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The Paleoecology and Taphonomy of Modern and Miocene Sclerobionts: Significance of Involving Undergraduates in STEM Research

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The Paleoecology and Taphonomy of Modern and Miocene Sclerobionts: Significance of Involving Undergraduates in STEM Research

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

Doctor of Philosophy

in

Earth and Planetary Sciences

by

Bridget Teresa Kelly

March 2022

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DEDICATION

I dedicate this work to my mom and dad, who have always fostered and supported my education. To my sister, whose perseverance and hard work have been an inspiration to me. And to husband, Rich, without whose support I could never have accomplished this endeavor.

ABSTRACT OF THE DISSERTATION

The Paleoecology and Taphonomy of Modern and Miocene Sclerobionts:
Significance of Involving Undergraduates in STEM Research

by

Bridget Teresa Kelly

Doctor of Philosophy, Graduate Program in Earth and Planetary Sciences
University of California, Riverside, March 2022
Dr. Mary Droser, Chairperson

Capitalizing on the diverse pool of students and early geoscience exposure in Riverside County, the NSF Geopaths Geoscientist Development (GEODE) Program at UCR is designed to remove barriers, recruit, and retain underrepresented students into the geosciences, the least diverse of the STEM fields. We report the results from the GEODE Internship Program that offered 10-week paid student internships, providing the opportunity for students to be exposed to the geosciences through research experiences. The students agreed that participating in research increased their interest in conducting scientific research in the future, reporting benefits of new research skills,

career preparation, and networking. The studies herein were conducted with the assistance of undergraduate interns, highlighting the potential for rigorous research while strengthening geoscience educational pathways and increase diversity in STEM.

The analysis of sclerobionts is a powerful tool for understanding ecological relationships and their trace fossils provide opportunities to study organisms not well-preserved. We examined sclerobionts on *Hyotissa hyotis* oysters from the Miocene Latrania Formation near Ocotillo, California, an ancient shoreline of the proto-Gulf of California. We analyzed occurrences and abundance of sponges, polychaetes, bivalves, phoronids, and corals. Combining taxonomic diversity with encrusting intensity yielded a more accurate representation of the dynamics of a hard substrate community than diversity alone. An *Entobia* ichnofacies, this assemblage supports a model of sediment starvation in the fan-delta deposits of the Latrania Formation.

We examined sclerobionts on modern *Mercenaria mercenaria* bivalves from Shelter Island, New York, in the Peconic Bay, an estuary with a history of pollution and hypoxia. We analyzed occurrences and abundance of sponges, polychaetes, bryozoans, barnacles, and molluscan attachment scars. Encrustation occurred with similar intensities on both surfaces of the valves and the co-occurrence of both deep- and shallow-tiered borings indicated the shells were exposed predominantly to a low energy environment, with periodic reworking events. For community studies involving encrusters, we found no added benefit from including heavily fragmented shells with complete shells. If complete valves are unavailable, we suggest examining valves >50% complete will yield robust results.

We present the preliminary data on a sclerochronological and isotopic analysis of the Miocene oyster *Hyotissa hyotis*.

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Strengthening Geoscience Educational Pathways for Diverse Students From 2Y to 4Y Institutions in Riverside, California:
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ABSTRACT

In the wake of potential shortages in the geoscience workforce, and as parts of efforts to reduce inequity, a need exists to draw students from historically underrepresented communities into the geosciences, the least diverse of the STEM fields. Riverside county, home to a diverse population, supports several community colleges with thriving geoscience programs where students can take a range of geology courses in preparation for a geology major at 4-year universities. Capitalizing on this diverse pool of students and early geoscience exposure, the NSF Geopaths Geoscientist Development (GEODE) Program at the University of California, Riverside, is designed to remove barriers, recruit, and retain underrepresented students into geosciences majors and careers. GEODE is a network for geoscience education and includes high school, 2-year college, and 4-year university programming consisting of classroom outreach, transfer advising, and internships. Here we report on the results from the GEODE Internship Program that offered 10-week paid student internships, providing the opportunity for students to be exposed to the geosciences through research experiences. We analyzed answers on program applications and exit surveys. The majority of the students agreed that participating in research increased their interest in conducting scientific research in the future, and many students expressed interest in or enrolled in more geoscience courses. The students reported benefits of new research skills, career preparation, and networking; they struggled with a lack of background

knowledge and a lack of research time. These results demonstrate a promising way to strengthen geoscience educational pathways and increase diversity in the geosciences.

INTRODUCTION AND LITERARY CONTEXT

Purpose and learning goals

Few students of color are successfully navigating through a geoscience education (Brown and Clewell 1995, Bembry et al. 1998, Levine et al. 2007, Riggs and Alexander 2007, Baber et al. 2010, NSF 2015, Wilson 2018). The educational pathways from high school (HS) and 2-Year Colleges to geoscience majors in the 4-year universities are oftentimes fragmented and ineffective, and a need exists for more diversity in the geosciences, the least diverse in the fields of science, technology, engineering, and mathematics (STEM; Dahl and Droser 2016, Wilson 2019, Dutt 2020, Marín-Spiotta et al. 2020). This problem is particularly alarming because previous research projects a shortage in the geoscience workforce attributed to the current failure to recruit new students into geosciences majors (Gonzales and Keane 2011, Zeigler and Camarota 2014, Dahl and Droser 2016, Houser et al. 2018, Wilson 2018). Several studies have recognized factors preventing students from entering and staying in the geosciences. These barriers which include a lack of social and cultural support, curriculum quality, unfamiliarity with career opportunities, and a lack of positive outdoor experiences limited by financial or physical abilities (Stokes et al. 2014, Dahl and Droser 2016, Carabajal et al. 2017, Szurmak et al. 2019), are further compounded by discrimination, harassment and hostile environments (Levine et al. 2007, Callahan et al. 2017, Marín-Spiotta et al. 2020).

The *NSF Geopaths Geoscientist Development Program (GEODE)* is a program designed to remove barriers and draw students from severely underserved and historically underrepresented communities into geoscience majors. GEODE is a network for geoscience education and includes high school, 2-year college, and 4-year university programming. Herein, we discuss the programming specific to recruiting and retaining students from 2-year colleges into 4-year universities, a critical educational junction we have identified where attrition from the geosciences pipeline frequently occurs. This programming consists of classroom outreach, including transfer advising, and paid research internships.

This study reports on the results from the GEODE Internship Program. We tested whether implementing a recruitment program with paid research internships would: (1) increase the students' interest in majoring in the geosciences and entering the geoscience workforce; (2) increase the students' interest in STEM majors and careers; (3) increase the number of students from underrepresented groups into geoscience majors and subsequently into the geoscience workforce; and (4) increase the students' likelihood of transferring from a 2-year college to a 4-year college. A secondary goal of this study is to describe our best practices, including information regarding the implementation of virtual research, an import branch of learning in today's educational environment, and fiscal ability.

Self-efficacy

Previous studies have demonstrated that internships, in addition to successfully training students for specific career paths, promote several benefits that fall outside the scope of career-specific training, particularly self-efficacy. It is critical for students to participate in opportunities that increase self-efficacy while engaging them in the research and integrating them into their academic institution; students leave college when they do not feel a sense of confidence and community (Tinto 1993, Stofer et al. 2021). The positive feelings, attitudes, and values that drive learning behaviors, and paying close attention to the emotional domain will ultimately enhance recruitment while reducing attrition in the geosciences (Barber et al. 2010, McConnell and van Der Hoeven Kraft 2011). Students who participated in internships gained confidence and broad professional skills that served to strengthen self-efficacy such as time management, the ability to work independently, and an overall understanding of how to conduct scientific research (McCormick and Brennnan 2001, Lopatto 2004, Lopatto 2007, Russell et al. 2007, Williams et al. 2016, Stofer et al. 2021). The student participants subsequently brought this confidence and competence with them into their professional careers.

Garnering interest and informing career choices

Internship programs have been successful at informing the career choices (Seymour et al. 2004, Allen 2011, Matsumoto 2015), and a link has been noted between student internships and a reduced rate of attrition (McCormick and Brennan (2001). Russell et al. (2007) found that research programs greatly increased the students' interest in STEM, subsequently influencing their desire to pursue a PhD. Jarrett and Burnley (2003), in a geoscience-focused, NSF-sponsored Research Experience for Undergraduates (REU), showed that the participants increased their interest in the geosciences and sought out more research-oriented career paths. Blake et al. (2018) conducted an internship involving specialized training in remote sensing, resulting in some of the participants moving on to other internships in the geoscience workforce. Garnering interest and exposing students to the numerous fields of geoscience employment and educational pathways are extremely influential elements in research and internship programs (Charlevoix et al. 2021).

Supporting transfer from 2Y to 4Y universities

Undergraduate research experiences have been shown to support students transferring from 2Y to 4Y colleges and universities (Higgins et al. 2011, Stofer et al. 2021). In their theoretical framework for creating an effective geoscience education pathway, Levine et al. (2007) recognized that certain experiences critically influenced students' decision to enter or leave the geosciences, and at the junction of 2Y to 4Y, these impactful experiences included geoscience awareness, career development, and internships. Townley et al. (2013) assessed students that transferred from local colleges into STEM majors at the University of South Carolina. Their study suggested a strong sense of community achieved through high participation in STEM activities positively contributed to the students' transferring to the 4Y university and succeeding academically post-transfer. Internships further support transferring to 4Y universities through student enjoyment and by supplementing traditional classroom learning, bridging the gap between theoretical learning and real-world, practical applications (Kolb and Kolb 2009, McCarthy 2010, Adetunji et al. 2012, Dombrowski et al. 2013, Blake et al. 2015).

Applications for increasing diversity

Internships and research experiences have been shown to engage, recruit, and retain underrepresented students, thereby acting as a successful pathway for these students into STEM fields (Lopato 2007). Hunter (2010) in an NSF report outlining the outcomes of the Internship Program at the University of California, Santa Cruz, describes successes in the areas of increasing diversity. This program included a high percentage of students from groups underrepresented in the STEM sciences and almost half of the students who participated were from 2Y colleges. The majority of students in this program continued on a STEM educational track. The majority of the program's alumni graduated with STEM undergraduate degrees. Internships and recruitment programs were shown to assist in creating an inclusive community and combating misconceptions about STEM and geoscience careers (e.g., geoscience jobs do not pay well, geology is one of the easiest sciences), crucial goals for enlisting and retaining underrepresented students (Hoisch and Bowie 2010, Blake et al. 2015, Haynes 2015, Stofer et al. 2011.) Further evidence has outlined the applications of internships and recruiting programs in effectively drawing students from severely underserved and historically underrepresented communities into geosciences education pathway. The successful recruitment and retention of underrepresented students into the geosciences can be improved if program designs included certain attributes that influenced students' decision to enter and remain in the geosciences; e.g., geoscience awareness and effective science instruction to factors specific to minority students like familial/cultural support and encounters with racism (Levine et al. 2007). Stofer et al. (2021) suggested that experiences, such as internships, research experience, mentoring, and team-building amongst their peers, could support recruitment and foster interest in geoscience for underrepresented students at 2Y colleges. Houser et al. (2018) focused on recruitment from 2Y colleges to increase the enrollment of students majoring in the geosciences at Texas A&M University (TAMU). After their program's inception, one third of the students in the Geosciences Department at TAMU were underrepresented students, a statistically significant increase. Miller et al. (2007) in a geoscience recruitment program involving Hispanic and Latino high school students, a demographic less likely to be exposed to the Geosciences or aware of career opportunities in the field, followed these students' college careers and found that more than half of them were still in STEM majors, with ten percent majoring specifically in geology.

STUDY POPULATION AND SETTING

Riverside County, located east of Los Angeles County in Southern California, is densely populated (2.5 million), and highly diverse with a population primarily made up of Hispanics (50.0%), non-Hispanic Whites (34.1%), Black and African Americans (7.3%), and Asians (7.2%; US Census Bureau 2020b). These demographics show parallels to the current US population (Table 1.1) as well as to what the US is projected to look like in the coming decades. The US Census anticipates that by 2060 the Hispanic population will nearly double to 27.5%, the non-Hispanic Whites will no longer be the dominant ethnic group in the US at 44.3%, the percentage of Black and African Americans will increase to 15.0%, and the Asian population will increase to 9.1% (Vespa et al. 2020). A recruitment program conducted among such a diverse demographic of students is an ideal test-setting and the results and best practices learned from this study can be applied more broadly across the country.

Riverside county is home to a wide range of geoscience career opportunities. Riverside County has a robust academic infrastructure in place that successfully ushers students from the local K-12 school district, through several 2Y community colleges, to local 4Y universities, including a large R1 university. The 2Y colleges in Riverside County host thriving geoscience programs, where students can take a variety of geology courses in preparation for a geology major at a 4-year university. Similar to the demographics in Riverside County, these 2Y colleges have a large population of underrepresented minority students, almost 60% Hispanic and 8% African American (Dahl and Droser 2016). An excellent opportunity exists in Riverside County to launch a geosciences recruitment program and capitalize on this early geoscience exposure and the diverse pool of students.

RESEARCH DESIGN AND METHODS

To measure the impact of the research internship on participants' interests in geoscience, we analyzed answers on program applications and exit surveys. Seventeen potential participants completed the program application and sixteen students completed the exit survey after completing their internship. Potential participants were recruited from local community colleges. Community college geoscience professors advertised the program to students enrolled in introductory geoscience courses. The program application form was used to evaluate students’ interest in participating and prior experiences in geoscience courses and to collect demographic information; e.g., gender identity, race/ethnicity, and first-generation college status.

The exit survey that the students completed included a questionnaire of twelve Likert scale questions (Likert 1932) and two open-ended short answer questions designed to measure student experiences in the program (Figure 1.1). We used a five-point Likert scale (strongly disagree, disagree, neutral, agree, strongly agree) which was later numerically coded along a five-point scale that ranged from -2 to 2. Using this scoring method allowed us to identify positive and negative student experiences.

RESULTS

Of the 17 students who applied to the program, eight (47.1%) identified with ethnic or racial groups that are underrepresented in STEM, one (5.9%) identified as multiracial, and eight (47.1%) identified as white. Eight (47.1%) students identified as female, eight (47.1%) identified as male, and one (5.9%) identified as nonbinary. Eight (47.1%) students were first-generation college students and nine (52.9%) had one or more parents or guardians who have earned a bachelor's degree or higher. A majority of students (58.5%) who applied to the program had not taken any Earth & Space Science coursework in high school, and a majority (82.4%) planned to major in geoscience in college. All but one student planned to transfer from their two-year college to a four-year university.

Students reported that participation in the internship had a positive impact on their attitudes towards scientific research (Figure 1.1). A majority of students agreed with all but two of the 11 statements they were asked to evaluate. The statement that students most agreed with was "Participating in research increased my interest in conducting scientific research in the future" (score: 1.81) followed closely by "I learned new research skills during my internship" (1.69) and "Participating in the internship program improved my understanding of how scientific research is conducted" (1.69).

Students also reported an increased interest in taking more geoscience coursework after participating in the internship program.

The two statements that students showed less agreement with were “I learned about career opportunities in geoscience during my internship” (score: 0.94) and “I learned about the community college to university transfer process during my internship” (0.13).

We conducted content analysis on the short answer questions to identify repeating themes. Six themes were identified for the first question (“Please describe the benefits of participating in the internship program”; Table 1.2). The most frequently reported benefit was “developing new research skills.” This benefit was reported by 14 of the 16 respondents (87.5%). Students commented on how during the internship they “gained hands-on experience with fossil preparation,” and “learned about Geophysics and how to map faults.” A student responded, “I learned so much about scientific research and got to practice useful skills in a meaningful, portfolio-building research project. It also led to me being able to do further research with my professor during which I was able to travel and help fieldwork.” One of the interns commented on how they “explored the research process and learned how to work with a team to achieve a common goal.” Another student stated, “I was able to conduct earthquake research that later became published and expanded on during my undergraduate senior thesis.”

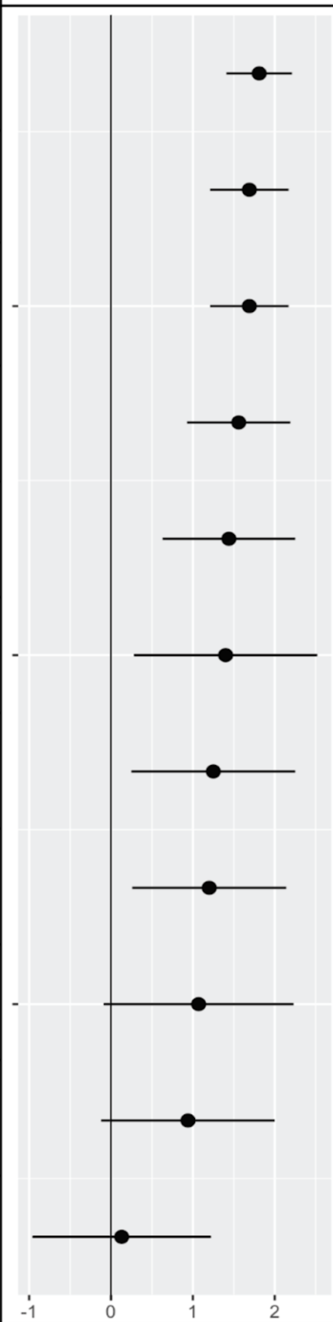
“Networking” and “career preparation” were also frequently reported (9 mentions each, 56.25%). For example, one student explained, “I learned SO much from my mentor. My mentor taught me about CV's, the academic process, and all helped me to get experience doing things I would have never been able to do otherwise, such as writing and submitting a paper for research. I also got to present our project on a poster at a symposium, and being able to attend that through the internship was an incredible and educational experience." Another student elaborated, "A major benefit was getting to interact with the graduate students in the geology department. They were really helpful the entire time and provided valuable insight about how graduate school works. They also gave great advice about school, research and life. I felt like they were great mentors and friends that I wouldn't have had if it weren't for the internship program."

The "Familiarization with the university environment" category was reported 5 times (31.3%). One of the participants stated that the program "exposed me to the Geology community at UCR that made me feel at home even before being accepted into the college," while another student "learned a great deal about life in a 4-year university." The "Decision to transfer" category was reported by 4 respondents (25%). One student explained, "Some benefits I encountered with the GEODE program were meeting faculty that motivated me to choose UCR for transferring. I was able to conduct research and maintain a research position after transferring." Other student comments included, "The experience of the internship very positively influenced my decision to go to UCR," and "Getting knowledge and more hands-on experience from those in the Department of Earth [and Planetary] Sciences allowed me to carry that same passion and transfer to a university to gain an undergraduate degree." Lastly, “monetary benefit” was reported twice (12.5%). One student noted, “The stipend definitely helped me pay for my usual costs of living and going to school.” Another student importantly elaborated that “The stipend greatly helped as my family and I have been struggling since many of us lost our jobs at the beginning of the pandemic.” Themes did not emerge as clearly in the second open-ended question (“Please describe any challenges or drawbacks to participating in the internship program”). Only three themes were reported by three or more respondents. “Complicated onboarding paperwork” was reported by 4 of the respondents (25%). One student noted, “The onboarding process was a little bit tricky.” While another student explained, “The stipend payment process can sometimes be a little challenging.”

Participants reported that they lacked requisite background knowledge for the research project that they were assigned. One participant described the challenge of “not knowing anything beforehand about how to conduct Geophysics research.” Students observed, “Professors sometimes didn’t fully explain the reasoning behind everything we did,” and “A lot of the research was out of my realm of understanding.” The participants also responded that there was not enough time dedicated to research. One student wrote, “I was washing lab equipment for over a month before getting to conduct any research.” Another student explained, “I just helped my advisor around the lab on other ongoing museum cataloging, which were all positive experiences, but I spent very little time by comparison on my actual GEODE project.”

Table 1.1. Summary of the demographics of the GEODE Internship participants, the geoscience majors in the U.S. (NSF 2019), the population of California (U.S. Census Bureau 2020a), and the population of the United States (U.S. Census Bureau 2020c).

CATEGORY	DEMOGRAPHIC	GEODE INTERNS	GEOSCIENCE MAJORS	CALIFORNIA	UNITED STATES
GENDER	Female	47.1% (8)	38.3%	50.3%	50.8%
	Male	47.1% (8)	61.7%	49.7%	49.2%
	Non-Binary	5.8% (1)	NA	NA	NA
RACIAL/ETHNIC GROUP	White, Non-Hispanic	47.1% (8)	75.4% (5,493)	36.5%	60.1%
	Hispanic, Latino or Spanish Origin of any race	41.2% (7)	8.8% (640)	39.4%	18.5%
	Black or African American	5.9% (1)	2.1% (155)	6.5%	13.4%
	Two or more races	5.9% (1)	3.1% (228)	4.0%	2.8%
	Asian	0.0% (0)	3.5% (256)	15.5%	5.9%
	American Indian or Alaska Native	0.0% (0)	0.5% (36)	1.6%	1.3%
	Native Hawaiian or other Pacific Islander	0.0% (0)	<0.1% (7)	0.5%	0.2%
	Race and ethnicity unknown or other	0.0% (0)	3.1% (225)	NA	NA



Survey Question	Score	Score	Standard Deviation
Participating in reserach increased my interest in conducting scientific research in the future		1.81	0.40
Participating in the internship program improved my understanding of how scientific research is conducted		1.69	0.48
I learned new research skills during my internship		1.69	0.48
I wanted to take more geoscience courses after participating in the internship program		1.56	0.63
Participating in the program INCREASED my interest in transferring from my community college to a 4 year university		1.44	0.81
I have taken more geoscience courses after participating in the internship program		1.40	1.12
I was planning to major in geoscience BEFORE participating in the internship program		1.25	1.00
Participating in the internship program INCREASED my interest in transferring from my community college to a 4 year university		1.20	0.94
Participating in the internship program impact my decision to pursure transferring from my community college to a four year university		1.07	1.16
I learned about career opportunities in geoscience during my internship		0.94	1.06
I learned about the community college to university transfer process during my internship		0.13	1.09

Figure 1.1. Student survey data with a focus on gaging the students' attitudes towards scientific research.

