# Distribution and Prevalence of Bioerosion Within Two Coral Species on Inshore and Offshore Reefs Across the Western Caribbean Sea

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# Abstract:

Bioerosion, the process by which organisms bore into hard substrate, weakens coral skeletons and degrades the quality of coral reef habitats. Prior studies reveal that bioerosion is enhanced by ocean acidification, eutrophication resulting from the addition of nitrogen into the environment, and other anthropogenic factors. However, these studies were primarily conducted in the Indo-Pacific region, while little is known about the distribution and prevalence of bioerosion across the wider Caribbean Sea. To address this shortcoming, we extracted 191 skeletal cores from two abundant and ubiquitous Caribbean corals (*Siderastrea siderea* and *Pseudodiploria strigosa*) in a hierarchical sampling design spanning inshore and offshore reef zones across three major reef systems that include the Florida Keys Reef Tract (FKRT), the Belize Mesoamerican Barrier Reef System (MBRS), and the Panama Bocas del Toro Reef Complex (BTRC). It was hypothesized that inshore corals are more severely impacted by bioerosion due to their closer proximity to local anthropogenic sources of stress and that species would differ in their susceptibility due to differences in skeletal architecture. The number of bivalve boring holes within cores of both species and the percent volume of *S. siderea* cores bioeroded was quantified. The percent volume of *P. strigosa* cores bioeroded was not quantified due to its very complex skeletal growth structure. Linear modeling and variance partitioning were employed to relate quantities of bioerosion to ambient environmental conditions on reef collection sites. The number of bivalve borings was higher in cores collected from inshore corals when compared to offshore corals. *Siderastrea siderea* cores were plagued by greater numbers of bivalve borings than *P. strigosa*, providing evidence for a host preference amongst bivalve bioeroders. The differences between reef zones and species are less pronounced in the Florida Keys Reef Tract; suggesting that Florida is distinct from the other two reef systems in the western Caribbean Sea. Modeling reveals a positive correlation between bivalve borings and the concentration of chlorophyll A in the ambient environment, supporting established links between eutrophication and bioerosion prevalence. Understanding the patterns of bioerosion across spatiotemporal scales highlights the impact of eutrophication on oceanic bioerosion and provides a foundation for further investigations into the impact of bioerosion on contemporary coral reefs under climate change.


# Introduction:

Nearly one-fourth of all marine species rely on coral reefs for habitat, shelter, or sustenance, either directly or indirectly [1]. For coral reef ecosystems to maintain these necessary functions, they must accrete calcium carbonate ($CaCO_3$) at a rate equal to or above that at which $CaCO_3$ is lost to the environment. Any changes to the delicate balance between $CaCO_3$ accretion and its destruction will alter the trajectory of the reef ecosystem. A phenomenon known to lower net $CaCO_3$ accretion rates is bioerosion, where organisms, such as fishes, poriferans, annelids, bivalves, and various microorganisms degrade coral skeletal structures via mechanical or chemical processes for either heterotrophic or sheltering purposes [2].

Though bioerosion is a naturally occurring interaction between corals and the invading taxa, any unnatural processes that augment bioerosion will indirectly increase reef skeleton degradation and lower the net calcification rate on a reef. Anthropogenic environmental changes, such as ocean acidification [3, 4, 5] and high nutrient concentrations [3], have previously been shown to increase bioerosion rates on reefs. As the effects of these human-mediated climate changes are expected to become more severe as time progresses, bioerosion rates may reach a level at which net calcification rates are significantly reduced on reef communities around the

world [4]. Unnaturally low rates of coral growth will negatively affect tropical marine ecosystems as unhealthy and weakened coral reefs cannot function well as buffers from severe weather events such as storms [6] and species dependent on the corals will likely leave, suffer reduced fitness, or perish.

Despite the perceivable role of bioerosion in future reef health trajectories, little is known about its current magnitude and distribution at large spatial scales across Florida and the western Caribbean Sea. Furthermore, how the distribution of bioerosion relates to the environmental heterogeneity across Florida and the western Caribbean Sea is also poorly understood.

It has previously been shown that physiochemical conditions vary widely across the Caribbean region [7]. Thus, small-scale studies of bioerosion trends may not accurately reflect the broader patterns throughout the region. To date, we still do not understand how bioerosion rates affect different coral taxa within the Caribbean Sea. Most previous studies were either conducted in other ocean basins or over a small geographic range [3, 4, 5], and focused on a single or multiple closely related species within the Caribbean [8]. However, different species, with different ecologies, morphologies, and natural histories, are likely to respond differently even when exposed to similar environmental conditions [2, 4, 8, 9].

Here, we investigate the distribution and prevalence of bioerosion on two abundant and ubiquitously distributed Caribbean coral species, *Siderastrea siderea* (Ellis & Solander, 1786) and *Pseudodiploria strigosa* (Dana, 1846), and between inshore and offshore across the Florida Keys Reef Tract, Belize Barrier Reef System, and Panama Bocas Del Toro Reef Complex in the western Caribbean Sea, a region spanning 15 degrees of latitude.

# Methods:

## Core Extraction

Coral skeletal cores were collected from three major regions throughout Florida and western Caribbean Sea: the Florida Keys Reef Tract (FKRT), the Belize Mesoamerican Barrier Reef System (MBRS), and the Bocas del Toro Reef Complex (BTRC) in Panama (Figure 1). Cores originating from the MBRS were collected in October and November 2015, while cores were extracted from the BTRC in May and June 2015, and cores were collected from the FKRT in May 2015 and 2016. Sites were selected based on the presence of apparently healthy *S. siderea* and *P. strigosa* colonies. Colonies were deemed healthy (i.e., exhibited little to no bleaching, lack of apparent disease, etc.) based on visual inspection. Each of the three reef systems consists of four regional inshore and offshore site pairs. Inshore reefs were closer to the mainland than their offshore counterparts. Though the exact distance the offshore sites occupied in relation to the mainland varies, most were at least a few kilometers from the mainland. The four inshore and offshore regional site pairs were distributed to ensure a more complete sampling regime across each of the three major reef systems.

Cores were extracted using a Model 2 hydraulic diamond core drill (*CS Unitec Inc, Norwalk Connecticut*) affixed with hollow extension rods and a 5 cm-diameter wet diamond core bit. Cores were extracted from the vertical growth axis of each colony. All collected cores were between 12 and 70 cm in length. After extraction, a concrete plug was inserted and secured in the drilled hole with an underwater epoxy to protect the colony from erosion and further physical damage. Thereafter, the collected cores were stored in capped PVC tubes filled with 100% ethanol (EtOH) and transported to the University of North Carolina at Chapel Hill where they were air-dried.

A total of 191 cores were collected, with 100 of those belonging to *S. siderea* and 91 belonging to *P. strigosa*. Of the total 191 cores, 91 were collected from inshore environments and 100 were collected from offshore environments. Seventy cores in total were collected from the FKRT, with 39 belonging to *S. siderea* and 31 belonging to *P. strigosa*. Of the same 70 FKRT cores, 39 were collected from corals inhabiting inshore environments and 31 were collected from corals inhabiting offshore environments. Sixty-two cores were collected from the BTRC, with 40 belonging to *S. siderea*, and 22 belonging to *P. strigosa*. Of the 62 cores collected from the BTRC, 22 were collected from inshore environments and 40 were collected from offshore environments. Fifty-nine were collected from the MBRS, with 21 belonging to *S. siderea* and 38 belonging to *P. strigosa*. Thirty of the MBRS cores were collected from corals inhabiting inshore environments and 29 were collected from corals inhabiting offshore environments.

**CT scanning**

All cores were CT scanned on a Siemens Biograph CT scanner at the University of North Carolina at Chapel Hill's Biomedical Research Imaging Center. Cores were placed in parallel rows on the scanning table. The CT scanner's parameters were set to 120 kV, 250 mAs, and 0.6 mm slice thickness with images constructed at 0.1 mm increments using the H70h "Very Sharp Spine" Window. Images were exported as DICOM files for bioerosion analyses [10].

