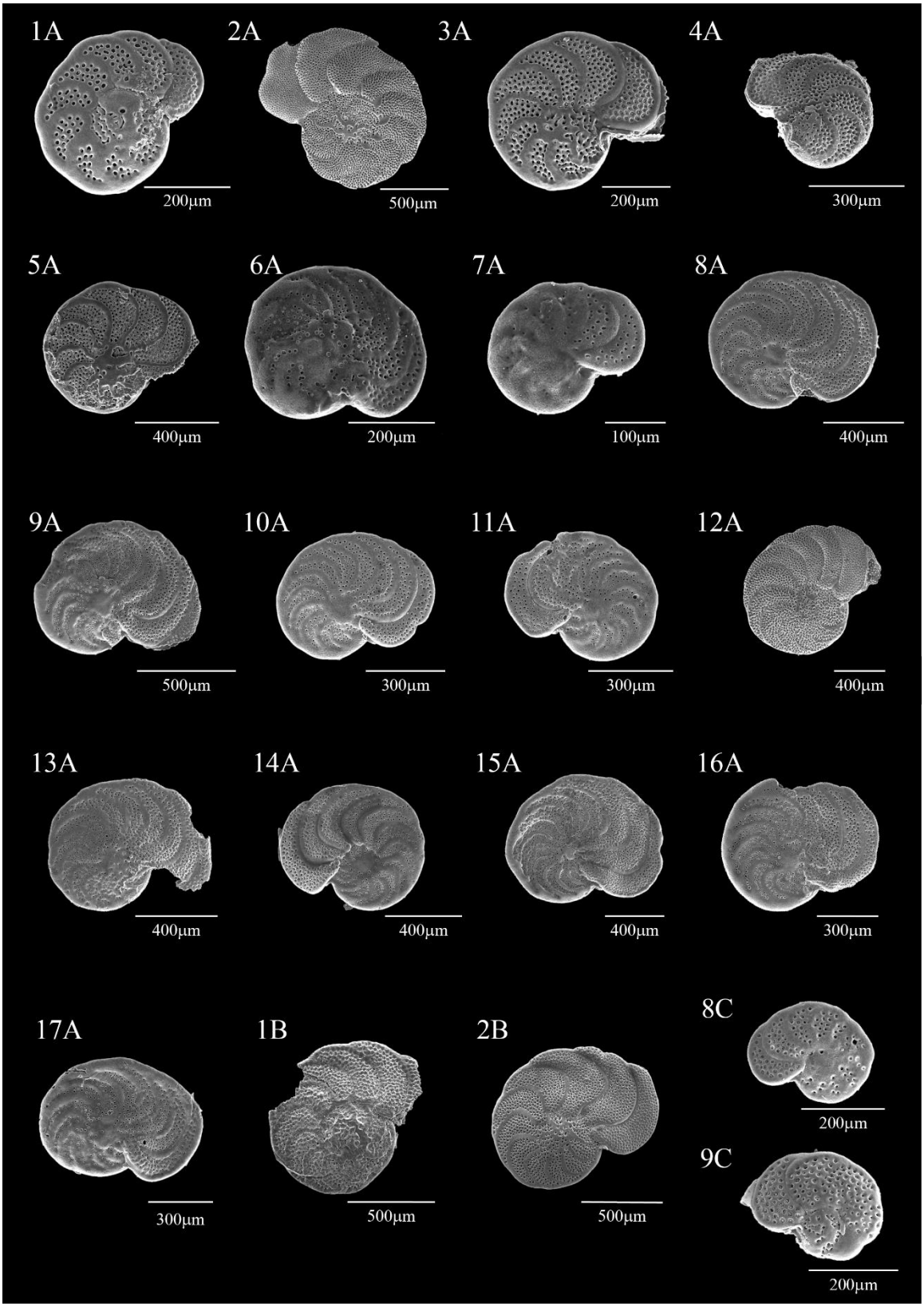
Core/Split	Station 12: 0 - 1 cm	Station 12: 1 - 1.5 cm	Station 12: 1.5 - 2 cm
Species			
Ammodiscus tenuis	0.00	0.00	0.00
Angulogerina carinata	0.00	0.00	0.00
Bolivina alata	0.00	0.00	0.00
Bolivina sp	0.00	0.00	0.00
Bolivina pacifica	0.00	0.00	0.00
Bolivina pseudopunctata	1.85	0.00	0.00
Bolivina spathulata	0.00	0.00	0.00
Bolivina spissa	0.00	3.33	15.38
Bulimina marginata	1.85	0.00	0.00
Bulimina pupoides	0.00	0.00	0.00
Cancris oblongus	0.00	0.00	0.00
Cassidulina carinata	0.00	0.00	0.00
Chilostomella oolina	0.00	3.33	0.00
Cibicidoides wuellerstorfi	7.41	3.33	0.00
Cornuspira involvens	5.56	16.67	15.38
Cyclammina sp	0.00	0.00	0.00
Deflated sphere	0.00	0.00	0.00
Eggerelloides sp A	0.00	0.00	0.00
Eggerelloides sp B	0.00	0.00	0.00
Eggerelloides sp C	0.00	0.00	0.00
Ehrenbergina trigona	0.00	0.00	3.85