Table 1.2. Coded concepts from the content analysis of the short answer questions given by the students.

OUTCOMES	CONCEPTS	SCORE
BENEFITS OF PARTICIPATING IN THE GEODE INTERNSHIP PROGRAM	Developed new research skills	14
	Career preparation	9
	Networking	9
	Familiarization with university	5
	Decision to transfer	4
	Monetary benefit	2
CHALLENGES OR DRAWBACKS OF PARTICIPATING IN THE GEODE INTERNSHIP PROGRAM	Start-up paperwork or payment	4
	Lack of requisite background knowledge	3
	Not enough research time	3
	Parking/travel to campus	2
	Limited choice in research projects	1
	Virtual learning	1
	Unsatisfactory workspace	1

DISCUSSION

Strengthening Interest in the Geosciences

One goal of this study was to test the hypothesis that participating in an internship would increase the students' interest in majoring in the geosciences. Despite the majority of the students entering the program with a preconceived desire to major in the geosciences, our results support this hypothesis. The students agreed that participating in this internship increased their interest in taking more geoscience courses in the future; and subsequently, they did enroll in additional geosciences courses upon completion of the internship. The increased interest these students showed in the geosciences indicates the efficacy of the GEODE Program to encourage students to take more geoscience courses, and also strengthened their resolve to major in the geosciences, a positive step towards retention. Our results are consistent with those of Jarrett and Burnley (2003), Blake et al. (2018), and Charlevoix et al. (2021). While there is a strong need for more data and programs involving internships that specifically conduct geosciences research, the success of the GEODE Program and the above geoscience-focused REU highlights the potential for success of other geoscience recruitment programs, lending justification for more institutions and departments to engage in such programs.

Implications for STEM

The GEODE program demonstrated success in cultivating the students' interest in STEM. In the survey responses, every student agreed that participating in this internship increased their interest in conducting scientific research in the future. It is noteworthy that the students also indicated that they learned new research skills and gained an understanding of how scientific research is conducted. We interpret these results to mean that the students during their internships gained knowledge and familiarity with the scientific process and the university research environment, invoking a sense of confidence and inclusion. One student wrote, "Learning how to conduct research has been a really valuable tool in college, I feel a lot more confident than I would have if ' didn't have this experience." It is this confidence and inclusion that made the students feel they not only could succeed in the sciences, but truly belonged in a career path in STEM, effectively contributing to their expressed intentions to continue STEM research. The students' desire to continue STEM research highlights the efficacy this program has on recruiting, informing career paths, and ultimately retention in the STEM sciences. Our findings were similar to several studies that examine undergraduate research programs in the STEM sciences (Lopatto 2004, 2007, Russell et al. 2007, Williams et al. 2016).

Despite being consistent with several of our above findings, the results of Lopatto (2004, 2007) also indicated that a very small percentage of students changed their existing career plans in favor of a career in STEM, and Williams et al. (2016) found that their students indicated low learning gains regarding their career paths; these findings initially appeared to contradict our own findings. Herein we discuss a possible explanation for this discrepancy. Many of the students in the Lopatto (2004, 2007) and Williams et al. (2016) studies entered into the research experience with their career paths already determined; these students did not initially choose their career paths as a direct result of their internships, an important distinction (Seymour et al. 2004, Lopatto et al. 2007). The majority of students in our study also had a preconceived intent to major in STEM. Our students agreed that participating in the GEODE internship program increased their interest in engaging in STEM research in the future, thus strengthening their predetermined choice of careers. The results of Lopatto (2004, 2007) and Williams et al. (2016) studies seem contrary to our own; however, the nature of their survey indicates that their results are not in direct conflict with our results.

Although the GEODE internship program was designed specifically for the geosciences, our results, i.e., the students gained an increased knowledge of how STEM research is conducted, indicate that this program has implications beyond the scope of the geosciences. The framework described herein can be applied towards multiple disciplines, contributing to the common goal of increasing interest and retention in the discipline and informing career choices. Matsumoto (2015) at the Monterey Bay Aquarium Research Institute, despite primarily conducting oceanographic research, focuses their internship program on introducing the students broadly to the process of conducting STEM research. Regardless of whether or not the students pursue oceanography as a career, Matsumoto has found that this approach is a success because it assists students in determining where their interests lie. Agreeing with Matsumoto's approach, one of our GEODE Internship participants stated, "The program successfully provided students the insight necessary to gain a better understanding of their field of interest."

Increasing Diversity in the Geosciences

Previous studies have shown that non-targeted recruitment alone is not enough; little headway has been made in the last 40 years to diversify the geosciences (Bernard and Cooperdock 2018, Marín-Spiotta et al. 2020). More than half of the GEODE Internship participants belong to groups underrepresented in the geosciences and each of these students indicated that this program increased their interest in the geosciences. Of these students, many are actively continuing down the geoscience pathway towards geoscience majors and careers as indicated by the high scores in students who have taken more geosciences courses since the completion of their internship. The GEODE program successfully capitalized on the diverse demographics that make up Riverside County, showcasing the potential that similar programs have to target-recruit and retain a diverse pool of students. Our results mirror previously reported data from studies involving geoscience and STEM research and recruitment programs (Miller et al. 2007, Lopato 2007, Hunter 2010, Houser et al. 2018, Stofer et al. 2021).

To better under the success that the GEODE and aforementioned programs have shown in increasing diversity, special attention must be paid to the theme of confidence, or self-efficacy (McConnell and van Der Hoeven Kraft 2011), that has emerged from the results of this study. The GEODE program has provided students with opportunities for positive experiences in the geosciences and it is these experiences that ultimately strengthened the confidence among our pool of diverse students, positively influencing their perceptions of geoscience majors and careers. Baber et al. (2010), in their study of two summer research programs at Pennsylvania State University, found that developing self-efficacy increased the students' interest in geoscience careers, underscoring the potential for the retention of underrepresented students through the geoscience education pathway. Jarrett and Burnley (2003) noted that the participants who indicated a high degree of ownership and understanding of their research projects were the same as those who shows an increased interested in the geosciences upon the completion of the REU. Van der Hoeven Kraft (2017) described that a student's interest is sparked by an external event and sustained support can lead to a well-developed interest in the geosciences; in our study, the event is the research opportunity and the sustained support comes from working with a mentor during the 10-week internship. In their blog, one of our students belonging to a group underrepresented in the geosciences posted, "This week has shown me that even someone like me who has never worked with software such as Trellis can learn through trial and error. I'm pretty excited to finish the mapping of these fault lines and see how we will be transferring it to the next program." This statement demonstrates how a student's confidence and comfortable acceptance that learning, including mistakes, can be an enjoyable part of the STEM process, and likewise, is a recipe for inclusive attitudes that contribute to the retention of diverse students.

Transferring from 2Y to 4Y Universities

Two of the lower scoring categories were "the internship impacted my decision to pursue transferring from my community college to a 4Y university" and "the internship program increased my interest in transferring from my community college to a four-year university." We are not discouraged by these results. Prior to entering the GEODE Internship Program, 94.1% of the students indicated that they had planned to attend a 4Y university. We interpret these results as an indication of students' strong prior resolve to attend a 4Y university; this program did not fundamentally change their determination to continue their educational journey. Several students indicated that "Decision to transfer" and "Familiarization with the university environment" were benefits they gained from the GEODE Internship Program. One student commented, "The internship program was a fantastic experience that allowed me to gain the confidence I needed to continue learning and pursuing a higher degree." Another student wrote, "The faculty I connected with during this internship greatly helped with my transition into a university setting." This evidence underscores the potential of the GEODE Internship Program to affirm the students' decision to transfer, while easing apprehensions and facilitating the comfortable transition of these students into the 4Y university system. Our results are consistent with the results reported by Townley et al. (2013).

CASE STUDY

As a child growing up in Southern California, Astrid loved the outdoors and could often be found digging in the dirt and collecting interesting rocks. After high school, she had a sense that she wanted to work in the sciences and began to consider a multitude of careers; e.g., medical examiner, environmental scientist, zoologist, and engineer. She enrolled at Riverside Community College (RCC), a 2Y college in Riverside County. At RCC, her interest in the geosciences was sparked when she enrolled in a course involving field excursions to several national and state parks, traveling as far as Salt Lake City. Discovering her love of working in the field inspired her to sign up for more geology courses.

Astrid applied and was accepted to the GEODE Internship Program, where she worked under the direction of a geophysicist to model earthquakes. She enrolled at the University of California, Riverside (UCR), as a geology major, and her results were published in a peer-reviewed scientific journal. Astrid graduated *cum laude* and accepted an internship working at the Florissant Fossil Beds National Monument in Colorado. Continuing to pay her experience forward, she recently spoke at a professional conference on engaging diverse audiences in the geosciences. Astrid was one of our first interns and we hope to be able to soon showcase many more success stories of our more recent interns.

BEST PRACTICES

Our best practices and suggestions are based on feedback and observation. The interns should work in pairs or groups. When students are able to come to campus as a cohort and form their own working groups, it is a less intimidating way to introduce them to a 4Y campus while fostering teamwork and reinforcing science as a collaborative effort. Offering complete flexibility and working around the schedule of the students is very important as many had varying class schedules, full and part-time jobs, and family obligations. It is valuable to use some of the research time for one-on-one mentoring with the faculty; this mentoring gives the students an opportunity to network and build a relationship with a faculty member outside of their 2Y colleges. Students should write blogs. We post to our department website; these resources are useful in promoting the program and framing the internships in a way that seems more approachable and encourages others to apply (Williams et al. 2016). In her blog, one student wrote, “Participating in the GEODE program, I found my desire to pursue geology as my career field. Through interacting with the faculty at UCR, I was instantly persuaded to choose UCR as my transfer school.” In another blog, a student commented, “At first, the Geology Building at UCR looked like a very daunting place where I couldn’t possibly ever fit in. However, through this unique experience, it’s become a place of refuge, comfort, and most importantly pride.”

Internship programs should provide opportunities for the students to strengthen their skills communicating science by presenting their research at a symposium or professional meeting. The interns should be encouraged to continue their research, either for credit or pay, after transferring to a 4Y institution. Some internships were so successful that the interns were able to earn an ongoing salary from their PIs to continue their research. The UCR Faculty members previously involved in the internship program are eager to continue their participation by taking on and mentoring more interns.

Virtual Research

During the Covid-19 pandemic, we discovered several benefits and suggestions for successfully implementing remote-learning internships. Similar to on-campus internships, flexible working hours were even more essential during this difficult time. It was a benefit for students to have flexibility of working location and removed barriers such as transportation, parking, and commute time. Using online tools like Google Drive, OneDrive, or Drop Box made it easy to collaborate and share data. Frequent meetings via an online platform like Zoom or WebX should be implemented to hold group meetings, maintaining a sense of community and support in a virtual lab setting. Virtual research has the potential to be highly inclusive, expanding the number of students who can participate in internships. Unlike field camps and other outdoor experiences where finances or physical abilities are potential barriers (Stokes et al. 2014, Dahl and Droser 2016), any student can participate in a remote-learning internship, regardless of physical ability, family commitments, or financial concerns. While it is possible that some students might not have access to their own computer or an internet connection, these barriers should be addressed and remedied on an individual basis; many institutions, upon transitioning to campus-wide online learning, now have resources to assist with these situations.

Funding

Our internships are paid at a rate of 15 dollars per hour for 100 hours and we offer assistance with public transportation to and from campus. We found that 1500 dollars was appropriate in our area for an internship stipend. For many professors and academic departments, 1500 dollars is an attainable amount to allocate for a student intern to conduct STEM research. Not all institutions have grants or funding for these stipends. The students considered the monetary component of the GEODE internship program to be the least important benefit, suggesting that all institutions can successfully implement an internship program regardless of funding. In the case of reduced funding, the internship program should decrease the number of expected hours per week so that students still have time to pursue other sources of income. The potential to develop new research skills, network, and prepare for their future careers scored the highest and are likely to draw students to an internship program regardless of monetary compensation.

LIMITATIONS AND AREAS FOR IMPROVEMENT

We have identified a few shortcomings that we hope to ameliorate during future iterations of this program. The lowest ranked responses were “learned about career opportunities in the geosciences," and "learned about protocol for transferring from 2Y to 4Y." Going forward, we will ask the participating faculty to either speak with the students more about geoscience careers or allow time for the GEODE program manager to work with the students to highlight geoscience careers. We have handouts and materials available that we use during our 2Y college visits that can guide these discussions, for example a handout we made for the program entitle, "Why be a Geology Major?" and diagrams such as, "Fields of Geoscience Employment" from the American Geosciences Institute (AGI). During these visits to the geology classrooms, we also distributed transfer information sheets and answered questions with the goal of clarifying the admissions process. These transfer sheets not only contain general admissions information, but were tailor-made with a list of the specific courses at their 2Y college required for admissions into the geology major at UCR. Previous studies have highlighted the benefits of discussing the potential salaries of geology careers as an effective method for recruitment (Hoisch and Bowie 2010, Blake et al. 2015); we will also implement this strategy in our program. Unfortunately, we neglected to carry these practices into the internship portion of our recruitment program, a point to be remedied going forward.

Students commented on feeling uncomfortable with the lack of background information needed to engage in their internship's area of research. We plan to address this issue by working with the faculty sponsor to compile a short list of relevant journal articles and background materials, such as diagrams or slides. These additional materials would be optional for the students, but the student can take advantage of them if they feel it would help ease their hesitancy or discomfort in engaging in a new research project.

The students indicated that time constraints were an issue; the students wanted more time to devote towards their research projects. This response is encouraging and we interpret this feedback to mean that the students became fully engaged in their work, taking ownership of their projects, and eager to continue their research. Mabrouk and Peters (2000), in a nationwide survey of biology and chemistry undergraduate research experiences, found that a high percentage of undergraduates who were given research opportunities earlier in their undergraduate tenures continued their research for over 2 years. Moving forward, we will encourage the participating faculty to consider extending a position to the student researcher for either pay or university credit. Students expressed concerns over the difficulties of the administration onboarding process; e.g., filling out employment paperwork and waiting for computer login assess to be granted prior to required online laboratory safety courses. While some of the administration difficulties were entirely out of our control, we can attempt to streamline this process by familiarizing ourselves with the paperwork requirements ahead of time; starting the process early is the key. Implementing a “buffer window” into the program specifically for the onboarding and necessary wait-time for the processing of paperwork will also make this process smooth-running.

CONCLUSION

This study demonstrates that the GEODE Internship Program increased the participating students' interest in the geosciences and STEM. We find that our program draws students from severely underserved and historically underrepresented communities into the geosciences. We outline evidence supporting this program's potential for increasing the students' likelihood of transferring from a 2-year college to a 4-year college. Our results, based on empirical data and feedback from the students, indicate that programs similar to the GEODE Internship Program would likewise yield successful results.

We have provided best practices and have highlighted the cost effectiveness and financial feasibility for institutions to engage in their own programs. Our success stories, while initially small in number, are beginning to accumulate. The framework discussed herein can be applied to the geosciences and other STEM sciences.

As geoscientists, we are putting forth a call to our community and the departments of other institutions to continue to grow or pilot their own geosciences internship and recruitment programs. If we are to succeed in circumventing workforce shortages and diversifying our discipline, then internships and recruitment programs are crucial and represent a promising path towards achieving these goals.

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CHAPTER 2

Encrusters on the fossil oyster *Hyotissa hyotis*: The paleoecological record of sclerobionts on a hard substrate community from the Miocene proto-Gulf of California

ABSTRACT

The analysis of sclerobionts is a powerful tool for understanding ecological relationships and their traces provide the opportunity to study organisms that may not otherwise be preserved in the fossil record. Herein, we report evidence of sclerobionts, on *Hyotissa hyotis* oysters from the Latrania Formation in the Southeast Coyote Mountains near Ocotillo, California. The upper Miocene Latrania Formation represents an ancient shoreline of the proto-Gulf of California. We examined target-collected, disarticulated specimens of the large, free-living oyster *H. hyotis* from this locality. To gain insight into the paleoecology, we analyzed occurrences and the areal coverage, a proxy for abundance, of sponges, polychaetes, bivalves, phoronids, and corals. *Entobia* was the most dominant occurring trace fossil found inhabiting the oysters in terms of occurrence and intensity; we identified this assemblage as an *Entobia* ichnofacies. The exterior surfaces of the oyster valves showed more encrusting intensity than the interiors. The abundance of bioerosion and trace fossils on the *H. hyotis* suggests that these oysters provided a hard, biogenic substrate for a diverse community of encrusting and boring sclerobionts. Utilizing areal coverage measurements was a useful method for elucidating encrusting intensity. The combination taxonomic diversity with an assessment of intensity yielded a more accurate representation of the dynamics of a hard substrate community then just the diversity alone. Analysis of the spatial distribution and areal coverage of the encrusters that inhabited the oysters in this study

supports a model of sediment starvation in the distal to the fan-delta deposits of the Latrania Formation.

INTRODUCTION

Sclerobionts, including encrusting epibionts and bioeroding endobionts (Taylor and Wilson 2002), inhabit hard-substrate communities. These sclerobionts, hereafter referred to as encrusters in this study, are a phylogenetically diverse and ecologically important functional group of filter feeders, representing a surprisingly significant percent of biomass and diversity in many marine communities (Taylor and Wilson 2003). The body fossils of calcified encrusters such as spirorbid worms, serpulid worms, and small ostreid and anomiid oysters can be found on mollusk shells and are common in Cenozoic California marine communities (Ricketts et al. 1985). Encrusters also leave a robust record of trace fossils. Trace fossils provide indirect evidence of behavior patterns and interactions of the trace-makers within an ecosystem (Ishikawa and Kase, 2007). The absence of body fossils of soft-bodied organisms, such as sponges, results in their underrepresentation in the fossil record. The traces left behind by soft-bodied organisms are often the only way to detect their presence. Hence, trace fossils bring more comprehensive understanding of paleoecology (Frey 1975, Taylor and Wilson 2003).

Encrusting species represent a powerful, often overlooked, tool for elucidating and understanding biological sensitivity to changing environmental and climatic conditions (Rodland et al. 2006). Establishing an ecological baseline of oysters and reef communities from a time before anthropogenic influence has become an important agenda of conservation paleobiologists (Dietl et al. 2015, Dietl and Flessa 2011, Harding et al. 2008, Harding et al. 2010, Kusnerik et al. 2018). The study of encrusting organisms also has economic relevance; encrusting organisms have a propensity for oysters and scallops and significant biofouling can cause problems for commercial aquaculture (Almeida et al. 1996, Caceres-Martinez et al. 1998, Handley 1998, Igic 1972, Korringa 1954, Thangavelu and Sanjeevaraj 1988).

Encrusters are preserved *in situ* retaining their spatial relationship to their molluscan hosts (Taylor and Wilson 2003). Because encrusters are sessile, they are easily assessed and appropriate for community studies involving abundance, diversity, distribution, and stability within ecosystems (Foster and Buckeridge 1987). Taylor and Wilson (2003) have used encrusters and their traces on mollusk shells to understand spatial competition in ecosystems. The study of encrusters provides insight into relative chronological interactions between encrusting organisms on ecological time-scales in the fossil record. Mollusk shells can be encrusted or bored while the mollusk is still alive (Berkman 1994, Ward and Thorpe 1991), but encrusting found on the interior surface of a mollusk shell is an indicator that the mollusk was dead at the time of the encrustation (McKinney 1995).

The Latrania Formation has been studied extensively to gain a better understanding of the sedimentation, tectonics, and physical processes surrounding the rifting of Baja California that led to changes in the Colorado River system and to the subsidence and marine inundation of the proto-Gulf of California in the Late Miocene (Dorsey 2010, Sawlan 1991, Winker and Kidwell 1996). Examining the encrusters of the Latrania Formation provides insight into the diversity and abundance of these organisms during the early stages of the Gulf of California. Studies like these can offer a baseline to understanding the impacts of the faunal interchange that occurred from the opening of the Central American Seaway or a baseline of the fauna in this region prior to human-induced environmental changes.

Previous work near this locality focused on the macrofauna and *Hyotissa hyotis* were recorded with bivalves, corals, and vermiculids (Winker and Kidwell 1996). The *H. hyotis* oysters found in Ocotillo, California (Figure 2.1), are heavily encrusted, presenting an opportunity to survey the associated encrusting fauna at this locality and explore the paleoecological implications of this oyster hard-substrate fossil community. Therefore, the main objectives of this study are to: assess the taxonomy of the encrusting organisms that inhabited the *H. hyotis* Miocene Latrania Formation, Ocotillo, California, and determine if the *H. hyotis* demonstrate a common ichnofacies; examine the abundance and intensity of the encrusters in this assemblage; understand the timing of when encrustation occurred on the *H. hyotis* oysters; and test the model of sediment starvation in the distal to the fan-delta deposits of the proto-Gulf of California proposed by Kidwell (1988).