**Quantifying Bioerosion**

Two independent procedures were used to quantify the intensity of bioerosion within the coral cores. The first method involved visually inspecting all cores for bivalve induced borings that had a diameter wider than approximately 5 mm. The total number of these large bivalve borings were summed for each of the 191 cores and standardized by the total length of the core, providing a bivalve-borings per meter metric for all coral cores. Bivalves presented themselves as one of the major causes of bioerosion on almost all cores based on visual inspection, however, most eroders were either absent from the core or had their remains destroyed in the collection process. Therefore, we do not know for certain which bivalve taxon or whether multiple taxa are responsible for these large borings. However, we presume that much of the bivalve erosion was created by members of the known Scleractinian bioeroding genus: *Lithophaga* [11]. This method allows us to compare the quantities of bioerosion exhibited by all corals of both species (*S. siderea and P. strigosa*) but is limited in that it only quantifies erosion from a select taxon of bioeroders.

In comparison, the MatLab program CoralCT was used to estimate the percent of a core that is absent due to erosive processes [12]. CT images were loaded into the program, and the percent volume eroded values were calculated manually. After the program calculated the percent volume absent due to bioerosion, it produced updated CT images with regions of bioerosion highlighted. Twelve DICOM file images for all collected *S. siderea* cores were considered for this method as the CoralCT cannot process the structurally complex skeletal architecture of *P. strigosa*.

**Statistical Analyses, Linear Modeling, and Variance Partitioning**

Overall, the data is zero heavy (*i.e.,* there are many cores with no bioerosion present) and skewed towards lower values, very much resembling a negative or chi-squared distribution. All

subsequent statistical methods were chosen as *a-posteriori* because they do not assume any specific distribution of bioerosion data.

All analyses were conducted in the RStudio (ver. 3.5.0) environment. Various statistical tests were conducted to determine how factors correlated to quantities of bioerosion on cores. Wilcoxon rank-sum tests allowed us to segregate cores into categories with respect to reef zone and species of coral to compare quantities of bioerosion between two groups. Kruskal-Wallis rank-sum tests were used to segregate cores with respect to reef zone, species of coral, and reef system of origin and compare quantities of bioerosion between three or more groups. Environmental data was collected from the National Oceanic and Atmospheric Administration's Ocean Acidification Product Site [18], allowing us to examine how environmental conditions (such as Chlorophyll A) related to the prevalence and distribution of bioerosion in Florida and the western Caribbean Sea. This geographic resolution of the data allowed us to correlate environmental conditions to all inshore and offshore sites. Variance partitioning was used to determine what proportion of the variance in bioerosion was explained by numerous known core-specific factors (reef zone, reef system, species of coral, chlorophyll A).

Linear modeling (LM) was used to isolate the effects specific parameters had on quantities of bioerosion. Certain parameters, such as coral species and reef zone, were chosen to be included in the model based on *a-posteriori* information displaying their significance in determining quantities of bioerosion. We created numerous models, as linear modeling has limited computing power and can only incorporate a few factors and variables in any given model.

Variance Partitioning was used to quantify how various factors and variables contributed to and ultimately explained the variance in bioerosion seen. Numerous models, each with a distinct combination of factors and variables, were produced as variance partitioning has limited computing power and can only incorporate a few factors and variables in any given model.

# Results:

## Major Trends in Bivalve Borings

We found evidence that the number of borings per meter was significantly higher (Table 1) in all inshore cores when compared to all offshore cores (Figure 2A) throughout Florida and the western Caribbean Sea. Also, evidence that the number of borings per meter throughout Florida and the western Caribbean Sea was significantly higher (Table 1) in all *S. siderea* cores when compared to all *P. strigosa* cores (Figure 2B) exists. Statistical analysis found evidence that the number of borings per meter was only different (Table 1) between cores collected from the FKRT and the MBRS, with the FKRT having higher numbers than the MBRS (Figure 2C).

## Reef System, Reef Zone, and Species-Specific Trends in Bivalve Borings

The number of borings per meter was not significantly different (Table 1) between inshore and offshore cores throughout the FKRT (Figure 3A) and the MBRS (Figure 3B), however, the number of borings per meter was significantly higher (Table 1) amongst inshore cores when compared to offshore cores throughout the BTRC (Figure 3C). We found no evidence for a difference in the number of borings per meter (Table 1) between *S. siderea* and *P. strigosa* cores throughout the FKRT (Figure 4A). However, statistical analysis showed that *S. siderea* cores have higher numbers of borings per meter (Table 1) than *P. strigosa* in both the MBRS and the BTRC (Figure 4B, Figure 4C).

The number of borings per meter did not differ (Table 1) between inshore cores collected from the MBRS, the FKRT, and the BTRC (Figure 5A). The number of borings per meter on offshore cores collected from the FKRT was higher (Table 1) than that on offshore cores collected from the MBRS and the BTRC (Figure 5B). However, we failed to find evidence that the number of borings per meter was different (Table 1) amongst offshore cores collected from the MBRS and the BTRC (Figure 5B). The number of borings per meter was not significantly different (Table 1) between *S. siderea* cores collected from the three reef systems (Figure 6A), nor was the number of borings per meter amongst *P. strigosa* collected from the three reef systems (Figure 6B).

**Trends in *S. siderea* Core Volume Erosion**

The percent volume eroded was not significantly different (Table 2) between inshore *S. siderea* and offshore *S. siderea* cores throughout the western Caribbean Sea (Figure 7A). However, the percent volume eroded was significantly higher (Table 2) amongst *S. siderea* cores from the FKRT when compared to those collected from the MBRS (Figure 7B). We found no evidence of a difference (Table 1) between cores collected from the FKRT and the BTRC and between cores collected from the MBRS and the BTRC (Figure 7B). The percent volume eroded was not significantly different (Table 1) between inshore and offshore core collected within the FKRT (Figure 8A) nor the BRTC (Figure 8C). However, inshore cores from the MBRS were found to have statistically higher amounts of volume eroded (Table 1) than their offshore counterparts (Figure 8B). The amount of erosion did not differ (Table 1) between inshore cores collected from the three reef systems (Figure 9A) nor did it differ amongst offshore cores collected from the three reef systems (9B).

**Relating Bivalve Borings and Core Volume Erosion in *S. siderea***

The relationship number of borings per meter and percent volume erosion amongst *S. siderea* cores is significantly different (Table 3) than zero (Figure 10A). The positive relationships suggest that on average, a 1.5% increase in the amount of core volume eroded should correspond to an increase in borings per meter by one.

**Relating Quantities of Bioerosion to Chlorophyll A**

Four linear models were conducted to examine how Chlorophyll A related to the number of borings per meter amongst all cores and the percent volume erosion amongst *S. siderea* cores. The first two models (LM-B & LM-C) found evidence that the relationship between the number of borings per meter and the concentration of Chlorophyll A amongst all cores is significantly different ($p < 0.001$) than zero (Table 3). We did not find evidence that the relationship between the percent volume erosion amongst *S. siderea* cores and the concentration of Chlorophyll A amongst all cores is significantly different from zero (LM-D & LM-E, Table 3).

**Variance Partitioning**

Amongst all cores, the species of coral (either *S. siderea* or *P. strigosa*) explained 3% of the variation in borings per meter (Figure 10B). Amongst all cores, the reef zone (either inshore or offshore) the core inhabited explained 4% of the variation in borings per meter (Figure 10C). Amongst all cores, the concentration of Chlorophyll A explained 5% of the variation in borings per meter (Figure 10B and 10C). Amongst all cores, the combination of the concentration of Chlorophyll A and species of coral explained 3% of the variation in borings per meter (Figure

10B). Amongst all cores, the combination of the concentration of Chlorophyll A and reef zone explained 3% of the variation in borings per meter (Figure 10C). At least 88% of the variation in bioerosion seen was unexplained amongst all cores (Figure 10B and Figure 10C).

Amongst *S. siderea* cores, the reef zone the core inhabited explained 7% of the variation in borings per meter (Figure 10D). Amongst *S. siderea* cores, the concentration of Chlorophyll A in the environment explained 3% of the variation in borings per meter (Figure 10D). Amongst *S. siderea* cores, the combination of concentration of Chlorophyll A and reef zone explained 5% of the variation in borings per meter (Figure 10D). This leaves 85% of the variation amongst S. siderea cores unexplained by the aforementioned variable and factors. Amongst *P. strigosa* cores, the reef zone the core inhabited, the concentration of Chlorophyll A in the environment, the combination of concentration of Chlorophyll A and reef zone explained less than 1% of the variation in borings per meter (Figure 10E), leaving almost all of the variation unexplained.

