The Molluscan Taphofacies of and Influence of Callianassid Shrimp on a Carbonate Lagoon (St. Croix, US Virgin Islands)

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ABSTRACT

Sediments collect in reef lagoons, and the shells within these can record changes in the environment as they accumulate. Smuggler's Cove (St. Croix, USVI) has been accumulating a sediment package for at least 5,000 years based on radiocarbon ages. Callianassid shrimp severely bioturbate this lagoon's sediment package by moving shell material into shelly, subsurface lags that have a high chance of becoming fossilized. Shell condition (taphonomy) was compared between surface and lag to see whether the lag is an accurate representation of the living surface fauna. Guild membership, taxon, and mollusk size between surface and lag assemblages were analyzed. It was found that the surface beds were more similar to each other than to lags regardless of habitat, and subsurface beds were also more like one another. The dominance of infaunal guilds and the scarcity of epifaunal guilds in the subsurface suggests that it is difficult for callianassids to bring down surface shells. The decrease in taphonomic alteration in the lower beds suggests that shrimp are not pulling shells down by size alone but rather by life guild, favoring infaunal over epifaunal organisms. Since infaunal organisms are less subject to taphonomic alteration than epifaunal ones and tend to be small, guild membership is driving the overall taphonomic signal and influences the results for species and size. Therefore, infaunal species may be overrepresented in the fossil record in these types of

environments. The epifaunal surface shells on the other hand, may persist there until degraded into sand.

INTRODUCTION

Taphonomy-- the study of how organisms decay and fossilize-- is a useful tool in paleontology, and especially paleoecology, because it offers insight into the changes between life and death assemblages related to the process of early fossilization (Kidwell and Bosence, 1991). These death assemblages are the result of the interactions between the supply of organic material, the inherent susceptibility of this material to decomposition, the environment, and the time scale of accumulation and exposure. These processes leave their mark on dead remains. In most cases, decay processes completely degrade the remains, removing them from any potential fossil deposit. Those that do fossilize; however, retain evidence of the processes they experienced after death and before fossilization.

In 1928, Rudolf Richter proposed taphonomy as a field of study (then called "actuopaleontology" and renamed taphonomy in 1940 by J.A. Efremov) to examine and untangle the processes that destroy and alter organic material before fossilization (Efremov, 1940). Unlike taxonomy, which is limited in scope due to the spatial and temporal ranges of species, taphonomic processes have been consistent for nearly all of geologic time. Taphonomic analyses can be applied to various death assemblages regardless of their taxonomic makeup, making it a valuable analytical tool for examining fossil beds and potential fossil beds. The field of taphonomy evolved and grew into what it is today when it was realized that taphonomic processes could confer positive information used to identify paleonenvironments in the 1970s (Cadee, 1991).

Several studies have been conducted to fully understand the nature of these positive taphonomic characteristics, and these have ranged from experiments on taphonomic processes using modern organisms to certain aspects of decay, to specific taxonomic groups' rate of decay, and to analyses of relationships between life and death assemblages (Parsons and Brett, 1991). The underlying theme of many of these studies is the concept of fidelity-- the degree of resemblance between life and death assemblages (Parsons and Brett, 1991). Many studies have examined how fidelity is lowered due to the absence of lightly skeletonized and soft-bodied organisms in the fossil record due to their low preservation potential (Dorjes, 1972; Jones, 1969; Schopf, 1978). Preservation potential, and therefore fidelity, is also affected by life habits, as infaunal organisms are more likely to be preserved due to already living in the subsurface. Other studies have examined the information lost between life and death assemblages with low fidelity (Boucot, 1953; Jones, 1969; Schopf, 1978; Warm, 1969; Warm et al., 1976).

When sediment accumulation rates are slower than organismal life spans, the death assemblage usually contains remains of several communities that lived and were preserved over a larger (usually decadal) time scale rather than that of a single community (Feser and Miller, 2014; Kidwell and Bosence, 1991; Kosnik et al., 2009). This process is referred to as time-averaging. In highly time-averaged assemblages, evidence of short-term changes are lost to the dominance of longer-term trends as the remains of more and more communities occupy the death assemblage. When stable environments change to another stable state, significant time averaging produces "taphonomic inertia" or a significant lag time— the amount of time it takes for changes in the life assemblage to be reflected in the death assemblage (Feser and Miller, 2014).

Another branch of study is the defining of "taphofacies" for different environments, i.e., groupings of taphonomic characteristics created from a specific environment and/or history (Speyer and Brett, 1988). Much modern taphofacies research has been done on shelly marine beds due to their relatively high preservation potential and the similarities between mollusk shell accumulations today and brachiopod assemblages of the Paleozoic (Parsons Hubbard et al., 2014). Studies utilize several taphonomic indices including abrasion, articulation, bioerosion, dissolution, edge rounding, fragmentation, orientation, encrustation, and size. Table 1 summarizes the origins and associations of each characteristic to specific processes and the environments in which they are important. These characteristics are preservable and can be studied in the formation of modern death assemblages. Through this, environmental signatures can be discovered by looking at how death assemblages are preserved in both modern and ancient beds.

Table 1: A summary of taphonomic indices and their implications for the conditions under which they alter assemblages from Parsons and Brett (1991).

Taphonomic Feature	**Implications**	**References**
Abrasion	The wearing-down of skeletons due to their differential movement with respect to sediments is an indicator of environmental energy. Significant abrasion is most often found on skeletal material collected from beaches, or areas of strong currents or wave action.	Driscoll and Weltin (1973), Driscoll (1976b).
Articulation	Multi-element skeletons are soon disarticulated after death. Articulated skeletons, then, indicate rapid burial or otherwise removing the skeleton from the	Allison (1986; 1988), Plotnick (1986).

	taphomically active zone (TAZ).	
Bioerosion	Bioerosion encompasses many different corrosive processes by organisms. The most pervasive causes of degradation are boring and grazing. Bioerosion erases a large amount of information from the fossil record, but it also leaves identifiable traces made by organisms on remaining hard skeletons. Therefore, bioerosion adds information on the diversity of ancient assemblages. Also, patterns and processes of bioerosion vary among environments due to the distribution of bioeroders, energy levels and other habitat differences.	Odum and Odum (1955), Warme (1977), Pleydell and Jones (1988), Boekschoten (1966), Perkins and Tsentas (1976), Futterer (1974).
Dissolution	Skeletal remains are often in equilibrium with surrounding waters, but changes in chemical conditions can cause skeletons to dissolve. Dissolution represents fluctuations in temperature. pH or pCOz in calcium carbonate skeletons. Silicious skeletons dissolve more readily because normal sea water is usually undersaturated with respect to silica.	Davies et al. (1989b), Flessa and Brown (1983), Alexandersson (1978).
Edge rounding	Broken edges of skeletons become rounded due to either dissolution or abrasion of the exposed surface. The processes that control edge rounding are not fully known, but are probably a combination of dissolution,	Davies et al. (1990).

	abrasion and bioerosion. Rounding gives an estimate of time since breakage.	
Encrustation	The overgrowth of hard skeletal substrates by other organisms is a common occurrence. Besides indicating exposure of the skeleton above the sediment—water interface, encrustation can specify environment. Different patterns of encrustation as well as different biota occur in different environments.	Rasmussen and Brett (1985), Driscoll (1967a), Driscoll (1968).
Fragmentation	Breakage of skeletons is usually an indication of high energy resulting from wave action, currents, tides or winds. Fragmentation can also be caused by other organisms through either predation or bioturbation.	Muller (1979).
Orientation	After death, skeletal remains are moved by the transporting medium and orientated relative to their hydrodynamic properties. Fossil skeletons in life position indicate rapid burial, attachment to a firm substrate or death of in-place infauna. Hard parts tend t oorientate long-axis parallel to unidirectional flow in current-dominated areas and perpendicular to wave crests on wave-dominated bottoms.	Nagle (1967), Johnson (1957), Emery (1968), Salazar-Jimenez et al. (1982), Clifton and Bogs (1970), Brenchley and Newall (1970).
Size	After death, a skeleton behaves as a sedimentary particle and is moved and sorted with respect to the carrying capacity of the flow	

	due to currents. Waves or tides. Size can, therefore, be an effective indicator of low capacity in a hydraulic or wind-driven system.	

Past research has been done to define taphofacies characteristics within certain environments, as well as the value of these taphofacies (Darroch, 2016; Forsey, 2016; Parsons Hubbard, 2005; Parsons Hubbard et al., 2014; Reich, 2012). Previous work has analyzed molluscan assemblages to determine taphofacies parameters for mixed carbonate and siliciclastic environments (Best and Kidwell, 2000; Parsons Hubbard, 2005; Parsons Hubbard et al., 2014; Zimmerman et al., 2001). This has been done by examining specimens and categorizing them through broad damage categories and the presence/absence of certain characteristics. These studies have also found that a composite signature of taphonomic characteristics reflects paleoenvironments as well as or even more accurately than ones based on faunal or life habit composition (Parsons Hubbard, 2005). In addition to this, composite taphonomic signatures from modern death assemblages can reliably indicate depositional environments in shallow carbonate systems, specifically in the Northeast Caribbean (Parsons Hubbard, 2005). Mollusks can also be used as proxies and indicators of other taphofacies as well (Parsons Hubbard et al., 2014). Accurately defined taphofacies can be especially invaluable to paleoecology research that focuses on organisms and environments with low preservation potential, such as seagrass.

Since seagrass itself is rarely preserved, there has been a focus on proxies for seagrass environments (Forsey, 2016; Reich, 2012). Many studies have been done to evaluate the value of different species as indicators of seagrass environments (Buchan et al., 2009; Darroch, 2016;

Reich, 2012; Vélez-Juarbe, 2014). Forsey (2016) found that ostracods work well as proxies. Vélez-Juarbe (2014) examined the presence of sirenians (seacows, manatees, and dugongs) and concluded that it could be a useful indicator due to their dependence on seagrass as a food source and their bones' having great preservation potential due to their high density. Mollusks as proxies also show promise, particularly lucinid bivalves such as *Codakia*. Others have examined forams due to their high preservation potential and relative abundance (Buchan et al., 2009; Darroch, 2016; Forsey, 2016; Parsons Hubbard et al., 2014; Reich, 2012). Because most taxa aren't restricted to seagrass environments, other information such as taphonomy, life habits, and species composition need to be considered when using them as a proxy (Reich, 2012). Reich (2012) analyzed death assemblages for species composition and life habits and found that these are useful tools for distinguishing vegetated areas from non-vegetated ones.

Darroch (2016) found that areas with (sparse) seagrass and vertical bioturbators (like callianassid shrimp) have a high amount of both pristine foram tests (shells) and heavily altered tests in comparison to sites without seagrass nor vertical bioturbators. The condition of pristine tests are preserved due to how seagrass baffles currents and therefore lowers the amount of alteration a test will undergo (Buchan and Lewis, 2009; Darroch et al., 2016). Other tests are heavily altered due to the dissolution promoting conditions of seagrass. Aerobic and anaerobic bacterial respiration around seagrass roots lowers the pH of pore waters through the production of carbonic acid and sulfate reduction, respectively (Darroch, 2016; Feser and Miller, 2014). Additionally, the carbonate saturation of sediment pore waters is lower beneath seagrass beds than in areas without seagrass. Another avenue for high alteration is the possibility of bioturbators bringing buried tests back to the surface and exposing them to

alteration once more. It is suggested that this pattern could apply to other shelly fauna; however, it is highly unlikely that bioturbators like callianassids could bring shelly material larger than fine sediment back to the surface, as they eject only fine material to their waste mounds (Meldahl, 1987). Additionally, this high proportion of both pristine and highly altered tests would be confined to areas of sparse seagrass and deep, vertical bioturbators.

This study attempts to bridge the knowledge between modern and fossil paleoenvironment studies by building on Parsons Hubbard et al. (2014)'s examination of shell beds from Smuggler's Cove, St. Croix (USVI) to evaluate whether the taphonomic condition of lagoonal mollusks can be used to infer variations in past seagrass density. Additionally, lag beds at the base of lagoonal cores were examined to determine their taphofacies as well as their relationship to the present surface shell beds. The modern taphofacies signatures from surface shells should be recording processes happening in the surface of that location most recently. A comparison of the taphonomic condition of mollusks within the lag shell beds should therefore provide insight into the recent history of the lagoon (i.e. a disparity between surface and lag beds should reflect environmental change at each core site over the time period in which those lagoonal sediments were deposited).

Study Site

St. Croix is part of the US Virgin Islands and is located in the eastern portion of the Greater Antilles (Fig. 1). The island is primarily made up of sedimentary rock and formed during the Pleistocene, over 27,000 years ago (Adey, 1977). The central area of the island mainly consists of carbonates within a graben, and the eastern and western ends consist of Cretaceous volcanoclastic sediment from the Caledonia Formation (Parsons Hubbard et al., 2014).

Smuggler's Cove—also known as Knight Bay and Tague Bay—is located on the northeastern corner of the island with a narrow insular shelf surrounding it. Sea level flooded the St. Croix shelf 9,000-8,000 years ago and slowed down between 7,000 and 5,000 years ago (Adey, 1977; Burke, 1989). Tague Reef formed after this, creating Smuggler's Cove.

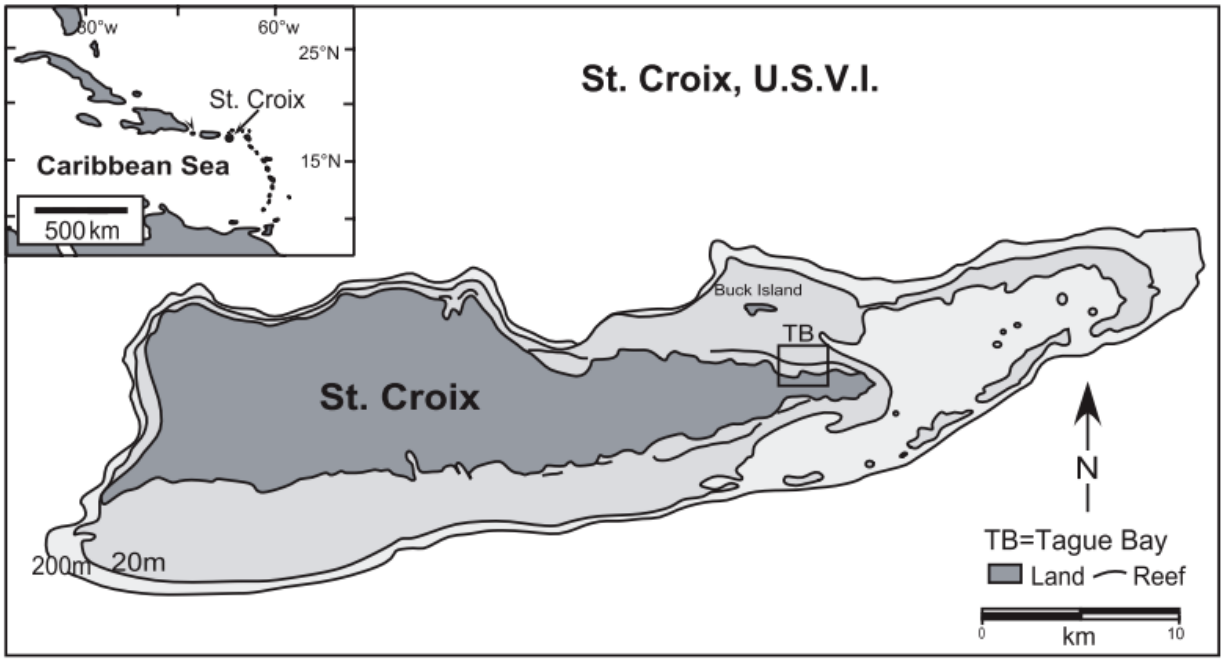

Figure 1: Location map for St. Croix, USVI from Parsons Hubbard et al. (2014). The study site, Smuggler's Cove (also known as Tague Bay and Knight Bay) is marked on the eastern end of the island in the box labelled "TB."

The bay is approximately 1 km wide, and sits behind an emergent reef that effectively protects the lagoon from wave action (Parsons Hubbard, 2005; Parsons Hubbard et al., 2014). Coral cover on the reef has decreased dramatically over the past 20 years, and carbonate sands make up the lagoon floor with sparse patch-reef development. Seagrass stabilizes the bottom, and macroalgae are also present (Ferguson and Miller, 2007; Parsons Hubbard et al., 2014). Seagrass increases in density to the east, and *Callianassa* shrimp actively burrow in areas of

sparser seagrass cover (Ferguson and Miller, 2007; Parsons Hubbard et al., 2014). The rhizome mats of the seagrass are thought to effectively discourage both erosion and callianassid activity; however, it has also been recorded that *Callianassa* can successfully take over seagrass areas due to the way sediments ejected by their burrowing activity smothers seagrass (Buchan et al., 2009; Suchanek, 1983). Because of both of these processes, seagrass zones near their burrows are more varied spatially and/or temporally (Ferguson and Miller, 2007). The dominant seagrass species is *Thalassia testudinum*; however, *Syringodium filiforme* and *halodule wrightii* are also present in the area (Feser and Miller, 2014). Seagrass has been present in Smuggler's Cove for at least the past 50 years, and its density has increased over the past 22 years (Ferser and Miller, 2014; Ferguson and Miller, 2007).

Callianassa spp. (Fig. 2) are burrowing ghost shrimp and typically live in the intertidal and shallow subtidal zone, becoming less numerous below water depths of 10.7 m (Shinn, 1968). They are most active below depths of 5 cm, which are below the rhizome mats of seagrass. Feeding and burrowing activities of callianassids create complex burrows with extensive networks (Fig. 3-4). Fine sediment (1-1.4 mm) is ejected out of the subsurface by currents created by the shrimp; although, these weaker currents cannot move shell debris and larger grains into burrow chambers (Curran, 2007; Kosnik et al., 2009; Roberts et al., 1981; Shinn, 1968; Suchanek, 1983). These ejected sediments form volcano-shaped waste mounds about 0.3 m high and 0.61 m in diameter (Shinn, 1968; Fig. 5). In their burrowing activities, *Callianassa* can even move large debris (e.g. a 2x2 cm glass plate) or work around dense and impenetrable areas (Curran, 2007; Curran and Miller, 2001).

Seagrass blades and other organic material are pulled down by the shrimp, along with sediment and surface shells. *Callianassa* activity pulls down shells specifically through this sediment ejection. As they remove fine sediment from the subsurface, the shell above the removed sediment naturally travels downward (Fig. 6a). This process continues as deep as their burrowing activity extends, eventually depositing the shell into a lag bed below all callianassid activity in a given area (Meldahl, 1987). Because infaunal organisms live below the sediment surface, the distance their shells have to move in order to enter the lag is shorter, and it is therefore easier for infaunal shell to be transferred into the lag. Conversely, it is harder for epifaunal shell to move into the lag due to the added distance they have to move from the surface all the way down to the lag. The rhizome mat of seagrass can further inhibit the downward movement of the epifaunal shell above them by acting as a net, catching the shell even as sediment from under it has been removed (Fig. 8b). It is also easier for small shells to be transferred downwards due to how much less sediment has to be removed below small shells for them to move downwards. This activity can create an over 2 m thick layer of moderately to poorly sorted medium and fine grained sediment above a poorly sorted gravel rich bed and in some cases-- like this study site and that of Meldhel et al. (1987)-- a lag shell bed (Kosnick et al., 2007; Parsons Hubbard et al., 2014; Tudhope and Scoffin, 1984).

Through this sorting, callianassids can create shell beds that accumulate shells of many ages (also known as time averaging) between the life and death assemblages in their environment. *Callianassa* spp. also lower the amount of encrustation and microboring in the death assemblage by speeding up their burial and movement out of the taphonomically active zone (Tudhope and Scoffin, 1984).

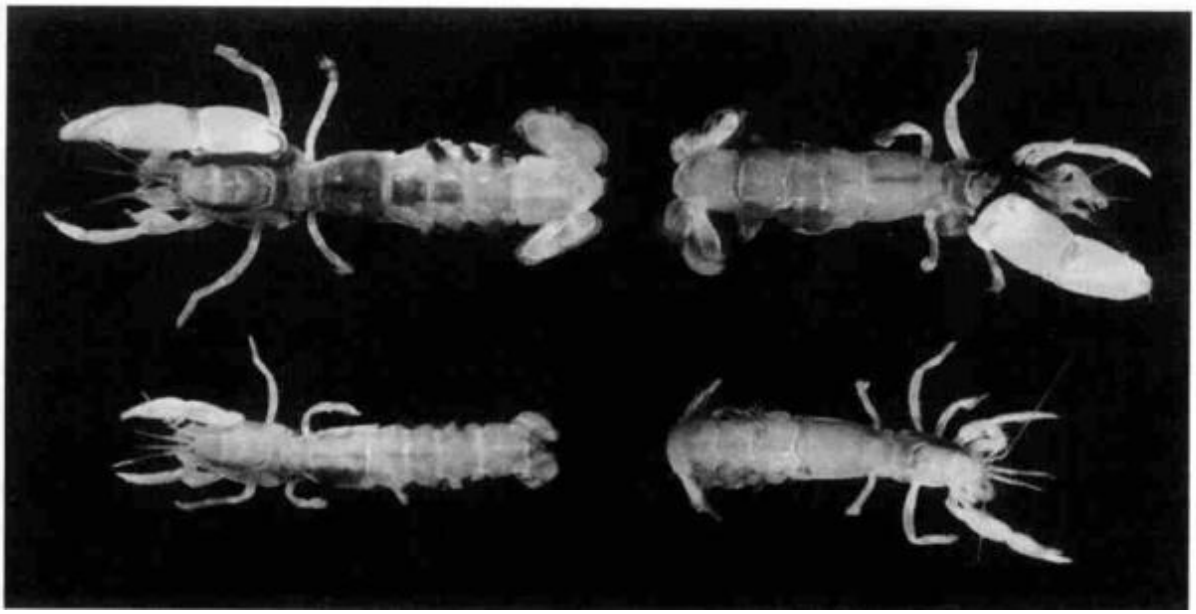

Figure 2: *Callianassa tyrrhena* (left) and *C. candida* (right; Dworschak, 1988). The upper specimens are male, and the lower are female. No scale bar was given in the original paper, but they can grow to be up to 8 cm long and are most likely 5 cm in length in this photograph (Tudhope and Scoffin, 1984).

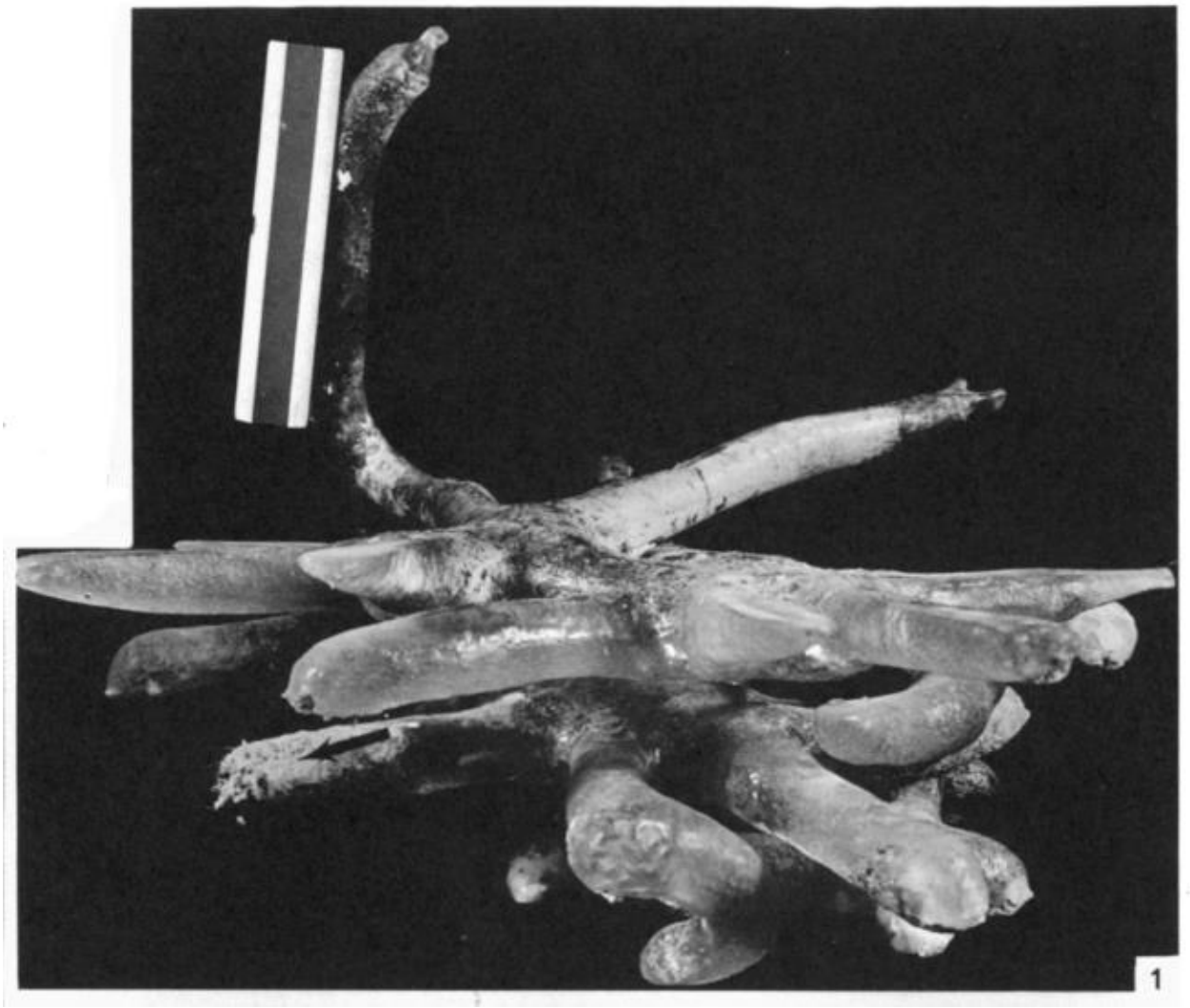

Figure 3: Side view of an epoxy resin cast of a *Callianassa* burrow from Shinn (1968). The arrows indicate burrow tunnels filled with marine grass and mollusk shells. The scale bar is 6 in length.