GEOLOGIC SETTINGS

In the Middle Miocene, southern California experienced tectonic extension on a long and relatively straight rift basin parallel to the pre-existing continental margin. In contrast to the typically complex fault system in Southern California during the Miocene, Baja California detached from North America as a rigid block to form the Gulf of California. By the Late Miocene, approximately 6 Mya, marine waters of the proto-Gulf of California had extended as far north as the present-day Riverside County, approximately 50 km from the Los Angeles Basin (Dorsey 2010, Sawlan 1991, Winker and Kidwell 1996). The Central American Seaway connected the Pacific Ocean and the Caribbean Sea (Coates et al. 1992) and temperatures in the proto-Gulf of California were subtropical to tropical, as indicated by microfossils (Quinn and Cronin 1984).

In this work, we focused on the Imperial Group of the Salton Trough region and employed the nomenclature revised by Winker and Kidwell (1996). The Miocene - Pliocene-age deposits of the Imperial Group overlay the non-marine volcanic and clastic units of the Miocene Split Mountain group and is stratigraphically lower than the non-marine Palm Springs Group (Figure 2.2). The Imperial Group consists of marginal marine evaporites near the base, the Latrania Formation, locally derived non-deltaic sediments that preserve marine fauna from the initial opening of the proto-Gulf of California, and the Deguynos Formation, deltaic sediment derived from the Colorado River. Outcrops of the Latrania Formation can be found in the Southeast Coyote Mountains near Ocotillo, California. It is within the fossiliferous Andrade Member of these outcrops that beds containing the fossil *Hyotissa hyotis* are recorded.

The Andrade Member is characterized by interbedded sandstones and limestones. Typically, active margins contain fewer shell accumulations; however, Kidwell (1988) interpreted the fossiliferous deposits, including oyster shell beds, bivalves, gastropods, and corals, of the Andrade Member to represent a period of sediment starvation. The *Porites* and *Solenastrea* corals found therein, while tolerant to turbid waters, generally infer shallow and clear waters. Subtidal ledges above the seafloor were likely protected from the high sediment accumulation despite the active margin (Kidwell 1988). The Andrade Member also exhibits deeper marine sedimentary rocks, deposited by sediment gravity flows, that contain thick bioturbated sandstones and *Thalassinoides* trace fossils (Winker and Kidwell 1996).

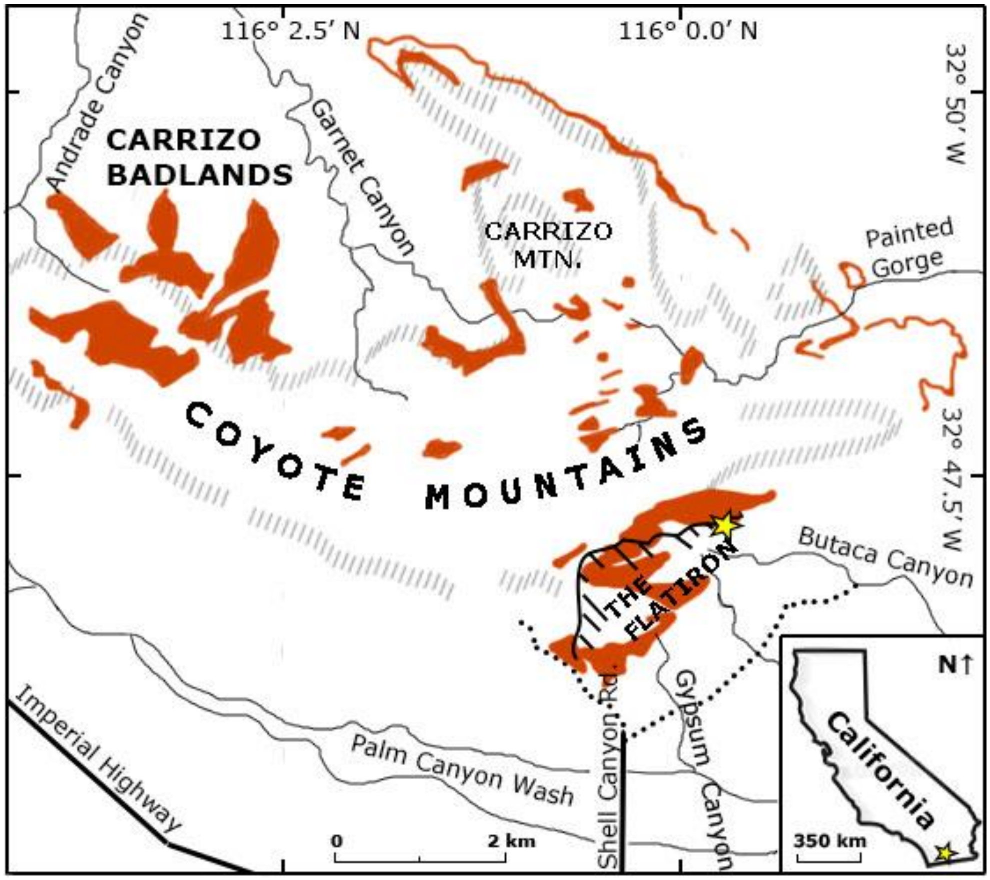


Figure 2.1. Locality map depicting the collection area in the southeast Coyote Mountains in Ocotillo, California. The outcroppings of the Latrania Formation are denoted in orange. Map after Winker and Kidwell (1996).

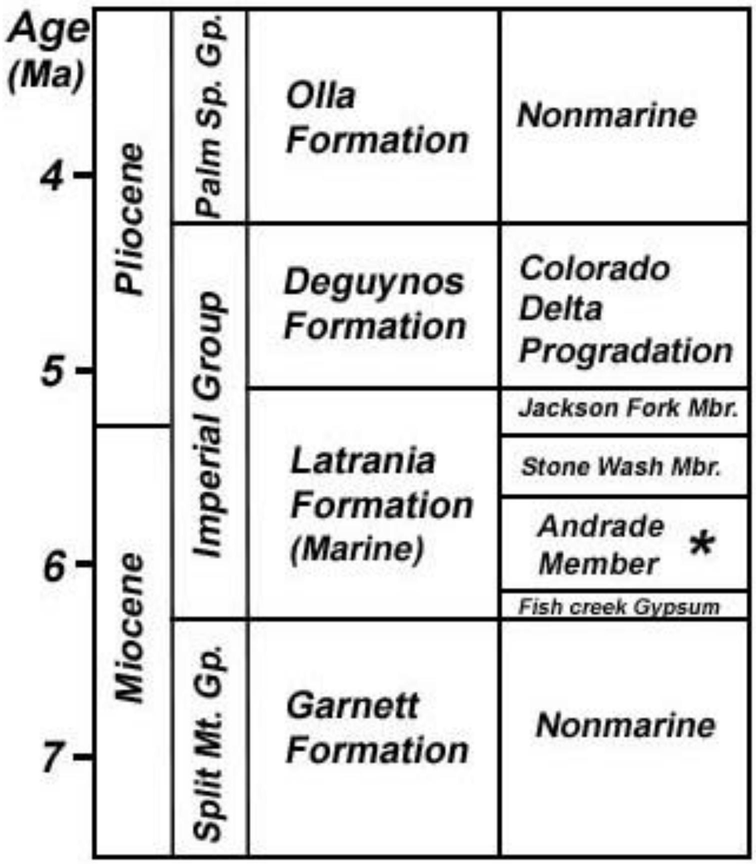


Figure 2.2. Diagram depicting the stratigraphy of the Latrania Formation southeast of the Coyote Mountains in Ocotillo, California. Adapted from Winker and Kidwell (1996) and Dorsey (2011).

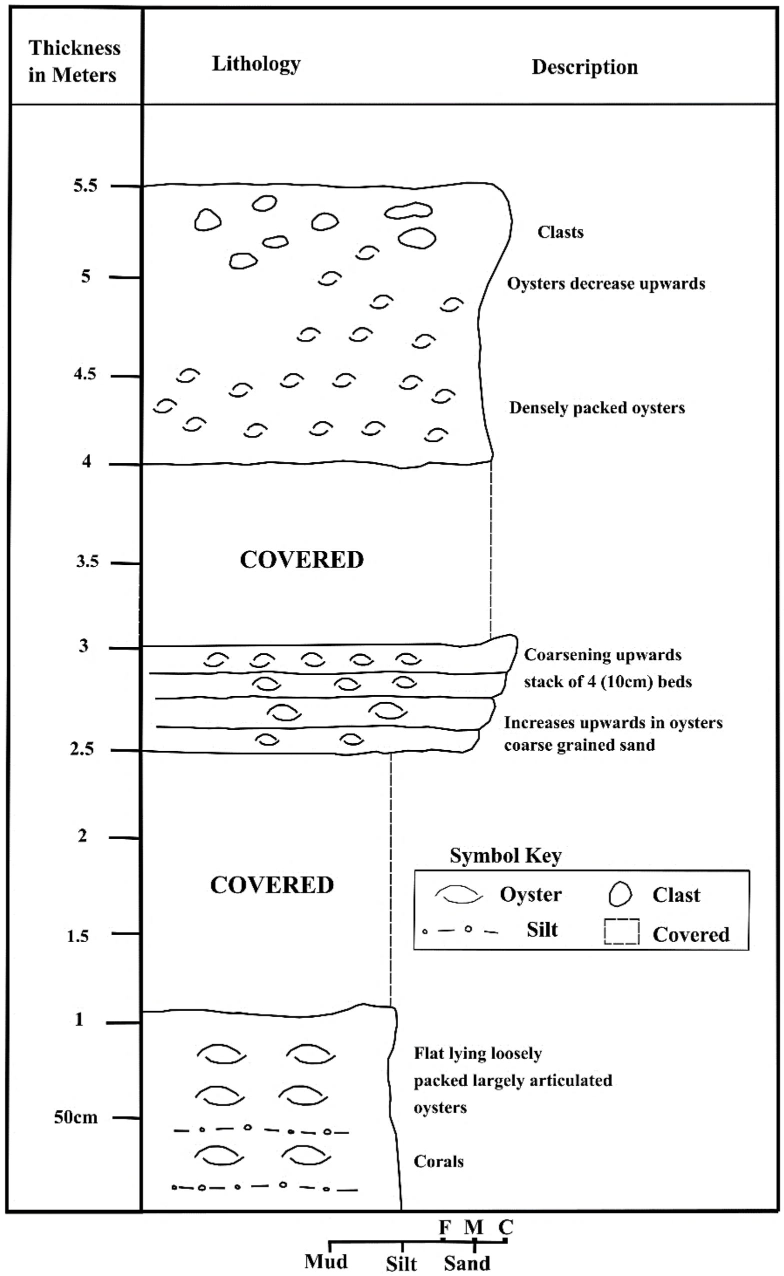


Figure 2.3. Diagram of the section of the Latrania Formation outcropping in the Southeast Coyote Mountains near Ocotillo, California.

MATERIALS

Kidwell (1988) originally described an oyster bed of *Pycnodonte heermanni* oysters in the Latrania Formation in Ocotillo, California. *Pycnodonte heermanni* have since been synonymized with the oyster *Hyotissa hyotis* (Cristin and Perrilliat 2013), a large and thick keystone oyster. Kidwell (1988) reported that these oysters were found alongside corals vermicularids and internal molds of bivalves and gastropods. She also noted that the oysters were infested by sponges and serpulid polychaete worms.

The *Hyotissa hyotis* exhibit strong radial ribs, large muscle scars, a large resilifer with distinct ligament growth tracks, and can grow to 30 cm in length. Both valves of the *Hyotissa hyotis* have a thick, convex morphology; however, the left valves grow larger and thicker than the right valves (Okutani 2000, Cristin and Perrilliat 2013, Hong et al. 2020). While frequently sub-circular, these valves can show strong morphological variations; the *H. hyotis* often grow to fit the relief of the available substrate (Cristin and Perrilliat 2013).

A total of 171 disarticulated valves were surface-collected from the locality. Oysters were collected from a narrow ravine that provided the only outcrop of the oyster beds. Although much of the section is covered, there are three intervals with oysters that are exposed (Figure 2.3). Articulated oysters occur loosely packed (Kidwell and Holland 1991) in a siltstone at the base of the section and in loosely packed to densely-packed shell concentrations (Kidwell and Holland 1991) with medium to coarse grained sandstone matrix in the other two exposures. Because of the steepness and instability of the ravine, it is not possible to collect material from the siltstone. Specimens used for this study are from the upper shell beds. Only valves that were more than 50% complete with intact hinges were included in this study in order to avoid overcounting. The specimens were washed and brushed with water and the remaining matrix dislodged with an engraving Dremel.

TAPHONOMY

The disarticulated valves of the *Hyotissa hyotis* collected from the site are overwhelmingly preserved as whole valves. Many of these valves showed little biostratinomic evidence of mechanical destruction indicating minimal transport. Some of the valves showed flaking of the laminae and chips around the margin likely from weathering out of the rock and the subsequent exposure to the surface. All of the valves displayed some degree of encrustation or bioerosion, indicating that encrusting organisms grew extensively in this assemblage. Oyster fragments also found on the surface suggest that despite many valves being found with heavy biologic encrustation, the biologic weathering was not enough to cause the complete destruction of these oysters after burial.

The *Hyotissa hyotis* from this locality all showed signs of diagenesis. Evidence of diagenetic alteration was inferred by the appearance of crystallization in the original calcite of these specimens. Despite diagenesis, the shells did not experience any substantial change in terms of their macrostructures; e.g., exterior surfaces, mantle cavities, laminae, hinges, and growth lines. Any recrystallization or chemical alteration did not eliminate the conspicuous evidence of encrustation, and thus, did not impair our ability to conduct a paleoecologic study.

METHODS

Each valve was examined using up to 30x magnification. Encrusters and borings visible to the naked eye were counted (approximately > 0.25mm). The encrusters were identified via ichnotaxa and, in the case of body fossils, to lowest taxonomic rank possible. The presence of encrusters on the interior and exterior surfaces of each valve was recorded. Multiple incidences of one type of taxon or trace on a valve was counted as a single occurrence. The life position of the encrusters, either on the interior or exterior surface of the valve, as also recorded.

The interior and exterior of each valve was photographed and the ImageJ Software Package was used to calculate the area occupied by each encruster and ichnotaxa on the valves in terms of the percentage of the total surface area. This areal coverage was used to determine the intensity of encrustation, a proxy for abundance. The results were analyzed statistically using the Chi-squared and Kruskal-Wallis tests in the Paleontological Statistics Software Package (PAST).

RESULTS

Taxonomic Composition of the Oyster Community

A total of six groups of taxa were found encrusting 171 valves of *Hyotissa hyotis*. Evidence for encrustation was found in the form of trace fossils (Figure 2.4) and body fossils (Figure 2.5). All of the valves examined have some encrustation (Figure 2.6). The trace fossil *Entobia,* inferred to be made by clionid sponges, was the most common encruster found inhabiting the oysters, but only a single ichnogenus was identified. The second-most dominant trace is *Gastrochaenolites.* They occur on 77.8% of valves. *Gastrochaenolites* is attributed to boring bivalves; however, there are various families (e.g., *Pholadidae* and *Mytilidae*) that are known to make these traces (Fischer 1990, Gibert et al. 1998, Warme 1975). No body fossils were found and casts of the burrows could not be obtained due to sediment infill. The bivalves that made these traces could not be identified.

Polychaete worms, represented by three ichnogenera, as demonstrated by fossil borings, and three taxa identified from the calcified body fossils, were the most diverse taxonomic group of encrusters. Polychaete borings, found on 59.6% of shells, were more common than body fossils, a rarity found on only 2.9% of shells. The body fossils included the calcified worm tubes of serpulids, spirorbids, and a sabellid. *Talpina* borings, inferred to be made by phoronids, were identified on 12.3% of the valves. Other rare encrusting taxa include the body fossils of corals and an oyster, found on 1.8% and 0.6% of shells respectively.

The patchy traces, herein this study referred to as Morphotype K, occur on 20.5% of valves. While we were unable to link Morphotype K to a specific ichnogenus, we interpreted this trace to be an attachment scar, possibly from an encrusting oyster or other bivalve. We assigned Morphotype K to it the ethological category of fixichnia, making this trace the only example of fixichnia found in this study with the remaining traces belonging to domicnia.

Distribution

Interior vs. Exterior. – Of the 171 valves, encrustation occurred on 168 of the exterior surfaces (98.2%) and 165 of the interior surfaces (96.5%). The areal coverage of the encrustation represents 26.5% of the total exterior surface area and 15.9% of the interior surface area of the valves (Figure 2.7). Of the individual valves, 120 exterior surfaces (70.2%), but only 80 interior surfaces (46.8%), showed encrustation of greater than 10% coverage (Figure 2.8); the difference between the number of exterior and interior surfaces with this degree of encrustation is statistically significant ($p = 0.0243$). *Entobia* occurred on the exterior surface of 167 valves (97.7%) and on the interior of 154 valves (90.1%). Sponges encrusted significantly more area on the exterior of shells (24.7% exterior area, 14.2% interior area, $p < 0.001$), and was the most dominant encrusters in the assemblage in terms of intensity. The majority of *Gastrochaenolites* were found on 132 exterior surfaces (77.2%) with occurrences on only on 12 interior surfaces (7.0%); this result was statistically significant ($p < 0.001$). The bivalve borings covered significantly more exterior area than interior (1.4% exterior area, 0.08% interior area, $p < 0.001$). *Entobia* and *Gastrochaenolites* have a high frequency of co-occurrence on exterior surfaces (166 valves, 97.1%)

Polychaetes, including traces and body fossils, occur on the interior of 90 valves (52.6%) and on the exterior of 66 valves (38.6%) with a significantly greater percentage of areal coverage on the interior surface of the shells (0.39% interior area, 0.09% exterior area, $p = 0.0116$). *Talpina* is found on the interior surface of 21 vales (12.3%) and on the exterior surface of only one valve (0.6%), indicating phoronids bored significantly more on the interior ($p < 0.001$), also with a significantly greater percentage of areal coverage on interior surfaces (1.0% interior area, 0.01% exterior area, $p < 0.001$). Morphotype K is only found on the interior surface of 35 valves (20.5%, $p <0.001$) with areal coverage of 0.19%. Coral encrustation is only found on the exterior surfaces of three valves (1.8%) with areal coverage of 0.24%. Only one occurrence of an encrusting oyster was found on the interior surface of a single valve (0.58%) with areal coverage of 0.003%.

Right vs. Left Valves. – The 171 valves analyzed in this study were comprised of 90 left and 81 right valves. Sponges and bivalves showed a higher percentage of borings on the left valves than the right, and the same is true for the left exterior surfaces (Figure 2.6); however, these differences were not statistically significant. Polychaetes, phoronids, and Morpho K showed no statistically significant difference between the left and right valves. The occurrences of corals and oysters, while low, also showed no preference between the right and left.

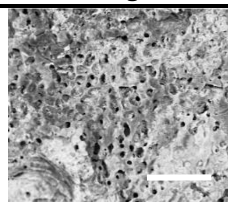
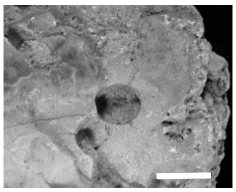
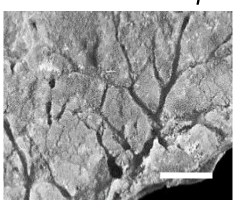
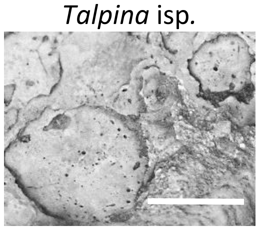
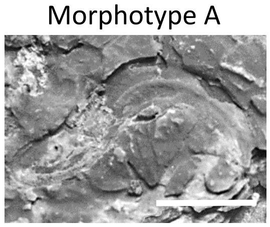
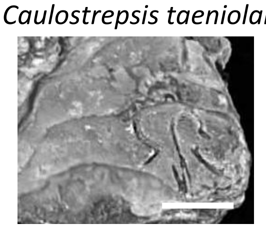
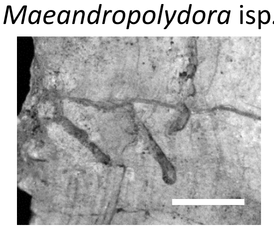
Encrusting Trace	General Features	Reference
 *Entobia* isp.	Small, circular apertures, on the surface ~1 – 2 mm in diameter, deep-tier network of chambered borings. Scale bar: 10 mm	Gibert et al. 1998, Bronn 1837, Gibert et al. 2007
 *Gastrochaenolites lapidicus*	Narrow Round aperture with a round – oval chamber, typically ~10mm in diameter, max 20mm Scale bar: 10 mm	Kelly and Bromley 1984, Gibert et al. 1998,
 *Talpina* isp.	Branching borings of consistent cylindrical diameter showing a systematic pattern and opening at regular intervals Scale bar: 10 mm	Bromley 1994, Parras and Casadío 2006
 Morphotype A	Circular to irregularly shaped scar, ~1 mm in depth, 3 – 20 mm in diameter with scalloped edges Scale bar: 10 mm	
 *Caulostrepsis taeniolar*	U-shaped borings separated by distinct vane. Cross section is flattened, with diameter 3 – 5 mm. Scale bar: 10 mm	Clarke 1908, Parras and Casadío 2006, Bromley and D'alessandro 1983
 *Maeandropolydora* isp.	Long, narrow, cylindrical borings, may be fused or unfused to each other and run parallel or in loops, 0.4 – 1.5 mm in diameter Scale bar: 5 mm	Bromley 1994, Barrier and D'Alessandro, 1985, el-Henedy 2007, Bromley and D'Alessandro, 1983, Parras and Casadío 2006
 *Trypanites* isp.	Circular cross section, relatively straight, rectilinear borings, 1 – 3 mm in diameter. Scale bar: 10 mm	Mägdefrau, 1932, Romero et al. 2017, Gibert et al. 1998

Figure 2.4. (Page 52) Taxonomic composition of the encrusting traces found *Hyotissa hyotis* from the Latrania Formation in Ocotillo, California.