# Discussion:

**Major Patterns in Bioerosion**

Inshore corals across Florida and the western Caribbean Sea have greater quantities of bivalve induced bioerosion than offshore corals. However, this pattern only persists in the BTRC when individual reef systems are examined. Inshore corals in all three reef systems have greater median boring per meter values and more skew towards higher borings per meter due to outlier than their offshore counterparts. The same general pattern, though not statistically significant, does exist when comparing the percent volume eroded of inshore *S. siderea* and offshore *S. siderea* cores throughout the region. Interestingly, there is only evidence of a statistical difference between the percent volume eroded of inshore *S. siderea* cores and offshore *S. siderea* cores in the MBRS when examining individual reef systems. We expect that the higher quantities of borings in inshore reefs may be a result of their proximity to human-mediated environmental changes, such as eutrophication [3], which have previously been known to benefit filter feeders such as bivalves [2].

Both procedures to quantify bioerosion on corals (*e.g.* the bivalve-borings per meter metric and the percent of a core that is absent due to erosive processes) failed to find significant differences between offshore and inshore corals in the FKRT which contradicts previous studies that have shown that inshore reef and offshore reef corals in the FKRT are ecologically distinct [10]. Our findings that inshore corals have greater quantities of bivalve induced bioerosion than offshore corals corroborate previous research suggesting that inshore reef and offshore corals in the MBRS respond accordingly to their distinct environmental conditions [13]. Interestingly, our finding that inshore *S. siderea* corals do not have a greater percent volume absence due to erosive processes does not corroborate this same line of previous research [13]. Statistical examination suggests that there is no difference in the quantity of bivalve induced bioerosion on inshore corals from the MBRS, the FKRT, and the BTRC; though the maximum quantity of bivalve induced bioerosion on corals from the FKRT is smaller than that of the either the MBRS or the BTRC. Also, the quantity of bivalve induced bioerosion on offshore corals from the FKRT is different from both the MBRS and the BTRC. This provides evidence that the environments of the MBRS and the BTRC are similar, while that of the FKRT is distinct within the wider western Caribbean Sea.

Across the western Caribbean Sea, *S. siderea* are parasitized by bivalves more than *P. strigosa*. This pattern persists in the MBRS and the BTRC, but not in the FKRT. *Pseudodiploria strigosa*, and other brain corals, are known to release substantial amounts of protective surface

mucosal polysaccharide layers when stressed [14]. We hypothesized that this protective mucous layer provides *P. strigosa* an effective defense against parasitism which *S. siderea* lacks. It is also possible that differences in skeletal architecture, specifically skeletal density play a role in the prevalence of parasitism present amongst the two species. Bivalve bioeroders may prefer the denser skeletal structure [10] of *S. siderea* when adopting a host. The data also suggests that the conditions causing bivalves to preferentially erode *S. siderea* in the MBRS and the BTRC are not present in the FKRT. The unique FKRT environment [7] may confer enough of an advantage to bivalve eroders that they are no longer limited to *S. siderea* [9]. Statistical examination suggests that there is no difference in the quantity of bivalve induced bioerosion on the *S. siderea* from the MBRS, the FKRT, and the BTRC. Statistical examination also suggests that there is no difference in the quantity of bivalve induced bioerosion on the *P. strigosa* from the MBRS, the FKRT, and the BTRC. These suggest that the distinct populations *S. siderea* and *P. strigosa* in the three different reef systems are either exposed to similar quantities of bioerosion or similarly respond to parasitism. These findings contradict multiple lines of evidence suggesting that phenotypic and genotypic differences exist between populations of the same coral taxon [15, 16, 17] as genetic differences between these populations may not affect their susceptibility to bioerosion.

There are strong, statistically significant, positive relationships between the concentration of Chlorophyll A present in the environment and the number of bivalve borings present in the cores. A positive relationship between the concentration of Chlorophyll A present in the environment and the percent of a core that is absent due to erosive processes is present, however, it is both weaker than that between Chlorophyll A and the number of bivalve borings, and is also not statistically significant. Since Chlorophyll A is an environmental proxy for net productivity[18], we assume net environmental productivity helps drive bioerosion. This finding corroborates previous work [2], as we would expect filter feeders such as bivalves to thrive in environments where there is a large amount of edible organic material present in the water column. We can expect corals inhabiting marine environments with a high number of anthropogenic sources of increased net productivity, such as eutrophication, to be riddled with unnaturally high amounts of bioeroders.

Variance partitioning showed that most of the factors and variables used throughout the study (species of coral, the reef zone inhabited, and the concentration of Chlorophyll A in the ambient) explain very little of the variation in the quantity of bivalve induced bioerosion on corals throughout Florida and the wider western Caribbean Sea. The variables examined in the variance partitioning shows that upwards of 85% of the variation or more is unexplained in this study. This finding should not be used to minimize the importance of our study, but to highlight how little we know about the factors that control bioerosion throughout Florida and the wider western Caribbean Sea, and throughout the Earth's greater marine biosphere.

## Conclusion

In conclusion, we found evidence that bioeroders infest *S. siderea* more often than *P. strigosa* in Florida and the wider Caribbean Sea. Corals inhabiting inshore reef zones suffer higher quantities of bivalve bioerosion than corals inhabiting offshore zones and this relationship is very likely a result of proximity to human activity. Our findings further support the notion that bioerosion is linked to net productivity of the immediate environment, with the real possibility that current and future anthropogenic activity will continue to exacerbate bivalve bioerosion. Future studies should try to expand our methods to include a greater breadth of distinct

environmental factors and variables to come to a more integrative understanding of bioerosion on corals across the globe.