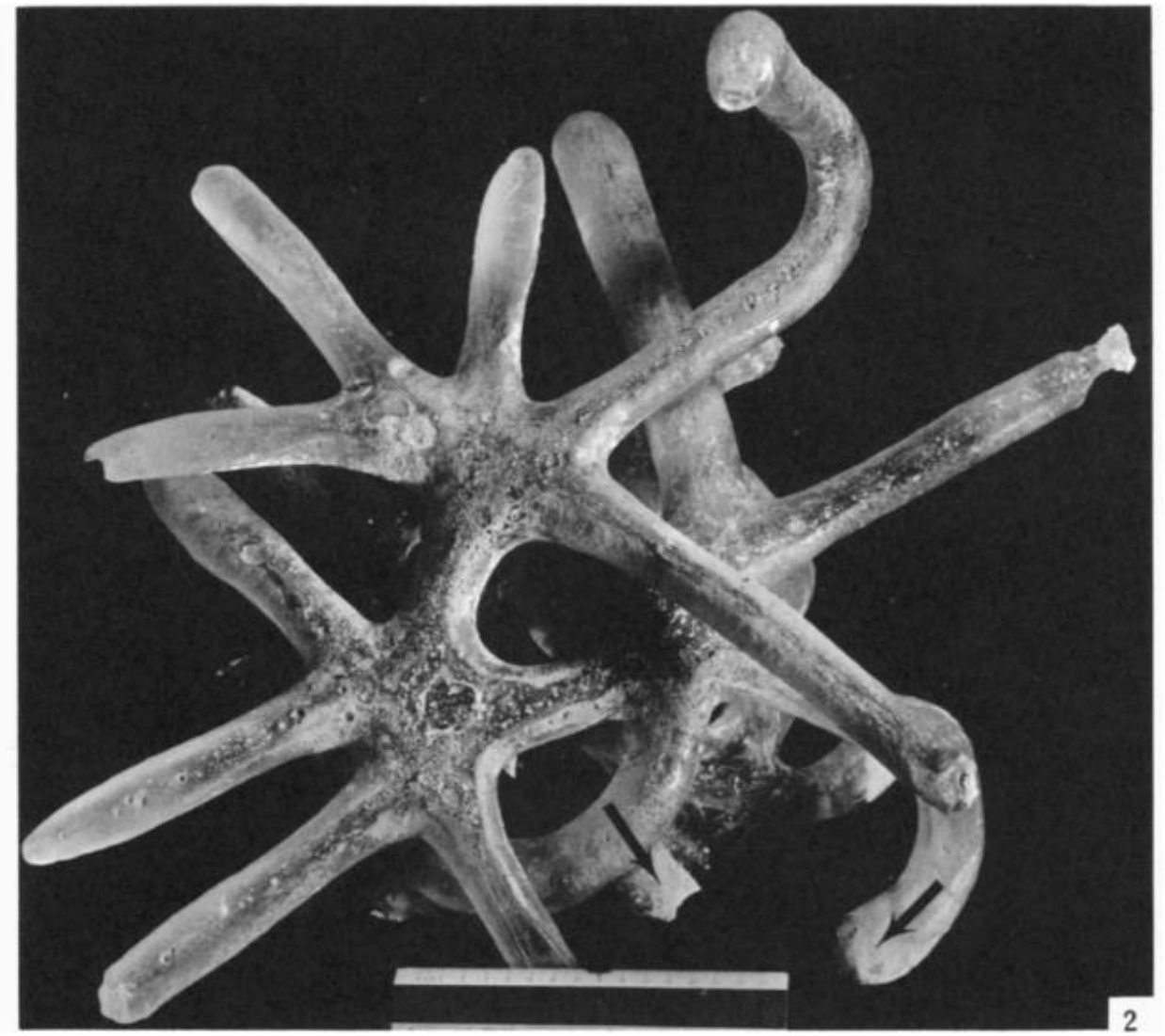

Figure 4: Plan view of a plastic cast of *Callianassa* burrow from Shinn (1968). Side chambers spread out from central rooms. The arrows indicate burrow tunnels filled with marine grass and mollusk shells. The scale bar is 6 in length.

Figure 5: Photograph example of an average lagoon floor with callianassid mounds from Smuggler's Cove (Parsons Hubbard et al., 2014).

Figure 6a: A cross-section of the seafloor (without seagrass) depicting the burrowing activities of Callianassa shrimp and how this facilitates shell movement into the lag bed. Callianssids move sediment surrounding their burrows out of their waste mounds (shown by white arrows). The removal of sediment below shell causes this shell to move downwards (shown by grey arrows).

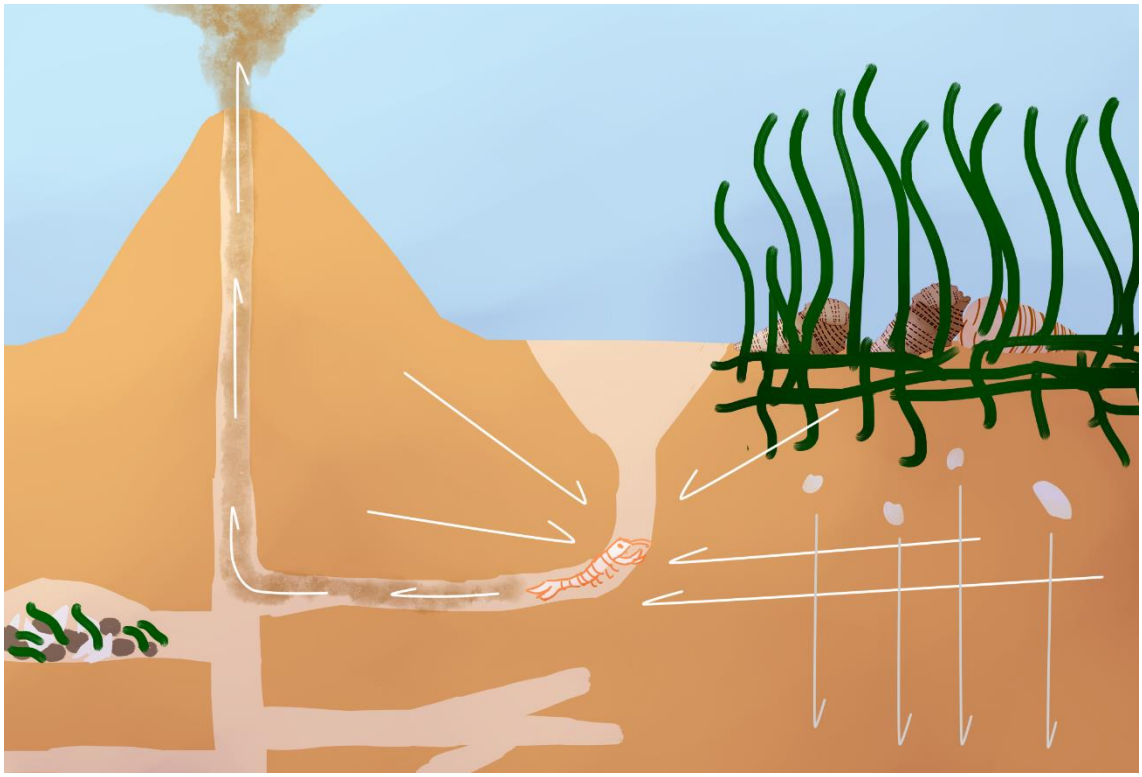

Figure 6b: A cross-section of the seafloor with seagrass depicting how rhizome mats interfere with shell movement into the lag bed (shown by grey arrows). The rhizome mats of seagrass act as a net, trapping epifaunal shell at the surface even as the sediment below them is removed by *Callianassa* shrimp.

Previous studies by Parsons Hubbard (2005, 2014) have examined surface shell beds and sediment cores in Smuggler's Cove on St. Croix (Fig. 7 and 8) to primarily describe the generic and life guild composition of shell beds but also to define the shell bed taphofacies. The taphonomic analysis used a scaled semi-qualitative analysis of shell characteristics such as the ones in Table 1. In this area, *Callianassa* burrowing has created a somewhat homogenous layer of fine sediment coarsening downwards in between the surface bed and a lag bed sitting on top of the Pleistocene subsurface (Fig. 8). She found the fauna within the lag bed (small, thin-shelled, infaunal bivalves with agglutinated polychaete tubes and decapod remnants) do not resemble the present-day surface's community (small, epifaunal gastropods and large bivalves).

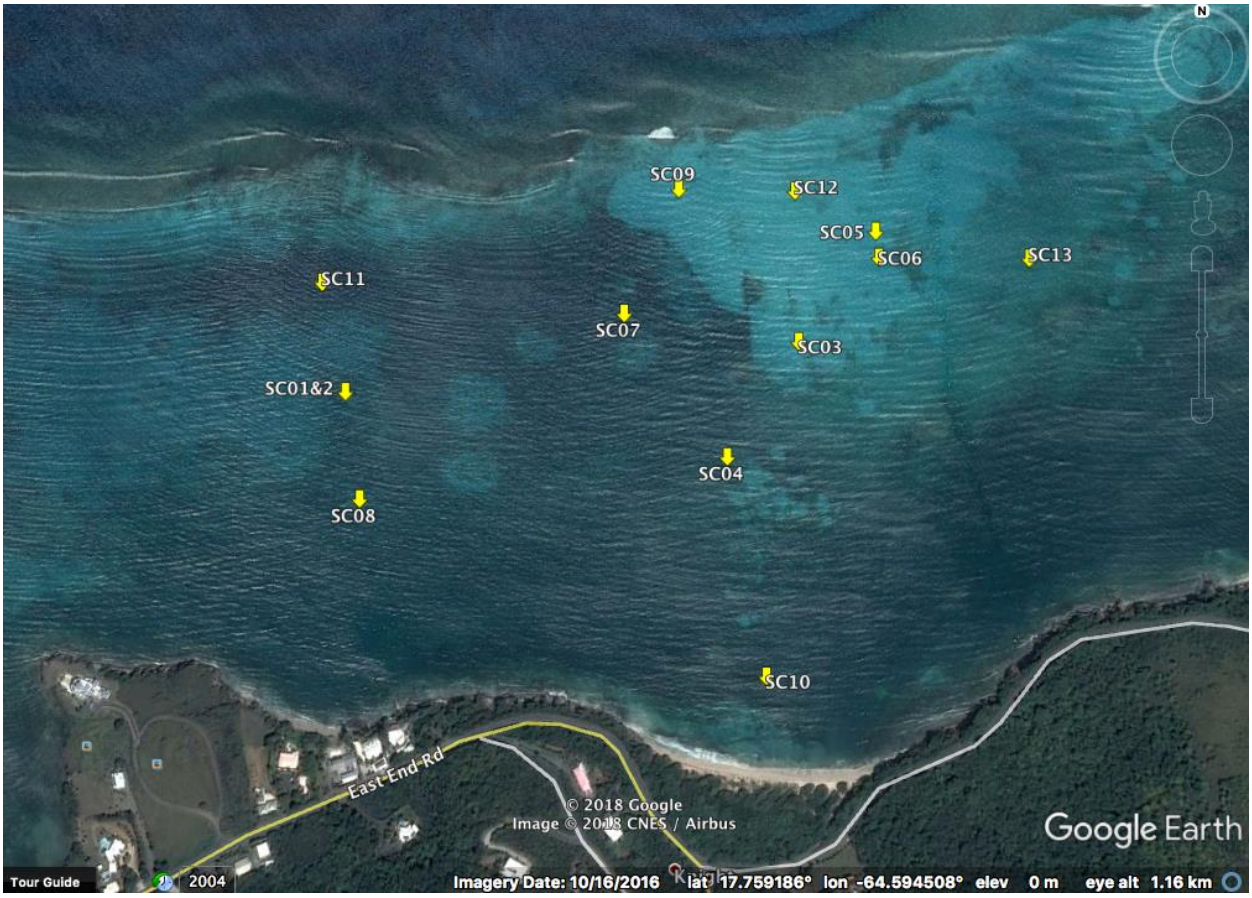

Figure 7: Smuggler's Cove, St. Croix from Google Earth. Core sites from previous studies are marked with yellow arrows (Parsons Hubbard et al., 2014). This study examines cores SC01/2, SC04, and SC08.

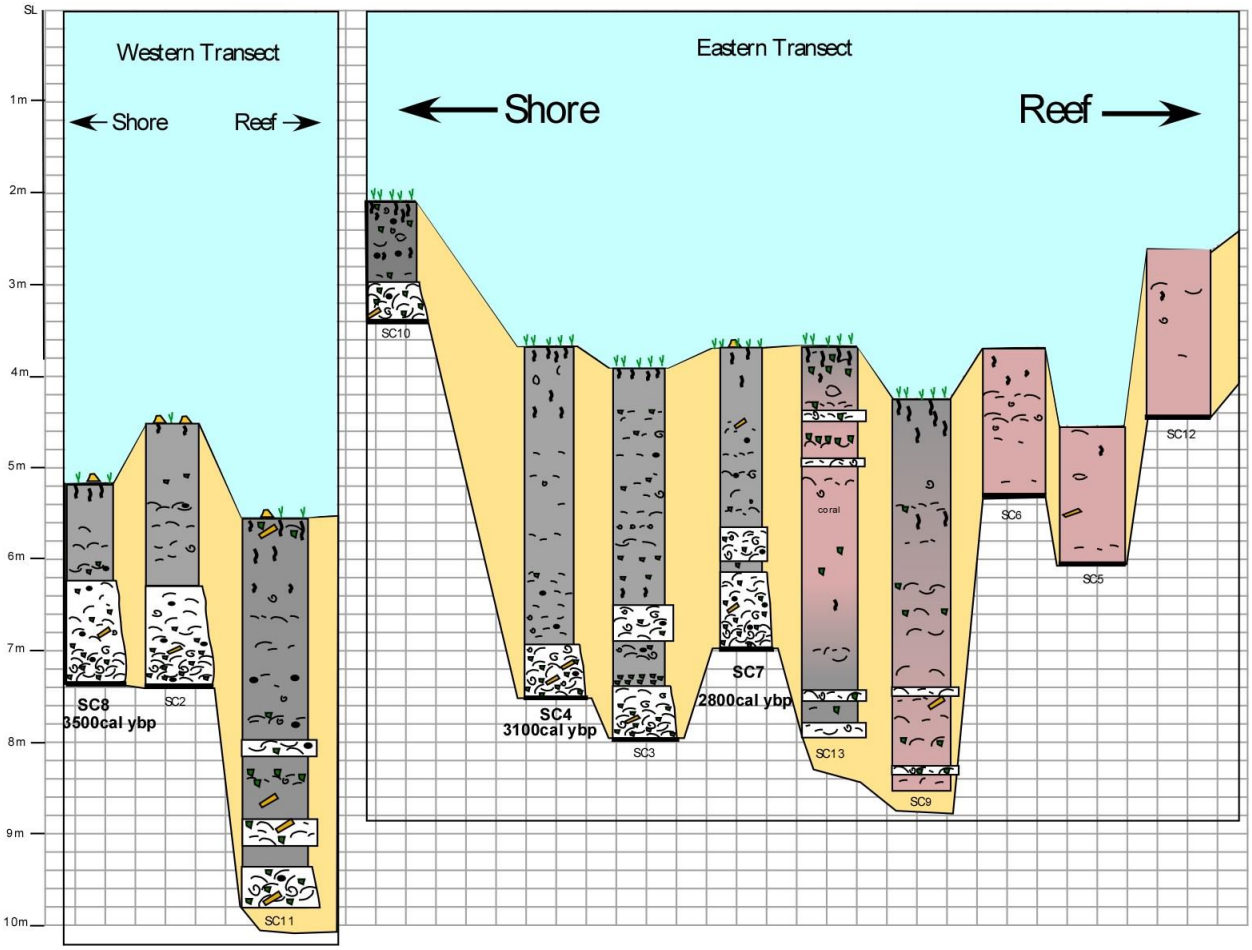

Figure 8: Cores at decompacted lengths arranged in transects from shore to reef from Parsons Hubbard et al. (2014). Sea level rests at the top of this diagram, and the cores are placed along the transect based on water depth and location within the lagoon. The green plant symbols on the surface convey seagrass density at each site, and the yellow mounds indicate the presence of several callianassid shrimp waste mounds. Gray indicates sand, and pink indicates sand originating from corals and red forams. The black symbols within these sediment layers indicate every instance of shell within them; although, the size of these symbols give the false impression that there was a significant amount of shell within these sediment layers. White layers represent concentrated lag shell beds. Black bars across core bottoms show those that reached the hard Pleistocene subsurface. SC4, SC7, and SC8's dates were radiocarbon dated at Beta Analytic, Inc., and the isotopic analyses were used to calibrate 14C ages to cal BP. The freeware program Calib 6 was also used to convert uncorrected ages from previous studies to cal BP.

The starkness the faunal difference made the explanation of *Callianassa* burrowing solely creating this sediment package and surface/lag difference seem unlikely. Another explanation is that the lag bed could have formed in the lagoon's early development and would

reflect the ancient environment. However, radiocarbon dates (see Fig. 8) suggest that shells within the lag bed were deposited more continuously over the past 6,000 years (Parsons Hubbard et al., 2014). In a more plausible environmental change scenario, the lag bed could have formed in a low-density seagrass or seagrass-free environment over thousands of years, and a more recent environmental change on the surface related to increasing seagrass densities could be responsible for the surface-lag bed difference. Google Earth imagery doesn't show significant change in seagrass cover over the course of the past 15 years, but it could be possible for a change from a seagrass-free to a seagrass-dense environment to occur over the course of 150-300 years.

In the case of either environmental change or shrimp sorting creating the lagoon's sediment package and low surface/lag bed fidelity, there should be more epifaunal genera and larger shell sizes at the surface than in the lag beds. In the environmental change scenario, this would occur due to the way seagrass influences faunal communities. A seagrass-free environment (such as is found in the lag shell bed) is mostly infaunal and has smaller species, while seagrass environments (such as found in the surface bed today) have more large and epifaunal species that graze and live on the seagrass blades (Parsons Hubbard et al., 2014) For the *Callianassa* sorting hypothesis, the high frequency of large, epifaunal shell on the surface is due to the fact that it is easier for small, infaunal shell to be sorted into the lag bed than it is for large, epifaunal shell.

For the environmental change hypothesis to be supported, the lag bed shells, representative of a seagrass-free environment, would be expected to be more taphonomically damaged than their corresponding surface shells because surface fauna in seagrass free sites

(SC05, SC09, and SC12) had more taphonomic damage that seagrass sites (Parsons Hubbard et al., 2014). This is likely caused by the exposure of the shell to increased amounts of wave energy, increasing taphonomic damage related to movement as well as making it easier for infaunal shells to be exposed to the surface.

For the *Callianassa* sorting hypothesis to be supported, the lag bed shells would be less taphonomically damaged than their corresponding surface shells. In this hypothesis, the lag bed is mostly composed of infaunal shells that have been shuttled into the lag through *Callianassa* bioturbation. Because the majority of infaunal organisms are rarely exposed at the surface after death, they are protected from the taphonomic processes that occur there and would be less altered than the primarily epifaunal surface bed shells (Kosnick et al., 2007).

The research described below builds on the work of Parsons-Hubbard et al. (2014) and attempts to use new sample data from 2016 to compare and contrast the taphonomic signatures of surface sites to those within the lags and to investigate why the surface and lag beds are so different. This research will contribute to understandings of fidelity and causes of low fidelity in areas with deep tier burrowers. It is very important to understand the fidelity of fossil beds and potential fossil beds because so many assumptions, inferences, and hypothesis about extinct organisms, paleocommunities, and the geologic past are made based on fossil beds. Additionally, these understandings of the past are instrumental in fields such as conservation paleobiology and in understanding climate change and its effects today.

The confirmation of either hypothesis—environmental change or *Callianassa* sorting as the cause of low fidelity—provides further insight into the processes occurring in environments with deep tier burrowers. If the environmental change hypothesis is supported, this study will

provide more insight into how environmental change is recorded in the sedimentary records of lagoons with deep tier burrowers. If the *Callianassa* sorting hypothesis is confirmed, even just the preliminary results from Parsons et al. (2014) show a massive bias in the fossil record caused by these deep tier burrowers. Furthermore, this study will contribute to the development and use of taphonomic analyses on modern prefossilized beds.

METHODS

Core Extraction and Sampling

The core specimens for this study were collected during Parsons Hubbard et al's 2014 core collection and from an additional data collection expedition in 2016. In the initial study, divers operated a vibracoring device to extract a core at each of the twelve sample site locations (Fig. 7-8). These core sites were chosen to get maximum coverage of the lagoon. A hydraulic concrete vibrator head (5 cm in diameter) was attached to a 7.6 cm diameter and 4.6 m long core pipe (aluminum irrigation pipe) with a custom-made clamp with handles (Fig. 9). A hydraulic motor was operated on an anchored, nearby vessel to provide power to drive the vibrating head. The pipe with the vibrating head attached, was moved into a vertical position, and divers used a control mechanism on the hydraulic hoses to start the vibracoring process. The process was stopped when about 50 cm of the pipe remained above the seafloor (enough to attach to an extraction device) or when it would no longer penetrate the seafloor, presumably hitting the pre-Holocene subsurface.

A hacksaw was used to remove excess pipe, and this length was measured to determine the length of the remaining core pipe (Parsons Hubbard et al., 2014). The length between the pipe and to the sediment surface, inside and outside of the pipe, was measured to calculate the

penetration depth and the degree of sediment compaction throughout the entire core during vibracoring. Next, the exposed pipe end was capped and handles were attached to aid extraction. An airlift bag and the diver's strength were used to pull the pipe from the seafloor, and a lower cap was attached to the bottom end of the pipe as soon as it was visible to avoid sediment loss. The core tube was kept vertical as it was extracted from the water and secured to a vertical mast on the vessel. After this, any excess pipe filled with water at the top was removed, and a new cap was placed.

At each core site, a 4.6 m long steel reinforcing rod (about 3 mm in diameter) was used to measure the thickness of the sediment layer. The rod was pushed vertically into the seafloor surface until it stopped, reaching the end of unconsolidated sediment, and the length was then measured. At each site, multiple measurements were made to find an average. A digital depth gauge was used to measure the water depth at each core location. The tidal range for Smuggler's Cove is less than 20 cm and was thus disregarded in water depth readings. Core and probing positions were located using a handheld GPS at the surface.

Figure 9: Karla Parsons Hubbard (lower) and Rebekah Shepard (higher) hold the core pipe steady before switching on the concrete vibrator. Photo taken by Rowan Lee during field research in Great Pond Bay, USVI 2018.

The core pipes were laid down in a cradle and sawed in half on shore. After they were photographed and logged, half of each core was sampled. Sampling was divided into alternating 8 cm and 12 cm intervals. Sediment for sediment-constituent and grain-size analysis was sampled from 8 cm; core material from 12 cm intervals was sieved with a 2 phi (0.25 mm) sieve to extract mollusks and other coarse materials. Both sediment and mollusk samples were washed with fresh water to remove the salt and dried.

Additional mollusk specimens were collected in 2016. Divers operated a vacuum device composed of plastic piping connected to a SCUBA tank and its regulator (Fig. 10). When the

lower end of the pipe was placed near the bottom surface, air released from the dive tank funneled into the pipe and traveled upwards, bringing up shell material and other debris to be caught in a mesh bag affixed at the upper end of the pipe. Seagrass and mollusks (larger than 2 mm) stayed in the bag, while finer sediment fell out. These airlift samples were collected in 0.25 m^2 sections at each site. On shore, samples were washed with freshwater, and had seagrass and mollusk flesh picked out of them. In the lab, most airlift and core samples were further sorted into bags by life guild.

Figure 10: Karla Parsons Hubbard (right) operating the vacuum device. Photo taken by Rowan Lee during field research in Great Pond Bay, USVI 2018.

Specimen Analysis

Specimens were taken from the cores and surface samples from the Parsons Hubbard et al. 2014 study and 2016 data collection and examined for taphonomic characteristics. Worm tubes, *Halimeda* debris, and crab remains were present in these samples but not counted. A total of 717 mollusks from the lagoon surface sediments and within cores from locations SC01/2, SC04, and SC08 were analyzed. Sites SC01/2, SC04, and SC08 were chosen because their cores had both surface and lag shell beds, and their surface beds had different seagrass densities. Site SC01/2 had *Callianassa* mounds and low density-seagrass cover, site SC04 had no mounds and high-density seagrass cover, and site SC08 had shrimp mounds and medium-density seagrass cover. The seagrass-free sites SC05, SC06, and SC12 were not chosen due to their lack of a lag shell bed. This was caused by their placement in an unusual location in the lagoon, where the Pleistocene subsurface is higher, causing their core heights to be much shorter. Additionally, the faunal communities of this site are disrupted by the unusually high amount of wave action in the area, so while they provide an idea of a seagrass-free community and death assemblage, they should not be used as the definitive example of this.

Table 2 summarizes the location, water depth, core length, and environmental characteristics of each sample site. Specimens from within the cores came from the basal lag in cores SC01/2 (208-220 cm) and SC08 (168-180cm). SC04's basal lag had been used for radiocarbon dating, so a mid-core shell layer at 194-224 cm was analyzed instead.