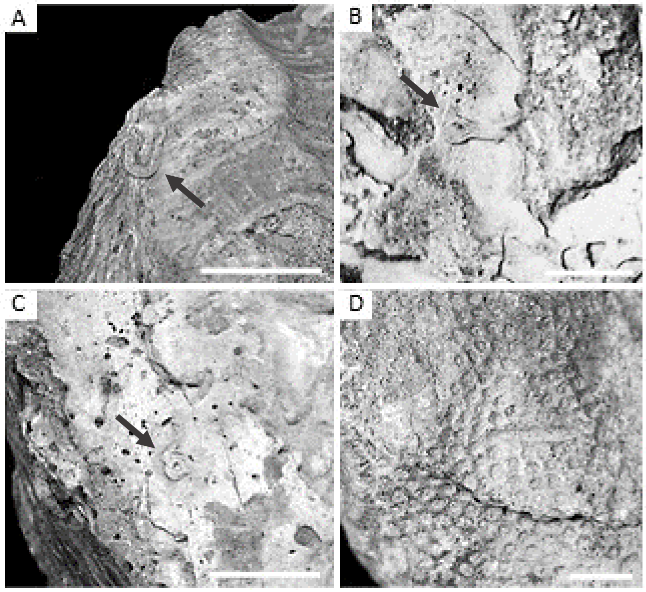


Figure 2.5. Body fossils found on the *Hyotissa hyotis* oysters. **A**) Serpulid worm tube. **B**) Serupid worm tube. **C**) *Spirorbis* sp. **D**) Coral, *Solenastrea* sp. Scale bar = 10 mm.

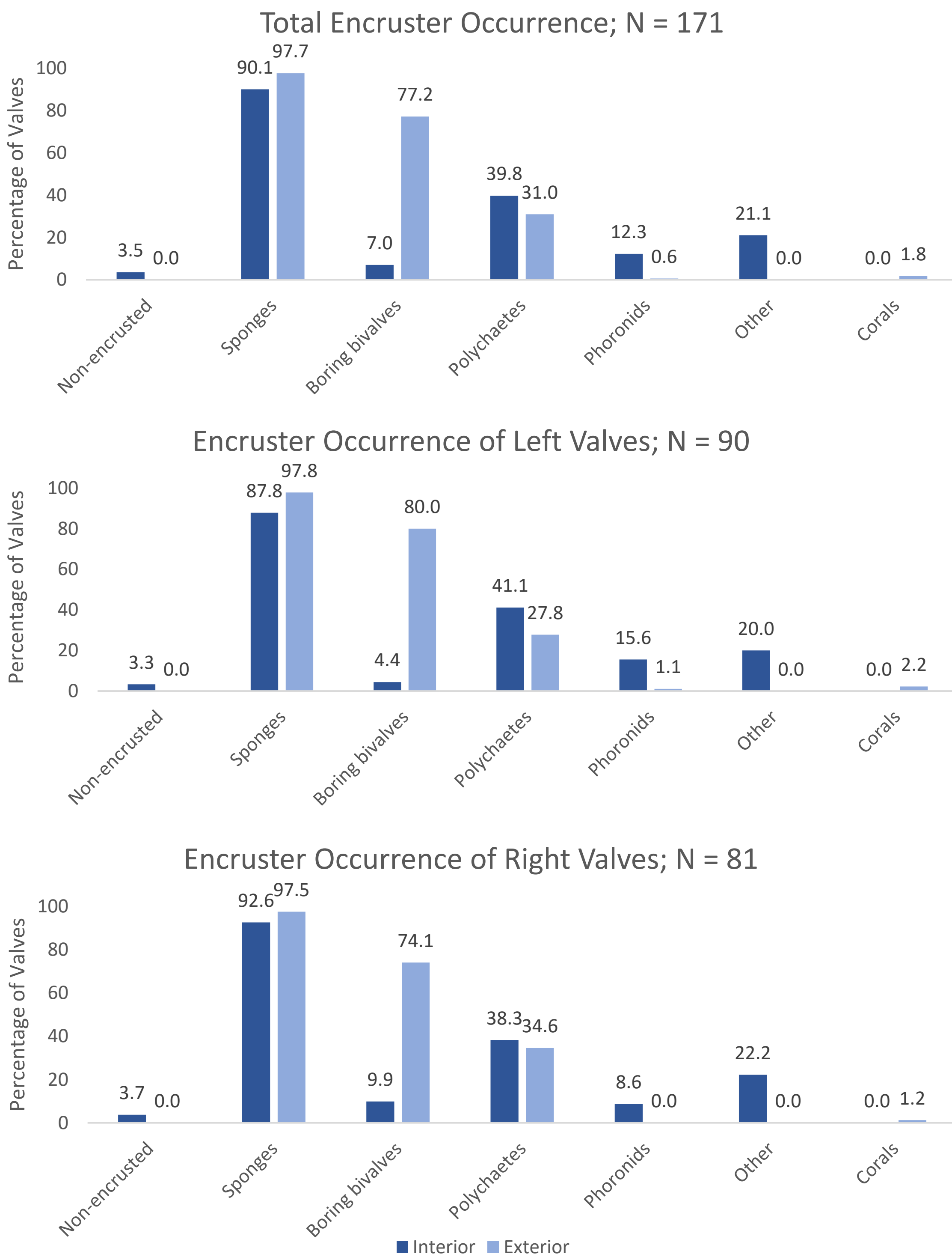


Figure 2.6. Distribution of encrusting organisms on the interior and exterior surfaces of the valves.

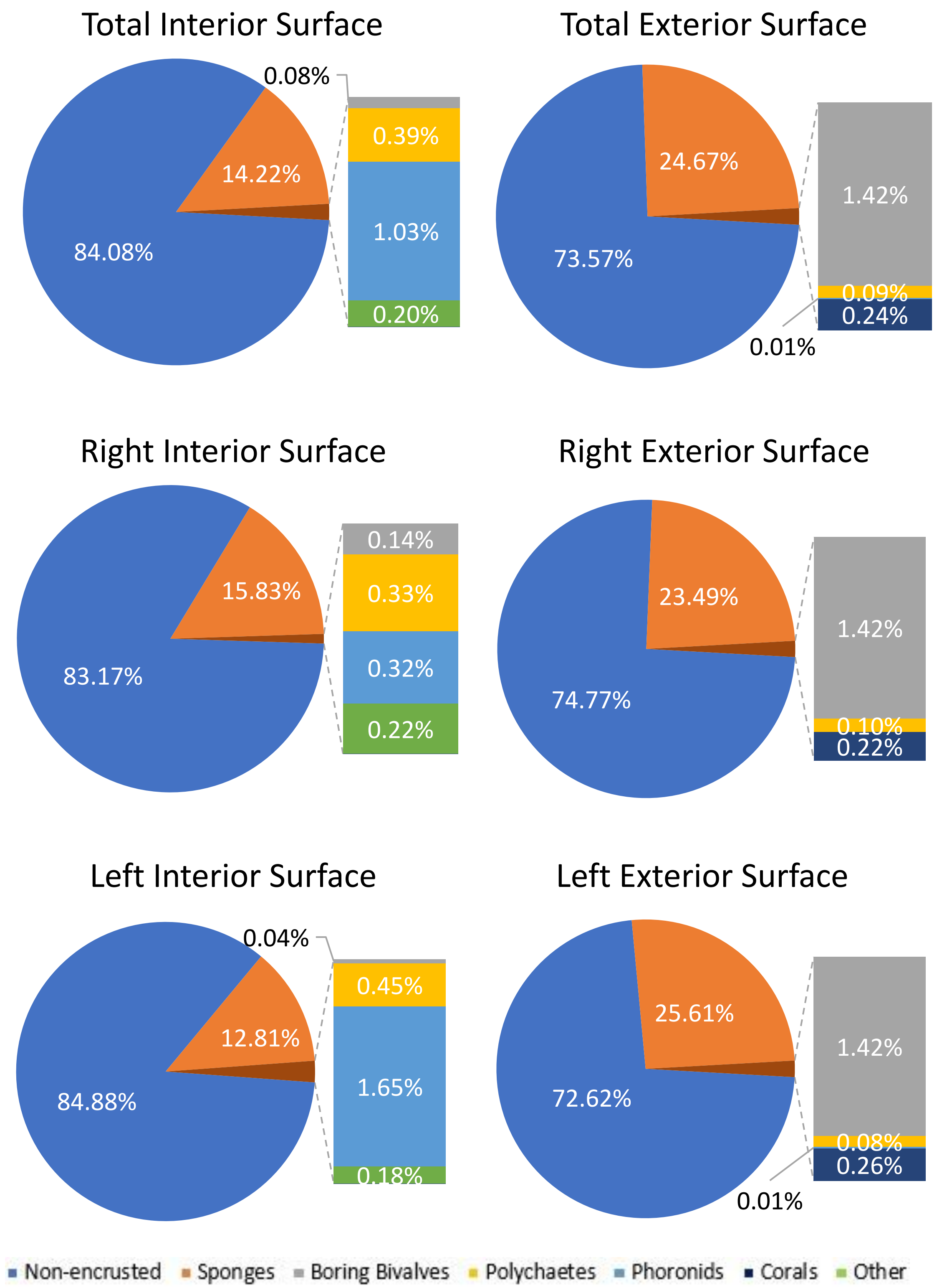


Figure 2.7. Coverage of the encrusting organisms on the *Hyotissa hyotis* by percent area.

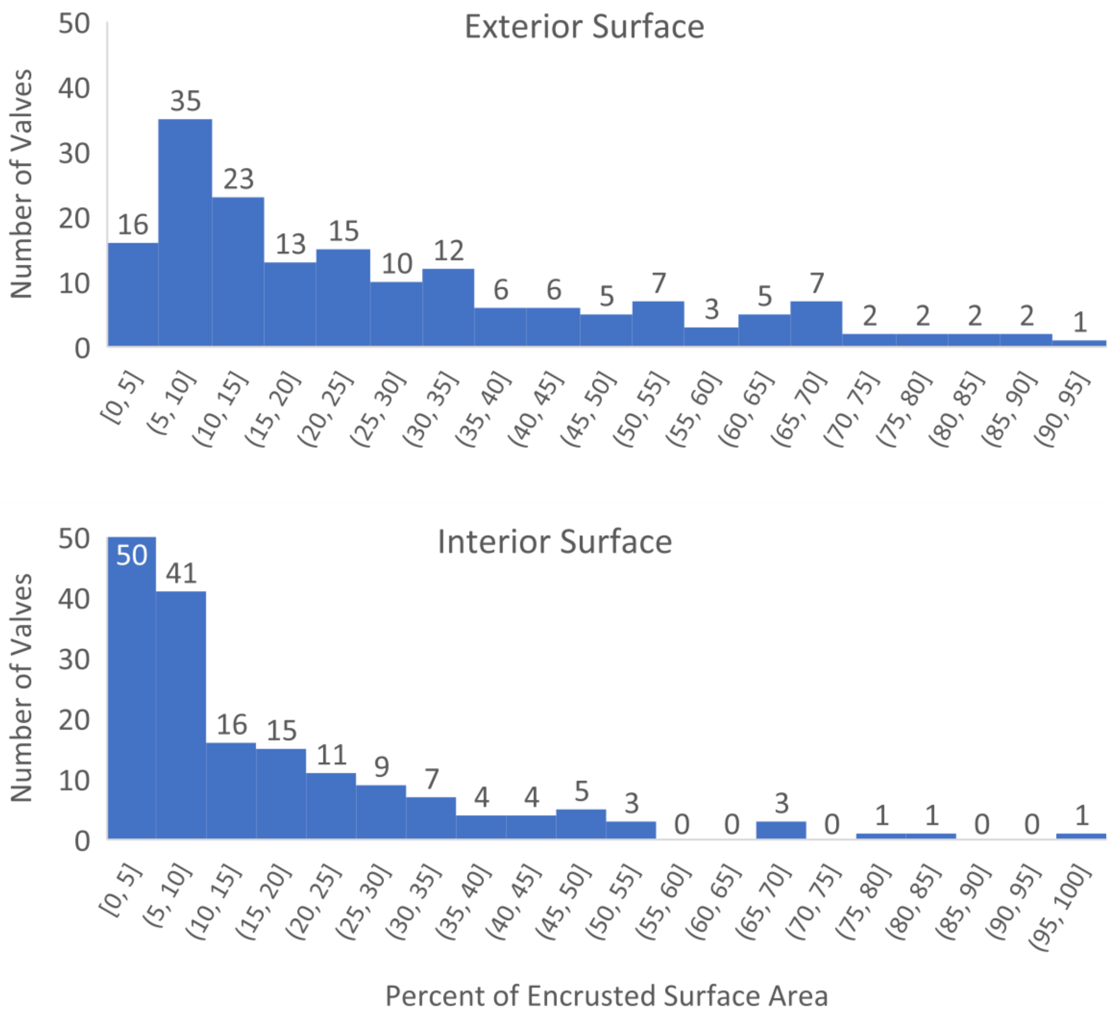


Figure 2.8. Histograms depicting the exterior vs. interior valve surfaces binned by percent coverage of encrustation.

DISCUSSION

Diversity

The previously reported taxonomic diversity of the Andrade Member of the Latrania Formation consisted of *Hyotissa hyotis*, and *Dendostrea* oysters, *Porites*, *Solenastrea*, and *Siderastrea* corals, and bivalves and gastropods such as *Vermicularia* and pectinids (Kidwell 1988, Winker and Kidwell 1996). Kidwell (1988) noted the encrustation of the *H. hyotissa* by sponges and serpulid worms. This study's in-depth look at the encrusting organisms of this assemblage added an additional clade, the phoronids, and significantly increased the diversity within the polychaetes, indicating that the Latrania Formation represents a more diverse and complex ecosystem that previously suggested.

Interior vs exterior/chronological interactions

The sequence of ecological interactions between encrusters and their hosts is a question often posed by paleoecologists. An exceptionally high number of both interior and exterior surfaces of the *Hyotissa hyotis* exhibit some degree of encrustation indicating that encrustation occurred pre- and postmortem. The encrusting intensity on the exterior surfaces of the oyster valves is significantly higher than on the interior surfaces of the valves. This is consistent with premortem exterior encrustation. Postmortem, the continued exposure at the water-sediment interface allowed for continued external encrustation, and despite the lower intensity, encrustation was common on the interior surfaces of the oysters by a variety of organisms, including sponges, phoronids, and polychaetes. The quantity of encrustation on the interior surfaces suggests that the shells were exposed to the water-sediment interface for periods on the order of ecological timescales. Sclerobionts and their trace fossils found on the interior surface of a shell indicates postmortem encrustation of the shell; the decomposition of the organic material exposes the interior surface of the mollusk (Luci 2014). Traces on the interior surface of shells made by parasites, such as trematodes, occur *in vivo* and are an exception (Huntley and Scarponi, 2021); however, the trace fossils in this study do not appear to have been cause by a parasitic infection.

The analysis of the spatial distribution and areal coverage of the encrusters on the interior and exterior surfaces of the oysters in this study tested the model of sediment starvation in the Latrania Formation presented by Kidwell (1988). Kidwell suggested, based on the sedimentological evidence combined with an analysis of the faunal composition of the shell beds, that the *Hyotissa hyotis* beds represent the sediment-starved seaward edge of the fan-delta complex of the proto-Gulf of California. The distribution of encrusters on the interior and exterior surfaces and the pattern of encrustation intensity suggest that sedimentation rates were slow enough to account for the valves being exposed at the sediment-water interface for ecological timescales.

Ichnofacies

Entobia and *Gastrochaenolites* co-occur in the Latrania Formation. These dominant borings, common throughout the Neogene, are commonly found with *Trypanites* and other polychaetes trace fossils such as those made by *Maeandropolydora* and *Caulostrepsis,* and are characteristic of the *Entobia* ichnofacies described by Bromley and Asgaard (1993). The deep tiering of the *Entobia* ichnofacies is indicative of long-term bioerosion resulting from extended periods of low sedimentation rates, and thus delayed burial. This continued activity of deep-tiering encrusters subsequently resulted in the overprinting, or destruction, of any traces left by early-colonizing, shallow-tiering encrusters. Physical abrasion, or the combination of abrasion and continued bioerosion, alternatively explains the absence of shallow-tiered traces in this oyster assemblage (Bromley and Asgaard, 1993; Gibert et al., 1998). The identification of this assemblage as an *Entobia* ichnofacies further supports the model of low sedimentation in the Latrania Formation.

Encrustation in the Latrania Formation

This study of *Hyotissa hyotis* shows a pattern of encrustation similar to other large oysters of the Miocene and Pliocene. Many studies of large Miocene-Pliocene oyster assemblages, including those with one lens-shaped valve and those more equivalved like *H. hyotis*, are dominated by *Entobia*, *Gastrochaenolites*, and various polychaete traces, indicative of the *Entobia* ichnofacies (Gibert 1998, Farinati and Zavala

2002, Parras and Casadío 2006, El-Hedeny 2007). Other studies, such as Gibert et al. (2007) and Romero et al. (2017), report Miocene-Pliocene oyster assemblages belonging to the *Gnathichnus* ichnofacies. *Gnathichnus* ichnofacies are dominated by *Gnathichnus* and *Radulichnus,* shallow-tier grazing traces such as those produced by echinoids and predatory gastropods. *Gnathichnus* ichnofacies reflect short-term encrustation in an environment with moderate energy.

Noticeably different from the findings of Gibert et al. (1998), Gibert et al. (2007), and El-Hedeny (2007), our study showed no indication of bryozoans. We also found no examples of algae, unlike Romero et al. (2017) who reported microalgal borings or Zuschin and Baal (2007) who reported crustose algae on a modern *Hyotissa hyotis* live-collected *in situ* from the Red Sea. Bryozoans and algae are shallow-tier borers, and if originally present at all on our assemblages, would not have been preserved due to the low sedimentation and long-term exposure to the sediment-water interface allowing deeper-tier borings to destroy them (Bromley and Agaard 1993). It is worth noting that there is a positive correlation between low primary productivity, abundant coralline algae, and lower biovolumes of sponges (Lescinsky et al. 2002, El Hedeny 2007). The absence of bryozoan and algal traces in this study is consistent with the strong intensity of *Entobia* and *Gastrochanolites,* an indication of high levels of primary productivity able to support the high biovolume of the encrusters in this assemblage.

Bivalve borings, primarily found on the exterior surfaces of the *Hyotissa hyotis*, indicate the bivalves encrusted *in vivo*. This is consistent with several studies of Miocene oyster reefs (Farinati and Zavala 2002, Parras and Casadío 2006). Interestingly, we found no significant difference between encrustation on the left and right valves of the *H. hyotis.* Zuschin and Baal (2007), and Romero et al. (2017), in their studies found that bivalves preferred the cryptic surface of the lower and more robust left valve. Conversely, Parras and Casidos (2006) found more boring bivalves on the lens-shaped right valves.

Many studies of Mio-Pliocene oysters typically report the preference of polychaetes on the exterior surfaces of oysters (Farinati and Zavala 2002, El-Hedeny 2007, Gibert et al. 2007), or in the case of Romero et al. (2017), reported no significant difference between coverage of polychaetes on the interior and exterior surfaces. This study reports the opposite; polychaete worms prefer to encrust the interior surfaces of the *Hyotissa hyotis* oysters. While Parras and Casidos (2006) found that the openings of *Maeandropolydora* borings more commonly occur on the exterior of the oyster valves, they also found abundant *Maeandropolydora* borings on the interior surfaces of right valves, consistent with our results. There are several possible reasons that polychaetes in this study preferred inhabiting the interior surfaces. The interior surfaces of the shells were exposed postmortem to the water-sediment interface for a period of time long enough for the settlement of polychaete worms (Bromley and Agaard 1993, Romero et al. 2017). The high intensity of sponge infestation on the exterior surface of the shells deterred the settling of these worms. Sponges are considered top spatial competitors that are rarely overgrown and prevent the settlement of other encrusters (Sears et al.

1990, Wulff 2006, Bell and Barnes 2003, Bell 2008). The chemical cues, such as metabolites, secreted from the sponges prevent the settlement of polychaete worms and other encrusting organisms; e.g., tunicates, barnacles, and bryozoans (Davis et al. 1991, Becerro et al. 1997, Hellio et al. 2005, Lee et al. 2006, Bell 2008). The abundance of the destructive, bioerosive sponges also could have overprinted any worm traces or body fossils (Bromley and Agaard 1993). Additional findings in this study support these latter two models; the sole occurrence of a sabellid worm is found on one of the rare examples of an exterior surface with no sponge borings, and phoronids, contrary to the findings of Parras and Casidos (2006), showed a significant preference for interior surfaces.