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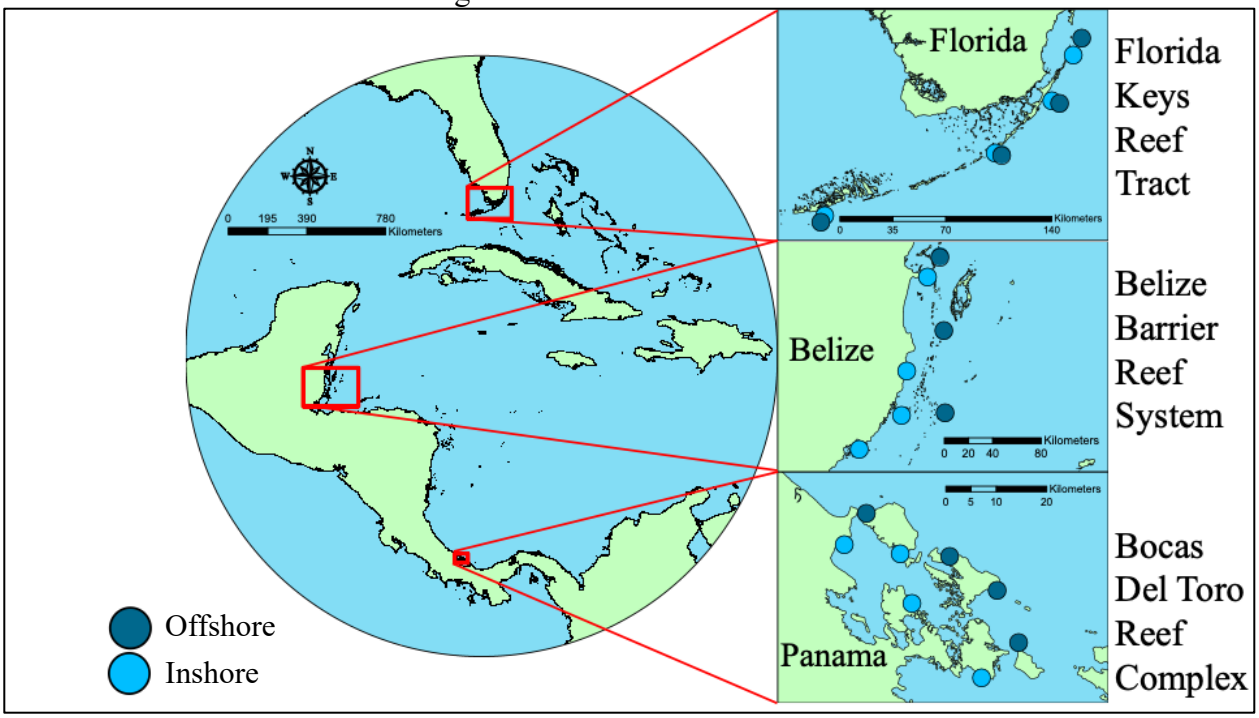
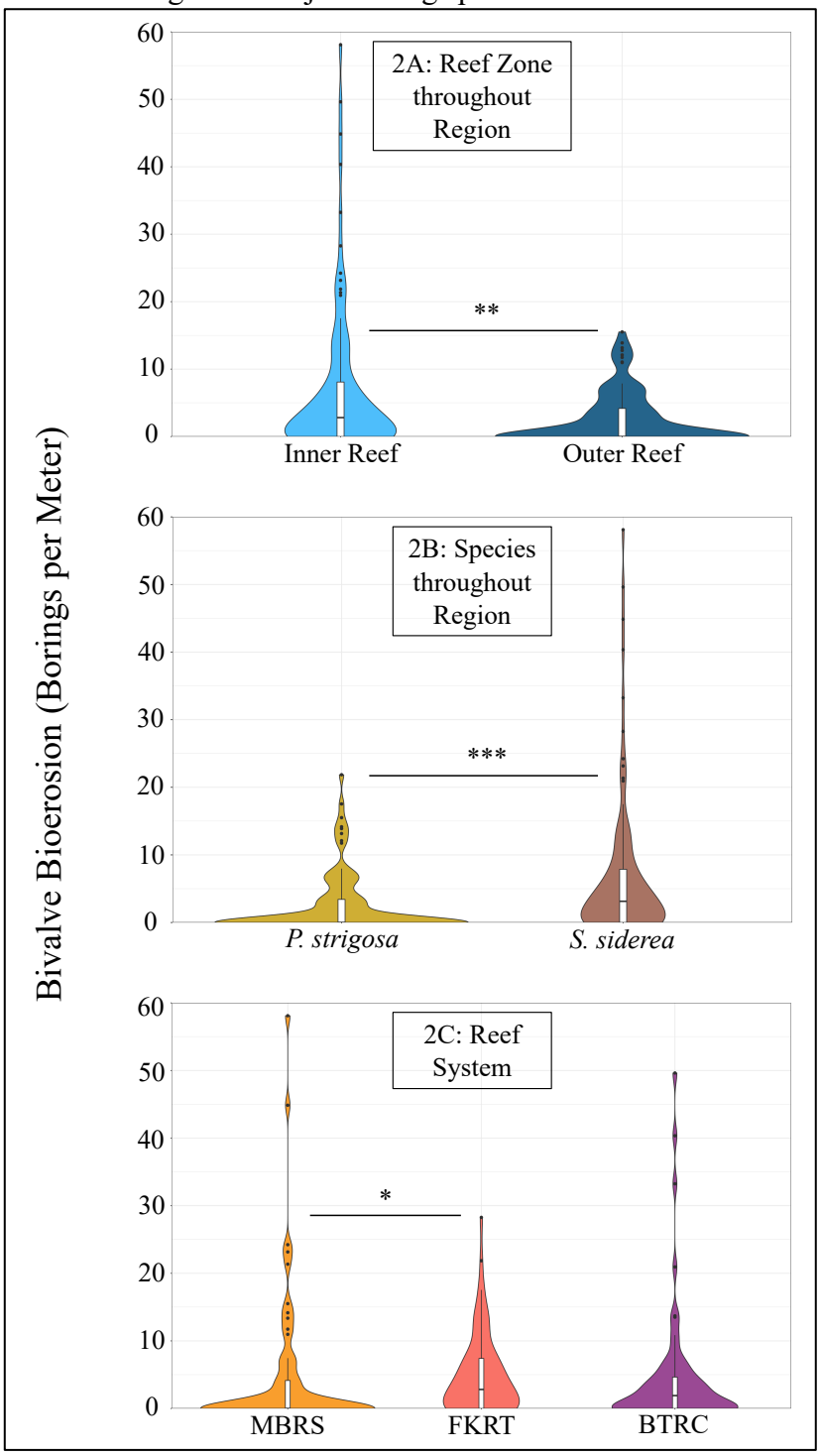
**Figures:**

Figure 1. Core Extraction Sites



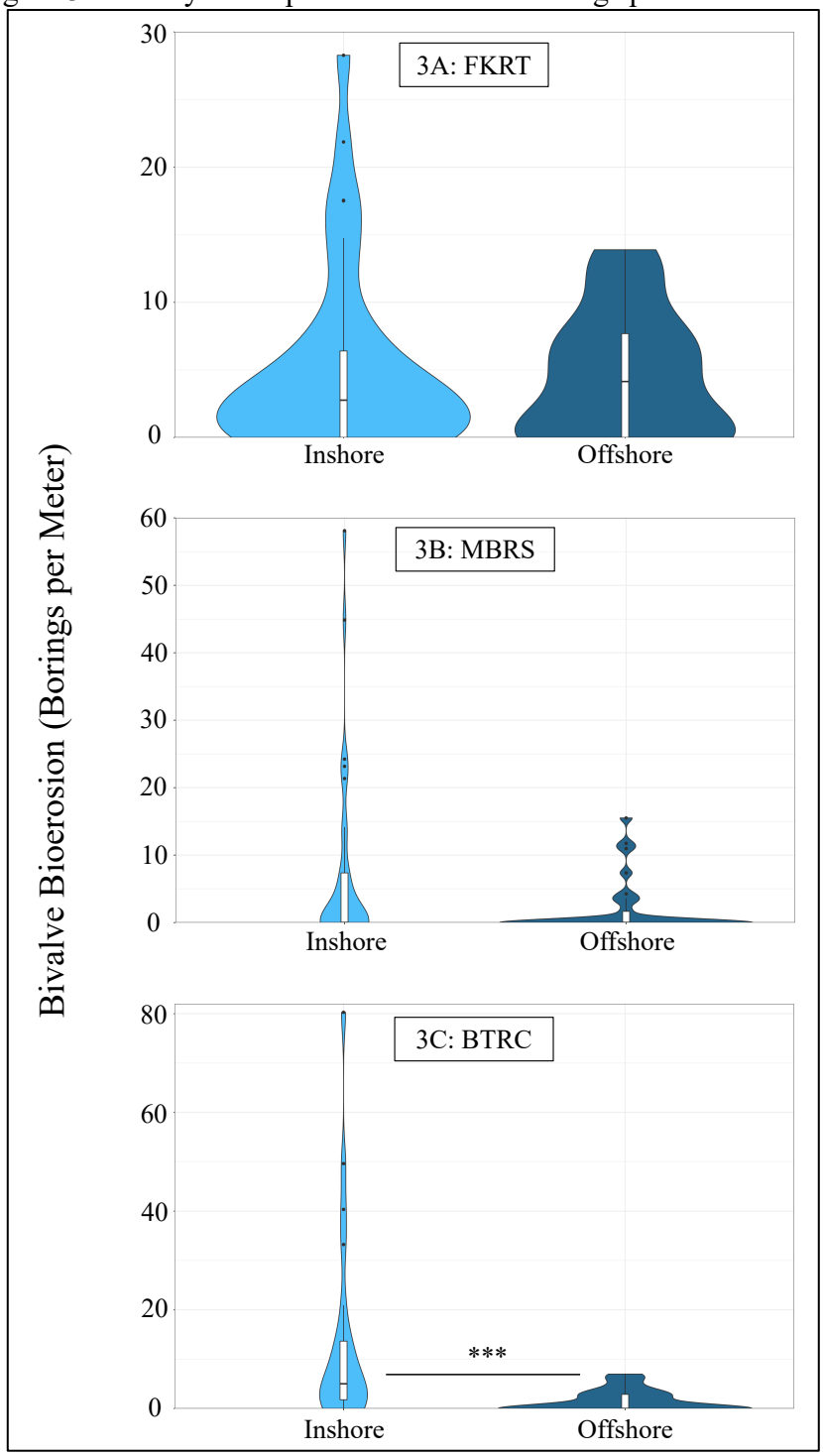

Map depicting the three major reef systems and the location of the inshore and offshore zone pairs for each.