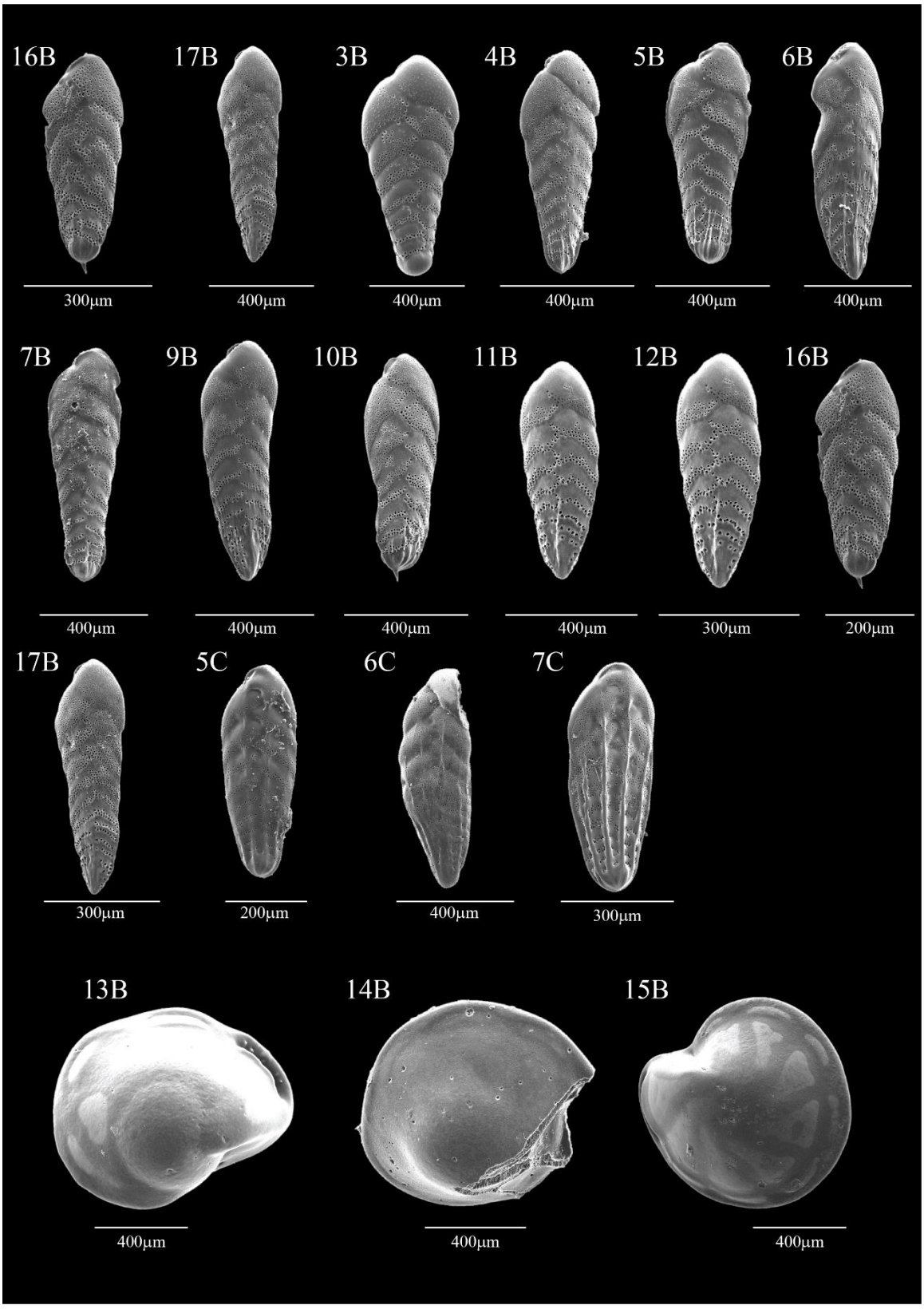
Eratidus foliaceus	0.00	0.00	0.00
Fissurina sp	0.00	0.00	0.00
Frondicularia sp	0.00	0.00	0.00
Globigerina eggeri	0.00	0.00	0.00
Globobulimina hoeglundi	0.00	0.00	0.00
Globobulimina pacfica	0.00	0.00	0.00
Globobulimina spinifera	0.00	0.00	0.00
Globocassidulina subglobosa	7.41	0.00	0.00
Haplophragmoides canariensis	0.00	0.00	0.00
Haplophragmoides sp	0.00	0.00	0.00
Hoeglundina elegans	100.00	56.67	46.15
Laticarinina pauperata	1.85	6.67	0.00
Martinottiella communis	0.00	0.00	0.00
Milliolid sp	0.00	0.00	0.00
Mutated Reophax sp A	1.85	3.33	3.85
Mutated Unknown	1.85	0.00	0.00
Nonionella glabra	1.85	0.00	0.00
Oridosalis umbonatus	14.81	3.33	7.69
Pullenia subcarinata	0.00	0.00	0.00
Pyrgo murrhina	0.00	0.00	0.00
Pyrgo sp A	0.00	0.00	0.00
Pyrgo sp B	0.00	0.00	0.00
Pyrgo williamsoni	0.00	0.00	0.00
Quinqueloculina laevigata	0.00	0.00	0.00
Reophax dentaliniformis	11.11	13.33	15.38
Reophax hispidula	0.00	0.00	0.00
Reophax horridus	18.52	13.33	15.38
Reophax pilulifer	18.52	6.67	0.00
Reophax scorpiurus	0.00	0.00	0.00
Rosalina bradyi	0.00	0.00	0.00
Sphere C	0.00	0.00	0.00
Sphere D	0.00	0.00	0.00
Spiral A	1.85	13.33	0.00
Spiral B	0.00	0.00	7.69
Spiroloculina tenuiseptata	3.70	3.33	3.85
Thurammina sp	0.00	0.00	0.00
Trochammina sp	0.00	0.00	0.00
Unidentified Agglutinate 1	0.00	0.00	0.00
Unidentified agglutinate juvenile	0.00	0.00	0.00
Unidentified juvenile	3.70	0.00	0.00
Uvigerina hispida	0.00	0.00	0.00
Uvigerina peregrina	22.22	33.33	7.69
Valvulinera glabra	0.00	0.00	0.00
Valvulineria minuta	0.00	0.00	0.00
Valvulineria oblongata	0.00	0.00	0.00
Valvulineria rugosa	0.00	0.00	0.00