Assessing encrusting intensity

Areal coverage measurements are a useful tool for elucidating encrusting intensity. It is necessary combine taxonomic diversity with an assessment of intensity; simply taking inventory of the organisms within a community does not yield the best representation of the dynamics of an ecosystem. For example, sponge borings occurred on the majority of interior and exterior surfaces, yet have a significantly greater encrusting intensity on exterior surfaces. Bivalves are also shown to encrust a high number of valves, but cover only a small percentage of surface area.

Using areal coverage as a proxy for encrusting intensity has its limitations. The openings of worm borings are small and can lead to a fairly large network of borings within the calcium carbonate of the oyster valves. These networks can usually only be seen when a shell is broken or eroded (Gibert et al. 2007). Only measuring the external apertures of the borings may underrepresent the intensity of encrusters in the fossil record. In this study, many worm traces identified on the interior surfaces of the oysters were visible in places where laminae had flaked off, contributing to the higher areal coverage. Gibert et al. (2007) had success using x-ray radiography on a Pliocene oyster to see the networks and chambers of sponge borings and a *Caulostrepsis* polychaete worm. Using a combination of areal coverage and x-ray radiography as a tool to assess encrusting intensity deserves further application.

CONCLUSION

The abundant encrusting organisms and their trace fossils on the *Hyotissa hyotis* suggests that these oysters supported a diverse community of sclerobionts. The *H. hyotis* oyster assemblage is identified as an *Entobia* ichnofacies, predominantly containing *Entobia*, *Gastrochaeonolites,* and various polychaete worms and traces. *Talpina* also occurs, adding phoronids to the known clades that existed within this ecosystem. The encrustation of the *Hyotissa hyotis* occurred pre- and postmortem.

This study demonstrates that utilizing areal coverage measurements is a useful proxy for quantifying encrusting intensity. Combining taxonomic diversity with areal coverage yields a more accurate description of the dynamics of a hard substrate ecosystem then just the diversity alone. The analysis of the spatial distribution and areal coverage of the encrusters on the interior and exterior surfaces of the oysters in this study supports a model of sediment starvation in the distal to the fan-delta deposits of the proto-Gulf of California proposed by Kidwell (1988).

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CHAPTER 3

The record of encrusters on the modern bivalve *Mercenaria mercenaria* from Shelter Island, New York: Implications for bioerosion and fragmentation in ecological and paleoecological studies

ABSTRACT

The analysis of sclerobionts and their trace fossils provides a non-invasive approach to studying ecological relationships, capturing the interactions of soft-bodied organisms that may not otherwise be preserved in the modern and fossil records. Changing climates and human-induced ecosystem pressures warrant a need for baseline studies; herein, we report on the record of sclerobionts that inhabit the thick-shelled bivalves *Mercenaria mercenaria* from Shelter Island, New York, in the Peconic Bay, an estuary with a history of pollution and hypoxic bottom water conditions. We examined target-collected, disarticulated specimens of the *M. mercenaria* from this locality. To gain insight into this community of encrusting organisms, we analyzed occurrences and the areal coverage, a proxy for abundance, of sponges, polychaetes, bryozoans, barnacles, and molluscan attachment scars attributed to *Crepidula* sp. and *Anomia* sp. Encrustation occurred on the interior and exterior surfaces of the valves with similar intensities. The co-occurrence of both deep- and shallow-tiered borings indicates that the shells were exposed predominantly to a low energy environment, with periodic reworking events, at the subtidal water-sediment interface on the order of ecological timescales. We found that it takes only minimal bioerosion to weaken shells, making them highly susceptible to taphonomic damage in the fossil record. We assessed the utility of using fragmented shells for community studies involving encrusters. We found no added benefit by including heavily fragmented shells with complete shells. If

primarily complete valves are not available, we suggest that utilizing valves that are greater than 50% complete will yield robust results.

INTRODUCTION

Sclerobionts, encrusting epibionts and bioeroding endobionts (Taylor and Wilson 2002) hereafter referred to as encrusters, are a phylogenetically diverse and an ecologically important functional group of filter feeders. These encrusters represent a surprisingly significant percent of biomass and diversity in many marine communities (Taylor and Wilson 2003). Encrustation on hard-substrates can provide habitat, protection, and food for other marine organisms (Auster et al., 1995; Steimle and Zetlin, 2000, Diaz et al., 2003; Scharf et al., 2006, Mercaldo-Allen et al. 2020). Some encrusters, e.g., calcified serpulid worms and barnacles, can be preserved as body fossils, but other encrusters leave only a robust record of trace fossils, providing indirect evidence of behavior patterns and interactions of the trace-makers within an ecosystem (Ishikawa and Kase, 2007). Because of the lack of body fossils, soft-bodied organisms, such as sponges, can be underrepresented in the fossil record. Examining the trace fossils of these organisms can bring a more comprehensive understanding of paleoecological systems (Frey 1975, Taylor and Wilson 2003).

Encrusters are an integral part of modern ecosystems. Some, like sponges, remove large amounts of organic matter from the water column through filter feeding (Taylor and Wilson 2003), providing the ecosystem service of filtering water and enhancing water quality through the reduction of pollutants (Rich et al. 2016). The degree of encrustation on mollusks is an indicator of nutrient levels and primary productivity (Voight and Walker 1995, Lescinsky et al. 2002). Grazing by encrusters is a natural control on eutrophication and a primary mechanism that removes planktonic particulate matter from the water, thus controlling phytoplankton populations (Cloern 1982, Officer et al. 1982, Ostroumov 2002). The study of encrusting organisms also has economic relevance: encrusting organisms have a propensity for bivalves and significant biofouling can cause problems for commercial aquaculture (Almeida et al. 1996, Caceres-Martinez et al. 1998, Handley 1998, Igic 1972, Korringa 1954, Thangavelu and Sanjeevaraj 1988).

Encrusters are preserved *in situ,* retaining their spatial relationship to their molluscan hosts (Luci and Cichowolski 2014, Luci and Lazo 2015, Liddell & Brett 1982, Taylor and Wilson 2003). Often overlooked, they are easily assessed and appropriate for community studies involving abundance, diversity, distribution, stability within ecosystems and elucidating biological sensitivity to changing climatic conditions (Foster and Buckeridge 1987). Encrusting organisms, tracking environmental changes and the migration of their host taxa into new habitats (Rodland et al. 2006), have already been used in studies of sensitivity to climate change, a principal driver of the geographic distribution of taxa and marine many organisms. For example, Blight and Thompson (2008) found that species richness of encrusters in kelp assemblages was sensitive to changing climates. Ortega et al. (2016) showed that as sea surface temperatures increased, the infestation by encrusters increased, negatively impacting host species of bivalves in Uruguay.

Thus, establishing an ecological baseline for marine communities has become an important agenda of conservation biologists and paleobiologists (Dietl et al. 2015, Dietl and Flessa 2011, Harding et al. 2008, Harding et al. 2010, Kusnerik et al. 2018). A major disruption of any part of a marine ecosystem could have significant impacts on global and local environments and economies (Hoegh-Guldberg et al. 2007). A need exists for baseline studies that specifically investigate encrusting organisms.

Peconic Bay

Long Island Sound (LIS) is an estuary located between the urban setting of New York City, Long Island, and Connecticut. Societally and economically important, the LIS has been used for transportation and fishing, both recreational and commercial (Andersen 2002, EPA 1998, Casey et al. 2014). Pollution, caused by agricultural runoff, urban sewage and garbage runoff, and industrial waste is a chronic problem affecting marine life in the LIS and has led to hypoxic and periodic anoxic conditions and eutrophication, a driver of toxic algal blooms (Parker and O'Reilly 1991, O'Shea and Brosnon 2000, Casey et al. 2014, Hoellein and Zarnoch 2014, Mackenzie and Tarnowski 2018). Changing climate is also a concern for the LIS. Estuarian marine organisms, already exposed in a range of fluctuating water temperatures, are extremely sensitive to temperature variations, such as those induced by climate warming. Recent evidence showing changes in abundance, diversity, distribution, and increased instances of disease in invertebrates have been well documented in estuaries (Bricker et al. 2008, Collie et al., 2008; Howell and Auster, 2012; Hoellein and Zarnoch 2014, Crosby et al., 2018, Roxanna 2018, Mercaldo-Allen et al. 2020).

The Peconic Bay, near the LIS, but not as widely studied, shares many of the same issues that negatively impact the LIS, such as pollution from nitrogen runoff and hypoxia (NYSDEC 2007). The Peconic Bay, lying between the North and South Forks of Long Island, is an estuary primarily fed by the Peconic River. Shelter Island lies in the eastern portion of the Peconic Bay, also known as Little Peconic Bay, and separates the Peconic Bay from Gardiners Bay, a small branch of the Atlantic Ocean. In this time of changing climates, toxic algal blooms, and ecological pressure from over-fishing, studies documenting the record of encrusters in the Peconic Bay are critical.

Mercenaria mercenaria

Mercenaria mercenaria, also known as the hard clam or northern quahog, is prevalent in inshore regions along the east coast of North America, and found at water depths of <1m–36m (Meldahl and Flessa 1990, Stiles et al. 1991, Turgeon et al. 2009). Environmentally sustainable and economically important, these bivalves are frequently used in aquaculture and have been farmed in the US since the 1970s (NOAA 2021, Zeng and Yang 2021). *Mercenaria mercenaria* is the subject of many studies related to water quality, temperature reconstruction, resource management and population dynamics

(Walker and Tenore 1984, Jones et al. 1989, Weiss et al. 2007, Casey et al. 2014, Jones et al. 2014). Research conducted on *M. mercenaria* in the context of providing a hard-substrate habitat for encrusters is limited. *M. mercenaria* is an infaunal bivalve and the encrustation found on both the interior and exterior surfaces is interpreted to be postmortem (Taylor and Wilson 2003). The *M. mercenaria* found in Peconic Bay provides an excellent opportunity to study the encrusting organisms that live on these bivalves, gaining insight into the ecology of this benthic community.

Previous studies have been conducted on encrusting organisms that inhabit *Mercenaria mercenaria.* Meldahl and Flessa (1990) examined the encrustation on *M. mercenaria* from Cape Cod, Massachusetts, along with other taphonomic factors, such as abrasion and corrosion. Using the occurrences of encrusters, they describe the taphonomic pathways of shelly assemblages, a bioerosion-dominated pathway indicative of the low-energy environments of the upper intertidal and deeper subtidal, and an abrasion-dominated pathway indicative of the high-energy environments of the lower intertidal and shallow subtidal. Using only whole *M. mercenaria* valves in their study, Meldahl and Flessa (1990) recorded occurrence, but not percent coverage of encrusters, nor did they assess the differences of encrustation on the interior and exterior surfaces of the valves. McKinney (1996) examined the encrusters on *M. mercenaria* and the oyster *Crassostrea virginica* from the Bogue Sound, North Carolina. McKinney (1996) determined that differing patterns of encrustation found on the shells was driven by the morphological differences between the two bivalves. Bogue Sound is a nitrogen-limited area with moderate nutrient levels, a stark contrast to the high levels of nitrogen recorded in the Peconic Bay (NSY DEC 2007).

Shell Breakage

The ability of bioeroding encrusters, like sponges and boring polychaete worms, to impact the fossil record by weakening and destroying shells has been well-documented (Kent 1981, Bromley 1994, Taylor and Wilson 2003, Best et al. 2007, Wilson 2007). Assemblages comprised of shell fragments are so prevalent in the fossil record that several studies have developed taphonomic frameworks for assessing the proportion of fragmented shells within a fossil assemblage as a means for elucidating energy, transport, and sedimentation rates (Brett and Baird 1986, Kidwell et al. 1986, Flessa et al. 1993). However, there is no universal rule for using fragmented bivalves in paleoecological studies (Daley 2017), nor is there consensus for what is classified as a shell complete enough for inclusion in such studies (e.g., Davies 1990, Hattori et al. 2014, Daley 2017, Cronin et al. 2018). Questions persist as to the relationship between bioerosion and the location on the shell where fracturing occurs, and whether it is appropriate and reliable to use individual fragmented shells for ecosystem community studies. A need exists to better understand the implications of including fragmented molluscan shells in studies focusing on encrusting organisms.

Objectives

The primary objective of this study is to examine the encrusting organisms that inhabited an assemblage of modern *Mercenaria mercenaria* from the coastline of Shelter Island, New York. A further objective is to examine the extent to which the distribution of bioeroders on the shells of this *M. mercenaria* assemblage have contributed to the occurrence of breakage through the shells. We will analyze and compare of the diversity and abundance of encrusting organisms on fragments and whole valves of *M. mercenaria* to assess whether using fragmented shells is appropriate for ecological, and paleoecological, studies on encrusters.

MATERIALS & METHODS

A total of 349 primarily disarticulated valves and fragments of the bivalve *Mercenaria mercenaria* were collected and examined. The shells were target-collected below the high tide mark, during low tide from the shoreline of Smith Cove on Shelter Island, New York (Figure 3.1). Smith Cove in Little Peconic Bay faces the South Fork of Long Island. All shells that could be confidently assigned as *Mercenaria mercenaria* were collected within a 200-meter section of the beach. The shells and their fragments ranged in size from 35mm to 140mm in length.

Specimens were cleaned by gently rinsing with water. To ensure proper identification, only the valves and fragments that were more than 25% complete were included in this study. A visual approximation of the completeness of the shells and the fragments was conducted and the shells were placed into bins; e.g., >75% complete, 50–74% complete, 25–49% complete.

Each valve was examined using up to 30x magnification. Encrusters and borings visible to the naked eye were counted (approximately > 0.25mm). The encrusters were identified by the ichnotaxon their activity produced or, in the case of body fossils, to lowest taxonomic rank possible. The presence of encrusters on the interior and exterior surfaces of each valve was recorded. Multiple incidences of one type of taxon or trace on a valve were counted as a single occurrence. The position of the encrusters, either on the interior or exterior surface of the valve, was also recorded.

The interior and exterior of each valve was photographed and the ImageJ Software Package was used to calculate the area occupied by each encruster on the valves in terms of the percentage of the total surface area. This areal coverage was used to determine the intensity of encrustation, a proxy for abundance. The difference in occurrence and areal coverage between binned groups was assessed.

The shells were assessed for breakage. Fragments and valves with large chips or missing sections of shell material were categorized as demonstrating breakage. Of the shells with breakage, whether or not the shell exhibited destructive bioerosion, from either sponge or polychaete borings, and the surface of the valve containing the bioerosion, either the interior or exterior, was recorded. It was also noted if the breakage on the shell occurred completely through, partially through, or not at all through an encruster (Figure 3.2). If bioerosion was found along the entire broken edge, this breakage was considered to be completely through an encruster. If bioerosion was found along only a portion of the broken edge, this breakage was considered to be partially through an encruster. If no bioerosion was found along the broken edge, this breakage was considered to be not at all through an encruster. The results were analyzed statistically using the Chi-squared and Kruskal-Wallis tests in the Paleontological Statistics Software Package (PAST).

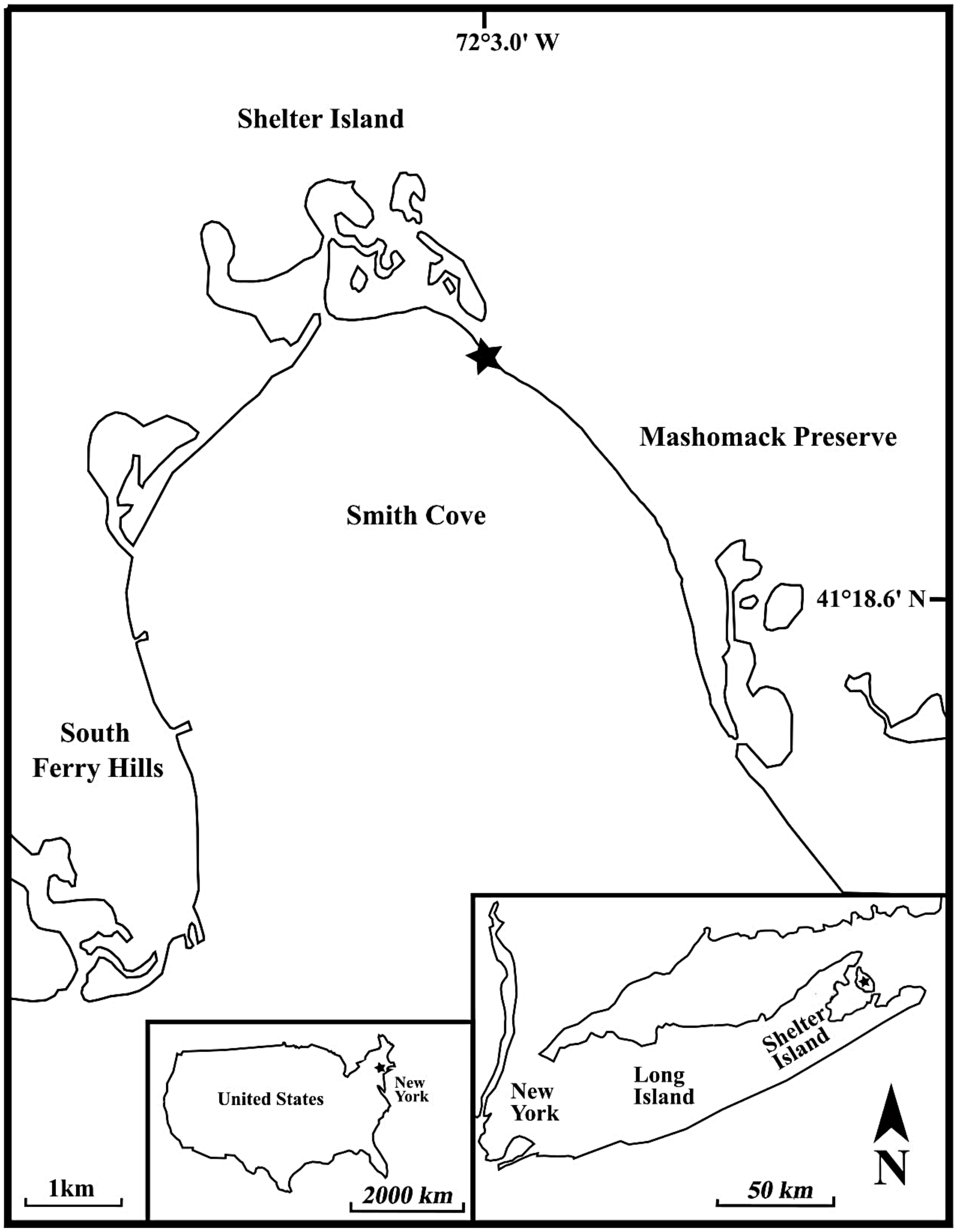

Figure 3.1. Locality map depicting the collection area along the shoreline of Smith Cove on Shelter Island, New York.

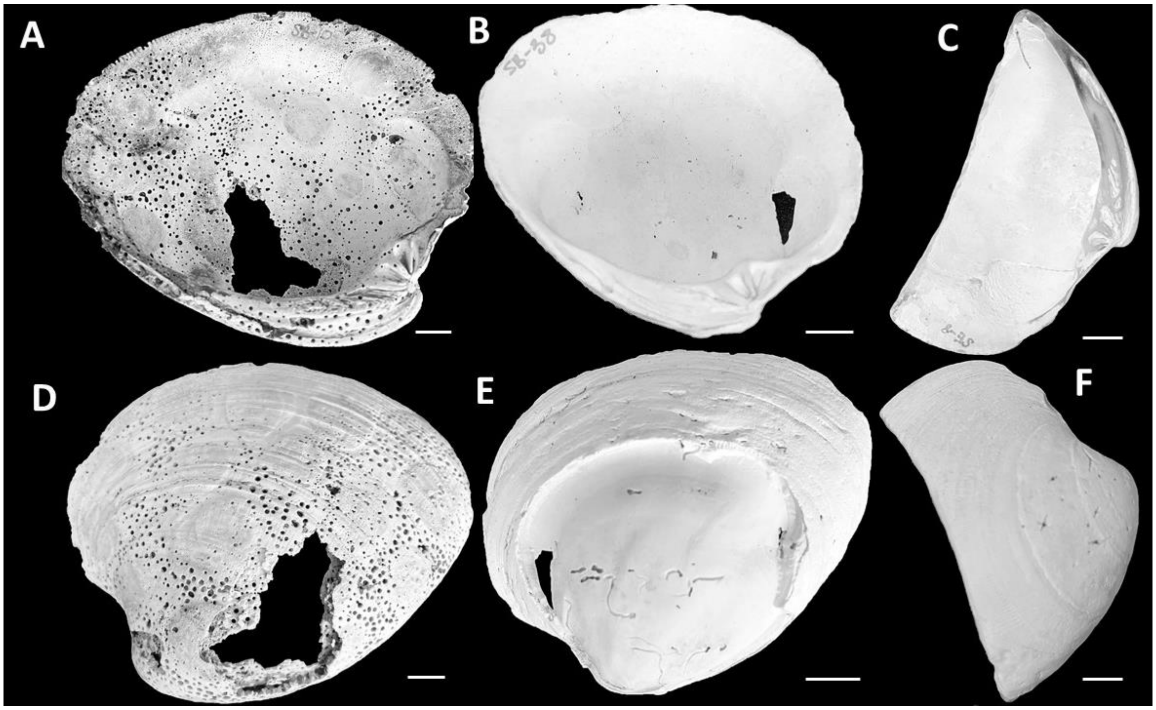

Figure 3.2. Examples of breakage through bioerosion on *Mercenaria mercenaria* valves. A) Breakage completely though sponge borings on interior surface. B) Breakage not through bioerosion on the interior surface. C) Breakage not through bioerosion on the interior surface of a shell fragment. D) Breakage completely though sponge borings on exterior surface. E) Breakage partially through polychaete worm borings on the exterior surface. F) Breakage not through bioerosion on the exterior surface of a shell fragment. Scale bar = 10mm.