Figure 2. Major Borings per Meter Trends



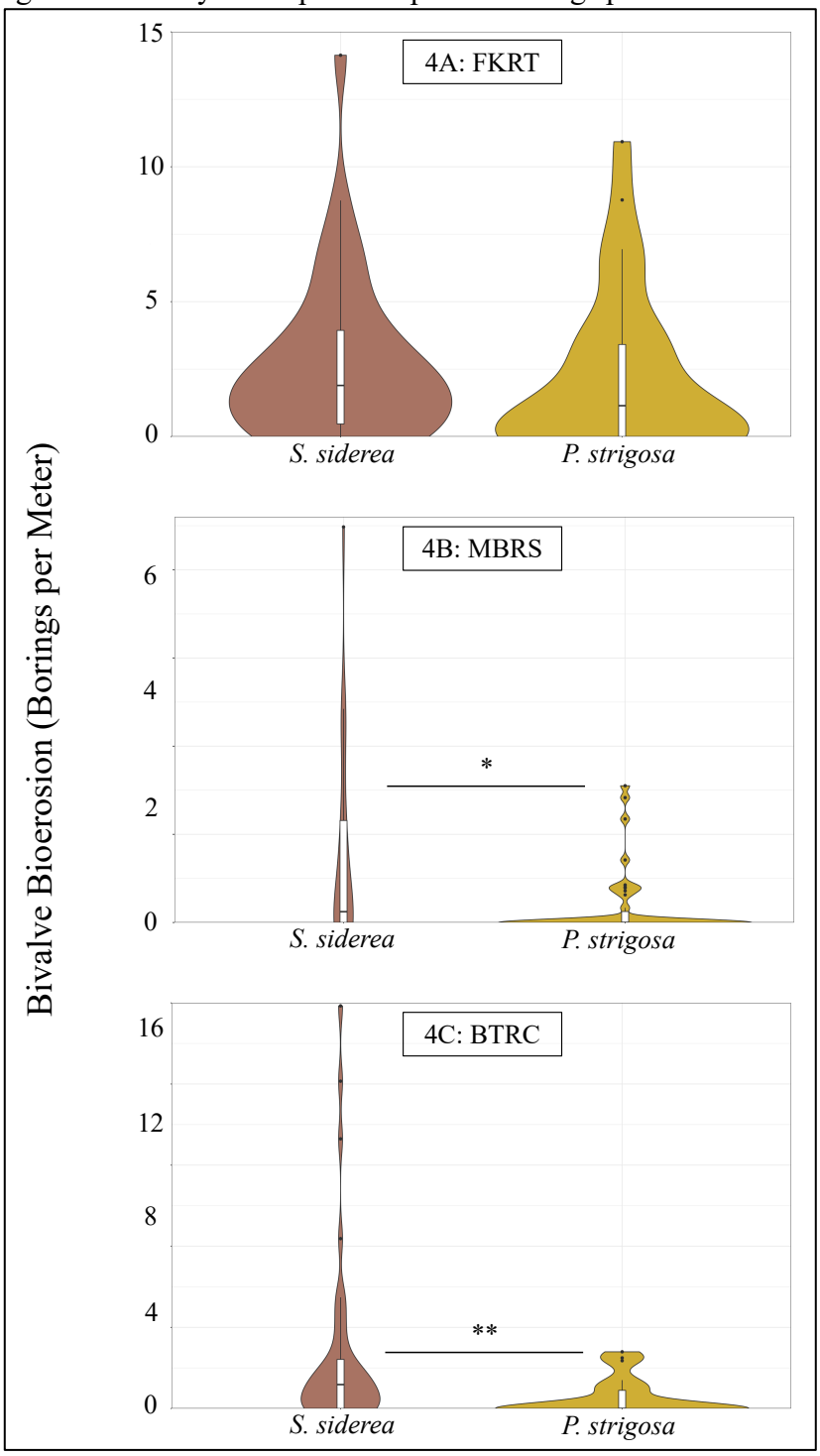

Graphs depict probability density distribution of borings per meter on cores with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 3. Reef System Specific Reef Zone Borings per Meter Trends



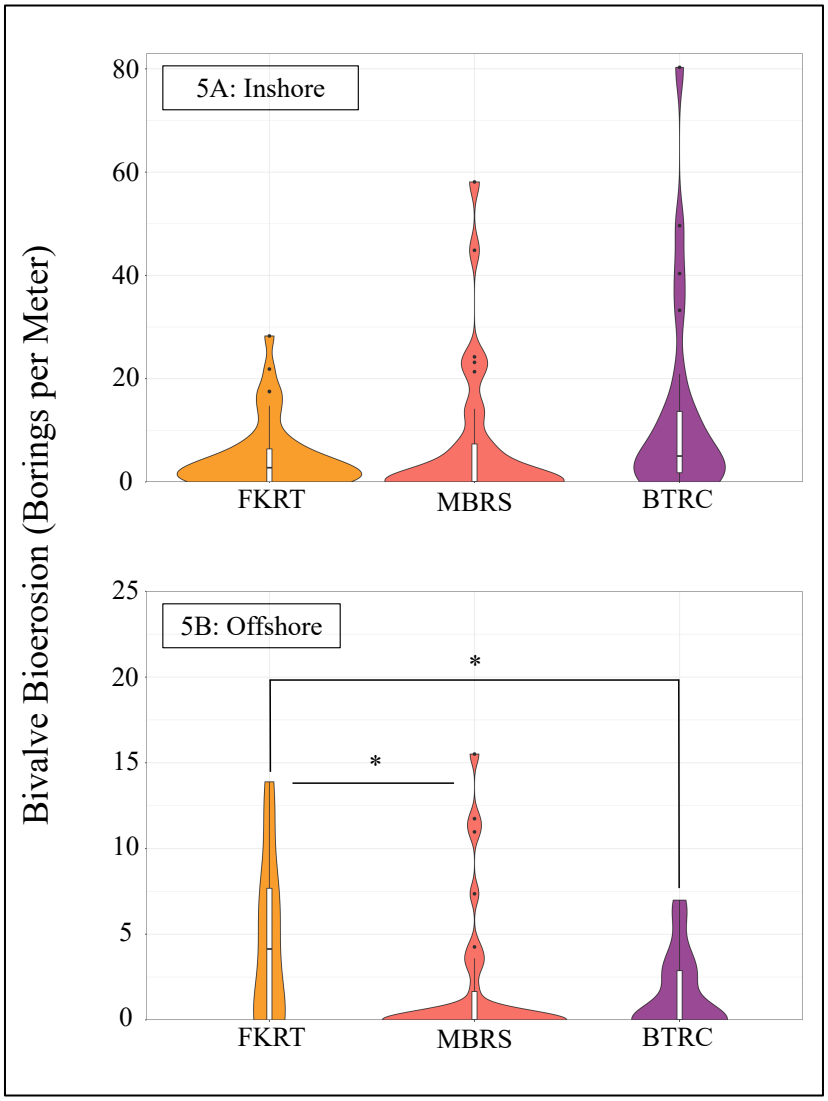

Graphs depict probability density distribution of borings per meter on cores with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 4. Reef System Specific Species Borings per Meter Trends