Table 2: Location, water depth, uncompacted core length, and environment for each core from Parsons Hubbard (2014)

Core	Location	Water Depth	Core Length	Environment
SC01/2	17.759600 N, 64.597310 W	4.5 m	3.1 m	Callianassid mounds, low density seagrass
SC04	17.758980 N, 64.593490 W	3.6 m	3.8 m	No mounds, high density seagrass
SC08	17.758581 N, 64.597156 W	5.2 m	2.2 m	Callianassid mounds, medium density seagrass

Specimens were examined under a Nikon SMZ1500 dissection microscope. Sample site, specimen location along the core, and specimen number were recorded for each shell. Genus and species were identified when possible as well as whether the specimen was alive or dead at the time of collection. Specimens were also measured along their longest dimension in mm using a digital caliper. After the data collection in 2016, live/dead status was recorded and specimens were combined by genus for life habit analysis by Megan Herrman (Oberlin College ’17). Genus was used to determine life habits using data from Parsons Hubbard et al. (2014) and is compiled in Table 3.

Table 3: Life habits by genus.

Epifaunal clam (Epi-clam)	**Epifaunal snail (Epi-snail)**	**Infaunal clam (In-clam)**	**Infaunal snail (In-snail)**	**Infaunal small clam (In-s-clam)**
Chama *Marcrocallista* *Modiolus* *Pinna*	*Acmaea* *Astraea* *Calotrophon* *Cerithium* *Columbella* *Conus* *Crepidula* *Cymatium* *Hyalina* *Littorina* *Modulus* *Nassarius* *Nitidella* *Pilsbryspira* *Pyrimidella* *Smaragdia* *Strombus* *Tegula* *Tricolia* *Turbo*	*Chione* *Codakia* *Heterodonax* *Laevicardium*	*Bulla* *Haminoea*	*Americardium* *Diplodonta* *Lucina* *Pitar* *Semele* *Tellina*

Specimens were analyzed by size class, life guild, genus, species, and bivalve articulation. A majority of the specimens in life guild bags (not entire shell beds) were randomly divided into halves or quarters to save time during data collection. The disproportionality created by this subsampling has been corrected in these data analyses. The correction was done by doubling the data entries of halved sample groups and quadrupling data entries for quartered sample groups to make them approximately their original size. In further data analysis in this paper, this will be referred to as “correcting the sample proportions.”

Taphonomic characteristics

Each specimen was analyzed for its taphonomic characteristics as well. Interior and exterior encrustation by other organisms was estimated as the percentage of the surface covered, with values above 10% rounded to the nearest 5. These estimates were based on visual percentage estimation from Terry and Chilingar (1955) and repeatability was tested and compared with a seasoned observer (Karla Parsons Hubbard). Drill holes, graze marks, articulation (for bivalves), and rhizome etchings (dissolved areas caused by contact with seagrass rhizomes/roots) were recorded as present or absent. Fragmentation, broken surfaces, abrasion, microboring, *Cliona* borings, dissolution, color loss, and luster loss (interior and exterior) were judged on semi-qualitative scales described in Table 4. Figures 11 and 12 show various examples taphonomic states and characteristics. For articulated and closed bivalves and other specimens whose interiors or exteriors are otherwise unobservable, the corresponding encrustation and luster values were marked as “NA.”

Table 4: The scales on which taphonomic features are described.

Characteristic	**0**	**1**	**2**	**3**
Fragmentation	Whole shell	Small chips on edges of bivalves or apex broken on gastropods	Major fragment (more than 50% of original shell)	Minor fragment (less than 50% of original shell)
Broken surfaces	Fresh, sharp broken edges	Edges look older, may have some dissolution or minor wear	Encrusted or completely altered to look like rest of shell	NA
Abrasion	None	Minor (slightly worn edges)	Moderate	Major (highly polished/beach worn shell)
Microboring	None	Present	Common	Very common
***Cliona* borings**	None	Present (one or two holes)	Common	Completely riddled with borings
Dissolution	None	Minor	Moderate	Major
Color loss	Fresh	Faded	Most color gone	White
Luster loss	Shiny	Somewhat dull	Dull	NA

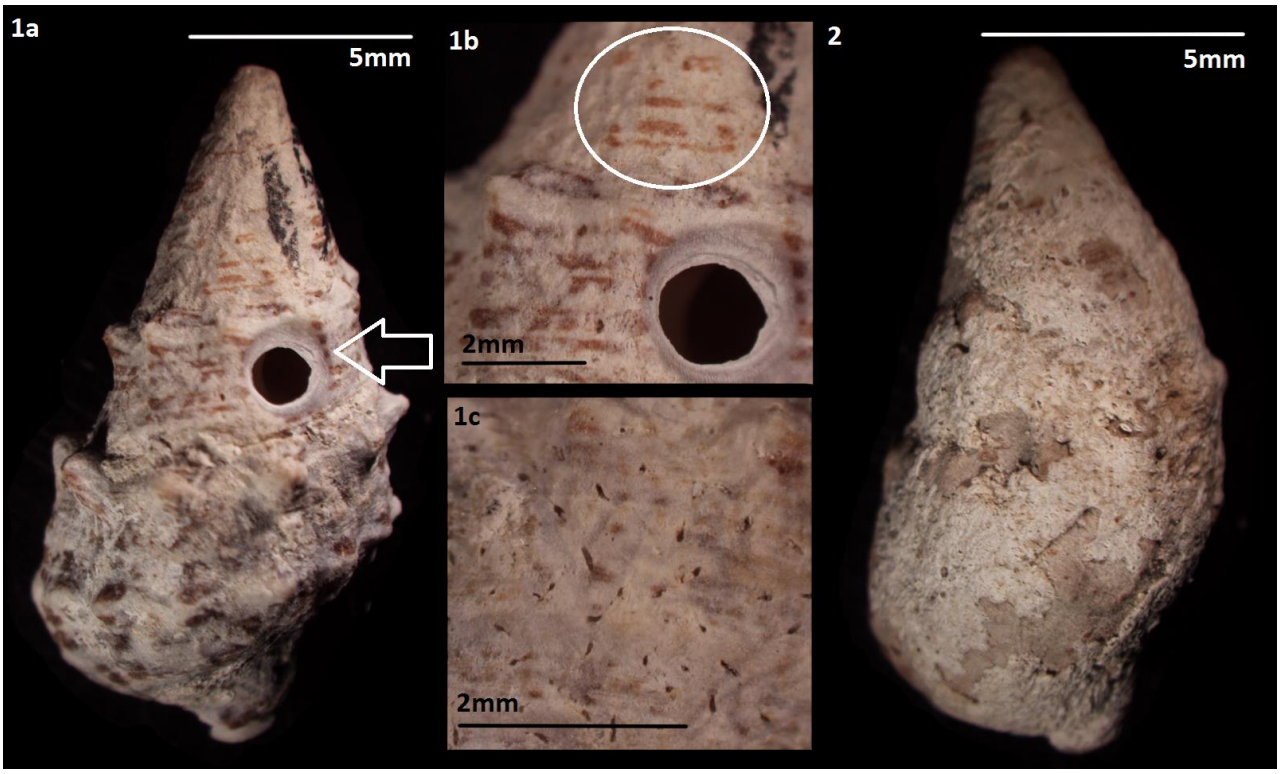

Figure 11: Examples of taphonomic characteristics. 1a: *Cerithium litteratum* that shows graze marks, a drill hole (indicated by arrow), low abrasion (assigned to category 1) moderate dissolution (category 2), mild abrasion (category 1), moderate color loss (category 2), and total outer luster loss (category 3). 1b: Close up of the same *Cerithium*'s graze marks (indicated by circle). 1c: Close up of the same specimen's *Cliona* borings on other side of shell. 2: *Cerithium sp.* with 80% exterior encrustation (lighter, differently textured areas) and moderate dissolution (category 2).

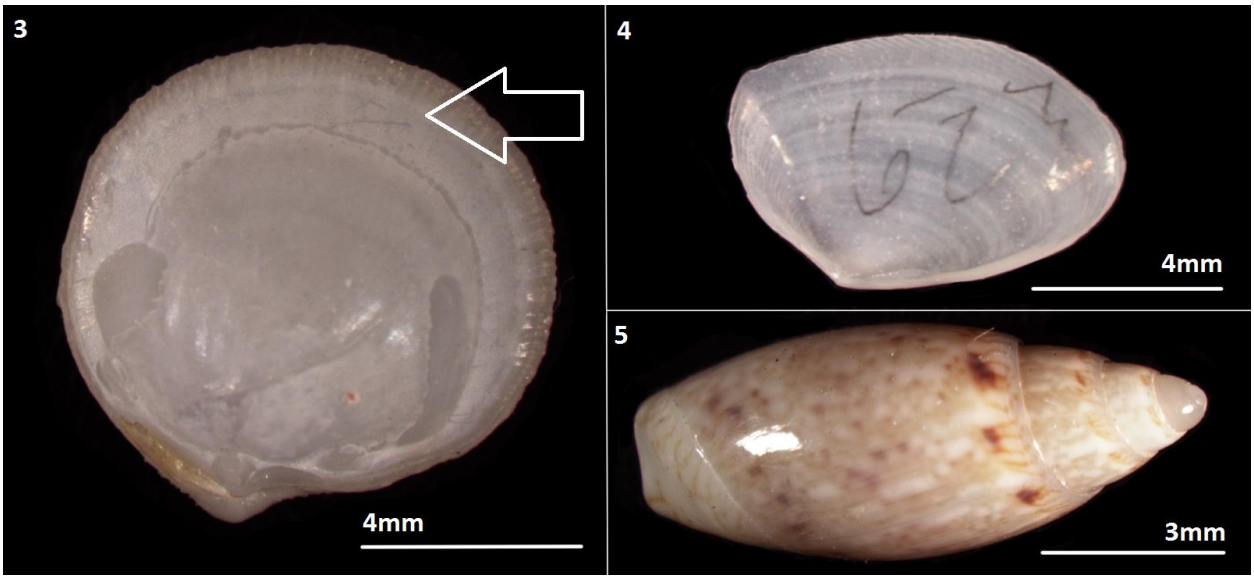

Figure 12: Examples of taphonomic characteristics. 3: *Codakia costata* with rhizome etchings (indicated by arrow) and mild luster loss (category 1). 4: *Tellina sp*. with mild microboring (assigned to category 2). 5: *Bulla striata* with 0% exterior encrustation, no luster loss (category 0), no dissolution (category 0), and low color loss (assigned to category 1).

Taphonomic characteristics were analyzed for infaunal and epifaunal organisms by modes and averages; confidence limits for averages were calculated. Nonmetric multidimensional scaling (NMMDS) was used to identify important patterns in the numerical taphonomic data. Ordination techniques like NMMDS seek and describe the strongest patterns in datasets that contain more than two variables, and plots individual specimens as data points on uncorrelated axes (Grace and McCune, 2002). NMMDs represents data dissimilarity and similarity through graphic distance and finds the most optimal positions for specimen data points through minimizing mathematical stress (Grace and McCune, 2002). Through this central concept, patterns are made clear; specimens with similar data plot as points close to one another and vice versa.

NMMDS is a highly defensible technique in peer review and is well suited to process non-normal data or those on discontinuous, arbitrary, or questionable scales (Grace and McCune, 2002). Furthermore, this dissuades assumptions of linear relationships among variables. Since the data collected in this study have different scales (i.e. some data are percentages, have 0-3 values, or are presence/absence data, etc.), this kind of multivariate statistical technique must be used. The NMMDS analysis was done using the free statistical software the Paleontological Statistics Software (PAST) v.3.2 (Hammer, et al., 2001).

For these taphonomic analyses, articulation and broken edges were omitted due to the possibility of specimens having no value in these categories (i.e. unbroken shells do not have a value for broken edges). Live/dead status, genus, and species data were not a part of these analyses as well due to their non-numerical nature. Size was omitted because shell size is partly determined by species and life habits in addition to age. For NMMDS specifically, the relatively higher magnitude of the size values gave them more weight and shifted the focus away from the taphonomic aspects. Additionally, the precision at which specimens were measured would not be conducive to modal analysis. Individual specimens with “NA” values for encrustation, color loss, or luster due to being a closed bivalve or lacking exterior material were not included in all taphonomic analyses.

For the size, life guild, genera, articulation, taphonomic modal, and taphonomic average analyses, halved and quartered subsamples’ proportions were corrected by doubling or quadrupling corresponding data entries. Because only parts of each shell bed were subsampled, the entire raw counts could not simply be doubled or quadrupled. The raw counts, corrected counts, and the number of specimens removed from analyses due to not having numerical

entries for all analyzed taphonomic categories are displayed in Tables 5-8. Proportionality was corrected for modal and average taphonomic analyses, but not the NMMDS analysis because duplicated and quadrupled specimen data would simply plot in the same location due to their identical data entries.

Table 5: Overall raw and corrected specimen counts for each bed.

	Raw specimen count	**Corrected specimen count**
SC01/2 Surface	145	356
SC01/2 Lag	55	200
SC04 Surface	206	592
SC04 Mid	77	236
SC08 Surface	151	500
SC08 Lag	83	332

Table 6: Raw and corrected number of specimens removed form life guild and generic analyses due to being unidentifiable.

	Raw specimen count	**Corrected specimen count**
SC01/2 Surface	19	37
SC01/2 Lag	5	20
SC04 Surface	52	196
SC04 Mid	11	22
SC08 Surface	1	4
SC08 Lag	24	96

Table 7: Raw and corrected number of bivalves for articulation analysis.

	Raw specimen count	**Corrected specimen count**
SC01/2 Surface	48	120
SC01/2 Lag	45	180
SC04 Surface	64	218
SC04 Mid	64	210
SC08 Surface	84	292
SC08 Lag	58	232

Table 8: Specimens removed from taphonomic analyses (modal, average, and NMMDS) due to having no numerical values for some of the analyzed categories. SC01/2 and SC08's were all bivalves whereas SC04's included bivalves and gastropods.

	Raw specimen count	**Corrected specimen count**
SC01/2 Surface	1	4
SC01/2 Lag	0	0
SC04 Surface	8	32
SC04 Mid	0	0
SC08 Surface	7	28
SC08 Lag	0	0

RESULTS

Size Analysis

All three surface beds had similar frequencies of shell sizes, and the lag and middle beds likewise had similar size frequencies relative to one another (Fig. 13-15). The surface beds almost always had more shells in the larger size categories than the lag and middle beds, and similarly, lower beds had more small shells (i.e. surface beds have larger shell sizes, and lag/middle beds heavily skew towards smaller shell sizes). The surface beds also had a wider size distribution than the middle and lag beds. The lower beds were better sorted with most of their shells in the 6-10mm size class.

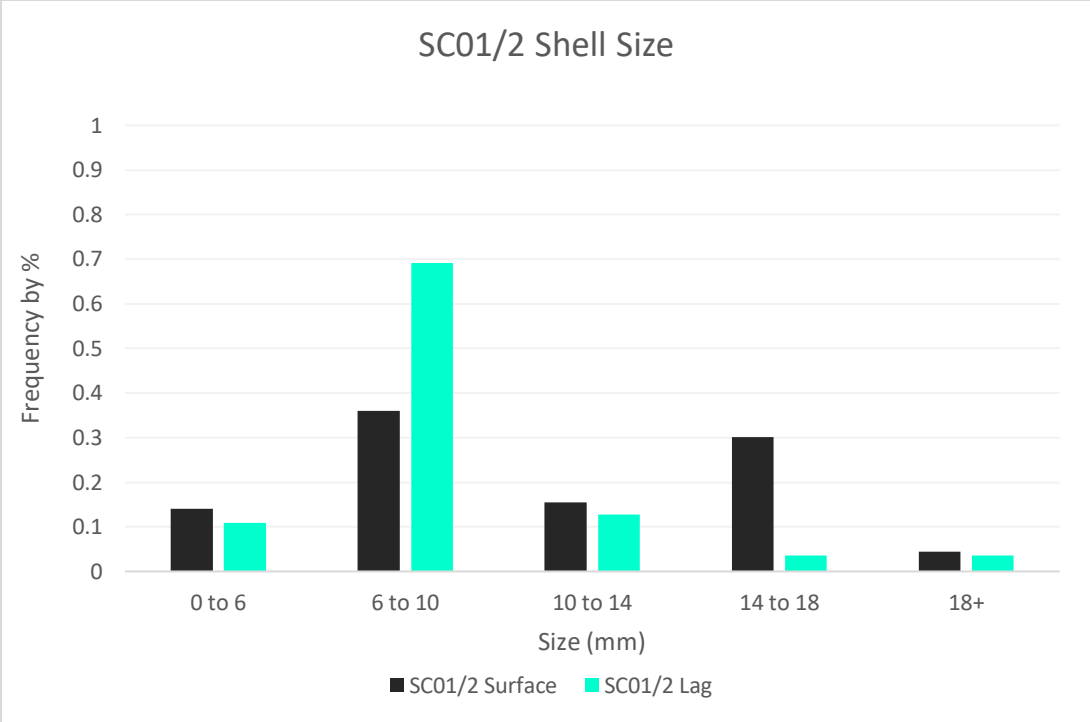

Figure 13: SC01/2's size distribution expressed as percentages. Surface shell sizes had a wider distribution with more shells in the 6-10mm and 14-18mm ranges. Lag sizes skewed heavily toward the 6-10mm range.

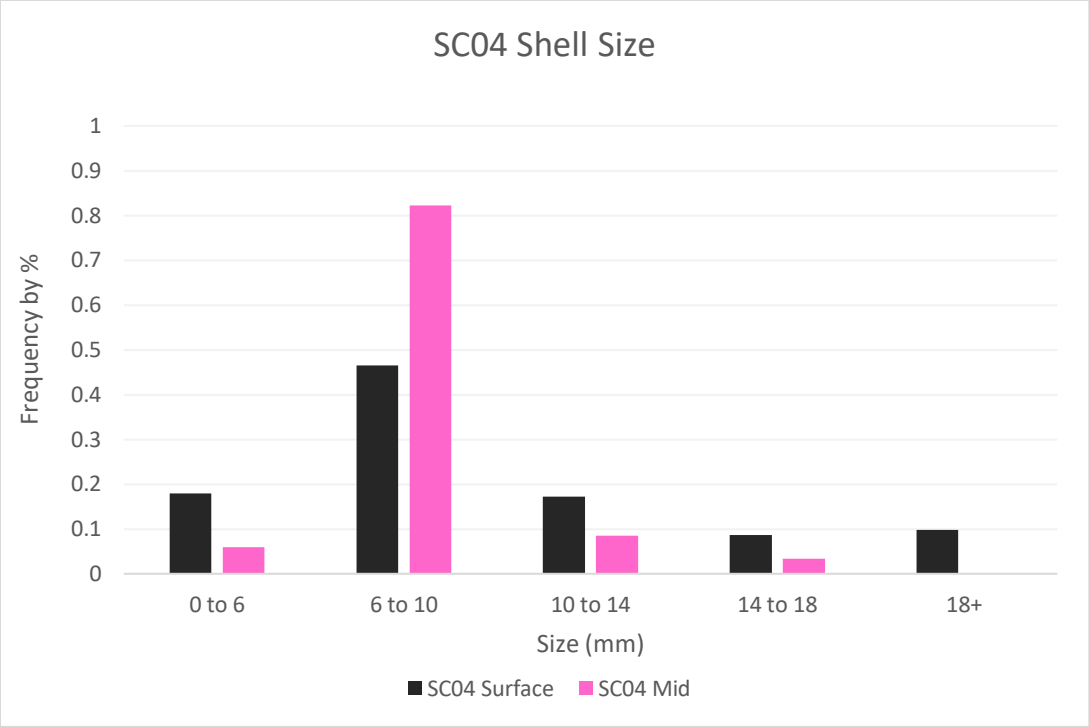

Figure 14: SC04‘s size distribution expressed as percentages. The surface shells had a wider size class distribution than the lower bed, but skewed towards the 6-10mm size class. The middle bed had a much smaller size distribution and skewed heavily towards the 6-10mm size class.

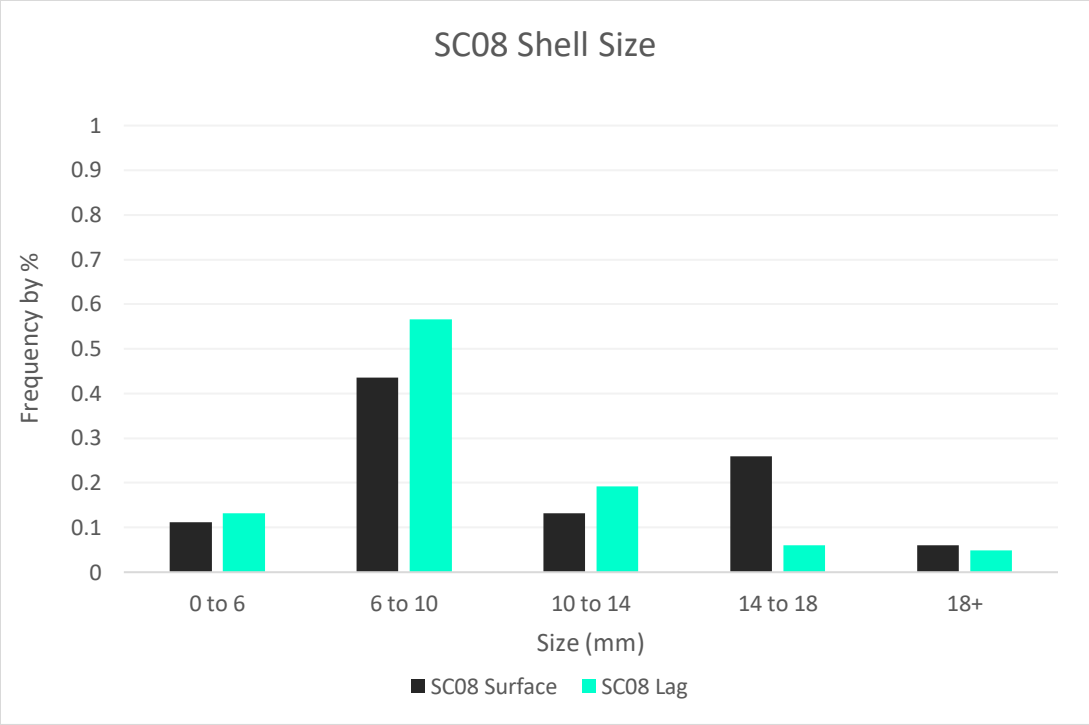

Figure 15: SC08's size distribution expressed as percentages. The surface and lag have similar size distributions, both skewing more towards the 6-10mm with the surface shells having a second peak at 14-18mm.

Life Guild Analysis

SC01/2 and SC04's surface beds were more similar to each other than to SC08's. SC01/2 and SC08's lag bed's life guild distributions were also more similar to each other than SC04's (Fig. 16-18). Overall, the surface beds were more similar to each other than to their corresponding lower beds and vice versa. Surface beds were dominated by epifaunal genera, while lag and middle beds had more infaunal ones, which in most cases, were made up of primarily infaunal small clams. There was far more variance in these results than in the size analysis results.

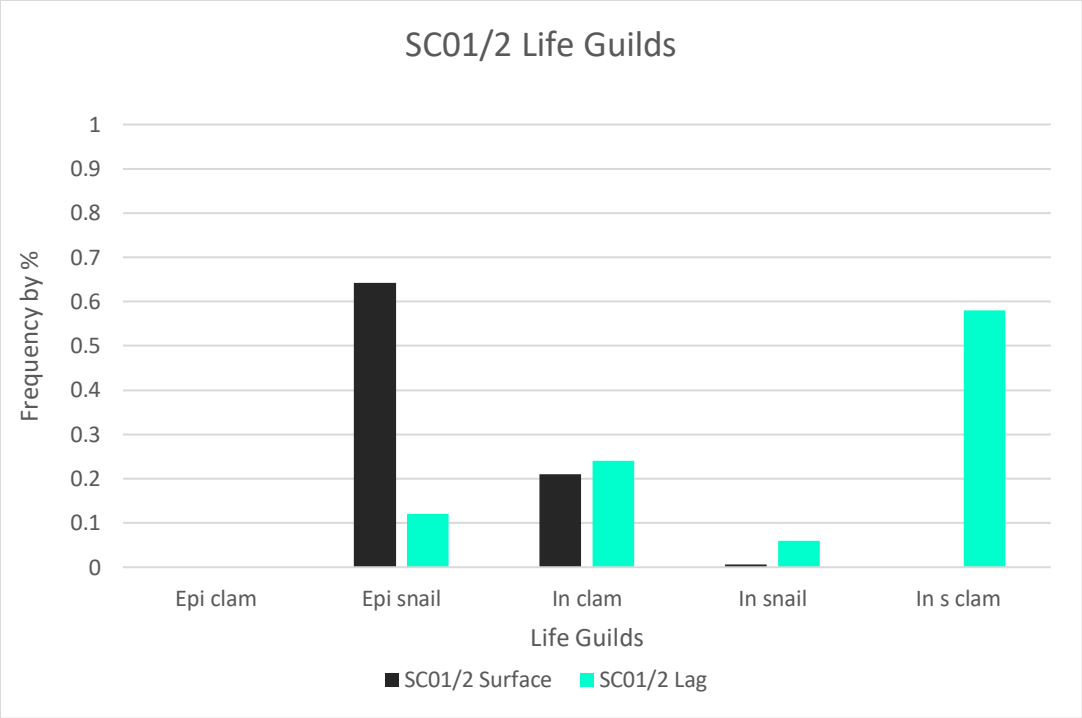

Figure 16: SC01/2's life guild distribution shown through percentages. The surface bed skewed heavily towards epifaunal snails, while the lag bed skewed towards infaunal clams and infaunal small clams.