Core/Split	Station 12: 2 - 2.5 cm	Station 12: 2.5 - 3 cm	Average Living Depth (cm)
Species			
Ammodiscus tenuis	0.00	0.00	
Angulogerina carinata	0.00	0.00	
Bolivina alata	0.00	0.00	
Bolivina sp	0.00	0.00	
Bolivina pacifica	8.33	16.67	2.58
Bolivina pseudopunctata	12.50	4.76	2.21
Bolivina spathulata	0.00	0.00	
Bolivina spissa	0.00	0.00	1.66
Bulimina marginata	4.17	0.00	1.71
Bulimina pupoides	0.00	0.00	
Cancris oblongus	0.00	0.00	
Cassidulina carinata	0.00	0.00	
Chilostomella oolina	0.00	0.00	1.25
Cibicidoides wuellerstorfi	0.00	0.00	0.73
Cornuspira involvens	8.33	0.00	1.51
Cyclammina sp	0.00	2.38	2.75
Deflated sphere	0.00	0.00	
Eggerelloides sp A	0.00	0.00	
Eggerelloides sp B	0.00	0.00	
Eggerelloides sp C	0.00	0.00	
Ehrenbergina trigona	0.00	0.00	1.75
Eratidus foliaceus	0.00	0.00	
Fissurina sp	0.00	0.00	
Frondicularia sp	0.00	0.00	
Globigerina eggeri	0.00	0.00	
Globobulimina hoeglundi	0.00	0.00	
Globobulimina pacfica	0.00	0.00	
Globobulimina spinifera	0.00	0.00	
Globocassidulina subglobosa	0.00	0.00	0.50
Haplophragmoides canariensis	0.00	0.00	
Haplophragmoides sp	0.00	0.00	
Hoeglundina elegans	29.17	2.38	1.17
Laticarinina pauperata	0.00	0.00	1.09
Martinottiella communis	0.00	0.00	
Milliolid sp	0.00	0.00	
Mutated Reophax sp A	0.00	0.00	1.31
Mutated Unknown	0.00	0.00	0.50
Nonionella glabra	0.00	0.00	0.50
Oridosalis umbonatus	0.00	4.76	1.25
Pullenia subcarinata	4.17	0.00	2.25
Pyrgo murrhina	0.00	0.00	
Pyrgo sp A	0.00	0.00	
Pyrgo sp B	0.00	0.00	
Pyrgo williamsoni	0.00	0.00	