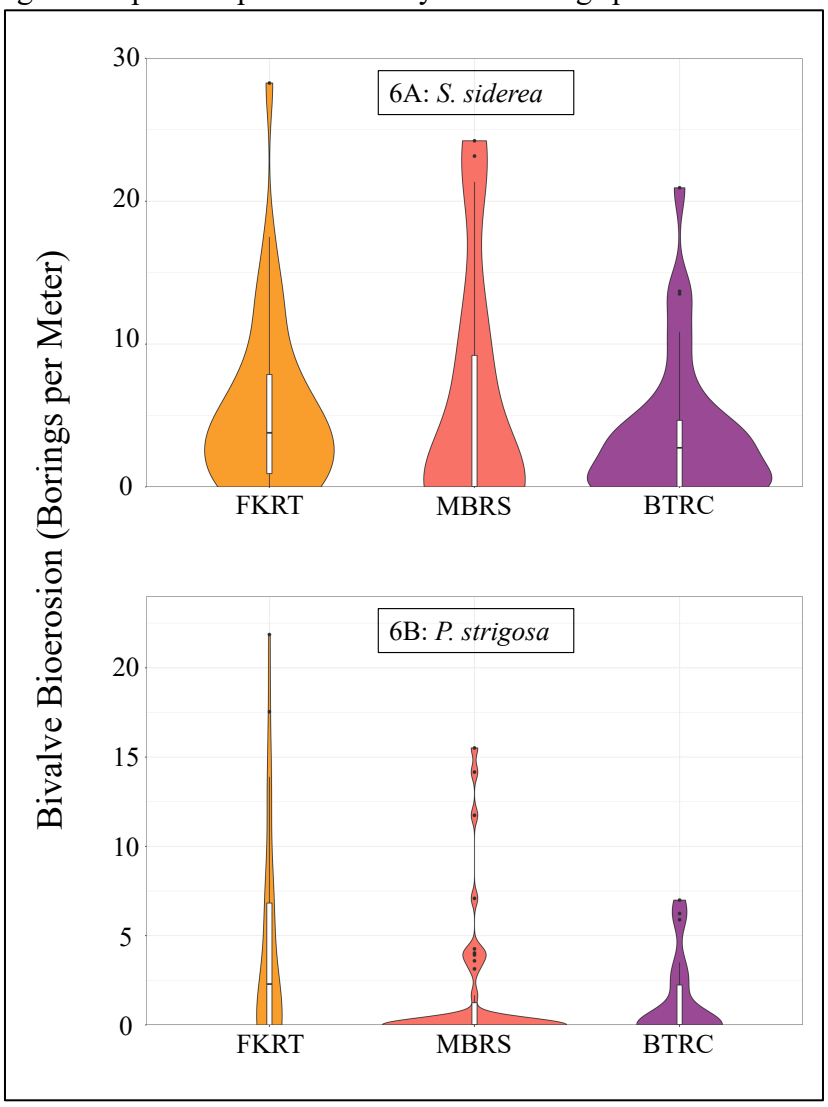

Graphs depict probability density distribution of borings per meter on cores with respect to groupings. Asterisks delineate the significance level of the test (P < 0.05 = *; P < 0.01. = **; P < 0.001. = ***).

Figure 5. Reef Zone Specific Reef System Borings per Meter Trends



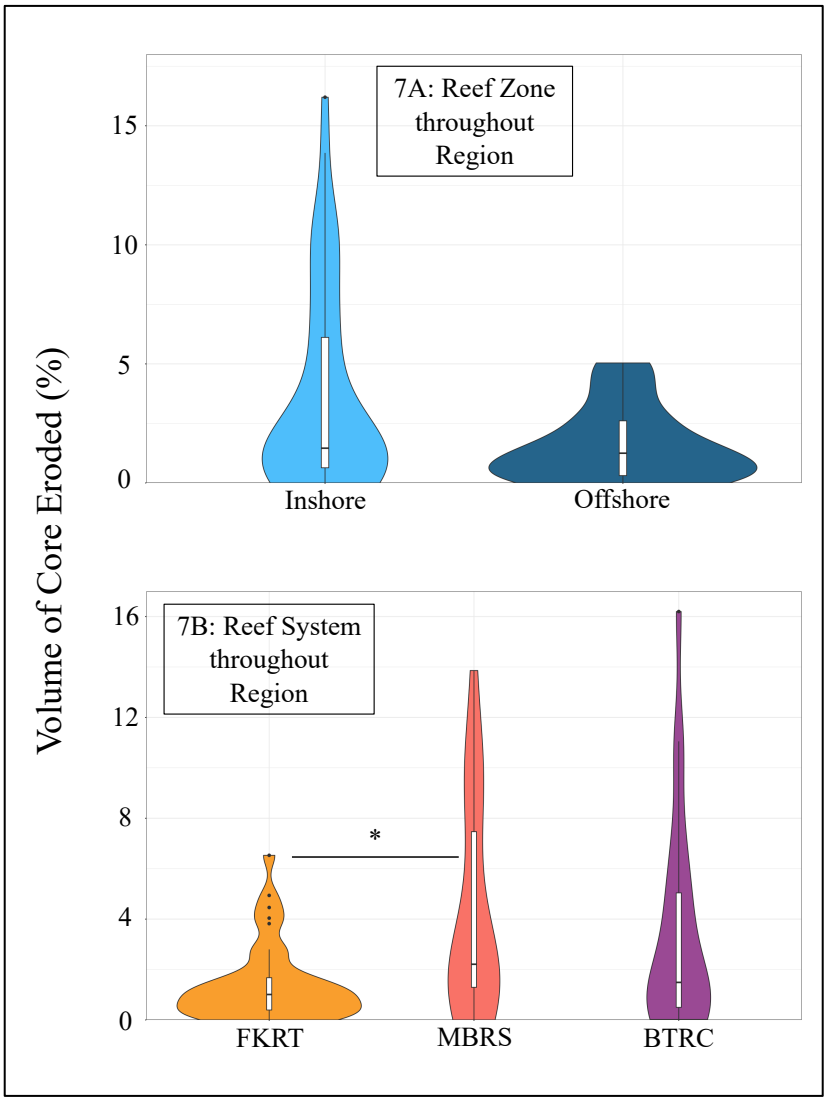

Graphs depict probability density distribution of borings per meter on cores with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 6. Species Specific Reef System Borings per Meter Trends