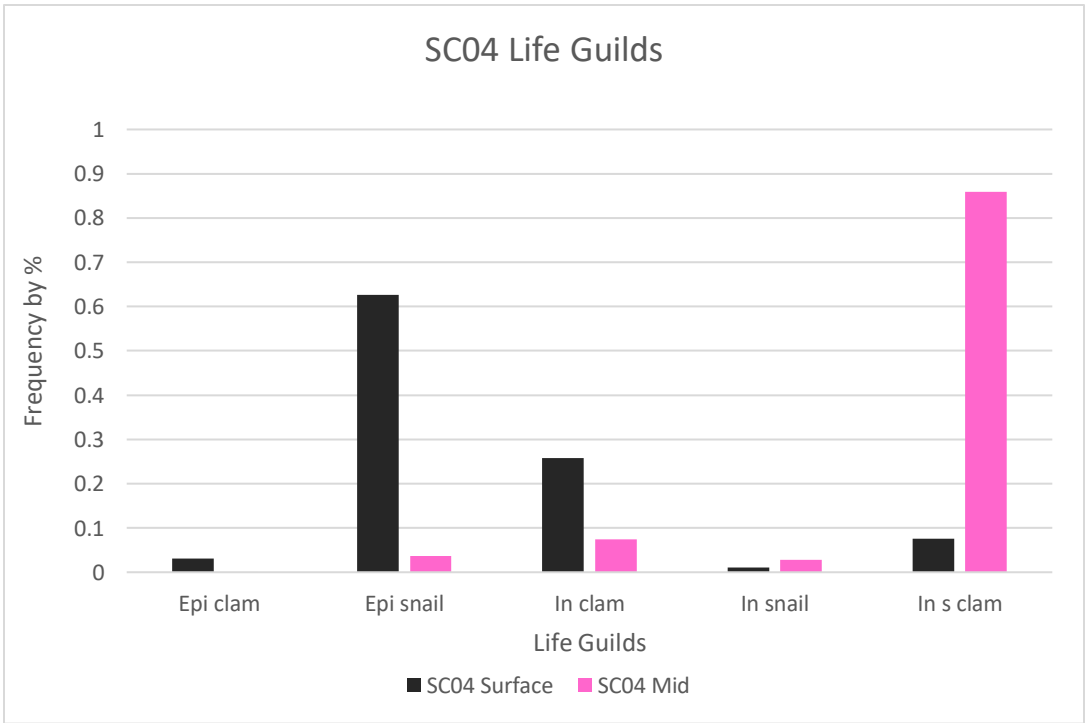

Figure 17: SC04's life guild distribution shown through percentages. The surface bed skewed toward epifaunal snails and the lag, heavily toward infaunal infaunal small clams.

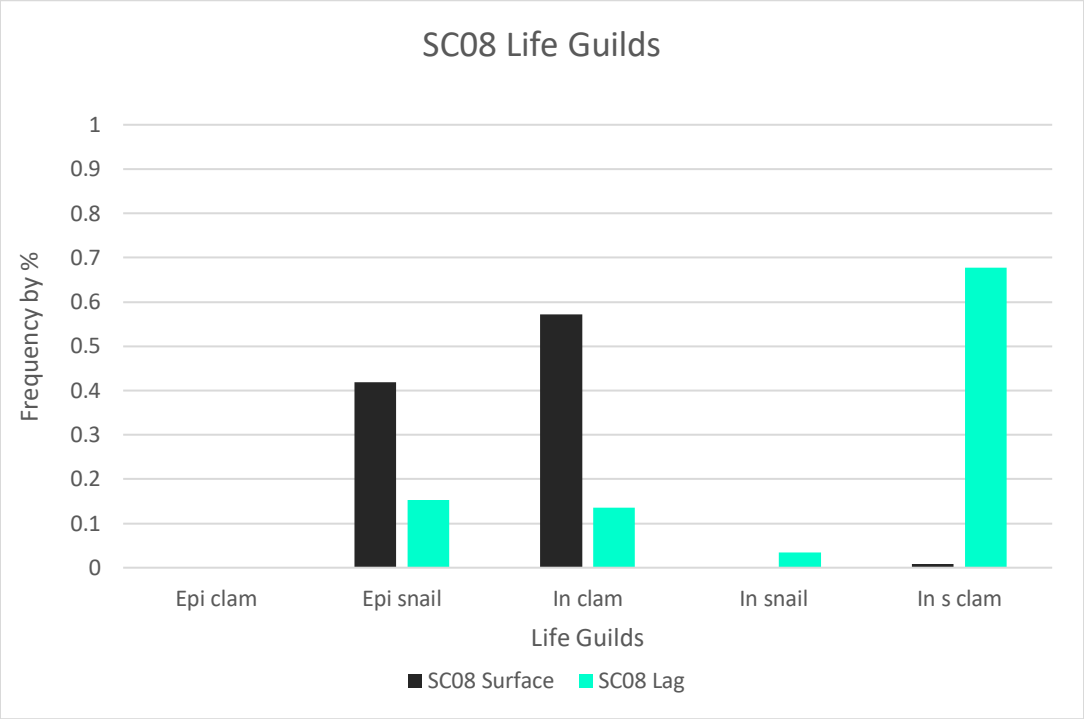

Figure 18: SC08's life guild distribution shown through percentages. The surface skewed toward infaunal clams primarily and epifaunal snails secondarily. The lag heavily skewed toward infaunal small clams.

Surface beds

Overall, these beds were dominated by epifaunal species. SC04, with the highest seagrass density, was the only site to have any epifaunal clams. All three surface beds had a significant percentage of epifaunal snails. It was the most numerous life guild in SC01/2 and SC04. In SC08, infaunal clams were the most numerous life guild (with epifaunal snails closely behind) but had distribution frequencies below 20% in SC01/2 and SC04. Similarly to epifaunal clams, the proportion of infaunal snail was very low at all three sites. Small infaunal clams were also less numerous but varied in number between the surface beds.

Lag and Middle beds

Unlike the surface beds, the subsurface beds were made up primarily of infaunal species and within that category— infaunal small clams. There were no epifaunal clams in the lag and middle beds. The percentage of epifaunal snails was over three times lower in the lag and middle beds than in the surface beds. The frequency of infaunal clams was higher in SC01/2, lower in SC04, and over four times lower in SC08 than in their corresponding surface beds. The amount of infaunal snails was still low in all subsurface beds but higher than in the surface beds. Infaunal small white-shelled clams were the most numerous in SC04 and SC08, but less common in SC01/2.

Species Analysis

Table 9 shows the five most common genera in each core level, Table 10 shows the total genera for each core bed, and Table 11 shows comparisons between the genera counts of the surface and lower beds. More detailed information is shown in Appendix 1. There is higher generic diversity in surface beds than in lag beds except in the case of SC08's surface bed, which had the lowest of all beds. SC04 had the highest diversity (highest seagrass density and no callianassid mounds). However, generic diversity does not appear to correlate with seagrass density, since the moderate seagrass density site, SC08, had the lowest diversity.

SC01/2 and SC04's surface beds have the same genera in their top five most common genera (*Cerithium, Codakia, Modulus, Nassarius*, and *Tellina*), and SC08's surface shares two of those (*Cerithium* and *Codakia*). All lower beds have *Americardia, Chione,* and *Tellina* in their top five, and SC01/2's and SC04's lower beds share *Nassarius* and *Pitar*. SC01/2 and SC08 share *Cerithium.*

In SC01/2*, Chione, Diplodonta, Laevicardium*, and *Pitar* were found only in the lower bed. For SC04, *Americardia, Diplodonta, Haminoea*, and *Lucina* were present solely in the middle bed. In SC08, *Bulla, Laevicardium, Littorina, Lucina, Pitar, Nassarius,* and *Tellina* were only found in the lower beds. For all core sites, *Diplodonata*, *Haminoea, Laevicardium*, and *Lucina* were exclusively found in the lower beds and had raw counts below 8 individuals. More information regarding raw counts and corrected proportions of all genera found is available in Appendix 1.

Table 9: Five most common genera in each core bed with the percentage of the total identified taxa they make up (calculated using corrected proportions). Genera that had the same percentage were both listed as a single entry out of the five.

SC01/2 Surface	**SC01/2 Lag**	**SC04 Surface**	**SC04 Middle**	**SC08 Surface**	**SC08 Lag**
Cerithium (39.5%) *Codakia* (18.8%) *Tellina* (13.5%) *Modulus* (7.83%) *Nassarius* (5.33%)	*Tellina* (32.0%) *Chione* (24.0%) *Americardia* (12.0%) *Haminoea* (20%) *Bulla* (6.00%) *Cerithium* (6.00%) *Nassarius* (6.00%)	*Codakia* (24.7%) *Cerithium* (15.4%) *Modulus* (10.3%) *Nassarius* (8.48%) *Tellina* (7.46%)	*Tellina* (77.14%) *Chione* (7.62%) *Nassarius* (3.81%) *Americardia* (2.86%) *Diplodonta* (2.86%) *Bulla* (1.90%) *Lucina* (1.90%)	*Codakia* (46.3%) *Cerithium* (36.7%) *Chione* (11.4%) *Astrea* (2.40%) *Pyramidella* (1.60%)	*Tellina* (45.0%) *Pitar* (13.3%) *Cerithium* (11.7%) *Chione* (8.33%) *Americardia* (5.00%) *Laevicardium* (5.00%)

Table 10: Total generic count for each core bed.

SC01/2 Surface	**SC01/2 Lag**	**SC04 Surface**	**SC04 Middle**	**SC08 Surface**	**SC08 Lag**
16	9	26	9	7	10

Table 11: Generic count comparisons between surface and lower beds.

	SC01/2	**SC04**	**SC08**
Genera Exclusive to Surface	13	21	4
Genera exclusive to Lower Beds	3	4	7

Bivalve Articulation

All of the bivalves of the lag and middle beds were disarticulated; both SC01/2 and SC04's surface beds had similar low percentages of articulated bivalves (Fig. 19). SC08's surface bed had a percentage of articulated bivalves over twice as high as the other two beds.

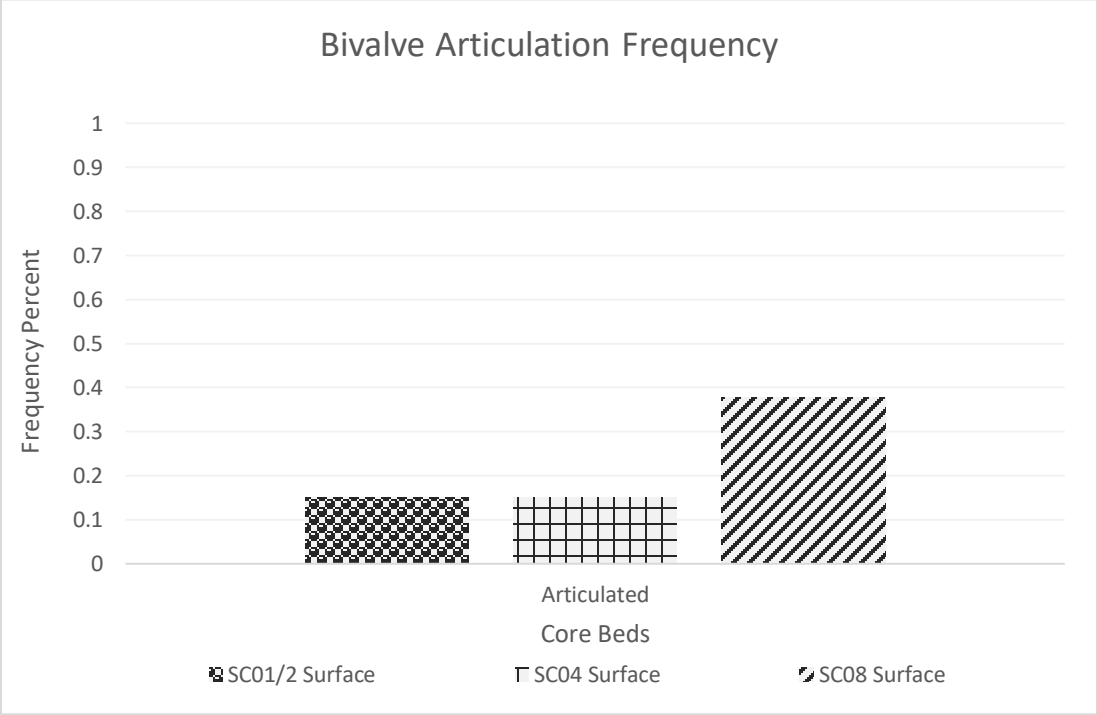

Figure 19: Percent of articulated shells in the surface beds of all three cores. There were no articulated bivalves in the subsurface beds.

Modal Taphonomic Analysis by Epifaunal and Infaunal Life Guilds

Modal analysis showed that surface beds are similar to each other regardless of location, and that the lower beds are internally consistent as well. Additionally, surface beds and epifaunal specimens had more taphonomic alteration than lower beds dominated by infaunal specimens.

Modal infaunal analysis showed the majority of infaunal specimens to have low fragmentation, dissolution, luster loss and high color loss regardless of location or depth (Table 12). Higher outer luster loss in surface beds and higher inner luster loss in lower beds were the only common patterns.

Table 12: Modal taphonomic values for infaunal specimens. Specimens with NA in any of the below categories were removed from this analysis.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Outlus	Closs
SC01/2 surface	0	0	1	0	0	0	0	0	0	2	0	2	2
SC01/2 lag	0	0	1	0	0	0	0	0	0	1	1	0	3
SC04 surface	0	0	1	0	0	1	0	0	0	1	1	2	3
SC04 middle	0	0	1	0	0	0	0	0	0	1	0	0	3
SC08 surface	0	0	1	0	0	0	0	0	0	1	1	2	3
SC08 lag	0	0	1	0	0	1	0	0	0	1	1	0	3

Epifaunal modal analysis showed that all beds had similar low modal values for fragmentation, microboring, and dissolution and higher values for outer luster loss and color

loss (Table 13). Surface beds typically had higher exterior encrustation and inner luster loss values than lower beds, and SC08's beds were the most taphonomically altered.

Table 13: Modal taphonomic values for epifaunal specimens. Swith NA in any of the below categories were removed from this analysis.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Outlus	Closs
SC01/2 surface	0	0.15	1	0	0	2	0	0	0	1	0	1	2
SC01/2 lag	0	0	1	0	0	1	0	0	0	1	2	2	2
SC04 surface	0	0	1	0	0	1	0	0	0	1	0	2	2
SC04 middle	0	0	1	0	0	1	0	0	0	1	0	1	3
SC08 surface	0	0.8	1	1	1	1	2	0	0	1	0	2	2
SC08 lag	0	0	1	1	0	1	0	0	0	2	2	2	2

Average Taphonomic Analysis by Epifaunal and Infaunal Life Guilds

Like the modal analysis, average analysis showed that surface beds are similar to each other regardless of location, and vice versa. 95% confidence limits for infaunal and epifaunal average analyses are displayed in Appendix 2.

Mean infaunal analysis showed that surface bed specimens typically had more taphonomic alteration in the encrustation, microboring, *Cliona*, rhizome, dissolution, outer luster loss, and color loss categories, while lower beds typically had higher values for inner luster loss and more drill holes (Table 14, Fig. 20).

Table 14: Average taphonomic values for infaunal specimens. Specimens with NA in any of the below categories were removed from this analysis. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Out lus	Closs
SC01/2 surface	0.01	0.00	1.00	0.00	0.06	0.37	0.09	0.35	0.00	1.23	0.60	1.07	2.76
SC01/2 lag	0.00	0.00	1.24	0.22	0.02	0.22	0.00	0.09	0.04	1.49	1.09	0.93	2.69
SC04 surface	0.06	0.11	1.21	0.02	0.01	1.45	0.05	0.11	0.00	1.25	1.21	1.56	2.91
SC04 middle	0.00	0.00	1.15	0.00	0.00	0.49	0.00	0.09	0.02	1.16	0.42	0.30	2.93
SC08 surface	0.05	0.05	0.72	0.00	0.01	0.30	0.02	0.49	0.01	1.28	0.78	1.91	2.77
SC08 lag	0.00	0.00	1.54	0.02	0.02	0.64	0.00	0.36	0.06	1.20	1.08	0.66	2.74

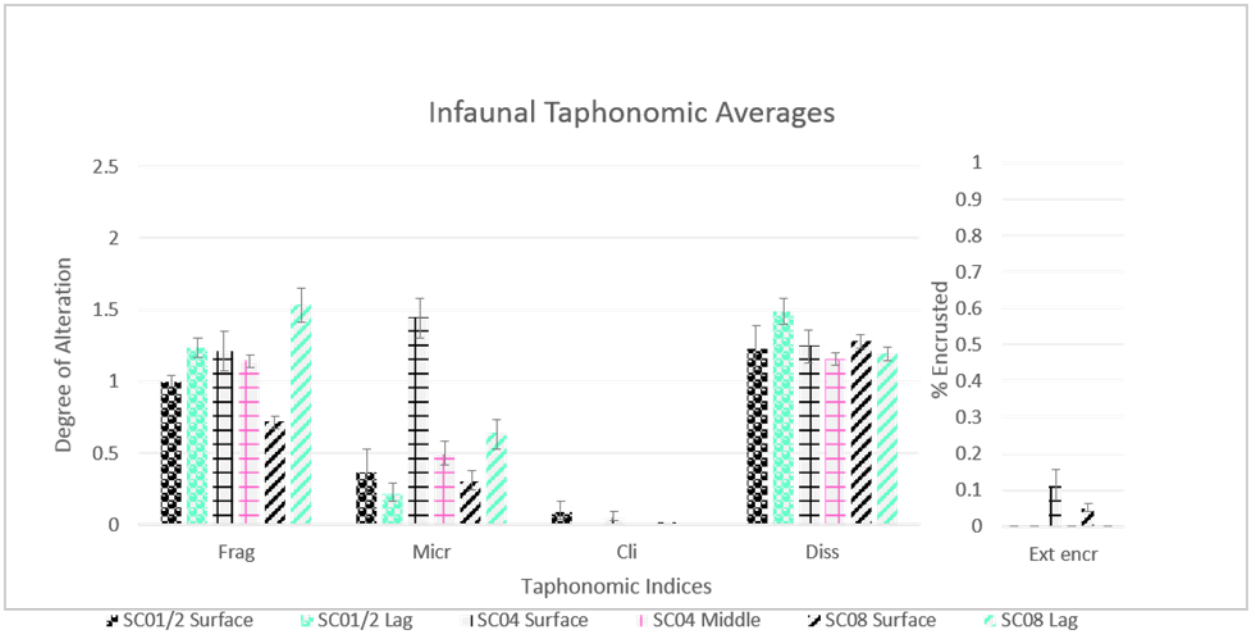

Figure 20: Taphonomic averages for exterior encrustation (%), fragmentation, microboring, *Cliona*, and dissolution values for infaunal specimens. 95% confidence limits show significant variations in data.

The average epifaunal analysis showed the surface beds had higher encrustation, abrasion, and *Cliona* values as well as more rhizome etchings and drill holes (Table 15, Fig. 21). The lower beds typically had higher fragmentation, microboring, dissolution, outer luster loss, and color loss values.

Table 15: Average taphonomic values for epifaunal specimens. Specimens with NA in any of the below categories were removed from this analysis. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Out lus	Closs
SC01/2 surface	0.05	0.37	1.29	0.27	0.26	1.48	0.51	0.11	0.15	1.23	0.70	1.45	2.13
SC01/2 lag	0.00	0.01	1.60	0.40	0.00	1.00	0.00	0.00	0.00	1.80	1.80	1.60	2.40
SC04 surface	0.13	0.43	1.33	0.35	0.35	1.26	0.68	0.20	0.05	1.32	0.95	1.55	1.97
SC04 middle	0.00	0.00	0.75	0.00	0.00	1.50	0.00	0.00	0.00	1.00	0.00	1.00	3.00
SC08 surface	0.04	0.61	1.11	0.79	0.73	1.43	1.50	0.06	0.01	1.18	0.57	1.73	1.88
SC08 lag	0.01	0.13	2.00	0.56	0.11	1.44	0.00	0.00	0.00	2.44	1.89	1.78	2.11

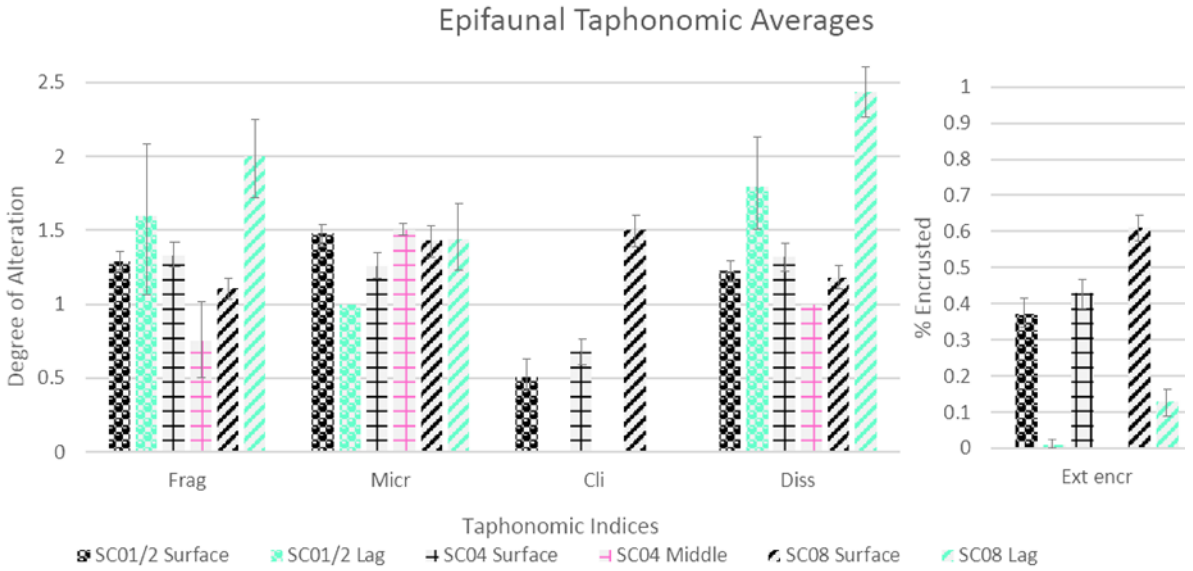

Figure 21: Taphonomic averages for exterior encrustation, fragmentation, microboring, *Cliona*, and dissolution values for epifaunal specimens. 95% confidence limits show significant variations in data.

NMMDS Analysis

NMMDS plots individual specimens in two-dimensional space, using graphic distance to show similarity and dissimilarity in their taphonomic data. Two points that plot close together have similar values for some if not all their taphonomic indices and vice versa. The formation of clouds of specimens indicates that these specimens have similar taphonomic data. Overlap between clouds shows similarities between different groups' taphonomic signatures.

While it cannot exactly be known what drives the differences between two coordinates, a clear idea can be drawn from referencing their taphonomic data entries. For every NMMDS graph, the data entries of four points from the highest, lowest, most leftward, and most rightward extents of the data clouds were analyzed to find a pattern for their data point distribution. The values that were most important for each direction were inferred, and each data cloud was judged along these as well as their position relative to one another. The range

of encrustation percentages and taphonomic values between these four specimens is depicted on each NMMDS plot along with the region they are located on the graph (Fig. 22-30; App. 3-6, Fig. 32-43). The percentage of these four specimens that had positive presence/absence data is also recorded. Taphonomic categories with ranges of 0 and presence/absence data that was not present in the four specimens is not displayed.

All Core Beds' Data Combined

In the combined bed analyses (App. 3, Fig 32), the lag and middle beds tended to form one or two distinct clouds that overlapped or partially overlapped with the greater surface cloud. The formation of their own clouds indicated they had a taphonomic signature and overlap between clouds showed similarities in the breadth of their signatures. The fact that the surface beds overall, tended to plot together, and the subsurface beds tended to plot together shows that the surface beds have similar taphonomic signatures to one another more than to their corresponding lag/middle beds and vice versa. Within the surface shells, SC08's surface bed tended to form its own cloud, showing it to be more distinct from SC01/2 and SC04's surface beds. Overall, color and luster loss values stayed relatively consistent between different areas of the plots.

In the combined mollusk analysis, the surface beds formed a large cloud within which, the lag and middle beds resided. The large size of the surface cloud indicates a relatively broad range for the surface beds' combined taphonomic signature compared to the subsurface beds. The overlap between the surface and subsurface clouds shows that the surface beds taphonomic signature shares some patterns with the subsurface beds. Specifically, this overlap

indicated the lag and middle bed specimens had similar low percentages of exterior encrustation as those surface specimens.

In the bivalve analysis (App. 3, Fig. 33), SC04's surface bed plotted lower on the y-axis than the rest of the beds, indicating its specimens had higher encrustation percentages, fragmentation, and slightly higher abrasion values as well as lower dissolution and microboring values than the other beds. SC08's surface bed plotted farther to the left than the other beds, showing its specimens had higher encrustation percentages, dissolution, *Cliona* boring, and luster loss values as well as lower microboring and fragmentation values compared to the other beds. For the bivalve analysis, SC04's surface bed was shown to have higher encrustation, fragmentation, dissolution, luster loss, microboring, and abrasion values as well as lower color loss values.

The gastropod analysis (App. 3, Fig. 34) showed beds forming clouds with less overlap, showing there was more distinct taphonomic data for the gastropods in different beds. SC08's surface bed plotted higher on the y-axis than other beds. This placement indicates these specimens had lower degrees of fragmentation, encrustation, and microboring as well as higher degrees of *Cliona* borings and microboring. SC08's surface bed also had more instances of graze marks than the other beds. The lag beds inhabited the lower-right region of the plot within the clouds of SC01/2's beds and SC04's surface bed. This shows that the lag beds had similar low encrustation percentages, abrasion, and *Cliona* boring values as well as high dissolution and more occurrences of drill holes as a portion of the other beds.