RESULTS

Composition of the Mercenaria Community

A total of five groups of taxa were found encrusting 349 valves and fragments of *Mercenaria mercenaria*. Evidence for encrustation was found in the form of trace fossils and body fossils (Figure 3.3). Of the examined shells, 66.8% showed some occurrence of encrustation. The trace fossil *Entobia,* inferred to be made by clionid sponges (Taylor and Wilson 2003), was the most common encruster occurring on 43.0% the bivalves. Polychaete worms, represented by three ichnogenera, evidenced by fossil borings, and the calcified body fossils of serpulids, were the second most dominant taxa, occurring on 37.5% of the shells, and the most diverse taxonomic group of encrusters. Polychaete borings, found on 33.8% of shells, were more common than body fossils, found on only 5.2% of shells. Molluscan attachment scars, inferred to be made by *Crepidula* sp. and *Anomia* sp., were identified on 12.0% of the shells. Bryozoans and barnacles were rare and found on 3.7% and 0.9% of shells respectively.

Distribution – Interior vs. Exterior

Encrustation occurred on 217 of the interior surfaces (62.2%) and 179 of the exterior surfaces (51.3%; Figure 3.4). The areal coverage of encrustation represents 20.3% of the total interior surface area and 22.2% of the exterior surface area of the shells (Figure 3.5). Of the total shell count, 170 interior surfaces (48.7%), but only 76 exterior surfaces (21.8%), showed encrustation of greater than 5% encrustation coverage (Figure 3.6); the difference is statistically significant ($p < 0.0001$). Sponge borings occurred significantly more on the interior surface of the shells (139, 39.8%) than on the exteriors (101, 28.9%, $p = 0.0342$). Sponges encrusted significantly more area on the interiors of shells as opposed to the exteriors (14.5% interior area, 10.8% exterior area, $p = 0.0016$), and were the most dominant encrusters in the assemblage in terms of intensity. The occurrences of polychaetes on the interior and exterior surfaces were similar on both, 28.4% and 27.2% respectively. Polychaetes covered a greater percentage of area on the exterior surfaces. Bryozoans occurred significantly more frequently on the interior surfaces (3.72% interior occurrence, 0.29% exterior occurrence, $p = 0.0015$), covering significantly more interior surface area (0.56% interior area, 0.07% exterior area, $p = 0.0012$). The occurrences of attachment scars were found consistently on both the interior and exterior surfaces, 8.31% and 7.16% respectively. The rare occurrences of barnacles are only found on interior surfaces.

Breakage through Bioeroders

Breakage was found on 305 of the 349 shells (87.4%). Of the 171 shells exhibiting destructive bioerosion from either sponges or polychaete borings on the exterior surfaces, 130 shells (76.0%) demonstrated breakage and the breakage occurred completely through a bioeroder on 76 shells (58.5%), partially through a bioeroder on 37 shells (28.5%), and not through any bioeroder on 17 shells (13.1%, Table 3.1). Of the 196 shells with destructive bioerosion on the interior surfaces, 127 shells (64.8%)

demonstrated breakage. The breakage occurred completely through a bioeroder on 73 shells (57.5%), partially through a bioeroder on 42 shells (33.1%), and not through any encrusters on 12 shells (9.4%). Breakage occurred completely or partially through a bioeroder on 100 shells that were encrusted on both the exterior and the interior surfaces, but only rarely did a bioeroder appear to completely penetrate the shell. On shells with destructive bioerosion on either the exterior or interior surfaces, breakage occurred more often completely or partially through the bioerosion; in both cases, these results are statistically significant ($p < 0.0001$). In only one example on an exterior surface (0.8%), and two examples on the interior surfaces (1.6%), breakage did not occur through a bioeroder; these results are also statistically significant in both cases ($p < 0.0001$).

Fragments vs. Whole Shells

The bin containing the valves that were 75–100% complete was compared to the groups binned as 25–100%, 25–49%, and 50–74% complete (Table 3.2). Among all four bins, there was no variation in the number of taxonomic groups identified. No additional taxonomic groups were observed when fragments were included in the 25–100% group and no taxonomic groups were lost when looking at only the fragments in the 25–49% and 50–74% complete groups. Of the compared bins, encrustation overall and the sponges had the most instances of statistical differences from the corresponding other bins made up of, or including, the fragments in terms of occurrence and areal coverage. The polychaetes and the barnacles showed no statistical difference between bins for either occurrence or areal coverage. Of the comparison between the 75–100% and 25–100% completion bins, only one instance between the sponges on the exterior surfaces, showed a statistical difference in taxonomic occurrence. Encrustation overall demonstrated the most instances of significant difference for areal coverage between the different bins for both the interior and exterior surfaces. In terms of areal coverage, comparison of the 75–100% and 25–49% completion bins showed the most statistical difference and comparisons of the 75–100% and 50–74% completion bins showed the least statistical difference. The areal coverage comparisons of the 75–100% and 25–100% bins also showed lower instances of statistical difference; only the exterior sponges were statistically different.

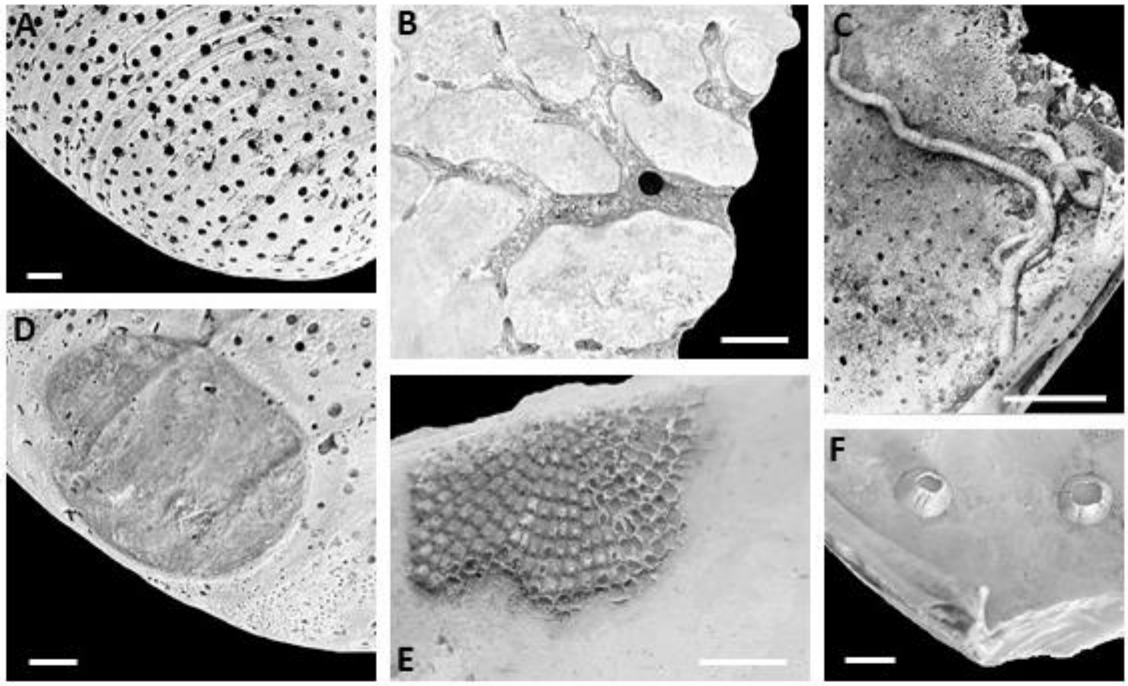

Figure 3.3. Examples of encrusters that use *Mercenaria mercenaria* as a hard substrate. A) Clionid sponge boring. B) Polychaete worm boring. C) Tubes made by serpulid worms. D) Attachment scar made by *Crepidula* sp. E) Cheilostome bryozoans. F) Barnacles. Scale bar = 5mm.

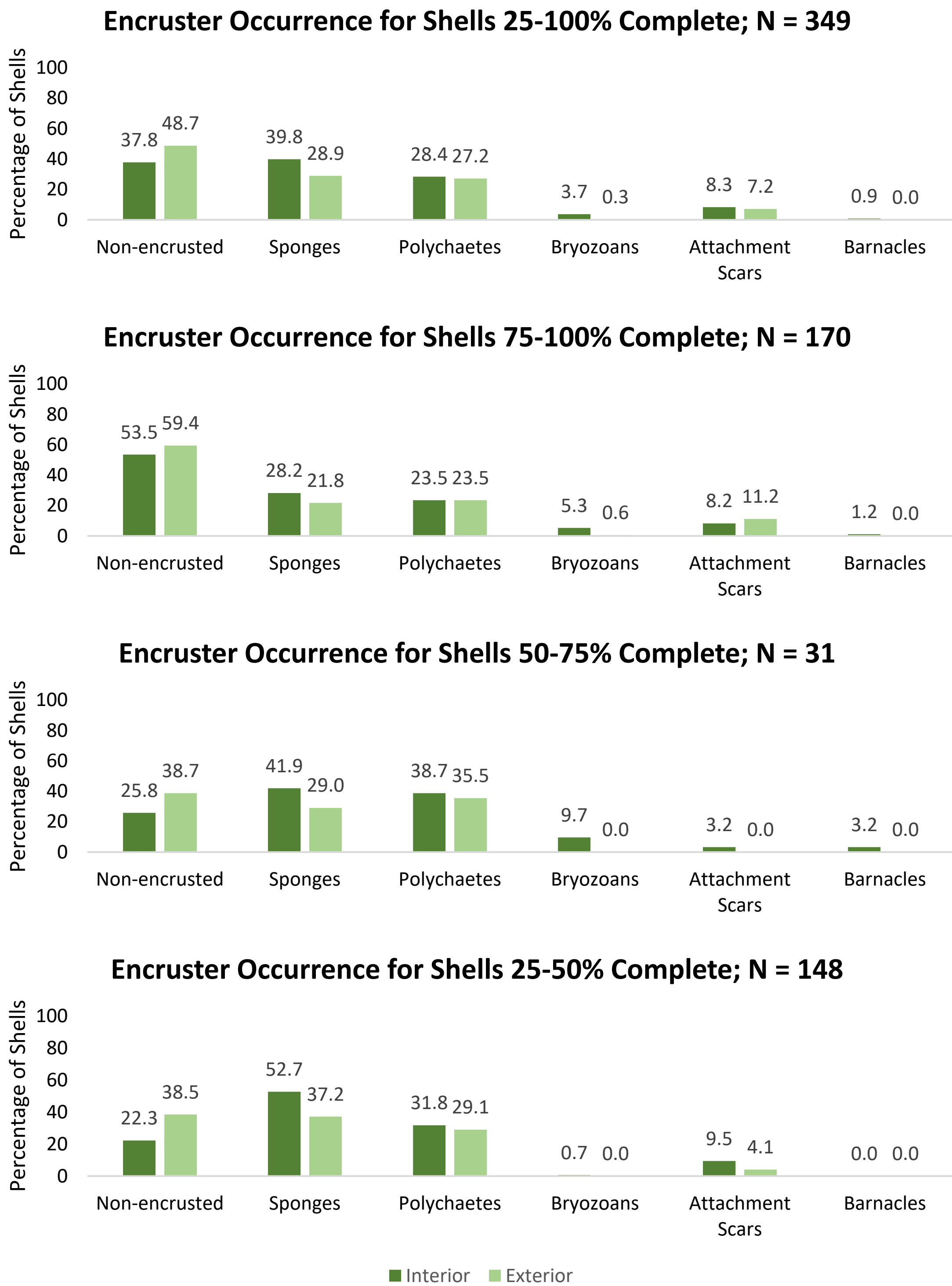

Figure 3.4. Distribution of encrusting organisms on the interior and exterior surfaces of the valves for the groups binned by percent of shell completion.

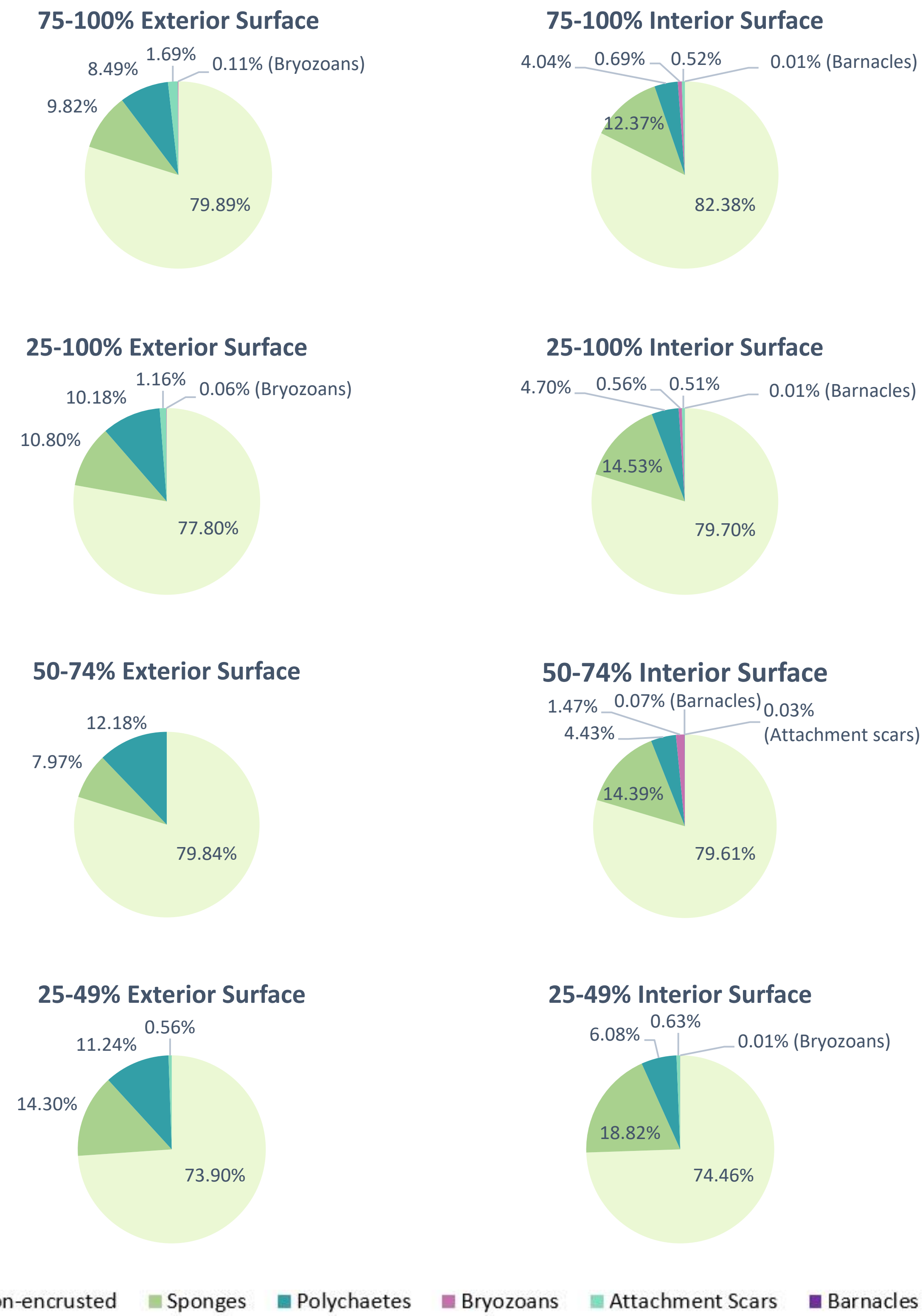
75-100% Exterior Surface
8.49%
1.69%
0.11% (Bryozoans)
9.82%
79.89%
75-100% Interior Surface
4.04%
0.69%
0.52%
0.01% (Barnacles)
12.37%
82.38%
25-100% Exterior Surface
10.18%
1.16%
0.06% (Bryozoans)
10.80%
77.80%
25-100% Interior Surface
4.70%
0.56%
0.51%
0.01% (Barnacles)
14.53%
79.70%
50-74% Exterior Surface
12.18%
7.97%
79.84%
50-74% Interior Surface
1.47%
0.07% (Barnacles)
0.03% (Attachment scars)
4.43%
14.39%
79.61%
25-49% Exterior Surface
11.24%
0.56%
14.30%
73.90%
25-49% Interior Surface
6.08%
0.63%
0.01% (Bryozoans)
18.82%
74.46%
Non-encrusted
Sponges
Polychaetes
Bryozoans
Attachment Scars
Barnacles

Figure 3.5. (Page 90) Coverage of the encrusting organisms on the *Mercenaria mercenaria* by percent area and binned by shell completion.

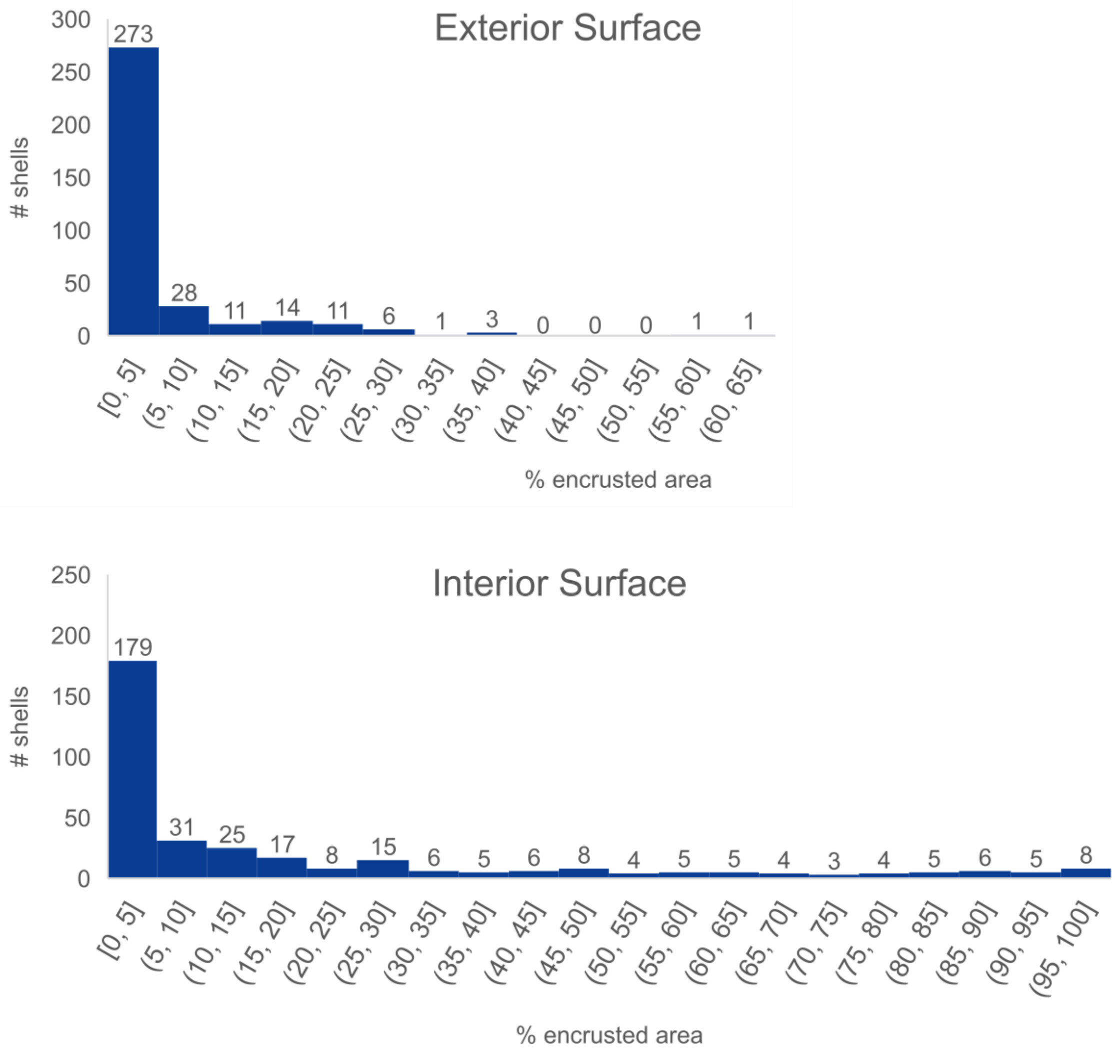

Figure 3.6. Histograms depicting the exterior vs. interior valve surfaces binned by percent coverage of encrustation.

Table 3.1. Distribution of the shells exhibiting breakage and evidence of destructive bioerosion on the exterior and interior surfaces. Denotes if the breakage occurred completely, partially, or not at all through a bioeroder.