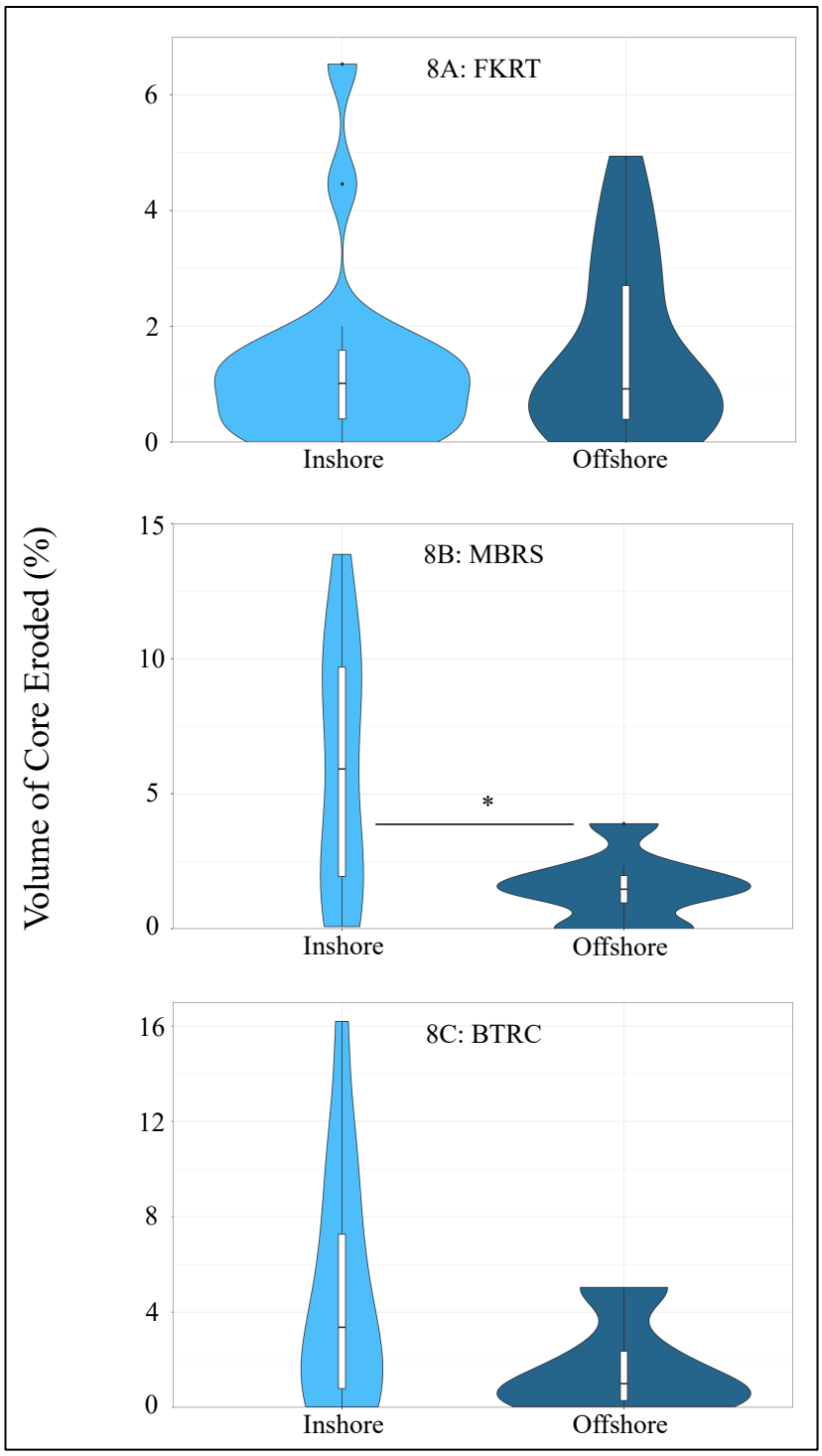

Graphs depict probability density distribution of borings per meter on cores with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 7. Major Percent Volume Eroded Trends



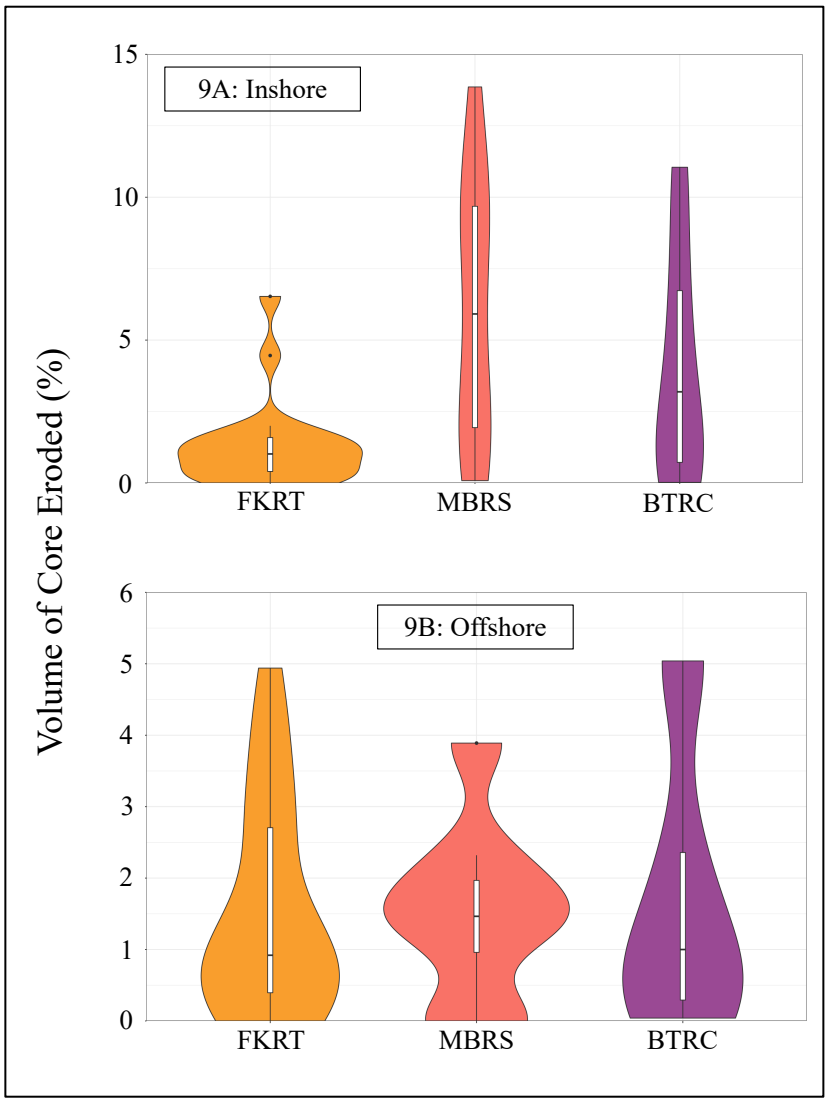

Graphs depict probability density distribution of percent volume eroded with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 8. Reef System Specific Reef Zone Trends



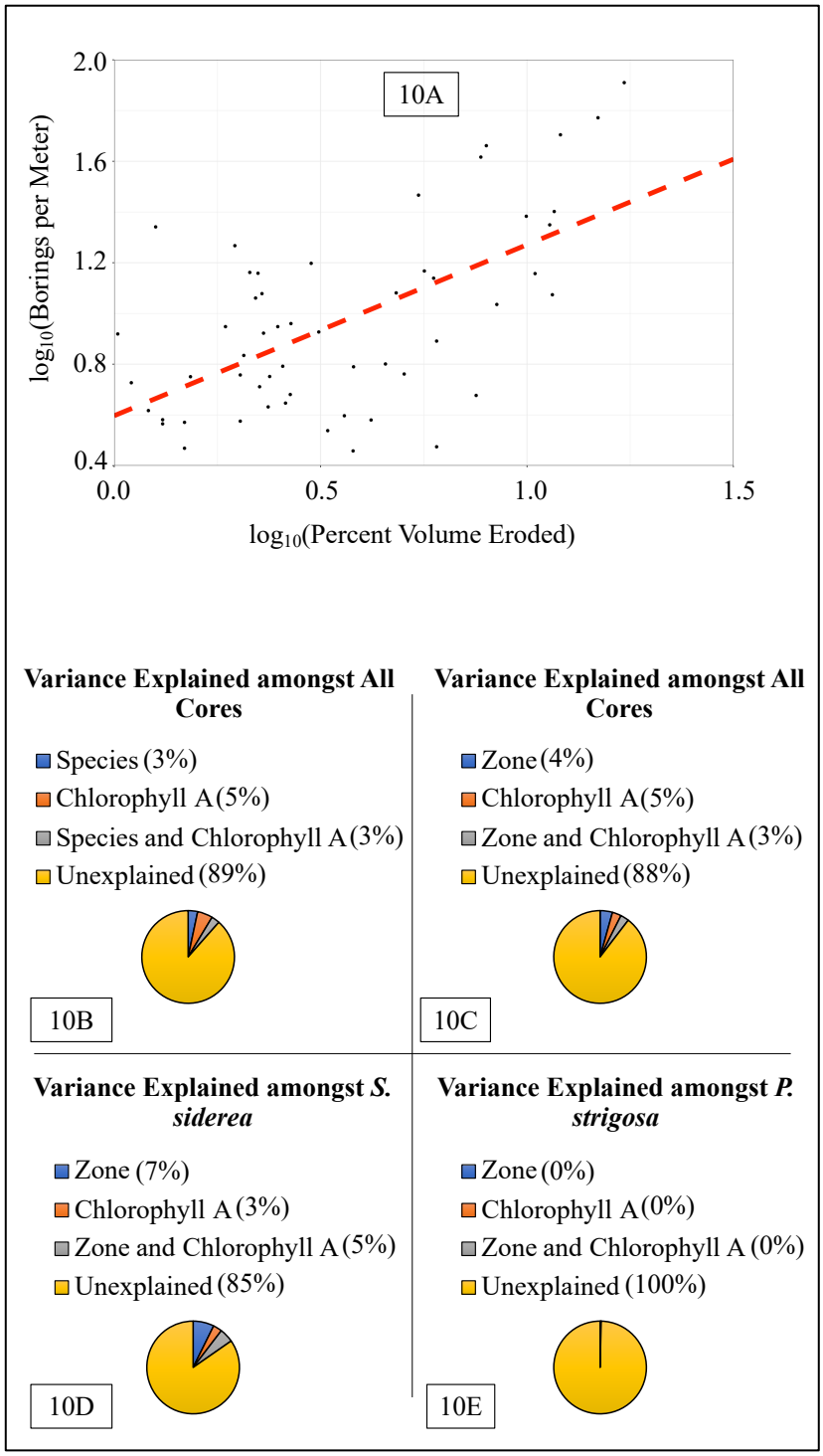

Graphs depict probability density distribution of percent volume eroded with respect to groupings. Asterisks delineate the significance level of the test (P < 0.05 = *; P < 0.01. = **; P < 0.001. = ***).