Surface Beds

In the combined mollusk analysis (App. 4, Fig. 35), there was significant overlap between the clouds of all three core's beds, with some more pronounced taphonomic variations and differences between them in the bivalve and gastropod analyses. But overall, surface shells, no matter where they came from, had similar taphonomic signatures.

For the combined mollusk analysis, SC08's specimens plotted in the upper half of the general specimen cloud, specifically due to having higher exterior encrustation percentages and higher occurrences of graze marks within the taphonomic range of the other core beds. These shells also had high microboring and abrasion values as well as low fragmentation values. SC01/2 had specimen points heavily concentrated in the left portion of the cloud, indicating it had many specimens with generally low alteration, moderate luster loss, and few rhizome etchings.

In the bivalve analysis (App. 4, Fig. 36), SC04 formed its own cloud with little overlap with SC01/2 and SC08's cloud. SC04's specimens, which plotted lower and more to the right than the other bed's, had more encrustation as well as higher microboring, abrasion, and fragmentation values than the other beds. For the gastropod NMMDS plot (App. 4, Fig. 37), SC08's specimens plot higher than the others due to having generally lower encrustation percentages and lower fragmentation values as well as higher microboring, dissolution, and abrasion values.

Lag beds

SC01/2 and SC08's specimens essentially formed one cloud for all analyses, proving them to be very similar taphonomically, regardless of surface seagrass density. In the combined mollusks analysis (App. 5, Fig. 38), SC08's specimens have a slightly higher range of taphonomic

values, allowing them to have higher encrustation, fragmentation, and microboring values as well as lower dissolution values and fewer occurrences of drill holes. For the bivalve analysis (App. 5, Fig. 39), only a handful of SC01/2 specimens plotted further to the left than the SC08 specimens. This wider spatial range reflects a wider range of taphonomic values in these specimens, allowing SC01/2's to have higher dissolution values along with lower microboring and fragmentation values. In the gastropod analysis (App. 5, Fig. 40), there were only a handful of points from SC08 that strayed from the range of the main cloud. This indicates a broader taphonomic range including higher exterior encrustation, fragmentation, and microboring values as well as lower dissolution values for SC08's specimens.

Lag and Middle Beds

In the analyses of all subsurface beds (the two lag beds and SC04's middle bed [App. 6, Fig. 41), there were more variations in the ranges of specimen clouds, but the strong overlap between all of them indicates their taphonomic data is very similar, regardless of surface environment (see Appendix 6 for graphs). In the combined mollusk analysis (App. 6, Fig. 41), SC04 has a slightly smaller cloud, concentrated in the right region of the other beds' clouds. This size and placement reflects a smaller range of taphonomic values limited to lower dissolution and abrasion and slightly lower fragmentation and microboring values in SC04 as compared to the rest of the beds. SC01/2 reaches further to the upper left, indicating the bed has a wider taphonomic range that includes higher dissolution, higher abrasion, lower fragmentation values and more occurrences of rhizome etchings. The bivalve analysis (App. 6, Fig. 42) showed a very strong overlap between taphonomic signatures from all three cores. The gastropod analysis had most separation between clouds (App. 6, Fig. 43). SC04's specimens plotted further to the left

than the other beds, and SC01/2's specimens plotted lower on the y-axis. SC04's cloud location reflects those specimens having lower fragmentation, dissolution, microboring, abrasion, and *Cliona* boring values. SC01/2's placement indicates these specimens had lower fragmentation values as well as higher dissolution and microboring values than the other beds.

Surface v. Lower Beds

The principle focus of this research was about the comparison between surface and lag/middle beds; therefore, these data plots are presented here as Fig. 22-30. In the surface v. lower bed NMMDS analyses, the surface and subsurface specimens consistently plotted away from each other, reflecting the significant difference of their taphonomic data. This difference is characterized by the surface beds having higher encrustation, microboring, and *Cliona* boring values, and the lag specimens generally having higher or only slightly lower fragmentation and dissolution values than surface specimens.

Overall, SC01/2's surface bed specimens had more taphonomic alteration than their corresponding surface specimens. In SC01/2's combined mollusk NMMDS plot (Fig. 22), the lag bed plotted higher than the surface bed, reflecting its lower encrustation, *Cliona* boring, fragmentation, and microboring values as well as its higher dissolution values. SC01/2's bivalve analysis showed more overlap, but the lag bed plotted higher than the majority of the surface bed, indicating that the lag specimens have lower microboring and abrasion as well as slightly lower fragmentation values than the surface specimens (Fig. 23). In the gastropod analysis, the lag specimens plotted high on the y-axis, overlapping slightly with the surface bed (Fig. 24). This shows the gastropod specimens of the lag does share its taphonomic signature with the surface bed, but only with a very small portion of those surface specimens. This signature is composed

of lower exterior encrustation, microboring, *Cliona* boring, dissolution, and abrasion values than the majority of surface bed specimens as well as fewer instances of graze marks and rhizome etchings

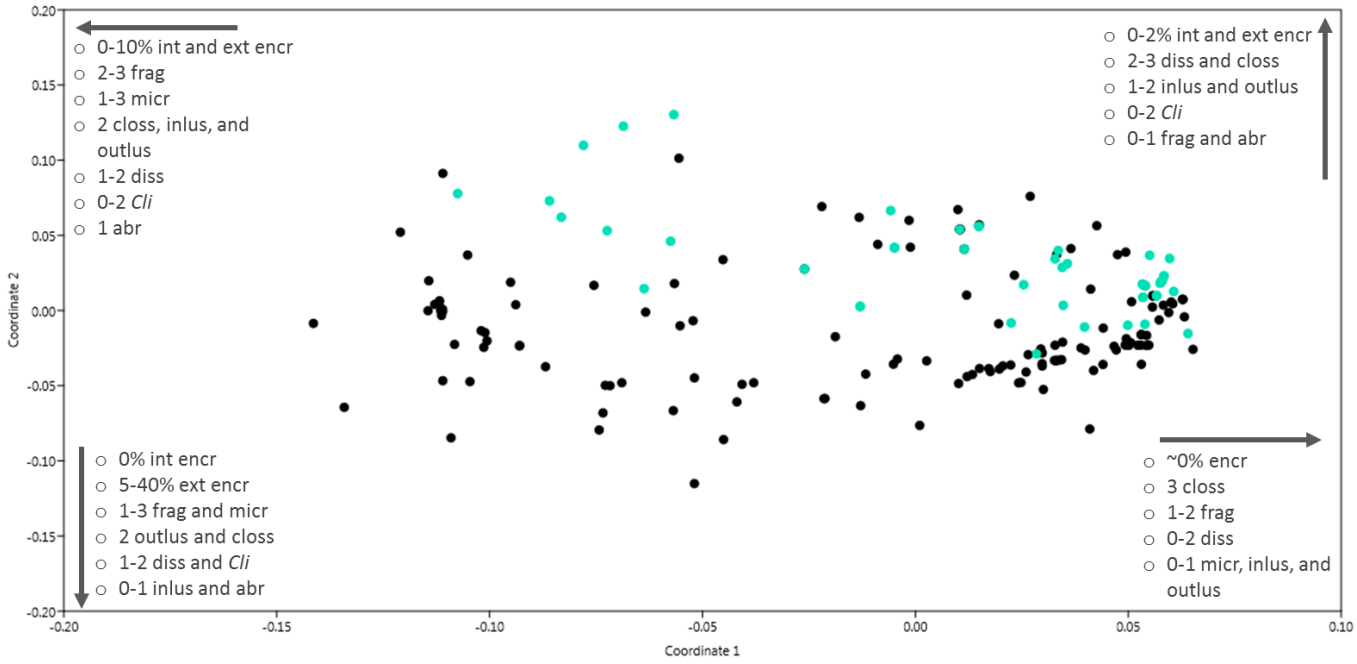

Figure 22: NMMDS graph for the combined mollusk analysis of all surface and lower core data for SC01/2. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

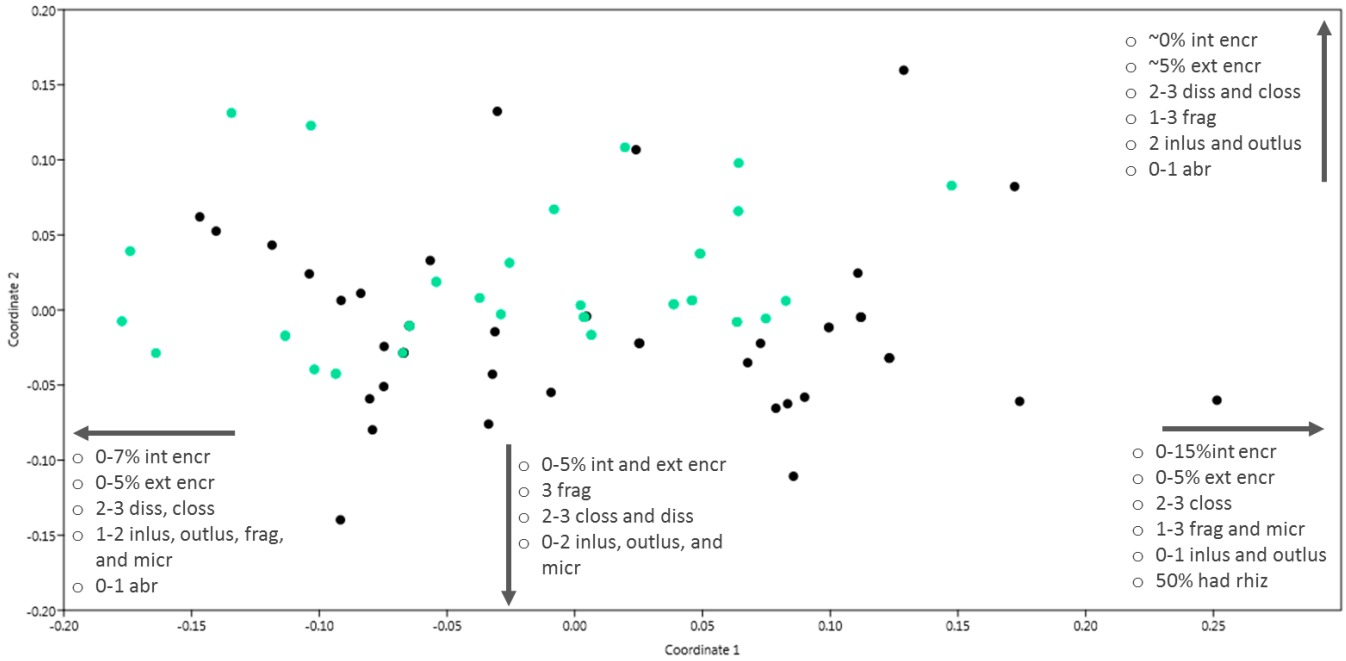

Figure 23: NMMDS graph for the bivalve analysis of all surface and lower core data for SC01/2. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

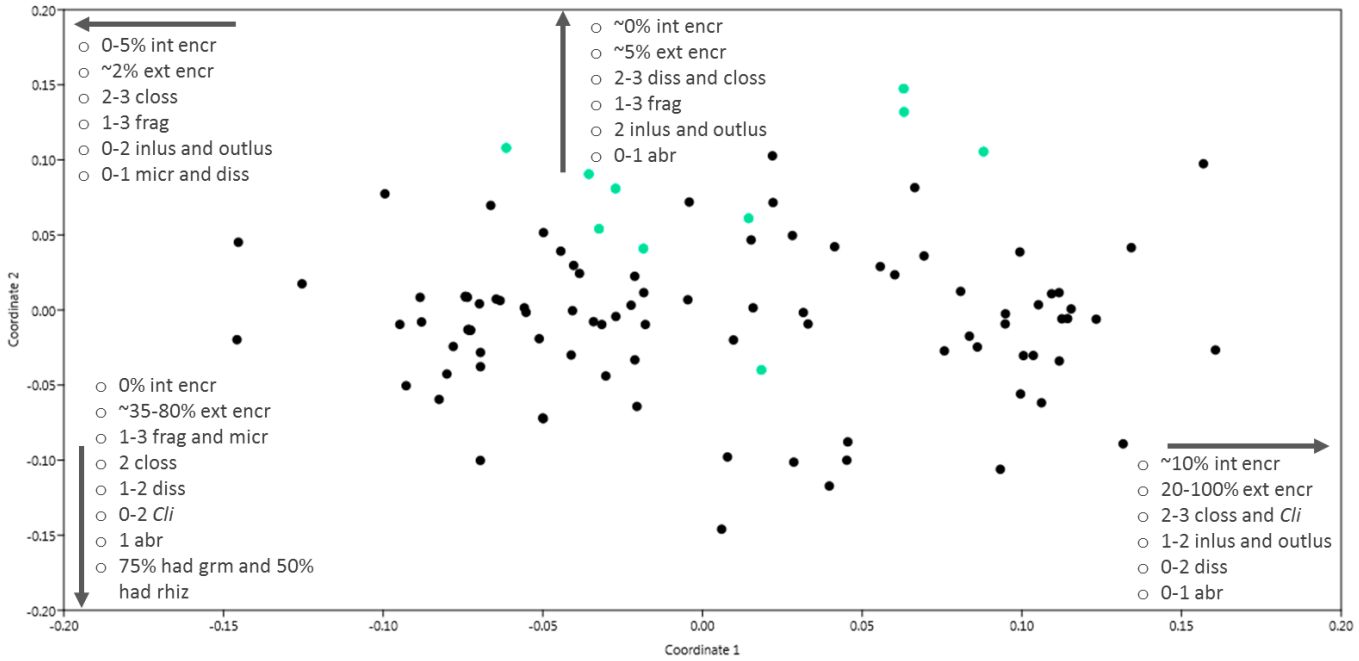

Figure 24: NMMDS graph for the gastropod analysis of all surface and lower core data for SC01/2. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

SC04's surface bed higher encrustation values and microboring, fragmentation, and *Cliona* values than its middle bed. The combined mollusks NMMDS analysis, showed taphonomic difference between the beds through how the middle bed plotted further to the right and slightly above than the surface bed (Fig. 25). This placement shows that the middle bed had lower encrustation percentages as well as slightly less fragmentation, less microboring, fewer instances of graze marks and more specimens with rhizome etchings. The bivalve analysis showed the subsurface specimens plotting further to the left than the surface ones (Fig. 26). This indicates that the middle specimens have lower encrustation percentages, fragmentation,

microboring, *Cliona* boring, and abrasion values than their surface counterparts. Like in SC01/2's gastropod analysis, there is some overlap between the surface and subsurface gastropod clouds of SC04, but the middle bed's smaller size, makes it somewhat distinct from the surface bed (Fig. 27). This distinction is caused by the middle specimens having higher fragmentation, dissolution, and encrustation percentages and lower microboring and *Cliona* boring values than the surface specimens.

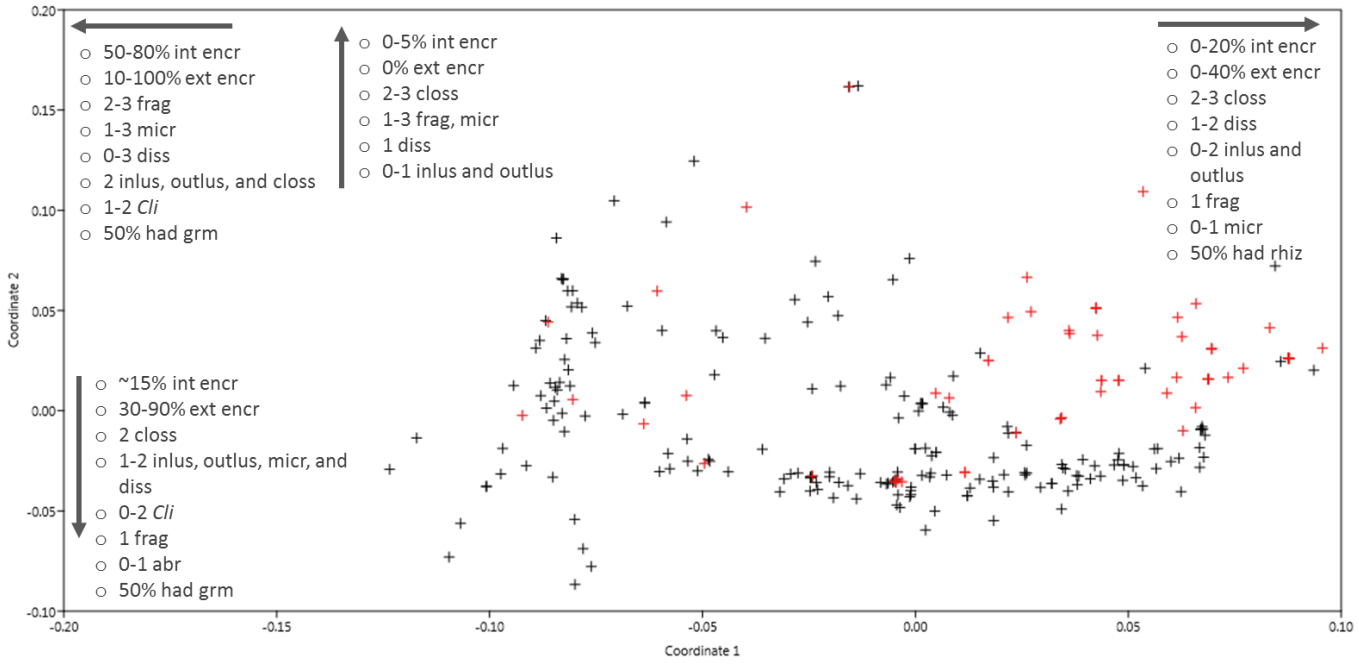

Figure 25: NMMDS graph for the combined mollusk analysis of all surface and lower core data for SC04. Black indicates specimens from surface beds, and pink indicates those from middle beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

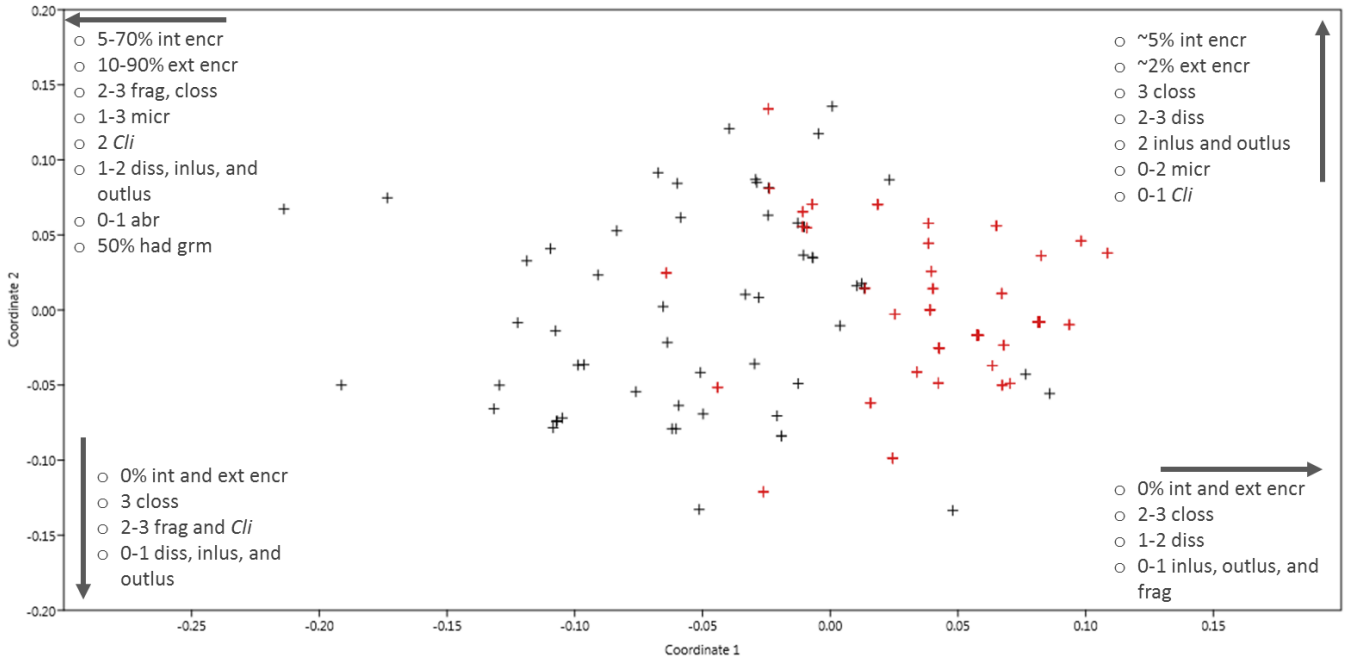

Figure 26: NMMDS graph for the bivalve analysis of all surface and lower core data for SC04. Black indicates specimens from surface beds, and pink indicates those from middle beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

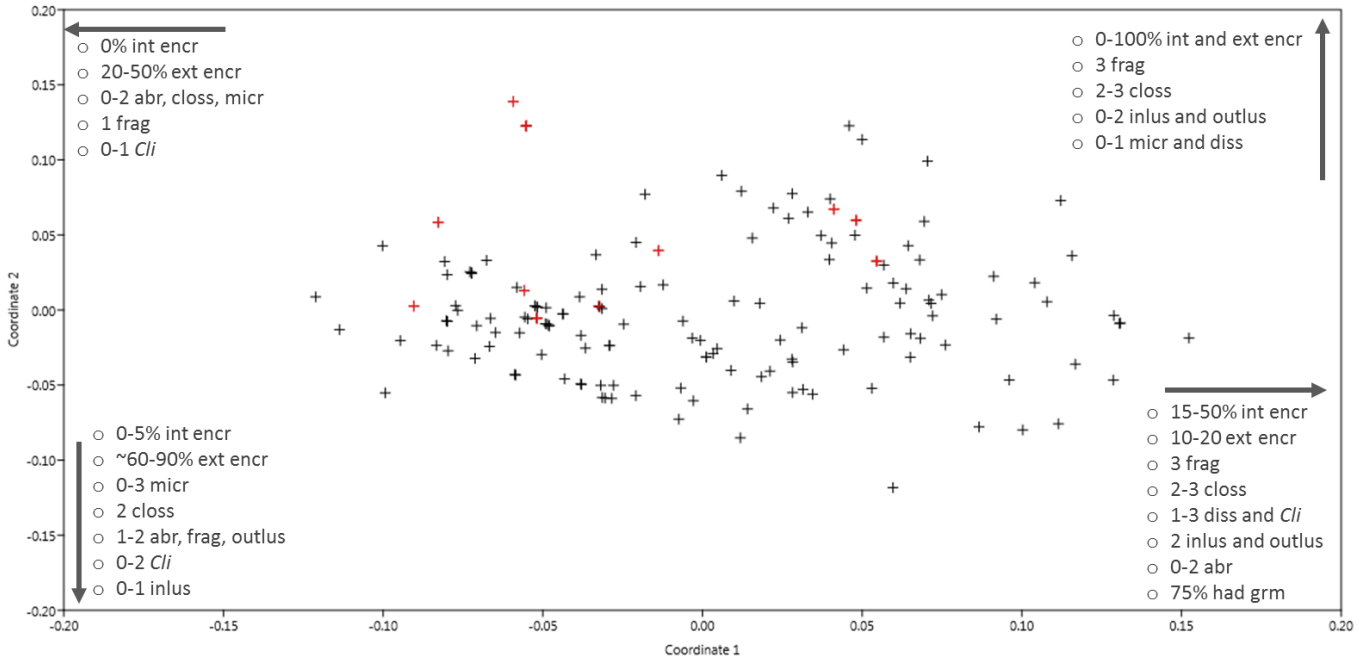

Figure 27: NMMDS graph for the gastropod analysis of all surface and lower core data for SC04. Black indicates specimens from surface beds, and pink indicates those from middle beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

Overall, SC08's surface bed specimens had more taphonomic alteration than the lag specimens, particularly in the categories of encrustation, microboring, and *Cliona* boring. The lag specimens had higher dissolution and fragmentation values than their surface counterparts. In the combined mollusk analysis, the lag specimens plotted far to the right and upper region of the plot, just barely overlapping with the surface specimens (Fig. 28). This shows a very distinct taphonomic signature in the lag specimens composed of lower encrustation percentages, *Cliona* boring, microboring and abrasion values; fewer specimens with graze marks; and higher fragmentation and dissolution values than surface specimens. The bivalve analysis showed a

very distinct separation of data clouds as well, the lag specimens plotting much further to the right than the surface ones (Fig. 29). This reflects the subsurface specimens having higher fragmentation and microboring values as well as lower encrustation percentages, dissolution, and *Cliona* boring values compared to the surface specimens. The gastropod NMMDS plot depicts the lag specimens in a cloud more towards the left than the surface ones, reflecting their lower exterior encrustation percentages; lower *Cliona* boring and abrasion values; and higher dissolution and fragmentation values (Fig. 30).