	BIOERODERS	COMPLETELY	PARTIALLY	NOT AT ALL
EXTERIOR SURFACES WITH BIOEROSION	Total	76	37	17
	Sponges	45	22	1
	Worm borings	17	14	0
	Cooccurring sponges and worm borings	14	0	0
INTERIOR SURFACES WITH BIOEROSION	Total	73	42	12
	Sponges	42	25	1
	Worm borings	17	17	1
	Cooccurring sponges and worm borings	14	0	0

Table 3.2. Statistical differences for occurrence data and areal coverage data between valves 75-100% complete and groups binned as 25-100%, 25-49%, and 50-74% complete. Occurrence data is given in as the number of valves with an encruster present over the total valves in the bin. NS = no significant difference. SIG = statistically significant difference. NA = number too low for statistical tests.

Taxa	Surfaces	Occurrence: 75-100% Complete	Comparison Bin	Occurrence: Comparison Bin	Occurrence Difference	Occurrence P-Value if Significantly Different	Areal Coverage Difference	Areal Coverage P-Value if Sig. Different
All Encrusters	Interior	48/170	25-100%	139/349	NS		SIG	p=0.00055
		48/170	25-49%	78/148	SIG	p=0.00351	SIG	p<0.00001
		48/170	50-74%	13/31	NS		SIG	p=0.01768
	Exterior	37/170	25-100%	139/349	SIG	p=0.00327	SIG	p=0.00227
		37/170	25-49%	55/148	SIG	p=0.02527	SIG	p=0.00027
		37/170	50-74%	9/31	NS		SIG	p=0.04972
Sponges	Interior	48/170	25-100%	139/349	NS		NS	
		48/170	25-49%	78/148	SIG	p=0.00351	SIG	p=0.00351
		48/170	50-74%	13/31	NS		NS	
	Exterior	37/170	25-100%	139/349	SIG	p=0.00327	SIG	p=0.00327
		37/170	25-49%	55/148	SIG	p=0.02527	SIG	p=0.02527
		37/170	50-74%	9/31	NS		NS	
Polychaetes	Interior	40/170	25-100%	99/349	NS		NS	
		40/170	25-49%	47/148	NS		NS	
		40/170	50-74%	13/31	NS		NS	
	Exterior	40/170	25-100%	95/349	NS		NS	
		40/170	25-49%	43/148	NS		NS	
		40/170	50-74%	11/31	NS		NS	
Bryozoans	Interior	9/170	25-100%	13/349	NS		NS	
		9/170	25-49%	1/148	SIG	P=0.02231	SIG	p=0.01868
		9/170	50-74%	3/31	NS		NS	
	Exterior	1/170	25-100%	1/349	NS		NS	
		1/170	25-49%	0/148	NS		NS	
		1/170	50-74%	0/31	NS		NS	
Attachment Scars	Interior	14/170	25-100%	29/349	NS		NS	
		14/170	25-49%	1/148	SIG	P=0.00240	NS	
		14/170	50-74%	1/31	NS		NS	
	Exterior	19/170	25-100%	25/349	NS		NS	
		19/170	25-49%	6/148	SIG	P=0.02913	SIG	p=0.02055
		19/170	50-74%	0/31	NS		NS	
Barnacles	Interior	2/170	25-100%	3/349	NS		NS	
		2/170	25-49%	0/148	NS		NS	
		2/170	50-74%	1/31	NS		NS	
	Exterior	0/170	25-100%	0/349	NA		NS	
		0/170	25-49%	1/148	NS		NS	
		0/170	50-74%	0/31	NA		NS	

DISCUSSION

Diversity

The diversity of encrusters in our study is consistent with those found in the bioerosion-dominated pathway of *Mercenaria mercenaria* described by Meldahl and Flessa (1990). This pathway, characterized by *M. mercenaria* with higher occurrences of sponges, barnacles, bryozoans, serpulid worms, indicates that the shells spent an extended period of time in stable, lower energy environments, not frequently reworked, in the salt marshes and inner flats or the deeper subtidal zone. Meldahl and Flessa (1990) found that bryozoans, sponges, and serpulids were limited to subtidal zones; following their model, it is likely the *M. mercenaria* in this study considerable spent time in the subtidal zone.

Many of the taxa McKinney (1996) found are consistent with those found in our study; e. g., sponges, bryozoans, *Crepidula* sp., barnacles and polychaetes. McKinney (1996) did find a number of organisms that we did not; e.g., hydrozoans, ascidians, encrusting bivalves, and a unicellular film. However, we are not discouraged by these results. McKinney (1996) live-collected encrusting organisms on an assemblage of disarticulated *M. mercenaria* by dredging 1–2 m below the low-tide level. McKinney (1996) further treated the *M. mercenaria* with sodium hypochlorite to simulate the loss of organic material in a fossil assemblage and found that the sponges, hydrozoans, ascidians, and some of the bryozoans did not preserve; his finding explain the absence of many of these body fossils in our assemblage.

Distribution and timing

We found no trace fossils indicating *in vivo* parasitic infestation by trematodes (Huntley and Scarponi 2021). The occurrence and cumulative intensity of encrustation are similar on the interior and exterior surfaces. However, significantly more interior surfaces exhibited a higher degree of encrusting intensity; instances of interior surfaces with more than 5% areal coverage of encrustation occurred more than twice as often than on exterior surfaces. The intensity of encrustation suggests that the shells were exposed to the water-sediment interface for periods ranging from, at the very least, weeks or months because barnacles can encrust in these short periods of time (Osman 1977, Meldahl and Flessa 1996), to likely on the order of years (Bromley and Asgaard 1993).

The encrustation on both surfaces indicates that the disarticulated valves were encrusted in both the convex up and convex down position. Initially, our findings appear to contradict McKinney (1996), who found that encrusting algal mats, erect bryozoans, and erect hydrozoans had a higher intensity of encrustation on the exterior surfaces of the valves. He interpreted this to mean that the shells had accumulated in a lower energy environment, with shells stable in a convex up position, inhibiting the growth on the interior surfaces as a result of low amounts of sunlight, food, and oxygen-rich water. An explanation for this discrepancy, we agree that the *M. mercenaria* in our study were subjected to low energy environments, again consistent with the aforementioned bioerosion pathway of Meldahl and Flessa (1996), but these shells were also likely subjected to periods, perhaps infrequent, of vigorous energy or reworking that subsequently caused the placement of many shells in both the convex up and convex down positions on the seafloor (Kidwell 1989). These results highlight the utility of combining occurrence data, cumulative areal coverage, and binning the shells' surfaces by percent areal coverage to elucidate the timing, distribution, and intensity of an assemblage of encrusting organisms on molluscan substrates.

Ichnofacies

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Breakage through Bioeroders

It is well-documented that bioerosion is capable of damaging and destroying shells (Kent 1981, Bromley 1994, Taylor and Wilson 2003, Wilson 2007). Our study confirms these previous claims; we found that when bioerosion made by sponges and polychaete worms was present, breakage on the *Mercenaria mercenaria* shells resulted from the weakness incurred from the actions of these bioeroders. There are likely some instances of encrusting bioeroders inhabiting already-fractured shells, but we do not see this explanation as being the main driver of our findings because the overwhelming majority of the breaks were associated with encrustation. It is an important distinction to note that the statistical correlation we found between the occurrence of the bioerosion and the location on the shell where breakage occurred does not indicate the cause of the breakage. Breakage of the *Mercenaria mercenaria* shells herein is attributed to tidal energy and shell-crusting predators, such as crabs and seagulls (Mackenzie 1977, Arnold 1984, Melhahl and Flessa 1990). However, due to the high occurrence of breakage due to the postmortem actions of the encrusters, and the dearth of examples demonstrating bioeroded shells that did not break through the bioerosion, we suggest that it takes only minimal perforation caused by a bioeroder to weaken the shell, making it highly susceptible to taphonomic breakage in the fossil record.

Our findings are consistent with several studies involving point-load compression experiments to assess the impacts of predatory bioerosion on shell strength. Roy (1994), examining thick-shelled bivalves, found that drilled shells were significantly weaker than non-drilled shells. Hagstrom (1996) showed that only shells drilled near the umbo were weaker. Interestingly, our findings differ from those of Zuchin and Stanton (2001), who determined that compaction in nature is more closely related to the compression of two shells, and not associated with the presence of drillholes. Kelley (2008) examined the bivalves from several fossil assemblage and found an abundance of bivalves containing breaks that did not pass though predatory drillholes, also determining that bioerosion from predatory borings did not weaken the shells significantly. These studies involve predatory bioerosion, as opposed to organisms in our study that use the molluscan substrates as a domicile.

Fragments vs. Whole Shells

In modern and ancient molluscan or brachiopod assemblages, it is common to find shelly assemblages comprised of largely of fragmented shells (Kidwell et al. 1986, Brett and Baird 1986, Flessa et al. 1993, Daley 2017), sparking questions about the robustness or appropriateness about using such fragments for ecological or paleoecological studies. At issue is the question: are there increased gains by including fragments with whole shells for community studies involving encrusters? We found no increased benefit of including shell fragments in determining taxonomic richness; using the group of 57–100% was adequate and no additional taxonomic groups were observed when fragments were included to comprise the 25–100% group. Another frequently asked question, if fragments are primarily available, is whether can these fragments be used for accurate determinations of evidence-leaving encruster taxonomic richness? We found that no taxonomic groups were lost when looking at only the fragments in the 25–49% and 50–74% complete groups, a promising prospect when examining encrusters in assemblages dominated by shell fragments. This is consistent with the findings of Daley (2017), who examined the richness of an assemblage of mollusks. Daley (2017) noted that despite the inclusion of non-hinged fragmented shells that greatly increased her sample size, only a gain of two new species were identified bringing the total to 45 species, a small return for the addition of almost 9000 fragments.

The suitability of using fragments in studies designed to estimate original abundance becomes more complex. Including fragments in our study, we found that comparing the 75–100% and 25–100% bins depicted very similar abundances for the encrusters with one exception; the abundance of sponges on the exterior surface of the shells were statistically different. The bin containing the valves that were 75–100% complete showed no statistical difference from the bin of fragments 50–74% complete, but showed the highest significant difference between the least complete fragments in the 25–49% bin. Including fragments along with whole shells may slightly alter the results when analyzing the abundance of encrusters. It is preferable to use primarily complete valves if enough are available to conduct a community study. To assess the abundance of encrusting organisms, including valves that are greater than 50% complete is preferred in the absence of whole shells.

CONCLUSION

This baseline study reports a diverse and abundant group of encrusting organisms that inhabit *Mercenaria mercenaria* bivalves from Shelter Island, New York. The *M. mercenaria* assemblage predominantly contains trace fossils left by clionid sponges, polychaete worms, *Crepidula* sp and *Anomia* sp. The body fossils of barnacles, bryozoans, and serpulid worms are also present. The presence of encrustation on both the interior and exterior surfaces and the co-occurrence of both deep- and shallow-tiered borings indicates that the shells were exposed to the water-sediment interface on the order of ecological timescales.

This work demonstrates that the breakage commonly occurs either completely or partially through the bioerosive traces fossils left by clionid sponges and boring polychaete worms, highlighting the destructive ability of bioeroding encrusters to weaken molluscan shells. Given the prevalence of fragments in the modern and fossil records, caution should be exercised when selecting fragmented shells for community studies involving encrusters. We found no added benefit from the inclusion of heavily fragments shells with primarily complete shells. We suggest using complete or mostly complete valves when accessible; but in the absence of complete shells, implementing valves that are greater than 50% complete will yield robust results.

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CHAPTER 4

Preliminary data and future research on Sclerochronological and Isotopic Analysis of the Fossil Oyster *Hyotissa hyotis* from the Miocene

ABSTRACT

Previous studies have shown that the growth rates of oysters living in temperate waters have slowed in modern times, highlighting the need to examine tropical oysters to determine if they are experiencing a similar trend. Modern oyster growth rates have slowed possibly from overfishing pressures, nitrogen runoff, pollution, and disease. Understanding the paleoecology and establishing a pre-human baseline from fossil oysters, a major contribution of paleontology to conservation efforts, is an effective way to evaluate trends in growth rate over time. *Hyotissa hyotis*, an extremely large and thick shelled oyster, is a keystone ecosystem engineer in many tropical to subtropical marine communities. Previous work has quantified the growth rate of modern *Hyotissa hyotis*, but the processes that drive the development of the internal growth increments of these oysters are poorly constrained. The existence of *H. hyotis* in the fossil record presents an excellent opportunity to compile a geohistorical baseline. Here we present the preliminary data on a sclerochronological and isotopic analysis of the oyster *H. hyotis* from the Latrania Formation in the Southeast Coyote Mountains near Ocotillo, California. The sediments from the upper Miocene Latrania Formation represent an ancient shoreline of the proto-Gulf of California. To gain insight into the paleoecology of the fossil oysters, the growth rate, thickness, and lifespans will be quantified by combining the use of morphology and stable isotope geochemistry. Testing if couplets of light and dark growth bands and the ridge-like steps on the surface of the hinge are

annual may provide for an efficient, less costly, way of determining the lifespans of these oysters.

INTRODUCTION

Hyotissa hyotis, an extremely large and thick keystone oyster, performs several important services to their ecosystems; e.g., filtering pollution and toxic algal blooms out of the water column, and providing valuable hard-substrate habitats for entire marine communities (Lenihan and Peterson 1998, Kirby and Jackson 2004, Zuschin and Baal 2007, Beck et al. 2011, Rick et al. 2016). Many people in coastal communities also depend on these oyster populations as a crucial food source (Andrus and Crowe 2000, Harding et al. 2008, Savarese et al. 2016). Economically, the seafood industry and its workers rely heavily on the harvesting of *H. hyotis* oysters (Grabowski et al. 2012), particularly in the Eastern Tropical Pacific Ocean where this food source is harvested in the wild and commercially fished (Rodriguez-Astudillo et al. 2005).

Studies have shown that the growth rates of oysters living in temperate waters have slowed in modern times, highlighting the need to determine if tropical oysters are experiencing a similar trend. Modern oyster growth rates have slowed from overfishing pressures, nitrogen runoff, pollution, and disease (Elmgren et al. 1989, Officer et al. 1984, Nixon 1995, Jackson et al. 2001, Lotze et al. 2006, Kirby 2004, Kirby and Miller 2005, Rick et al. 2016). The growth rate and the controls on growth of many oyster species, including *Hyotissa hyotis*, are not well understood. To assess trends in growth of modern oysters, we address oyster growth traits and population lifespans of the past (Jackson et al., 2001; Kraeuter et al., 2007; Mann et al., 2009a; Mann et al., 2009b). Establishing a baseline of oyster growth from a time before anthropogenic influence has become an important agenda of conservation paleobiologists (Harding et al. 2008, Harding et al. 2010, Dietl and Flessa 2011, Dietl et al. 2015, Kusnerik et al. 2018). Most ecological studies on growth rates are based on modern field studies that encompass only a few years. Those studies that include historical records rarely include data prior to the 1950s and do not include data on the lifespan of the oysters (Jackson 1991, Jackson 1997, Dayton et al. 1998, Jackson et al. 2001).

Oyster Ecology and Growth

Oysters grow by accreting layers of $CaCO_3$ in the form of calcite onto their existing shells. Studies on oyster growth focusing on the hinge, the ligamental area that connects the two oyster valves, has been demonstrated to be an effective and promising strategy (e.g., Kirby et al. 1998, Titschack et al. 2010, Gillikin et al. 2013, Durham et al. 2017, Zimmt et al. 2019). The hinge forms easily identifiable internal growth increments along the axis of growth, toward the ventral margin (Figure 4.1). Two types of incremental layers can clearly be seen in the interior cross section of a bisected hinge and while both are calcitic layers, they have different microstructures. The light chalky layer is typically more capacious and porous with a honeycomb-shaped crystalline structure. The dark foliated layer comprises densely arranged crystals (Kirby et al. 1998, Checa et al. 2007, Dauphin et al. 2013, Zimmt et al. 2019). The shell thickness perpendicular to the axis of growth is another metric often used to describe oysters (Kirby 1999). Some oysters are known to cease growing in response to excessive temperature tolerance thresholds and cannot record the upper and/or lower chemical signature from the seawater during these growth breaks (e.g., *Crassostrea virginica*; Kirby et al. 1998).

Sclerochronology is the study of the physical and chemical structures accreted by an organism, e.g., growth increments, in a temporal context (Hudson et al., 1976, Jones 1983, Jones 1985, Jones and Quitmyer 1996, Gröcke and Gillikin 2008). Combining sclerochronology with stable isotope geochemistry has previously been an effective way to obtain lifespan data on species of oysters with unidentified annual growth bands (Durham et al. 2017). In several studies, a profile of the $\delta^{18}O$ values of the oyster plotted against the axis of growth yielded a sinusoidal curve that identified annual growth increments (Jones 1985, Jones and Allmon 1995, Titschack et al. 2010, Gillikin et al. 2013, Durham et al. 2017). In these studies, the lifespans of certain species of oyster are determined by counting the ridge-like steps on the surface of the hinge or the couplets of light and dark bands on the interior cross-section of the hinge. Titschack et al. (2010) found a strong correlation between the number of ridge-like steps on the surface of the hinge and the lifespan of modern *Hyotissa hyotis.*

This is the first study to evaluate the trends in the growth rates of *Hyotissa hyotis* using fossil data from the Miocene. The main objectives are to: use isotope geochemistry to quantify growth rate, and to test the hypothesis that one hinge-step and one couplet of light and dark banding is equivalent to one year of growth on the fossil *H. hyotis.* If this hypothesis is verified, then this morphological information can be used to determine the lifespans of the *H. hyotis*. This approach may be less costly and more efficient than stable isotope analysis. Here I report the preliminary results from this research.

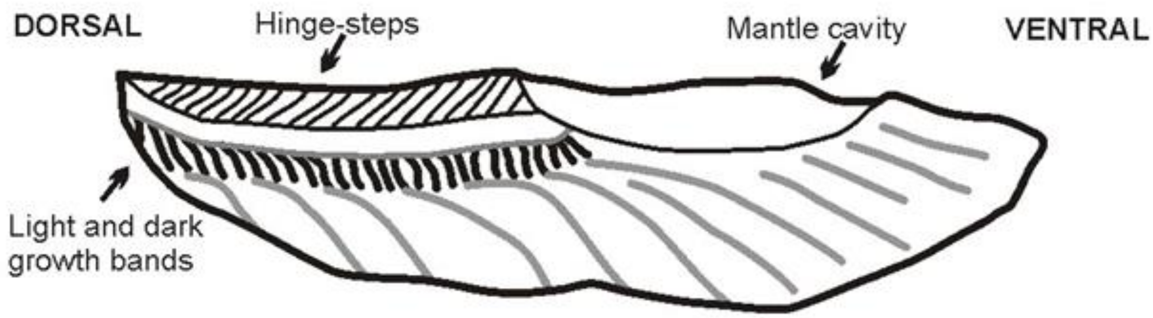

Figure 4.1. Sketch showing the internal cross section of the oyster *Hyotissa hyotis.*

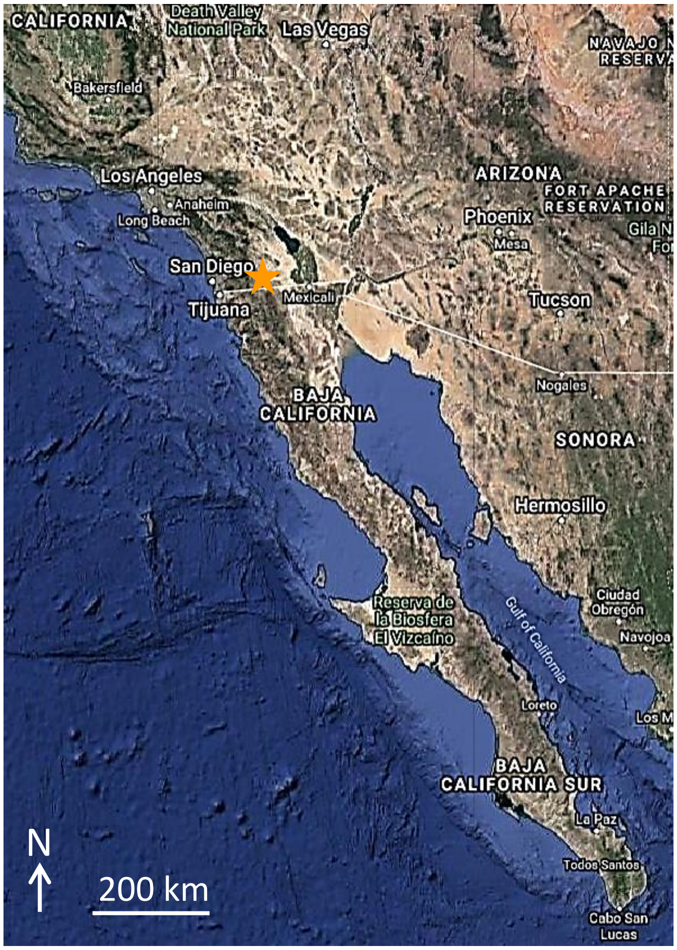

Figure 4.2. Field work locality, indicated by the orange star at Ocotillo, California.