Figure 9: Reef Zone Specific Reef System Trends




Graphs depict probability density distribution of percent volume eroded with respect to groupings. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Figure 10: Linear Modeling and Variance Partitioning




Graph 10A depicts relationship between the two methods of bioerosion quantification. 10B-10E depict how much various factors and variables explain variation in bioerosion amongst cores.

**Tables:**

Table 1. Bivalve Borings per Meter Group Comparison Results

| Group A (Median) | Group B (Median) | Wilcoxon rank-sum test P-value | Kruskal-Wallis rank sum test P-value |
|---|---|---|---|
| *S. siderea* (3.210) | *P. strigosa* (0.000) | $3.959 \cdot 10^{-5}$*** | |
| Inshore (2.820) | Offshore (0.000) | $1.532 \cdot 10^{-3}$** | |
| MBRS (0.000) | FKRT (2.815) | $4.8 \cdot 10^{-2}$* | $4.353 \cdot 10^{-2}$* |
| MBRS (0.000) | BTRC (1.930) | $6.41 \cdot 10^{-1}$ | $4.353 \cdot 10^{-2}$* |
| FKRT (2.815) | BTRC (1.930) | $4.82 \cdot 10^{-1}$ | $4.353 \cdot 10^{-2}$* |
| MBRS *S. siderea* (3.005) | MBRS *P. strigosa* (0.000) | 0.008111** | |
| FKRT *S. siderea* ( 3.790) | FKRT *P. strigosa* (2.290) | $1.851 \cdot 10^{-1}$ | |
| BTRC *S. siderea* (2.45) | BTRC *P. strigosa* (0.000) | 0.01288* | |
| MBRS Inshore (0.000) | MBRS Offshore (0.000) | $1.11 \cdot 10^{-1}$ | |
| FKRT Inshore (2.760) | FKRT Offshore (4.140) | 1 | |
| BTRC Inshore (5.020) | BTRC Offshore (0.000) | $1.562 \cdot 10^{-4}$*** | |
| MBRS *S. siderea* (2.45) | FKRT *S. siderea* (3.790) | 1 | $8.581 \cdot 10^{-1}$ |
| MBRS *S. siderea* (2.45) | BTRC *S. siderea* (3.005) | 1 | $8.581 \cdot 10^{-1}$ |
| FKRT *S. siderea* (3.790) | BTRC *S. siderea* (3.005) | 1 | $8.581 \cdot 10^{-1}$ |
| MBRS P. strigosa (0.000) | FKRT *P. strigosa* (2.290) | $8.7 \cdot 10^{-2}$ | $4.983 \cdot 10^{-2}$* |
| MBRS P. strigosa (0.000) | BTRC *P. strigosa* (0.000) | 1 | $4.983 \cdot 10^{-2}$* |
| FKRT P. strigosa (2.290) | BTRC *P. strigosa* (0.000) | $1.91 \cdot 10^{-1}$ | $4.983 \cdot 10^{-2}$* |
| MBRS Inshore (0.000) | FKRT Inshore (2.760) | 1 | $1.009 \cdot 10^{-1}$ |
| MBRS Inshore (0.000) | BTRC Inshore (5.020) | $1.7 \cdot 10^{-1}$ | $1.009 \cdot 10^{-1}$ |
| FKRT Inshore (2.760) | BTRC Inshore (5.020) | $2.5 \cdot 10^{-1}$ | $1.009 \cdot 10^{-1}$ |
| MBRS Offshore (0.000) | FKRT Offshore (4.140) | $3.0 \cdot 10^{-2}$* | $6.476 \cdot 10^{-3}$** |
| MBRS Offshore (0.000) | BTRC Offshore (0.000) | 1 | $6.476 \cdot 10^{-3}$** |
| FKRT Offshore (4.140) | BTRC Offshore (0.000) | $1.8 \cdot 10^{-2}$* | $6.476 \cdot 10^{-3}$** |

Distribution specific data included for all of groups considered. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Table 2. Percent Volume Eroded Group Comparison Results

| Group A (Median) | Group B (Median) | Wilcoxon rank-sum test P-value | Kruskal-Wallis rank sum test P-value |
|---|---|---|---|
| Inshore (1.4600) | Offshore (1.250) | $8.918 \cdot 10^{-2}$ | |
| MBRS (2.210) | FKRT (1.010) | $2.1 \cdot 10^{-2}$* | $2.206 \cdot 10^{-3}$** |
| MBRS (2.210) | BTRC (1.490) | 1 | $2.206 \cdot 10^{-3}$** |
| FKRT (1.010) | BTRC (1.490) | $2.76 \cdot 10^{-1}$ | $2.206 \cdot 10^{-3}$** |
| MBRS Inshore (5.915) | MBRS Offshore (1.465) | $3.38 \cdot 10^{-2}$* | |
| FKRT Inshore (1.0150) | FKRT Offshore (0.920) | $7.894 \cdot 10^{-1}$ | |
| BTRC Inshore (3.365) | BTRC Offshore (1.000) | $1.513 \cdot 10^{-1}$ | |
| MBRS Inshore (5.915) | FKRT Inshore (1.0150) | $6.3 \cdot 10^{-3}$** | $7.095 \cdot 10^{-3}$** |
| MBRS Inshore (5.915) | BTRC Inshore (3.365) | 1 | $7.095 \cdot 10^{-3}$** |
| FKRT Inshore (1.0150) | BTRC Inshore (3.365) | $1.627 \cdot 10^{-1}$ | $7.095 \cdot 10^{-3}$** |
| MBRS Offshore (1.465) | FKRT Offshore (0.920) | 1 | $9.623 \cdot 10^{-1}$ |
| MBRS Offshore (1.465) | BTRC Offshore (1.000) | 1 | $9.623 \cdot 10^{-1}$ |
| FKRT Offshore (0.920) | BTRC Offshore (1.000) | 1 | $9.623 \cdot 10^{-1}$ |

Distribution specific data included for all of groups considered. Asterisks delineate the significance level of the test ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).

Table 3. Bioerosion Quantification Linear Models

| Model Name | Dependent Variable | $\beta_0$ (Intercept Value) | $\beta_1$ (Slope Variable and Value) | Equations |
|---|---|---|---|---|
| A | Bivalve Borings per Meter | 0.59674*** | Percent Volume Eroded 0.67428*** | $\mathbf{R^2 = 3.525 \cdot 10^{-1}}$ $\log_{10}$(Borings per Meter) = 0.59674 + 0.67428•$\log_{10}$(Percent Volume Eroded) |
| B | Bivalve Borings per Meter | 2.302* | Wet Season Chlorophyll A 1.592*** | $\mathbf{R^2 = 7.652 \cdot 10^{-2}}$ (Borings per Meter) = 2.302+1.592•(Wet Season Chlorophyll A) |
| C | Bivalve Borings per Meter | 3.1610*** | Dry Season Chlorophyll A 1.3631*** | $\mathbf{R^2 = 5.317 \cdot 10^{-2}}$ (Borings per Meter) = 3.1610+1.3631• (Dry Season Chlorophyll A) |
| D | Percent Volume Eroded | 2.0794*** | Wet Season Chlorophyll A 0.2942 | $\mathbf{R^2 = 1.995 \cdot 10^{-2}}$ (Percent Volume Eroded) = 2.0794+0.2942•(Wet Season Chlorophyll A) |
| E | Percent Volume Eroded | 2.3676*** | Dry Season Chlorophyll A 0.1874 | $\mathbf{R^2 = 5.375 \cdot 10^{-4}}$ (Percent Volume Eroded) = 2.3676+0.1874• (Dry Season Chlorophyll A) |

Linear Models results determining the relationships between methods of bioerosion quantification and Chlorophyll A in the environment. $R^2$ values reveals how well specific methods of bioerosion quantification are explained by model. Asterisks delineate the significance level of the ANCOVA derived relationship ($P < 0.05$ = *; $P < 0.01$. = **; $P < 0.001$. = ***).