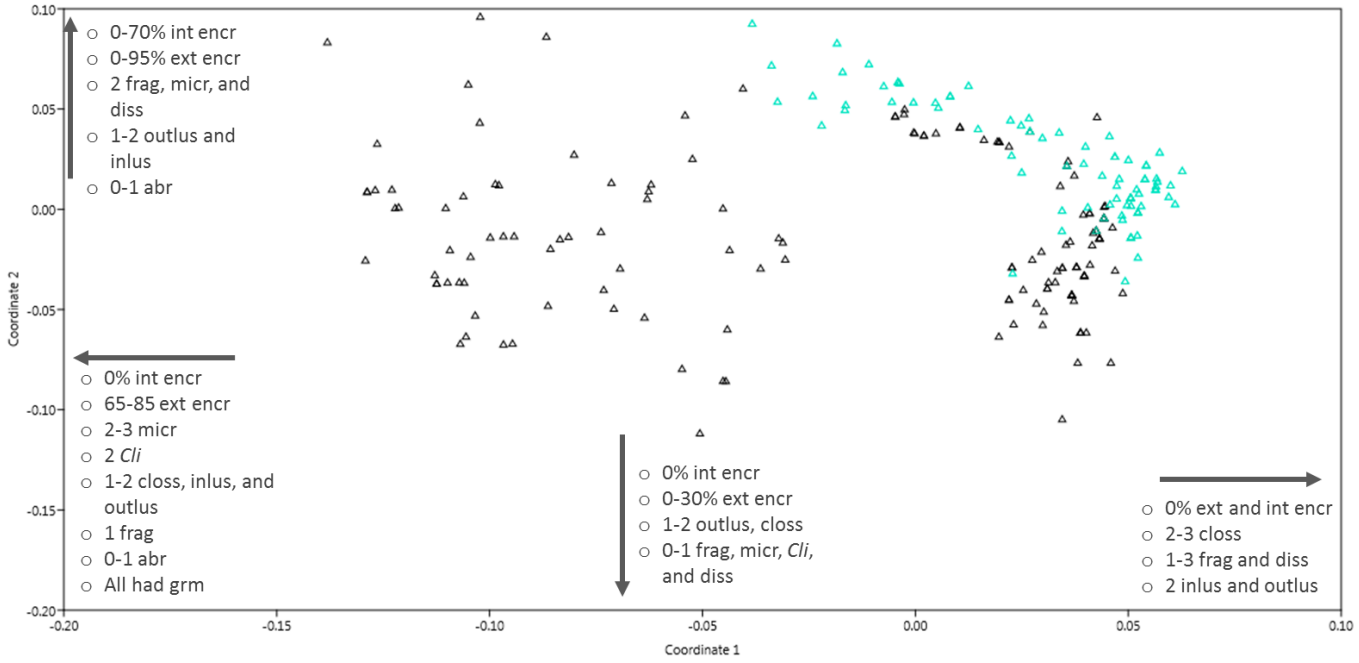

Figure 28: NMMDS graph for the combined mollusk analysis of all surface and lower core data for SC08. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

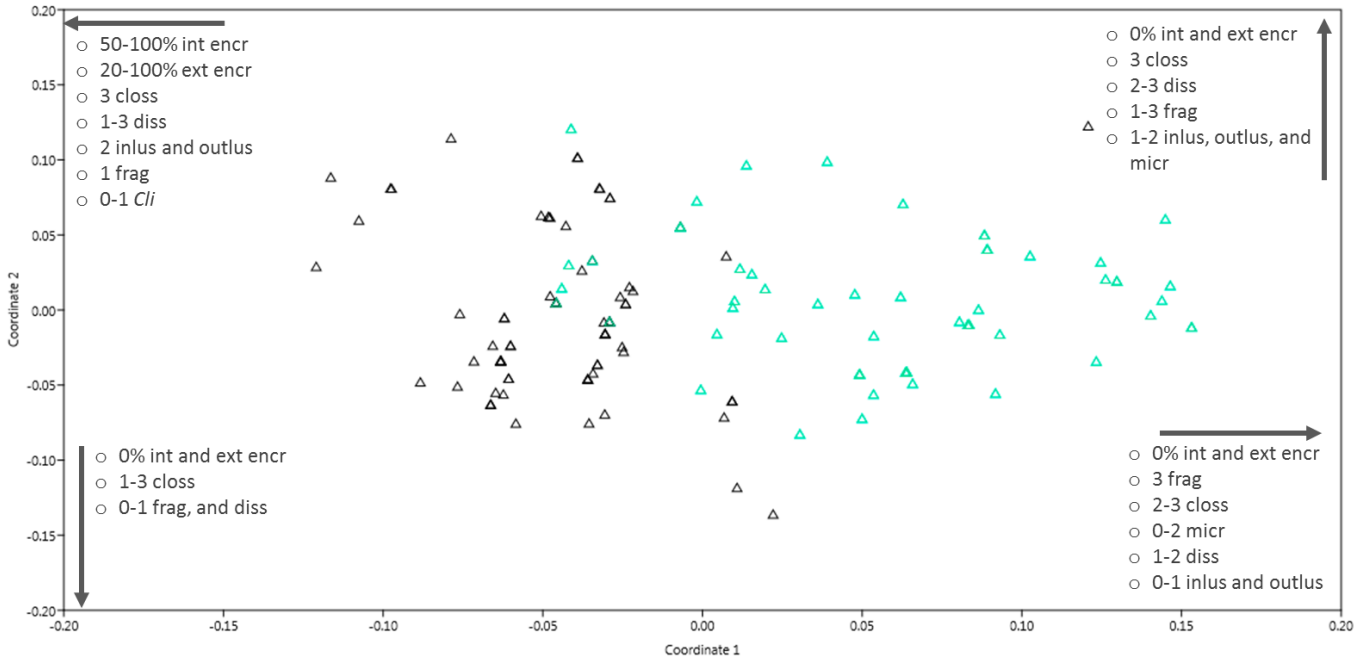

Figure 29: NMMDS graph for the bivalve analysis of all surface and lower core data for SC08. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

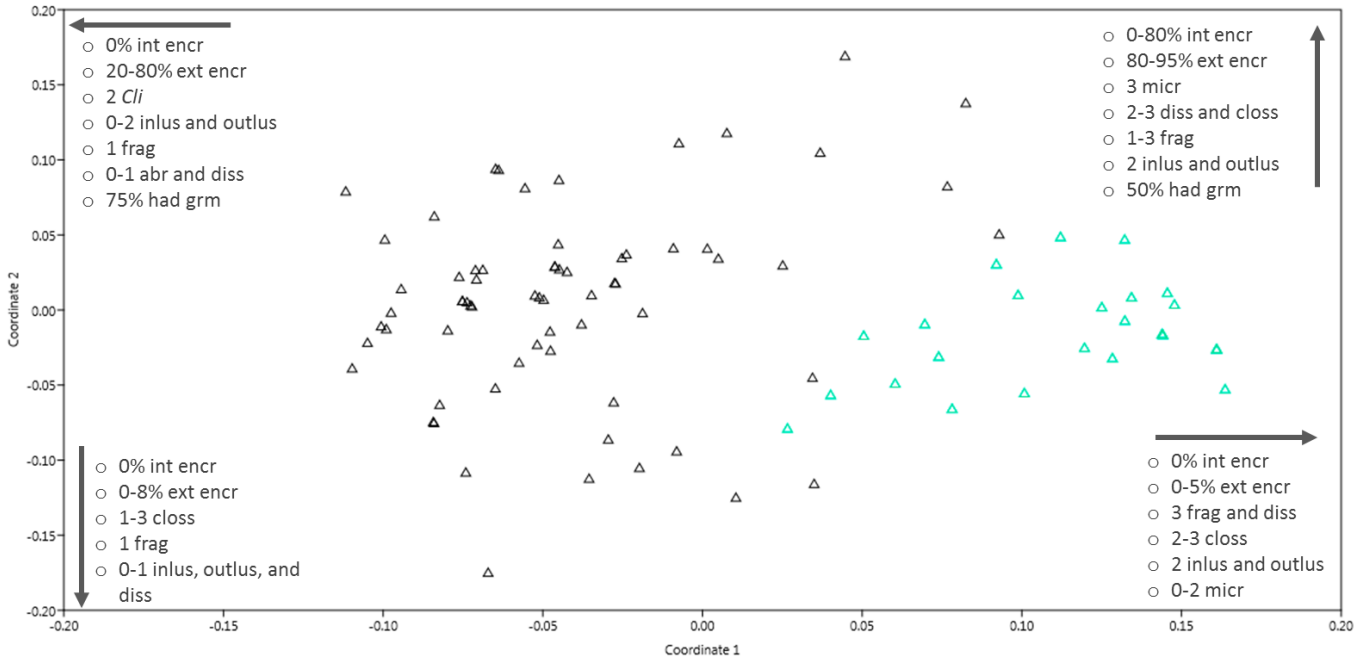

Figure 30: NMMDS graph for the gastropod analysis of all surface and lower core data for SC08. Black indicates specimens from surface beds, and blue indicates those from lag beds. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

In summary, the surface beds resembled each other regardless of present surface habitat (variation in seagrass cover density), and subsurface beds and lags resembled each other as well. Surface beds skewed towards larger shell sizes and epifaunal species, while subsurface beds were primarily dominated by smaller shell sizes and infaunal species, primarily, infaunal small clams. Generic diversity varied between surface beds but did not correlate with seagrass density, and generic diversity was lower in the lag beds than the surface ones. All lag bivalves were disarticulated, and 15-38% of surface bivalves were articulated. In general, surface mollusks were typically more taphonomically altered than subsurface ones. Color and

luster loss stayed relatively consistent between all specimens, and subsurface specimens had higher or only slightly lower dissolution and fragmentation values than surface specimens.

DISCUSSION

There were several significant differences between the modern death assemblage and the lag bed mollusks that could survive to fossilize. All core sites' beds skewed towards the 6-10mm size class, but the lower beds had a much heavier skew compared to their surface counterparts. Fig. 13-15 show this pattern as well as smaller variations between beds. Size is a function of taxon or life guild as well as fragmentation, so these differences could be linked to those aspects, especially since SC04 had a large percentage of small infaunal clams. Life guild analysis does not explain the trends in shell size in other beds however. This could be due to the increased range of sizes for epifaunal snails and infaunal clams as compared to the very common small infaunal clams. NMMDS analysis showed that generally fragmentation increases from surface to subsurface beds. However, the analyses based on bed averages do not show a significant overall increase in fragmentation from surface to subsurface nor a pattern that supports fragmentation as a principle cause for decreasing shell size, so it is likely that genus plays a larger role in these size class differences.

Surface life guilds skewed towards epifaunal snails and to a smaller extent, infaunal clams, while specimens from the lower beds were concentrated into the infaunal small clam life guild, with SC04's having the highest distribution. As in size classes, there were variations in this overall trend. SC08 stood out from the other core sites. All surface beds had a higher proportion of epifaunal snails except for SC08's, which favored infaunal clams slightly more. Its lag bed fell into a similar pattern as SC01/2's. SC04 also had the highest generic diversity and

SC08, the least. SC08 lacked the some of the most common genera in the other cores (*Tellina, Nassarius*, and *Modulus* in the surface; *Nassarius* in the subsurface). SC08 also has the most genera exclusive to its lower bed, but this could just be a function of its overall low diversity and how it was overwhelmingly composed of *Cerithium* and *Codakia*.

Life guild and taxonomic patterns do not appear to be primarily influenced by seagrass density and/or *Callianassa* activity. While SC04 does have the highest generic diversity and seagrass density with no callianassid mounds, SC08 has the lowest diversity and medium seagrass density. One possibility for the primary factor driving molluscan diversity could be distance from shore since SC08 was much closer to shore than the other two and had much lower diversity. Generic diversity decreases from surface to subsurface for all core sites, and this analysis suggests that this is due to taphonomic filtering, likely exacerbated by callianassid activity. The nine small infaunal clam genera that are only present in the lower beds could suggest environmental change as an explanation for the surface/subsurface bed difference. However, with the exception of *Tellina* in SC08, there are so few of these specimens in the raw count that these could just be rare genera, and SC08 already stands apart from the other cores in terms of generic diversity. Additionally, several genera only found in one core site's lower bed are present in another site's surface bed. In all three cores combined, there are only four genera exclusive to subsurface beds and they have raw counts of six (*Diplodonata*), four (*Laevicardium*), one (*Haminoea*), and four (*Lucina*). Therefore, it is unlikely that these subsurface exclusive genera are a result of a previous environment and more likely simply a result of being rare genera and/or this study's limits based on samples from single cores at each location.

Taphonomic analyses show that infaunal shells generally experience less alteration than epifaunal shells for the categories of rhizome etchings, dissolution, inner luster loss, and color loss. Surface infaunal and epifaunal shells had close to the same amount of fragmentation and dissolution (except in the case of SC08's lag bed) as their corresponding subsurface specimens but had higher averages for all other taphonomic indices. Lower luster and color loss values are expected since infaunal organisms are less exposed to sunlight and other factors that fade color and dull luster due to their life habit. They would also be more likely to be exposed to rhizomes below the surface, and the environment is more acidic in the subsurface due to both seagrass and callianassid burrowing. *Callianassa* activity can increase dissolution rates by increasing fluid flow, impeding alkalinity, and promoting carbonic acid production via aerobic respiration and sulfide oxidation (Walker and Goldstein, 1999). The aerobic and anaerobic bacterial respiration associated with seagrass roots and lower carbonate saturation also facilitate dissolution just underneath seagrass beds (Darroch, 2016; Feser and Miller, 2014). Taphonomic alteration (excluding dissolution) in gastropods could be higher not only because of the majority of them being epifaunal and therefore less likely to enter subsurface beds and become sheltered, but also from their larger surface area as compared to bivalves (Walker and Goldstein, 1999). Fig. 31 visualizes these areas in an environment with both seagrass and calllianassid activity.

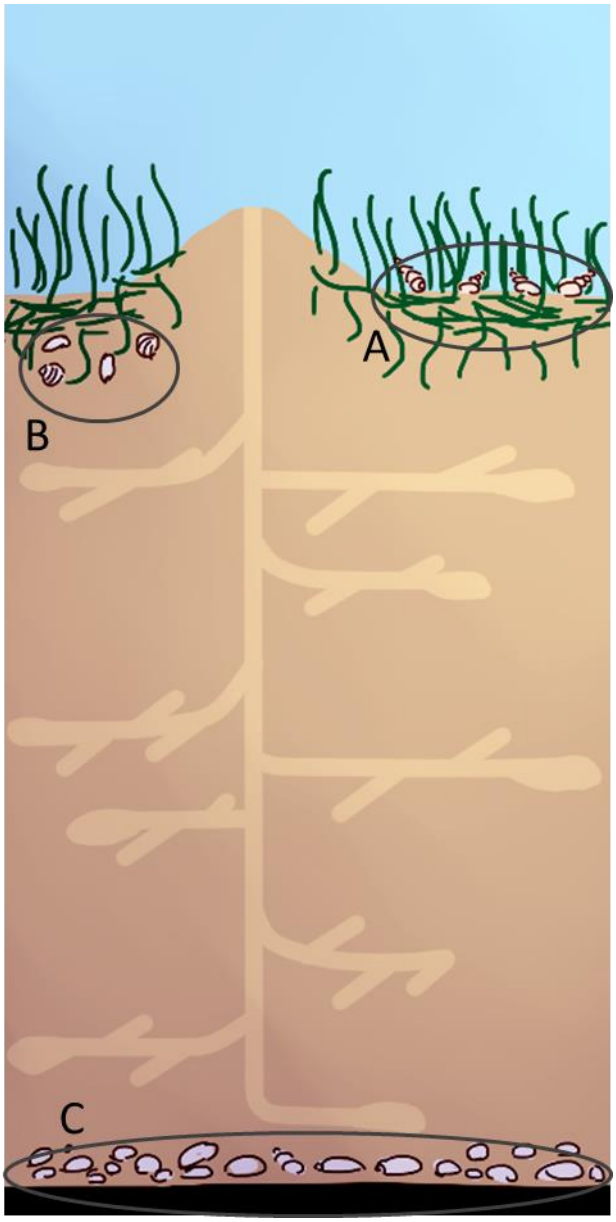

Figure 31: A cross-section of the seafloor extending from the surface to the Pleistocene subsurface (shown in dark brown) not to scale. Seagrass, their rhizome mats, a callianassid waste mound and burrow, and sediment package are shown. Group A shows epifaunal shells on the surface, group B shows infaunal shells below the rhizome mat, and C shows shells in the deep subsurface right above Pleistocene material.

Additionally, the surface specimens are more altered than subsurface ones for the categories of *Cliona* borings, microboring, and encrustation. The NMMDS analyses for bivalves (the vast majority of which were infaunal) support these two differences but suggests that

subsurface bivalves also rank higher or only slightly lower in the categories of dissolution and fragmentation. Comparisons of bivalve and gastropod NMMDS plots also showed subsurface bivalves (the majority of which were infaunal) to be less altered than the (mostly epifaunal) gastropods of the same bed. NMMDS comparisons of all surface beds, all subsurface beds, and just lag beds show at all surface beds and all subsurface beds have much more overlap with each other than between surface and subsurface beds of the same core for both bivalves and gastropods. Infaunal shells had averages that were relatively consistent with each other's overall, with some significant variations. This and the fact that composition of the subsurface was mostly infaunal implies that subsurface specimens are sheltered from most taphonomic forces and that these have a higher likelihood of being pulled down into the deep subsurface beds.

SC01/2's and SC08's surface had low fragmentation averages and SC08's lag had high fragmentation averages. SC01/2's low fragmentation was also shown in NMMDS, but fragmentation was not shown as important for SC08. Wave action is likely not a significant factor due to the infaunal nature of these specimens. For SC08, the low fragmentation average could be due to the fact that most surface specimens had thicker shells (mostly *Codakia*), while its subsurface specimens had thinner shells and were also larger and therefore, easier to break (*Tellina*). Although SC04's middle bed was overwhelmingly composed of small infaunal clams, their small size might make them harder to break during transportation to the lag than larger ones. The cause of low fragmentation in SC01/2's infaunal shells could be similar to SC08's in that it is mostly composed of thicker shelled mollusks.

The subsurface bed's zero or near zero averages for *Cliona* borings and exterior encrustation could be due to the high likelihood that they were never exposed at the surface to be made susceptible to these kinds of bioerosion. However, microboring averages are not split into this particular pattern, with SC01/2's subsurface and SC08's surface shells having low averages. This could be due to microboring processes not being constrained by shallow burial. The distribution of seagrass densities, core proximities to shore, and microboring averages do not suggest that they are linked.

SC01/2's lag has high mean dissolution and this is puzzling. Since both seagrass and callianassid activity contribute to more acidic conditions, SC04 or SC08 should have higher dissolution averages. SC01/2's lag bed had the most infaunal clams and least small infaunal clams of the subsurface beds, so it could be possible that the former are less susceptible to dissolution. Additionally, mean analysis shows infaunal subsurface bed specimens to have higher values for inner luster loss and the presence of drill holes. This is puzzling but can be explained through a possible exposure of infaunal specimens to the surface. These infaunal organisms could have been exposed, acquired drill holes and/or died, disarticulated, and then lost interior luster before reburial. This could have been caused by the wave action of a storm event or a series of storm events.

Average analyses show that epifaunal organisms had more variation in their degree of alteration but overall, were more altered at the surface than the subsurface except in the categories of fragmentation dissolution, luster loss, and color loss. The increased variation could be due to differences in environmental conditions having more effect at the surface than the subsurface, especially with regards to wave action and bioeroders. The higher

fragmentation in the subsurface is likely not due to shell thickness, as the dominant epifaunal subsurface fauna were not thin shelled like the infaunal shells were. The higher fragmentation in the subsurface could be due to breakage resulting from transportation to the lag beds. Higher luster and color loss for surface specimens is expected due to their increased exposure to taphonomic forces and sunlight, respectively. NMMDS plots support these results, but showed SC01/2's surface gastropods to be less altered than the other surface beds, only having higher encrustation, fragmentation, luster loss, and dissolution. This is unexpected and is not supported by mean analysis.

SC04's epifaunal middle bed shells had a low fragmentation average, and SC08's epifaunal lag bed shells had a high one. Wave action would be more significant in epifaunal organisms' fragmentation due to their life on the seafloor surface. SC04's middle having low fragmentation could be due to its high seagrass density lowering flow around the area and its distance from shore reducing wave action, reducing the shells' chance of breakage while they were close to the surface. The lack of waste mounds shows that callianassid activity was lower in this area and could also lower the chance of breakage during downward transport. SC08's higher fragmentation in the lag could be due to the inverse of these conditions (being close to shore, having less dense seagrass beds, and more callianassid activity). However, for both of these to be plausible, *Callianassa* would have to quickly shuttle shell fragments to the subsurface otherwise the surface bed would have a higher fragmentation average.

SC01/2's lag had low microboring, all subsurface beds had low *Cliona* boring means, and SC08's surface bed had high *Cliona* boring averages. Additionally, all subsurface beds had low exterior encrustation, and SC08's surface bed had high encrustation. The low to 0 *Cliona* boring

and exterior encrustation averages in the subsurface beds are consistent with the infaunal averages' pattern, so it is likely that these are controlled by exposure at the surface. SC08's high *Cliona* and exterior encrustation averages could be linked to shoreline proximity. Considering the values and patterns of the other beds, the low microboring average of SC01/2's lag bed is unlikely due to shoreline proximity, core length, or seagrass density.

All lag beds had high dissolution, and SC04's middle bed had low dissolution. As discussed before, this is most likely due to the subsurface environment being more acidic than the surface one. The low dissolution value of SC04's middle bed is puzzling and could be due to the previously stated possibility of infaunal small clam shells being less susceptible to dissolution. NMMDS does not consistently depict high dissolution in the subsurface as a significant differentiating factor in the beds (Fig. 25-27).

Despite the abundance of these variations, which are likely due to the unavoidable variation in core sites, they do not obscure overall, dominant patterns between these sites: infaunal shells experience less alteration than epifaunal ones, and the subsurface beds are dominated by small, infaunal shells with less taphonomic alteration than their mostly large, epifaunal surface counterparts. Dissolution is generally higher in subsurface specimens, and as discussed earlier, the higher dissolution values in subsurface shells could be due to the acid promoting effects of both callianassid bioturbation and seagrass below the surface.

Due to their life habit, infaunal specimens are more likely to experience less taphonomic alteration and more likely be buried and preserved (Kosnick et al., 2009). The results showed that the lag was dominated by these kinds of specimens and therefore, the results support a hypothesis for callianassid sorting rather than environmental change. Furthermore, Ferguson

and Miller's (2007) study has already shown that there is a strong taphonomic bias between the life and death assemblages in the upper 40 cm of the seafloor in Smuggler's Cove. They found that there was a much higher abundance of epifaunal gastropods than infaunal bivalves in the life assemblage, and this was not reflected in the death assemblage that formed from it.

The dominance of infaunal guilds and the small distribution of epifaunal guilds in the subsurface suggests that it is much more difficult for the shrimp to bring down surface shells. Since, the bulk of *Calliannassa* burrows typically start at 5 cm and can extend up to 3m below the sediment water interface with only burrow entrances and sediment exit tunnels reaching the surface, it is reasonable to assume that it would be easier for infaunal organisms to be pulled down by callianassids and would therefore have higher representation in the lower beds (Tudhope and Scoffin, 1984). Figures from Stanley (1970) suggest that some tellins can burrow 3-5cm deep, but any amount of burrowing would make it easier for shells to be shuttled down than if they sat on the surface. Tague reef surrounding Smuggler's cove lowers the amount of wave action in the bay, and could protect the seafloor from significant disruption from minor storms (Parsons Hubbard, 2007; Parsons Hubbard et al., 2014).

The decrease in most taphonomic alteration and increase in dissolution in the lower beds supports the idea of a strong callianassid induced taphonomic filter as well. Because the surface beds resembled each other more than their corresponding subsurface beds in regard to genus, life guild, size, and taphonomy, it would seem as if these results support the environmental change hypothesis more strongly. However, this does not disprove the callianassid sorting hypothesis and can be seen as evidence of the shrimps' strong taphonomic filter. Additionally, several other studies have taken note of the large sediment package and lag

shell bed Callianassids create, so it should be remembered that this study site is not an anomaly in that regard (Meldahl, 1991; Roberts et al., 1981; Shinn, 1968; Tudhope and Scoffin, 1984).

This strong taphonomic filter suggests that the majority of large, epifaunal shells are left on the surface to break down into sediment. A previous study by Parsons Hubbard examining shell taphonomy over the course of 13 years in a similar carbonate environment in the Bahamas supports this (Parsons Hubbard, personal communication, 2018). Shells were placed at 15 and 30 m water depths and were found to be broken, encrusted, bored by *Cliona*, and lost luster and color. From this, it was concluded that the likelihood of shell surviving for more than 20-50 years exposed at the seafloor surface in a well-lit, shallow carbonate setting to be very low (Parsons Hubbard, personal communication, 2018). Additionally, a study by Meldahl et al. (1997) found shell beds in carbonate pocket bays to have half-lives of about 90 years. Smuggler's Cove has been collecting sediment for approximately 7,000 years based on sea level rise calculations from Burke et al. (1989). Lag shell bulk dates from Parsons et al. (2014) were about half that, suggesting they represent an average accumulation over 7,000 years. Therefore, a ~100 year "life span" of a dead shell points to a complete recycling of surface shells and erasure of much of the life assemblage from the fossil record.

Additionally, the results show that variations in seagrass density do not produce distinct taphonomic signatures, and the lag does not resemble a low seagrass density environment in the slightest. There is likely a "with seagrass" signature in the surface beds, but this should be further analyzed in relation to a seagrass-free bed. If there were environmental change, the lag is not the result of a previous seagrass environment of any density; although, a change from seagrass-free to seagrass could still be possible. There could be a stronger distinction between

dense and seagrass free areas as Ferguson and Miller (2007) found that lucinid bivalves and grazing gastropods are more common in dense seagrass areas while other bivalves and predatory gastropods are more common in heavily bioturbated areas (i.e. likely seagrass free). Additionally, callianassid activity creates ideal conditions for fast burrowing tellins and leads to their dominance in bivalve assemblages and strongly discourages the presence of infaunal echinoids (Tudhope and Scoffin, 1984). A future study could more closely examine the size, faunal, and taphonomic differences between seagrass-free and seagrass sites.