Quinqueloculina laevigata	0.00	0.00	
Reophax dentaliniformis	4.17	4.76	1.47
Reophax hispidula	0.00	0.00	
Reophax horridus	25.00	14.29	1.72
Reophax pilulifer	0.00	0.00	0.70
Reophax scorpiurus	0.00	0.00	
Rosalina bradyi	0.00	0.00	
Sphere C	0.00	0.00	
Sphere D	0.00	0.00	
Spiral A	0.00	0.00	1.16
Spiral B	4.17	0.00	1.93
Spiroloculina tenuiseptata	0.00	0.00	1.17
Thurammina sp	0.00	0.00	
Trochammina sp	0.00	0.00	
Unidentified Agglutinate 1	0.00	0.00	
Unidentified agglutinate juvenile	0.00	0.00	
Unidentified juvenile	0.00	0.00	0.50
Uvigerina hispida	0.00	0.00	
Uvigerina peregrina	12.50	2.38	1.29
Valvulinera glabra	0.00	0.00	
Valvulineria minuta	0.00	0.00	
Valvulineria oblongata	0.00	0.00	
Valvulineria rugosa	0.00	0.00	

APPENDIX B: SPORE SEM Plates




16B
17B
3B
4B
5B
6B
300µm
400µm
400µm
400µm
400µm
400µm
7B
9B
10B
11B
12B
16B
400µm
400µm
400µm
400µm
300µm
200µm
17B
5C
6C
7C
300µm
200µm
400µm
300µm
13B
14B
15B
400µm
400µm
400µm