GEOLOGIC SETTING & MATERIALS

In the Miocene, southern California experienced tectonic extension on a long and relatively straight rift basin parallel to the pre-existing continental margin. This extension and the subsequent detachment of Baja California from North America formed the Gulf of California. By the Late Miocene, approximately 6.5 Mya, marine waters of the proto-Gulf of California, had extended north across the present-day Salton trough region to San Gorgonio Pass (Winker and Kidwell 1996). Microfossils indicate subtropical to tropical climates in the Gulf during this interval (Quinn and Cronin 1984) and the sediments found in the Salton Trough preserve the first marine fauna from the initial separation of Baja from the mainland.

A total of 171 disarticulated valves were surface-collected from the late Miocene Latrania Formation in the Southeast Coyote Mountains near Ocotillo, California (Figure 4.2; Kidwell 1988). Large and free-living *Hyotissa hyotis* oysters are found articulated and *in situ* at this locality, suggesting minimal transport. *Hyotisa hyotis* specimens are recrystallized. Diagenesis modifies the original isotopic signature and distorts paleoenvironmental signals (Schöne 2013). Recrystallization resets the primary $\delta^{18}O$ values but may provide useful cyclicity indicative of seasonal changes (Ivany and Runnegar 2010, Angiolini 2011).

METHODS

Specimens were bisected though the hinge, parallel to the axis of growth (Figure 4.3; Kirby et al. 1998, Surge et al. 2001, Andrus and Thompson 2012, Durham et al. 2017, Zimmt et al. 2019) using a water-cooled table saw. The halves were polished using a lapping plate and fine-grit polisher to achieve a smooth and planar surface for sampling and measuring.

To determine the growth-periodicity of the *Hyotissa hyotis,* I applied sclerochronology combined with stable isotope geochemistry to the specimen. Powder carbonate samples were milled from the internal dark and light growth bands of the hinge following the axis of growth (Figure 4.4). Samples were milled using a New Wave/Merchantek Micromill with a 0.5 mm carbide micro-drill bit located at the University of California, Santa Cruz. Using the computer-controlled micromilling system, 4–6 samples were milled per mm and approximately 30-50 µg of the carbonate powder was analyzed from each sample, achieving high resolution results.

Forty samples were analyzed for the $\delta^{18}O$ and $\delta^{13}C$ isotopic values using a Thermo Fisher Delta V Plus isotope ratio mass spectrometer (IRMS) interfaced with a Thermo Fisher Kiel IV carbonate perception device located at the University of California, Riverside. The samples were run with a known standard to verify the precision of the instruments and the resultant isotopic values. The $\delta^{18}O$ and $\delta^{13}C$ values were plotted against the axis of growth (Figure 4.5).

The hinge-steps on the surface of the hinge of each oyster were counted. To test that each hinge-step represents one year of growth, the number of hinge-steps were compared to the lifespan of the oysters. If the data supports this test, the lifespan of *H. hyotis* can be estimated by counting the number of steps on the hinge.

To test if one couplet of light and dark bands on the interior cross-section of the hinge is equivalent to one year of growth, the number of couplets were compared to the lifespan of the oyster. If one couplet of light and dark bands corresponds to one year, this will show that the controls on the internal growth structures of *Hyotissa hyotis* are annual.

Additional data on the physical characteristics of these oysters was collected; e.g., shell thickness, shell length, hinge length. The width of each light and dark growth band of the interior cross-section of the hinge was measured along the axis of growth using the ImageJ software program.

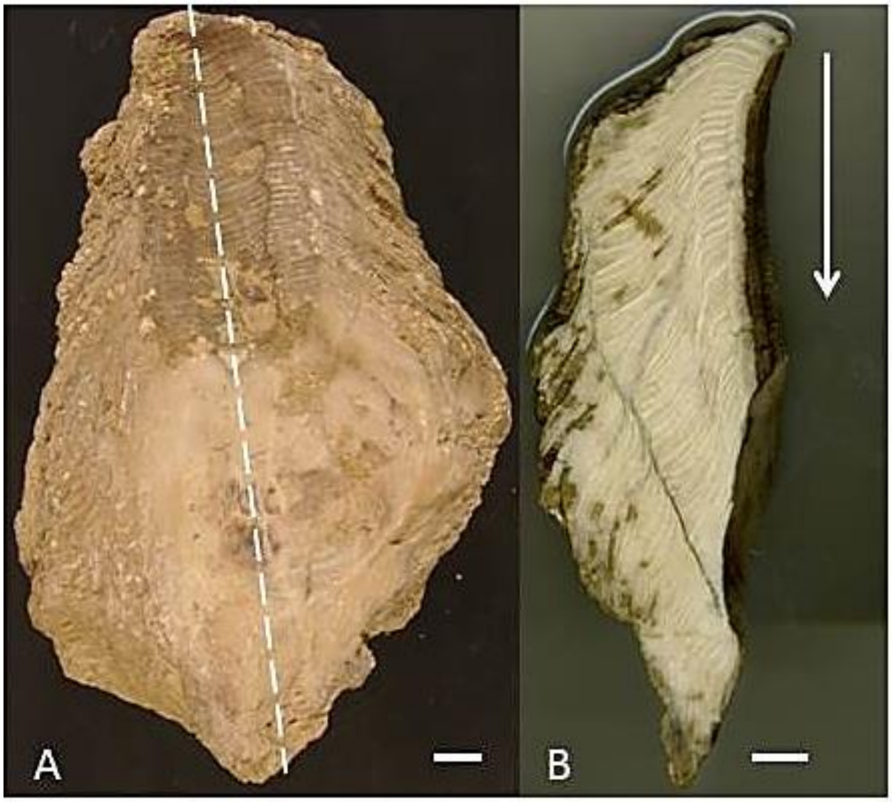

Figure 4.3. A) *Hyotissa hyotis* valve from Ocotillo, California. This oyster has 37 hinge-steps. White line indicates bisection through the hinge. B) Interior cross-section of the bisected valve showing the internal growth increments. White arrow indicates direction of growth. Scale bar = 10 mm.

PRELIMINARY DATA

Isotopic data

As expected from diagenetically altered material, the $\delta^{18}O$ values, prone to early signal degradation upon diagenesis, are abnormally low. The $\delta^{13}C$, while still negative, demonstrate a more typical range.

Hinge data

Hinge-steps were counted for 165 individual valves; 89 were left valves and 76 were right valves. Six valves were not counted because the hinges were eroded. The number of hinge-steps ranged from 9 to 114 with an average of 32.8 steps. The number of hinge steps were plotted against the interior surface area of the valves (Figure 4.6); the trend lines indicate that increasing the number of hinge-steps only slightly increases the interior surface area. The right and left valves were binned by the number of hinge-steps, with both showing a right-skewed distribution (Figure 4.7).

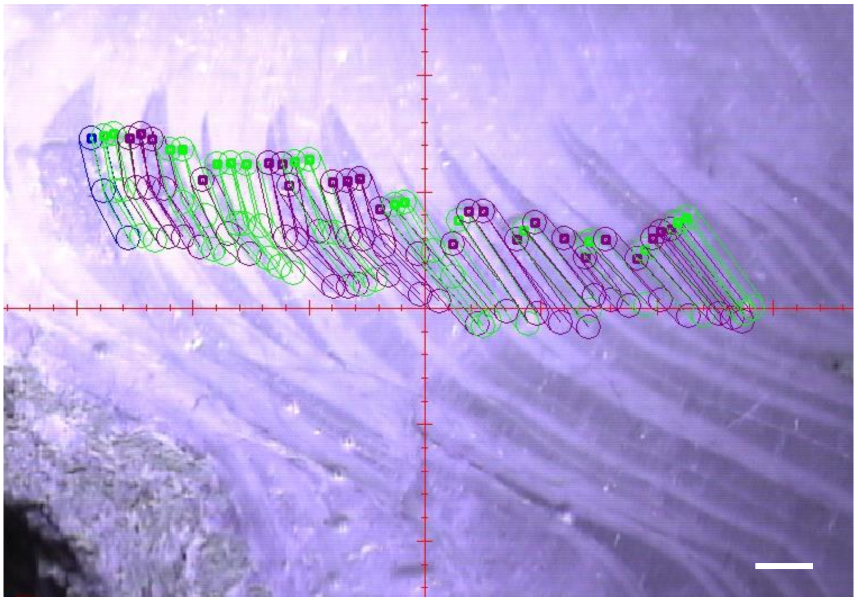

Figure 4.4. Screen capture from New Wave/Merchantek Micromill showing drilled transect lines through the hinge of the fossil *Hyotissa hyotis*. Scale bar = 1mm.

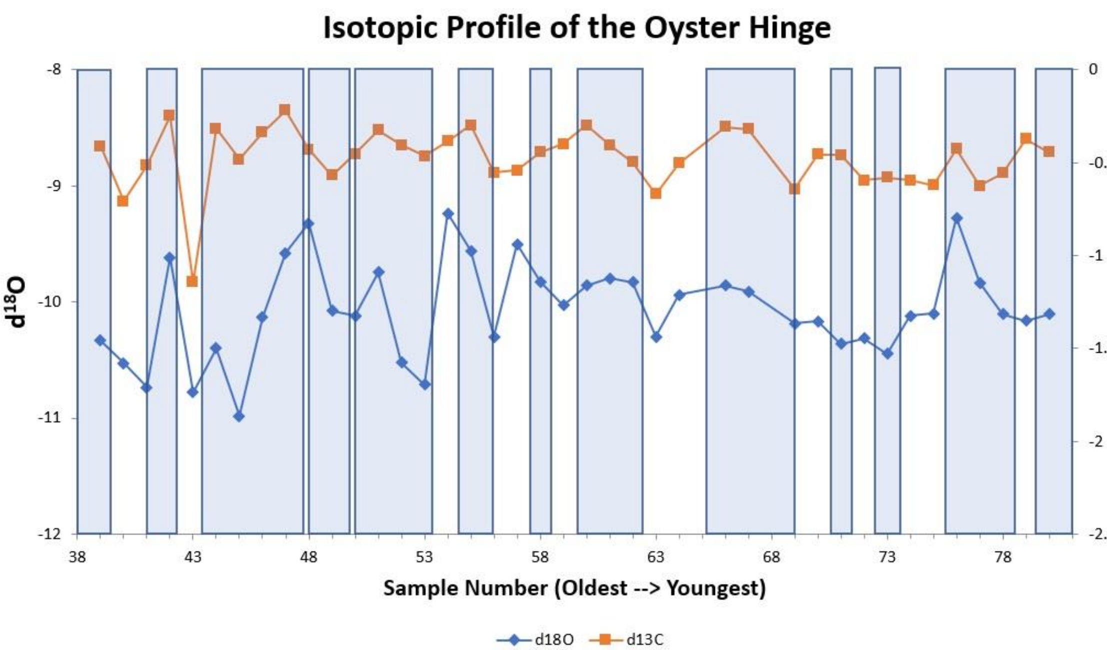

Figure 4.5. Profiles showing $\delta^{13}C$ and $\delta^{18}O$ isotopes from the hinge of *Hyotissa hyotis*. Direction of growth follows left to right. White and blue intervals on the graph indicate light and dark growth bands respectively.

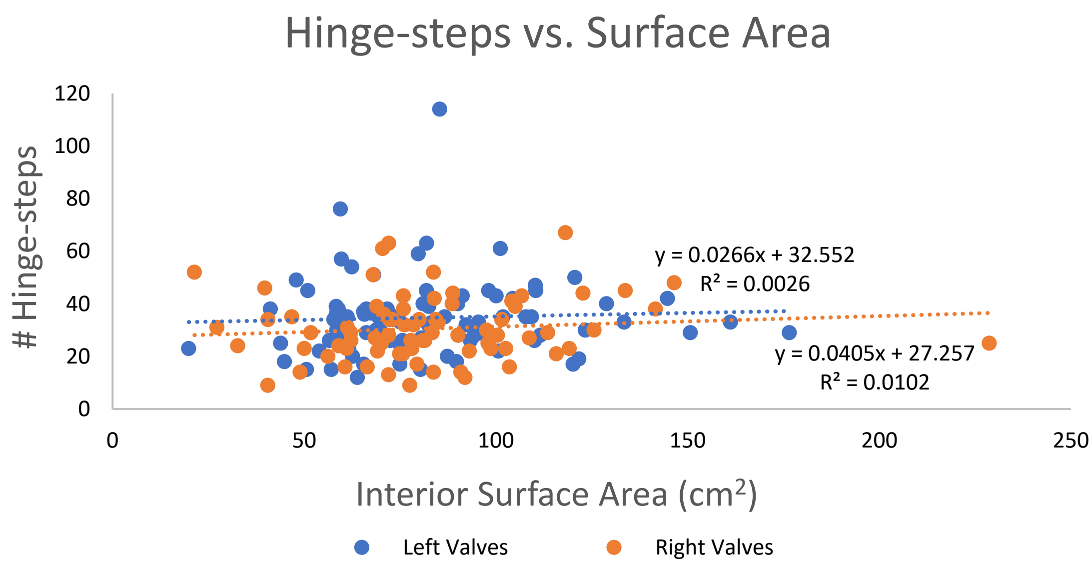

Figure 4.6. The number of hinge-steps vs. the interior surface area of the valve. The linear trend lines with equations shown for both sets of valves.

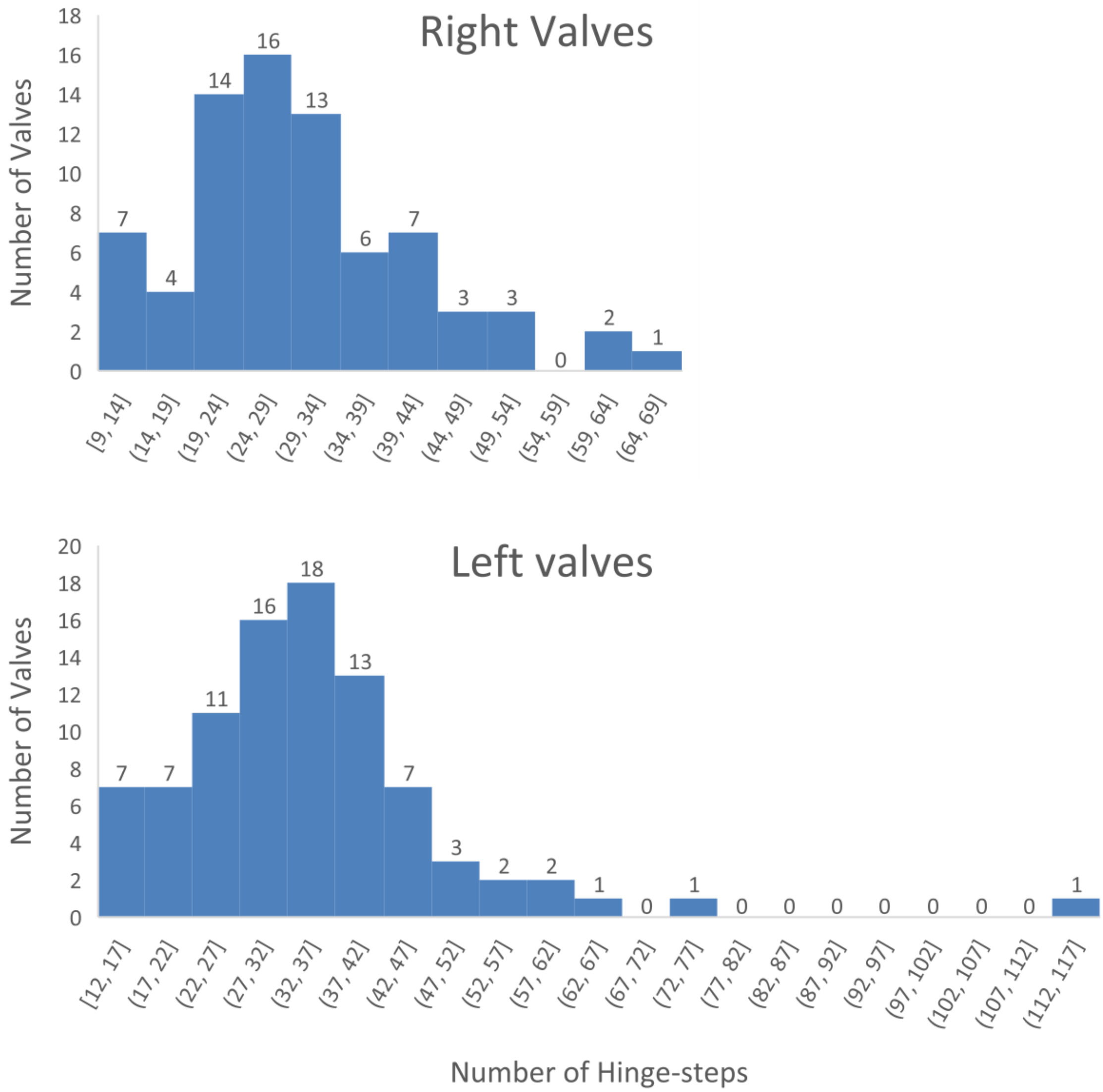

Figure 4.7. The number of right and left valves binned by number of hinge-steps.

FUTURE RESEARCH

More data collection will be needed to finish this study. Once all of the data is collected and analyzed, the original objectives of this study will be carried out: to determine if the hinge-steps and couplets of light and dark growth bands are annual, and to calculate the growth rate of the fossil *Hyotissa hyotis* oysters.

Paleoclimate

The *Hyotissa hyotis* lived during the middle Miocene climatic optimum, an extended period of warmth during the Miocene that acts as a useful analogue for predicting future scenarios in response to climate change (Holbourn et al. 2014). The *H. hyotis* also endured the Pleistocene, a period of colder climates and abrupt climate oscillations driven by glacial-interglacial orbital cycles and millennial scale Dansgaard-Oeschger cycles (Anklin et al. 1993, Dansgaard et al. 1993) related in part to the closing of the Central American Seaway approximately 3.5 Mya (Coates et al. 1992, Jones and Allmon 1995). The survival of *Hyotissa hyotis* in interglacial and glacial periods highlights the need to understand the water temperatures in the proto-Gulf of California.

Stable oxygen isotopes of fossil oysters can be used as a proxy for determining paleotemperatures from the source water (Epstein et al. 1953, Grossman and Ku 1986, Jones and Allmon 1995, Kirby et al. 1998, Andrus and Crowe 2008, Goodwin et al. 2013). Oysters incorporate isotopes from the surrounding water into their shells; the shells contain a biogeochemical record of the environmental and climatic conditions experienced throughout their lifetimes (Jones 1985, Jones and Quitmyer 1996). Although some organisms do not precipitate their shells in equilibrium with seawater (Brenchley and Harper 1998), the physiologic effects, or species-dependent fractionation, among mollusks are minimal (Jones 1985). *Hyotissa hyotis* has a long lifespan providing multi-decadal records of climate (Titschack et al. 2010).

Most oxygen occurs as either the heavier ^{18}O isotope or the lighter ^{16}O isotope and the $\delta^{18}O$ value (the ratio of ^{18}O to ^{16}O) of marine carbonates is primarily controlled by the $\delta^{18}O$ of the source waters. A $\delta^{18}O$ decrease of 1‰ corresponds to an approximate water temperature increase of 4°C (Epstein et al. 1953, Hudson and Anderson 1989, Jones and Allmon 1995). Stable oxygen isotope values are reported in the standard (δ) notation where:

$$\delta^{18}O = [(\delta^{18}O/\ \delta^{16}O)_{SAMPLE}\ /\ (\delta^{18}O/\ \delta^{16}O)_{STANDARD} - 1] \times 10^3 \text{ per mil} \quad (1)$$

The $\delta^{18}O$ value of seawater can vary seasonally due to changes in temperature, evaporation, precipitation, terrestrial runoff, or current dynamics (Ruddiman 2008). Some controls on $\delta^{18}O$ may not be seasonal; e.g. higher frequency storm events, and lower frequency multi-year droughts. Sampling multiple shells is useful for identifying any anomolous values (Surge et al. 2001). To distinguish between lower-frequency annual variability and higher-frequency intra-annual variability, the $\delta^{18}O$ values will be linearly detrended, centering the results around zero by substracting the linear trendline values from the raw data (Durham et al. 2017, Zimmt et al. 2019).

While it is impossible to determine exact temperatures using paleotemperature equations for calcite, a range of paleotemperatures of the proto-Gulf of California can be estimated by using the $\delta^{18}O$ value of standard mean ocean water (SMOW) during the Pleistocene, obtained from proxies such as ice-cores or foraminifera, with the $\delta^{18}O$ values from calcite shells in a calcite specific paleotemperature equation such as from Wanamaker et al. (2007):

$$T°C = 16.28 (\pm 0.10) – 4.57 (\pm 0.15) \times [\delta^{18}O_{SHELL} - \delta^{18}O_{SMOW}] + 0.06 (\pm 0.06) \times [\delta^{18}O_{SHELL} - \delta^{18}O_{SMOW}]^2 \quad (2)$$

To gain insight into the marine chemistry of the shallow, near-shore environment of the proto-Gulf of California, it will be necessary to examined and interpret the isotopic data from fossil oysters with little to no diagenesis. Cristin and Perrilliat (2013) described and collected Pleistocene *Hyotissa hyotis* from Baja California Sur that we would like to examine. Therefore, the primary objective of our future research is to create an isotopic record, $\delta^{18}O$, of the well-preserved *H. hyotis* from Baja California Sur to gain insight into the composition of the water chemistry and the seasonal temperature variations of the shallow-marine environment of proto-gulf of California.

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