Smuggler's Cove has, no doubt, experienced recent environmental changes, so that hypothesis is not completely out of the question, especially due the fact that this study did not include a completely seagrass free site. Images from Google Earth and Ferguson and Miller (2007) show that seagrass cover in Smuggler's Cove has increased over the past 50 years. Additionally, Feser and Miller (2014) found evidence of rapid taxonomic changes (seasonal to decadal in scale) in the surface life and death assemblages. However, they posit that these temporal dynamics affecting taxonomic composition may not be primarily influenced by the substrate and seagrass. Feser and Miller (2014) suggest that nutrient-input fluctuations could be driving mollusk population fluctuations, and that the surface death assemblage is able to track the lagoon's sub-decadal ecological changes.

Studies have found that iron is a limiting factor in seagrass growth and that increases in iron via terrestrial sedimentation could increase the growth of seagrass nearby (Duarte et al., 2005; Fourqurean et al., 2008). Ferguson and Miller's (2007) transect analysis also suggested that the nearshore zone of dense *Thalassia* was spatially stable while the offshore zone of mixed seagrass and *Callianassa* burrows was more varied, spatially and/or temporally, so

sediment influx from the island could be linked to this. Additionally, Feser and Miller (2007) noted that since 1980, the eastern end of the island has experienced increased residential development, and this could increase the frequency and content of runoff from this region to Smuggler's Cove. These changes were measured in surface shells, and the results of this study show that these changes may be on a time scale too small to be recorded and shown in the lag beds.

If environmental change were the cause of the stark differences between the surface and lag beds, it would likely be in the form of significant changes in discharge and sedimentation rates influencing mollusk communities, and this could be anthropogenically driven. Marine molluscan communities are affected by river discharge rates, as low flow rates allow sediment to stabilize, creating favorable conditions for infaunal suspension feeding bivalves (Allller and Stupakoff, 1996). Archeology research has shown that Indigenous people (most likely the Taino or Carib people) drastically changed the environments of the US Virgin islands through agriculture after their migration and settlement around 4500-2500 BCE (Ramos et al., 2013). Ceramics research suggests that St. Croix was first inhabited by Saladoid peoples who used swidden and casual cultivation to cultivate food. Other research suggests that later groups inhabiting the island also used swidden agriculture and relied on marine life for protein (Keegan, 1992; Ramos et al., 2013). There was also a rapid shift from inland to coastal settlements, possibly resulting from a depletion of land resources, a shift to drier conditions, and/or population growth and expansion.

In addition to this, after the arrival of Columbus, white settlers burned and deforested nearly all of St. Croix in 1651 and continued to do so in the 1730s-1750s, changing the islands

microclimate to a more arid one (Lawaetz, 1991). The drastic decrease in plant cover would have increased runoff as well as altered precipitation patterns around the island. But that said, the results of this study suggest that all of these changes happening in the last 400 years of a 7,000 year record are overwhelmed by the actions of the callianassids who are creating a subsurface pre-fossilized bed that is quite different from what likely existed on the surface. Therefore the view of the past recorded in these deep subsurface beds could be badly skewed.

CONCLUSION

While the environmental change hypothesis is not completely ruled out, the data of this study support the idea that callianassid sorting has far more influence on the disconnect between surface and subsurface beds in terms of guild structure, taxonomy, size, and taphonomy than the hypothesis for environmental change. Furthermore, this taphonomic filter is far stronger than expected for a shelly marine bed and suggests the immense and rapid loss of larger, epifaunal shells at the surface. Evidence of past environments and communities could be greatly distorted through callianassid-caused selective preservation in the pre-fossilized bed.

There are several avenues of ecological change that could be reflected in these beds. Seagrass, sedimentation, and discharge changes are possible causes for taxonomic change. Differences between seagrass free areas and seagrass areas are yet to be examined. Further research into the taphonomic signature of a non-seagrass core in Smuggler's Cove to better understand the role of seagrass vs. the role of *Callianassa* (who avoid heavy seagrass areas) as well as the island's environmental history must be done to confidently and definitively answer the question of why the surface and lag beds are so different. The results of this analysis could more confidently refute or confirm the callianassid sorting hypothesis.

This research shows that there is likely a taphonomic signature for callianassid sorting and other deep tier burrowers. This signature consists of an infaunally dominated subsurface bed with small shell sizes, overall low taphonomic alteration, and medium to high dissolution beneath a thick, coarse grained sediment package fairly devoid of shell. A surface bed of large, epifaunal shell with high taphonomic alteration may be preserved above due to a rapid burial event, but is unlikely to be preserved often. This taphonomic siganture can potentially be used to identify callianassid or other deep burrowing in paleobeds and other lagoons and shallow marine areas. Additionally, this signature could be used with other stratigraphic tools to detect areas that had been shallow at one point in time, as callianassids tend to stay within shallow water to the intertidal zone and thin out at depths of over 10.6m (Shinn, 1968). More importantly, it should be noted that these fossil or subfossil beds show a strong taphonomic bias and are not remotely reflective of their corresponding life assemblage.

Future studies could also examine other callianassid and seagrass dominated lagoons to further test if these taphonomic signatures are specific to St. Croix's environment or whether they are simply the product of callianassid burrowing. Additionally, research could further explore and investigate the variations between beds, particularly the effects of proximity to shore and conditions favored by bioeroders.

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APPENDIX 1. FULL GENERA COUNT

Table 16: Genera count and percentages for SC01/2's surface and lag beds. The corrected proportions values were used to calculate the percentages.

	SC01/2 Surface			SC01/2 Lag		
	Raw Count	**Corrected Proportions**	**Percentage of Total**	**Raw Count**	**Corrected Proportions**	**Percentage of Total**
Acmaea						
Americardia	1	2	0.63%			
Astrea	1	4	12.5%			
Bulla	1	2	0.63%	3	12	6.00%
Calotrophon						
Cerithium	46	126	39.5%			
Chama						
Chione						
Codakia	21	60	18.8%			
Columnella						
Conus						
Crassipiea						
Crepidula	1	1	0.31%			
Cymatium						
Diplodonta				5	20	10.0%
Haminoea						
Heterodonax	4	7	2.19%			
Hyalina	2	3	0.94%			
Laevicardium				1	4	2.00%
Littorina	4	8	2.51%			
Lucina						
Macrocallista						
Modiolus						
Modulus	10	25	7.84%			
Nassarius	8	17	5.33%	3	12	6.00%
Nitidella	4	5	1.57%			
Pinna						
Pitar				1	4	2.00%
Pyramidella	2	6	1.88%			
Smaragdia	1	2	0.63%			
Strombus						
Tegula						
Tellina	18	43	13.5%	16	64	32.0%
Tricolia	2	8	2.51%			
Turbo						

Table 17: Genera count and percentages for SC04's surface and middle beds. The corrected proportions values were used to calculate the percentages.

	SC04 Surface			**SC04 Middle**		
	Raw Count	**Corrected Proportions**	**Percentage of Total**	**Raw Count**	**Corrected Proportions**	**Percentage of Total**
Acmaea	10	10	2.57%			
Americardia				3	6	2.86%
Astrea	1	2	0.514%			
Bulla	1	4	1.03%	2	4	1.90%
Calotrophon	1	1	0.257%			
Cerithium	27	60	15.4%			
Chama	2	2	0.514%			
Chione	2	6	1.54%	8	16	7.62%
Codakia	24	96	24.7%			
Columnella	3	9	2.31%			
Conus	2	8	2.06%			
Crassipiea	1	2	0.514%			
Crepidula	5	16	4.11%			
Cymatium	1	1	0.257%			
Diplodonta				1	2	0.952%
Haminoea				1	2	0.952%
Heterodonax						
Hyalina						
Laevicardium						
Littorina	5	10	2.57%			
Lucina				2	4	1.90%
Macrocallista	1	4	1.03%			
Modiolus	1	1	0.257%			
Modulus	19	40	10.3%			
Nassarius	11	33	8.48%	4	8	3.81%
Nitidella						
Pinna	5	5	1.29%			
Pitar	1	1	0.257%	1	2	0.952%
Pyramidella	1	1	0.257%			
Smaragdia						
Strombus	1	2	0.514%			
Tegula	6	20	5.14%			
Tellina	9	29	7.46%	41	162	77.1%
Tricolia	7	16	4.11%			
Turbo	3	10	2.57%			

Table 18: Genera count and percentages for SC08's surface and lag beds. The corrected proportions values were used to calculate the percentages.

	SC08 Surface			**SC08 Lag**		
	Raw Count	**Corrected Proportions**	**Percentage of Total**	**Raw Count**	**Corrected Proportions**	**Percentage of Total**
Acmaea						
Americardia	1	4	7.98%	3	12	5.00%
Astrea	3	12	2.40%			
Bulla				2	8	3.33%
Calotrophon						
Cerithium	61	184	36.7%	7	28	11.7%
Chama						
Chione	14	57	11.4%	5	20	8.33%
Codakia	69	232	46.3%			
Columnella						
Conus						
Crassipiea						
Crepidula						
Cymatium						
Diplodonta						
Haminoea						
Heterodonax						
Hyalina	1	4	7.98%			
Laevicardium				3	12	5.00%
Littorina				2	8	3.33%
Lucina				2	8	3.33%
Macrocallista						
Modiolus						
Modulus						
Nassarius				1	4	1.67%
Nitidella						
Pinna						
Pitar				8	32	13.3%
Pyramidella	2	8	1.60%			
Smaragdia						
Strombus						
Tegula						
Tellina				27	108	45.0%
Tricolia						
Turbo						

APPENDIX 2. MEAN TAPHONOMIC CONFIDECE LIMITS

Table 19: 95% confidence limits for infaunal taphonomic averages analysis.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Out lus	Closs
SC01/2 surface	0.002 - 0.012	0.001 - 0.006	0.949 - 1.051	0.000 - 0.000	0.012 - 0.098	0.230 - 0.504	0.017 - 0.166	0.259 - 0.438	0.000 - 0.000	0.959 - 1.298	0.473 - 0.719	0.912 - 1.234	2.681 - 2.842
SC01/2 lag	0.000 - 0.000	0.001 - 0.004	1.168 - 1.321	0.161 - 0.283	0.001 - 0.044	0.154 - 0.291	0.000 - 0.000	0.047 - 0.131	0.014 - 0.075	1.384 - 1.594	1.014 - 1.594	0.808 - 1.058	2.621 - 2.757
SC04 surface	0.027 - 0.087	0.072 - 0.153	1.073 - 1.348	-0.001 - 0.042	-0.008 - 0.026	1.316 - 1.579	0.011 - 0.094	0.055 - 0.173	0.000 - 0.000	1.120 - 1.371	1.078 - 1.343	1.428 - 1.700	2.860 - 2.964
SC04 middle	0.000 - 0.000	0.000 - 0.001	1.010 - 1.215	0.000 - 0.000	0.000 - 0.000	0.405 - 0.567	0.000 - 0.000	0.049 - 0.126	0.001 - 0.038	1.106 - 1.205	0.349 - 0.495	0.218 - 0.384	2.900 - 2.966
SC08 surface	0.025 - 0.067	0.030 - 0.067	0.665 - 0.783	0.000 - 0.000	-0.003 - 0.018	0.231 - 0.366	0.005 - 0.040	0.425 - 0.545	-0.003 - 0.019	1.212 - 1.341	0.707 - 0.860	1.876 - 1.945	2.710 - 2.827
SC08 lag	0.000 - 0.000	0.000 - 0.000	1.421 - 1.659	0.001 - 0.039	0.001 - 0.039	0.553 - 0.039	0.000 - 0.000	0.293 - 0.427	0.027 - 0.093	1.138 - 1.262	1.019 - 1.141	0.557 - 0.762	2.679 - 2.801

Table 20: 95% confidence limits for epifaunal taphonomic averages analysis.

	Int encr	Ext encr	Frag	Abr	Grm	Micr	*Cli*	Rhiz	Dhol	Diss	Inlus	Out lus	Closs
SC01/2 surface	0.034 - 0.067	0.329 - 0.409	1.221 - 1.362	0.211 - 0.333	0.202 - 0.322	1.392 - 1.560	0.401 - 0.628	0.069 - 0.155	0.102 - 0.199	1.154 - 1.302	0.582 - 0.816	1.373 - 1.520	2.081 - 2.172
SC01/2 lag	0.000 - 0.000	0.001 - 0.019	1.060 - 2.140	0.180 - 0.620	0.000 - 0.000	1.000 - 1.000	0.000 - 0.000	0.000 - 0.000	0.000 - 0.000	1.464 - 2.136	1.620 - 1.980	1.380 - 1.820	2.180 - 2.620
SC04 surface	0.100 - 0.152	0.393 - 0.475	1.235 - 1.427	0.282 - 0.424	0.293 - 0.406	1.178 - 1.352	0.584 - 0.784	0.071 - 0.335	0.025 - 0.078	1.262 - 1.451	0.849 - 1.055	1.492 - 1.611	1.926 - 2.023
SC04 middle	0.000 - 0.000	0.000 - 0.000	0.429 - 1.071	0.000 - 0.000	0.000 - 0.000	1.130 - 1.870	0.000 - 0.000	0.000 - 0.000	0.000 - 0.000	1.000 - 1.000	0.000 - 0.000	1.000 - 1.000	3.000 - 3.000
SC08 surface	0.017 - 0.056	0.579 - 0.651	1.041 - 1.171	0.705 - 0.872	0.670 - 0.791	1.314 - 1.552	1.388 - 1.612	0.026 - 0.089	0.056 - 0.136	1.101 - 1.265	0.477 - 0.657	1.665 - 1.797	1.830 - 1.939
SC08 lag	0.001 - 0.022	0.043 - 0.214	1.729 - 2.271	0.391 - 0.720	0.007 - 0.215	1.218 - 1.671	0.000 - 0.000	0.000 - 0.000	0.000 - 0.000	2.280 - 2.610	1.785 - 1.993	1.640 - 1.916	2.001 - 2.215

APPENDIX 3. ALL CORE DATA NMMDS PLOTS

The range of encrustation percentages, taphonomic values between these four specimens, and the percentage of these four specimens that had positive presence/absence data is also recorded is depicted on the plot along with the region they are located on the graph. Taphonomic categories with ranges of 0 and presence/absence data that was not present in the four specimens is not displayed.

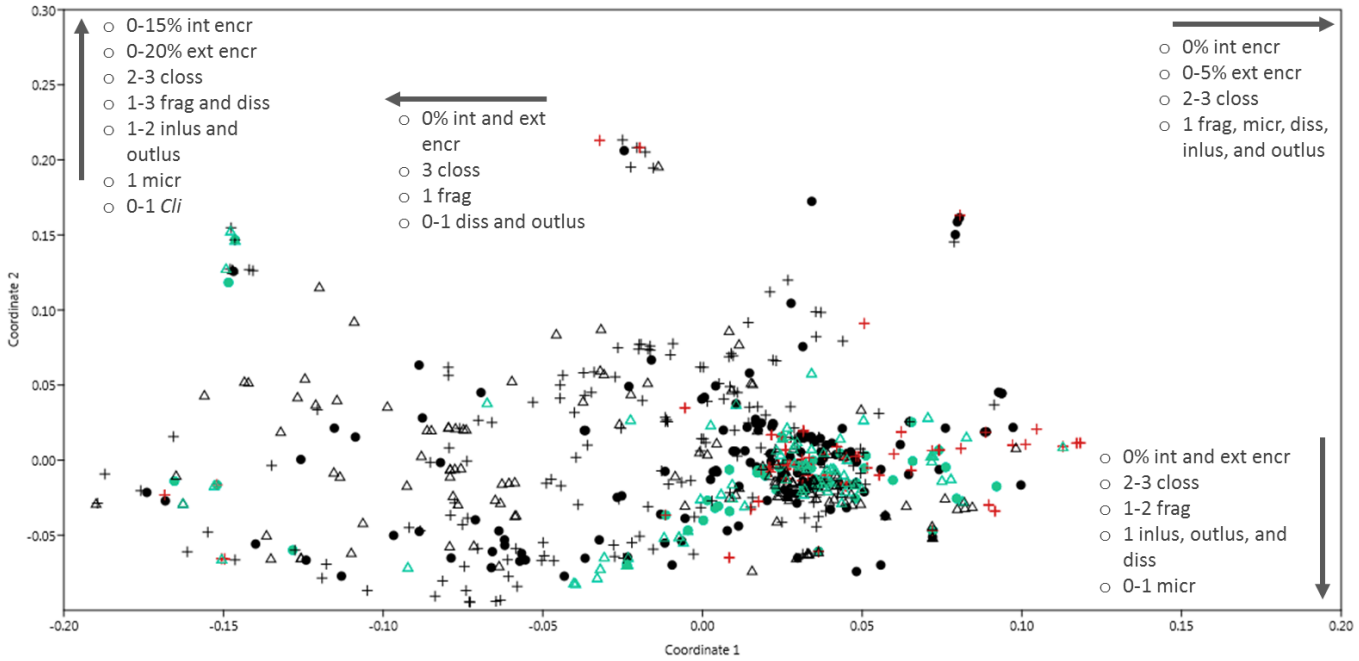

Figure 32: NMMDS graph for the combined mollusk analysis of all core data. Black indicates specimens from surface beds, pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

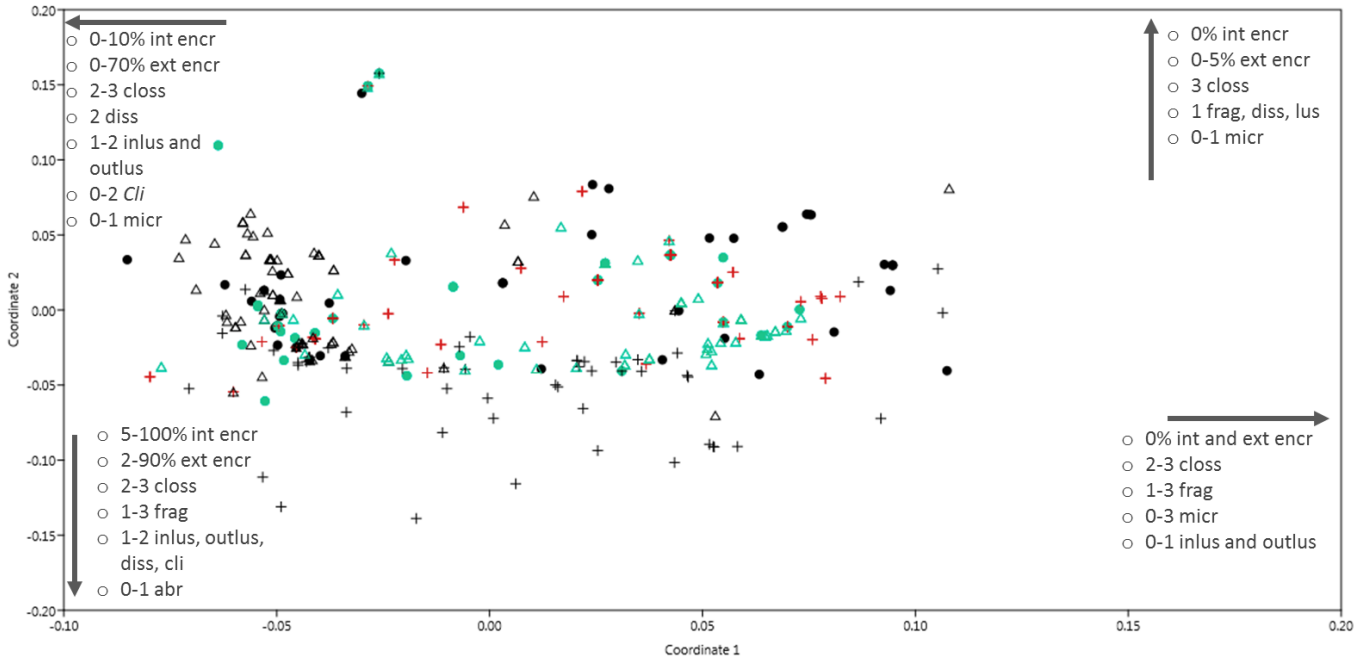

Figure 33: NMMDS graph for the bivalve analysis of all core data. Black indicates specimens from surface beds, pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

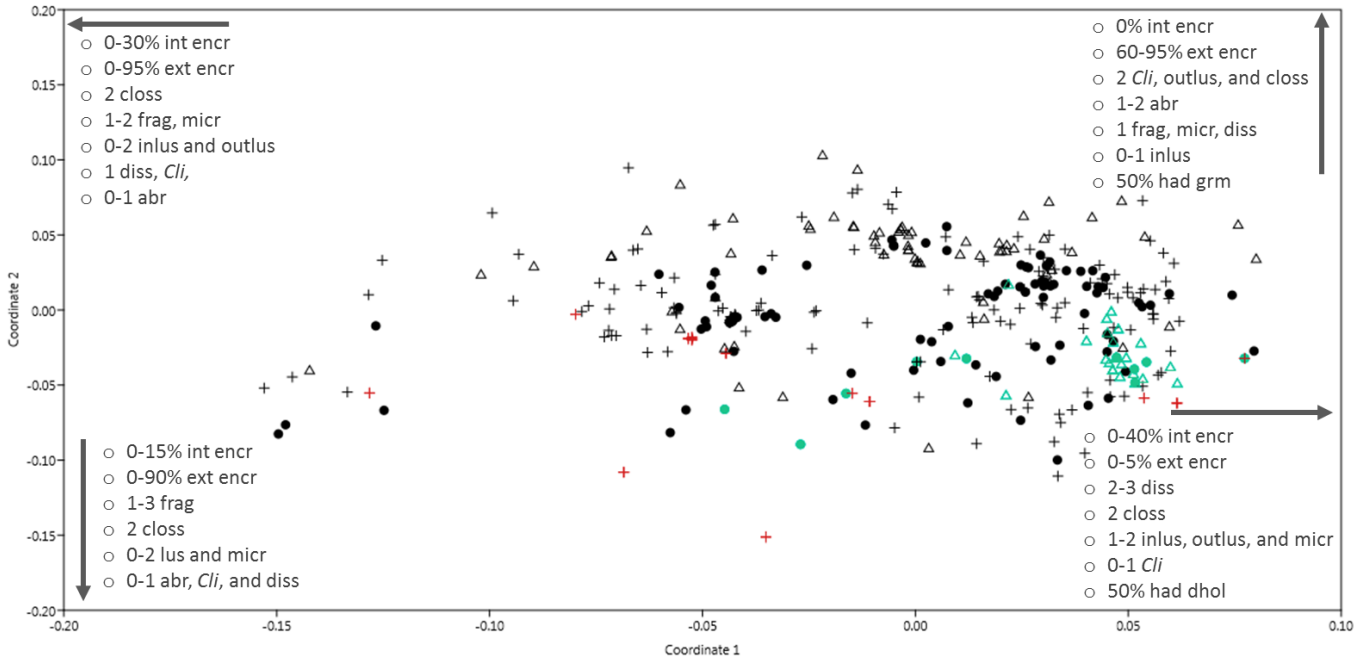

Figure 34: NMMDS graph for the gastropod analysis of all core data. Black indicates specimens from surface beds, pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

APPENDIX 4. SURFACE NMMDS PLOTS

The range of encrustation percentages, taphonomic values between these four specimens, and the percentage of these four specimens that had positive presence/absence data is also recorded is depicted on the plot along with the region they are located on the graph. Taphonomic categories with ranges of 0 and presence/absence data that was not present in the four specimens is not displayed.