APPENDIX C: SPORE Plate Descriptions

Stub ID	Chamber of Interest	Station #	Depth (m)	O2 (mL/L)	Species	Dead or Alive	Pore (%)	Non-pore (%)
1A	Penultimate	STN 6	617.9	1.071	C. wuellerstorfi	Alive	21.39%	78.61%
	Antepenultimate		617.9	1.071			22.63%	77.37%
2A	Penultimate	STN 6	617.9	1.071	C. wuellerstorfi	Dead	16.54%	83.46%
	Antepenultimate		617.9	1.071			20.84%	79.16%
3A	Penultimate	STN 6	617.9	1.071	C. wuellerstorfi	Alive	21.15%	78.85%
	Antepenultimate		617.9	1.071			23.43%	76.57%
4A	Penultimate	STN 6	617.9	1.071	C. wuellerstorfi	Dead	10.80%	89.20%
	Antepenultimate		617.9	1.071			25.33%	74.67%
5A	Penultimate	STN 6	617.9	1.071	C. wuellerstorfi	Dead	17.87%	82.13%
	Antepenultimate		617.9	1.071			17.24%	82.76%
6A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Alive	14.37%	85.63%
	Antepenultimate		1001	1.274			11.95%	88.05%
7A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Alive	8.80%	91.20%
	Antepenultimate		1001	1.274			9.37%	90.63%
8A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	16.11%	83.89%
	Antepenultimate		1001	1.274			13.05%	86.95%
9A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	11.64%	88.36%
	Antepenultimate		1001	1.274			11.45%	88.55%
10A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Alive	9.57%	90.43%
	Antepenultimate		1001	1.274			8.69%	91.31%
11A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	7.25%	92.75%
	Antepenultimate		1001	1.274			7.50%	92.50%
12A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	10.49%	89.51%
	Antepenultimate		1001	1.274			9.75%	90.25%
13A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	5.92%	94.08%
	Antepenultimate		1001	1.274			7.61%	92.39%
14A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Alive	13.01%	86.99%
	Antepenultimate		1001	1.274			6.43%	93.57%
15A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	11.65%	88.35%
	Antepenultimate		1001	1.274			10.51%	89.49%
16A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	11.97%	88.03%
	Antepenultimate		1001	1.274			10.25%	89.75%

17A	Penultimate	STN 7	1001	1.274	C. wuellerstorfi	Dead	10.91%	89.09%
	Antepenultimate		1001	1.274			8.30%	91.70%
1B	Penultimate	STN 1	1001	0.9065	C. wuellerstorfi	Dead	45.08%	54.92%
	Antepenultimate		1001	0.9065			39.74%	60.26%
2B	Penultimate	STN 1	863	0.9065	C. wuellerstorfi	Dead	9.92%	90.08%
	Antepenultimate		863	0.9065			8.88%	91.12%
3B	Penultimate	STN 1	863	0.9065	B. spissa	Live	5.97%	94.03%
	Antepenultimate		863	0.9065			4.37%	95.63%
4B	Penultimate	STN 1	863	0.9065	B. spissa	Live	3.55%	96.45%
	Antepenultimate		863	0.9065			4.58%	95.42%
5B	Penultimate	STN 1	863	0.9065	B. spissa	Live	4.07%	95.93%
	Antepenultimate		863	0.9065			3.93%	96.07%
6B	Penultimate	STN 1	863	0.9065	B. spissa	Live	3.16%	96.84%
	Antepenultimate		863	0.9065			4.17%	95.83%
7B	Penultimate	STN 1	863	0.9065	B. spissa	Live	4.03%	95.97%
	Antepenultimate		863	0.9065			3.20%	96.80%
8B	Penultimate	STN 6	617.9	1.071	B. spissa	Live	0.42%	99.58%
	Antepenultimate		617.9	1.071			1.37%	98.63%
9B	Penultimate	STN 6	617.9	1.071	B. spissa	Live	3.49%	96.51%
	Antepenultimate		617.9	1.071			2.93%	97.07%
10B	Penultimate	STN 6	617.9	1.071	B. spissa	Live	4.74%	95.26%
	Antepenultimate		617.9	1.071			6.19%	93.81%
11B	Penultimate	STN 6	617.9	1.071	B. spissa	Dead		
	Antepenultimate		617.9	1.071				
12B	Penultimate	STN 7	1001	1.274	B. spissa	Live	3.21%	96.79%
	Antepenultimate		1001	1.274			4.83%	95.17%
16B	Penultimate	STN 12	328	0.533	B. spissa	Live	4.60%	95.40%
	Antepenultimate		328	0.533			4.25%	95.75%
17B	Penultimate	STN 12	328	0.533	B. spissa	Live	4.59%	95.41%
	Antepenultimate		328				5.74%	94.26%

VITA

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