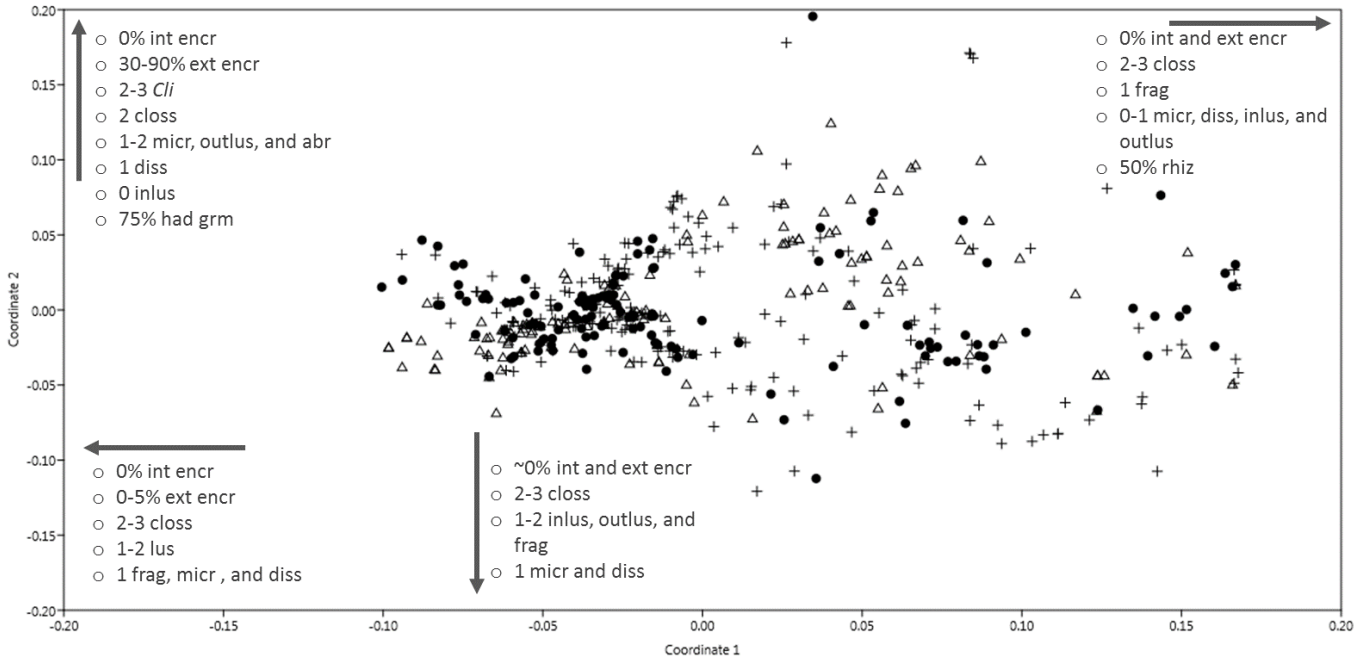

Figure 35: NMMDS graph for the combined mollusk analysis of surface core data. Black indicates specimens from surface beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

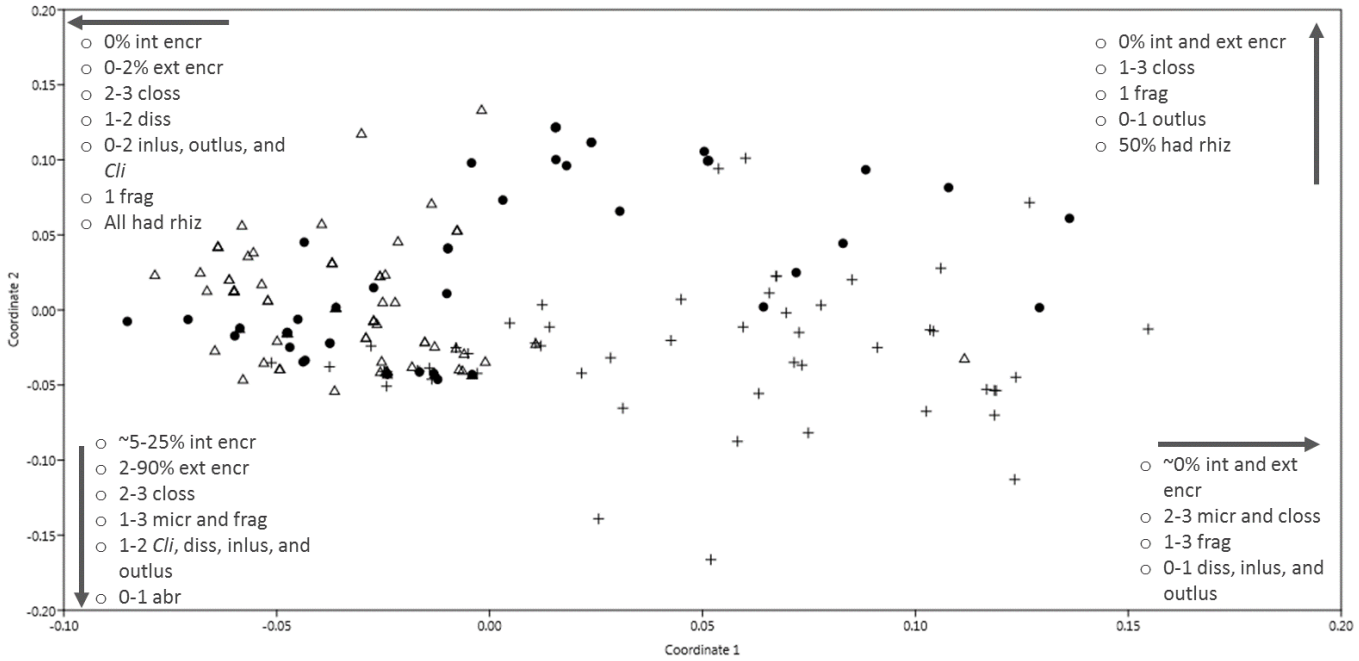

Figure 36: NMMDS graph for the bivalve analysis of surface core data. Black indicates specimens from surface beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

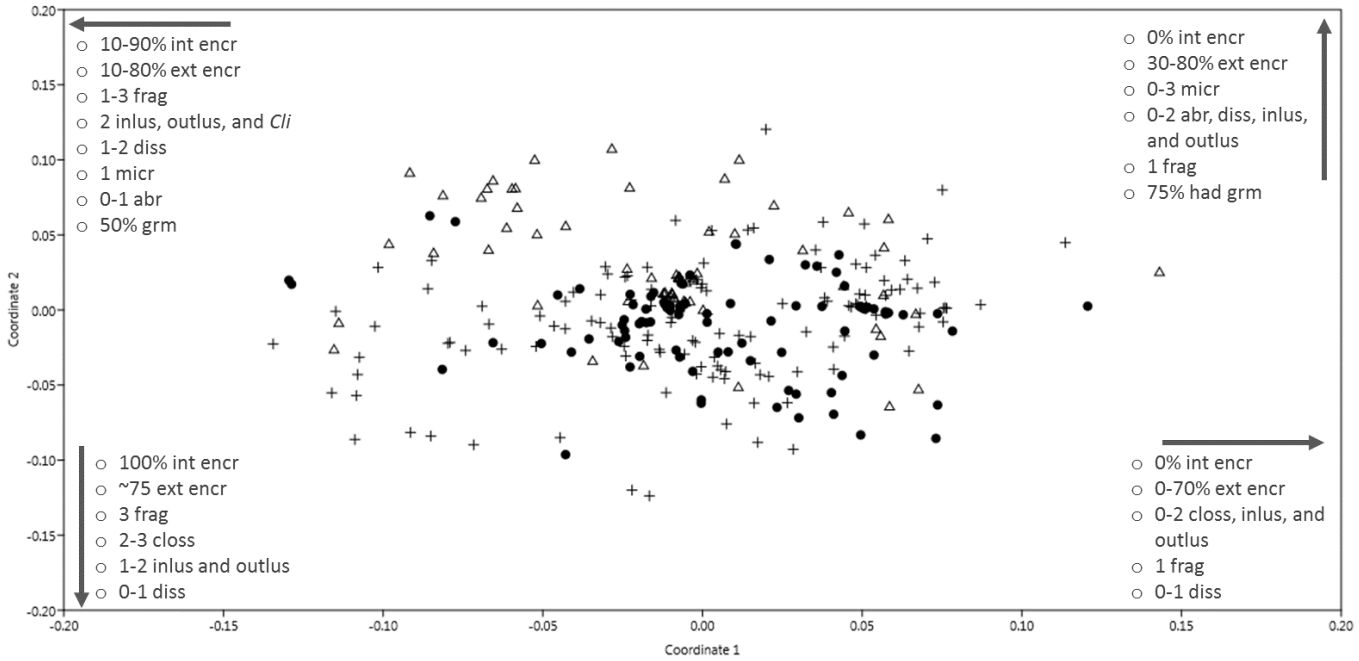

Figure 37: NMMDS graph for the gastropod analysis of surface core data. Black indicates specimens from surface beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

APPENDIX 5. LAG NMMDS PLOTS

The range of encrustation percentages, taphonomic values between these four specimens, and the percentage of these four specimens that had positive presence/absence data is also recorded is depicted on the plot along with the region they are located on the graph. Taphonomic categories with ranges of 0 and presence/absence data that was not present in the four specimens is not displayed.

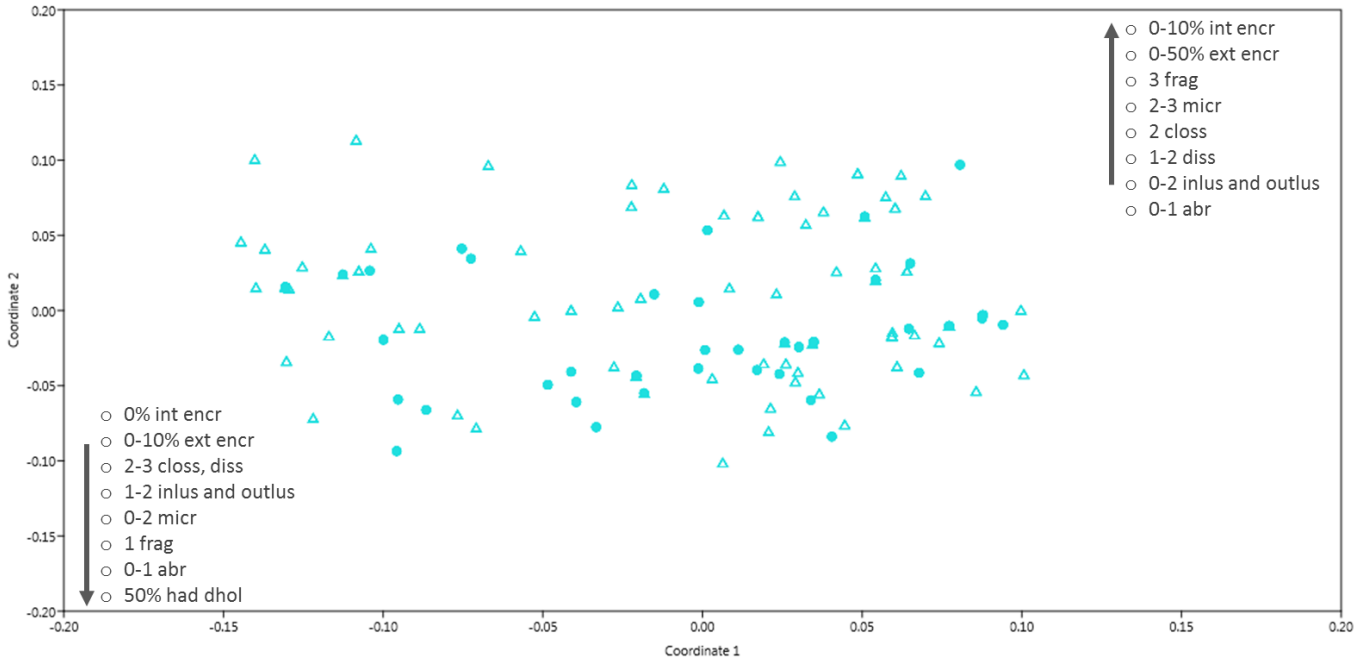

Figure 38: NMMDS graph for the combined mollusk analysis of both lag beds. Blue indicates those from lag beds. Circles indicate those from SC01/2, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

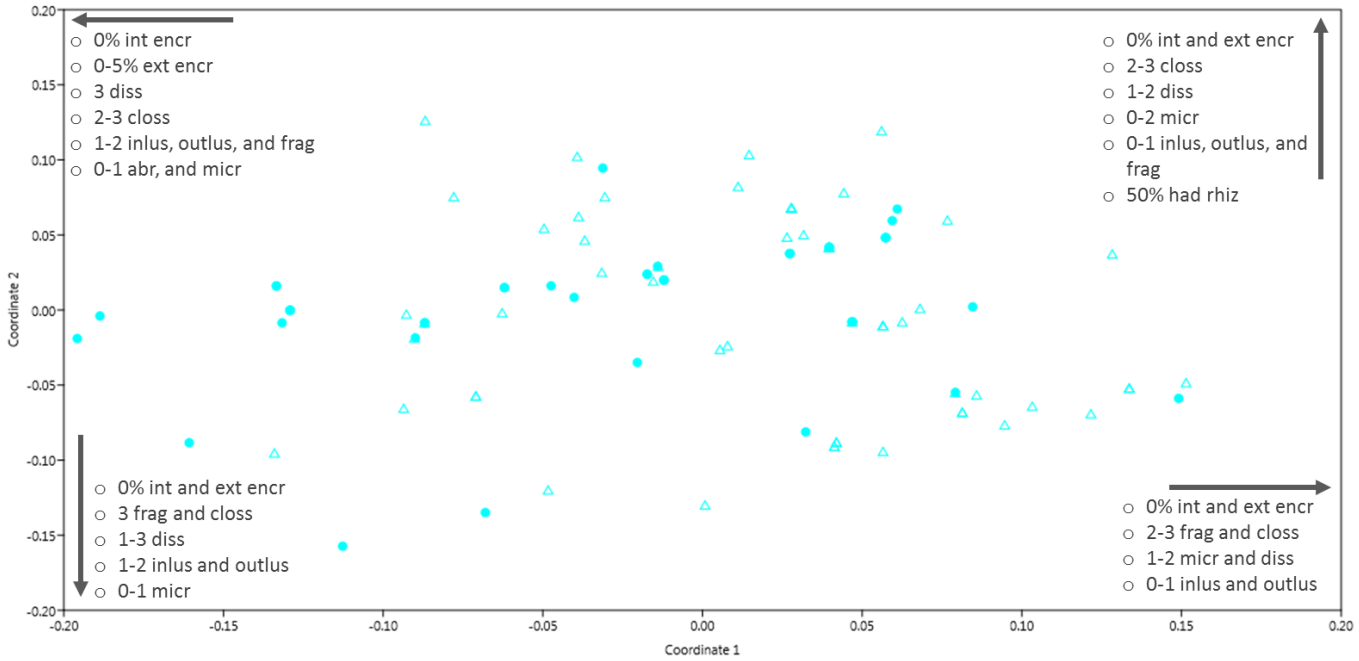

Figure 39: NMMDS graph for the bivalve analysis of both lag beds. Blue indicates those from lag beds. Circles indicate those from SC01/2, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

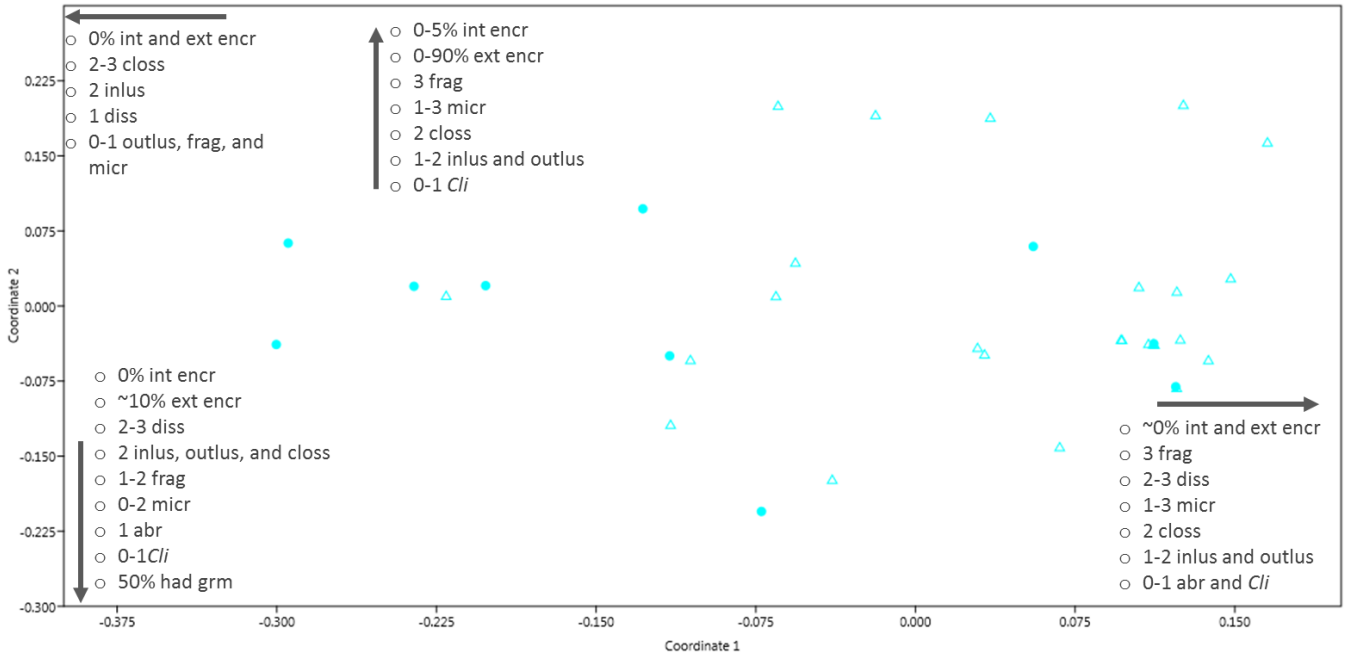

Figure 40: NMMDS graph for the gastropod analysis of both lag beds. Blue indicates those from lag beds. Circles indicate those from SC01/2, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

APPENDIX 6. LAG AND MIDDLE NMMDS PLOTS

The range of encrustation percentages, taphonomic values between these four specimens, and the percentage of these four specimens that had positive presence/absence data is also recorded is depicted on the plot along with the region they are located on the graph. Taphonomic categories with ranges of 0 and presence/absence data that was not present in the four specimens is not displayed.

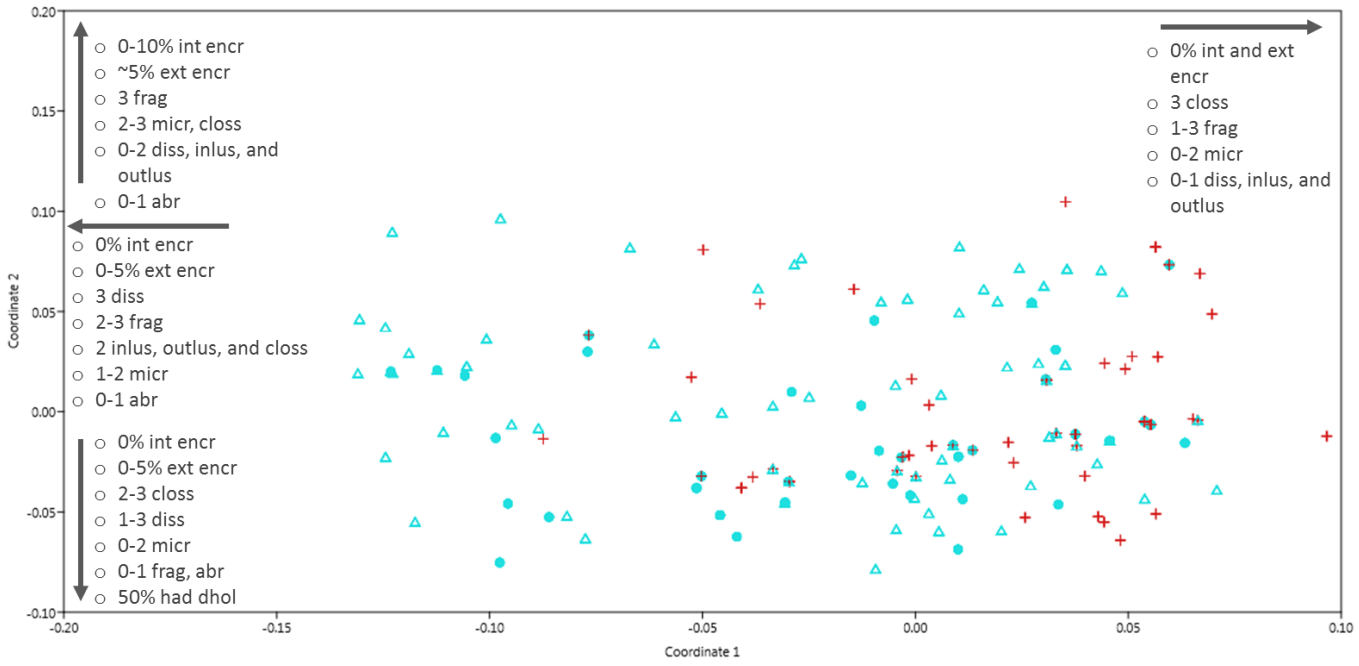

Figure 41: NMMDS graph for the combined mollusk analysis of lag and middle core data. Pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

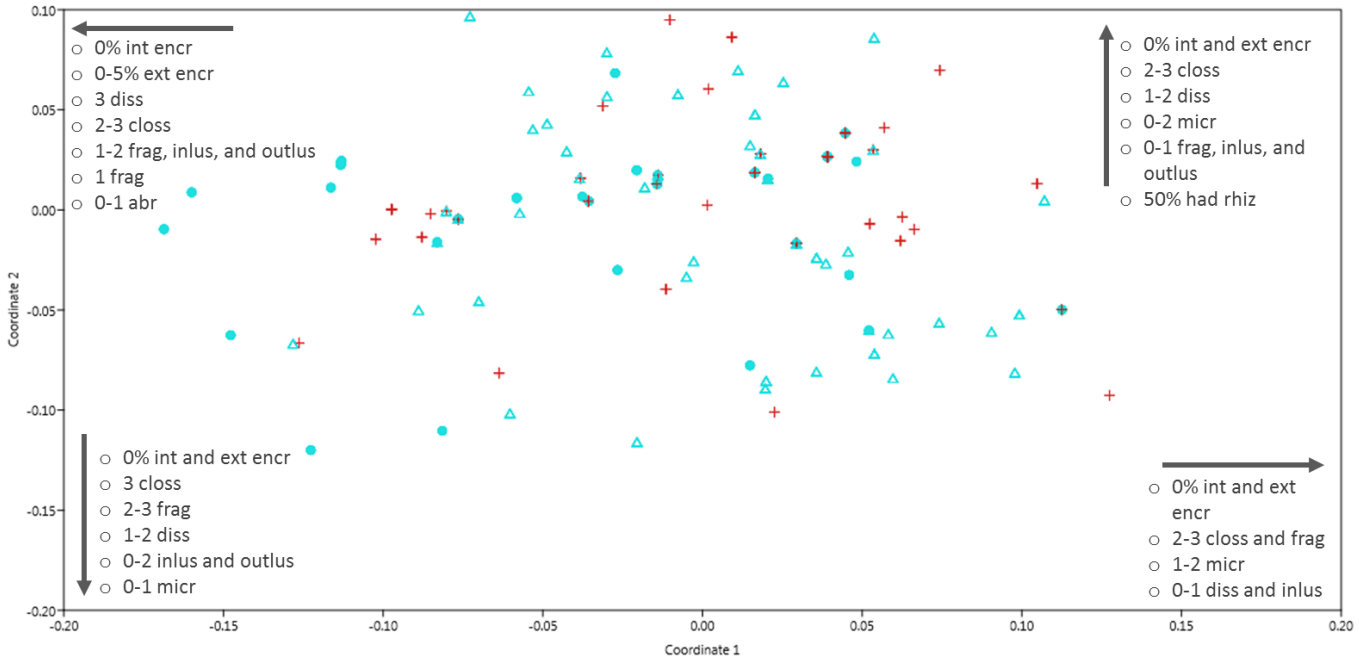

Figure 42: NMMDS graph for the bivalve analysis of lag and middle core data. Pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

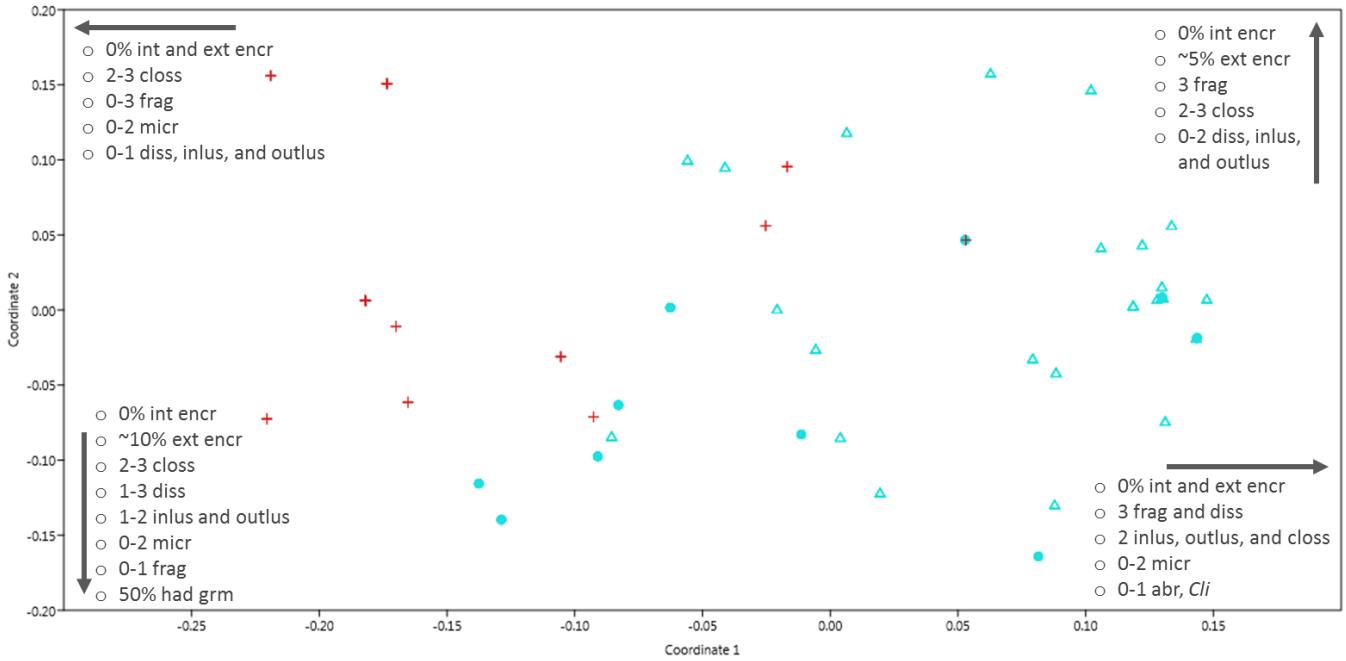

Figure 43: NMMDS graph for the gastropod analysis of lag and middle core data. Pink indicates those from middle beds, and blue indicates those from lag beds. Circles indicate those from SC01/2, plus signs from SC04, and triangle from SC08. These taphonomic characteristics are abbreviated as such, int encr = interior encrustation, ext encr = exterior encrustation, frag = fragmentation, abr = abrasion, grm = graze marks, mcr = microboring, *Cli* = *Cliona* borings, rhiz = rhizome etchings, dhol = drill hole, diss = dissolution, inlus = internal luster, outlus = outer luster, closs = color loss.

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