Biodiversity of Coral Species in Selected Caribbean Regions

Hannah-Marie Lamle, Sarah M. Muckerheide, Jenna H. Baelz, Carley J. Divish
Faculty Mentors: Dr. Claudia C. Johnson & Charles D. Beeker
Indiana University Bloomington

ABSTRACT

Indiana University's Center for Underwater Science (IU) has been monitoring shipwreck sites in the Florida Keys and Dominican Republic for more than three decades. This paper is a synthesis of all coral species data collected at six sites from 1988 to 2021 to understand biodiversity differences including alpha, beta, and gamma species richness. The goal of this study is to analyze biodiversity within the context of dispersal and historical legacy. Biodiversity comparisons of sites within the Florida Keys and Caribbean yielded similar results, but in comparing the two ecoregions, results indicated greater differences in biodiversity between rather than within ecoregions. Results of surface current patterns and phylogenic analyses showed that both dispersal and historical legacy played a role in the current biodiversity of the ecoregions, further speculating that modern-day anthropogenic causes may be driving differences in biodiversity.

KEYWORDS: coral reef, ecology, biodiversity, biogeography, phylogeny

INTRODUCTION

Coral reefs worldwide have been studied extensively due to the extreme ecological importance of these ecosystems relative to their size. The coral reef ecosystem comprises just 1% of total ocean floor but harbors approximately 25% of all known fish species in the oceans, making these ecosystems biodiversity hotspots that provide benefits both to the ecosystem and to humans (Moberg & Folke, 1999). However, anthropogenic factors such as climate change have catalyzed the decline of reefs in the Caribbean. Corals are under threat from rising sea temperatures, ocean acidification, pollution, and coral diseases (Gardner Toby A. et al., 2003). Specific conditions need to be met for these animals to flourish, including water temperature, depth, water movement, pH level, and a calcium carbonate substrate to settle on. Therefore, when conditions change rapidly, corals may not be able to adapt quickly enough to overcome these stressors, and they undergo a process called bleaching (Rohwer et al., 2010). Corals are animals with a symbiotic relationship to photosynthetic algae known as zooxanthellae, and when conditions are not met for a coral (warmer water temperature, decreasing pH, etc.) the coral expels the algae from its colony, resulting in the bleaching of their tissue, as the zooxanthellae give coral their unique colors (Hughes et al., 2003). When bleaching occurs, the corals become deprived of nutrients, as zooxanthellae photosynthesize energy for the coral animal to use for growth. Corals cannot sustain prolonged episodes of bleaching, and they will eventually succumb to the stress events caused by the bleaching (Rohwer et al., 2010).

Focusing specifically on coral reefs found in the Caribbean Sea, biodiversity of coral species varies based on the region within the Caribbean Sea. The book Marine Ecoregions of North America categorizes areas of the Caribbean Sea based on location and commonality of ecological parameters (Wilkinson et al. 2009). The Indiana University Center for Underwater Science (IU) has over three decades of coral data in two of these ecoregions, the Florida Keys (Region 12.1.2, "Florida Keys") and the Dominican Republic (Region 15.2.1, "Caribbean Sea"), (Figure 1). However, coral data are comprised mainly of coral growth on shipwreck sites, which are artificial reefs. Unlike a natural coral reef that grows on benthic substrate unaltered by humans, an artificial reef is a reef with substrate that was placed underwater by humans, either purposefully or by accident, as is the case with most shipwrecks (Ammar, 2009). Shipwrecks and associated artifacts often provide excellent coral growth substrate, an elevated

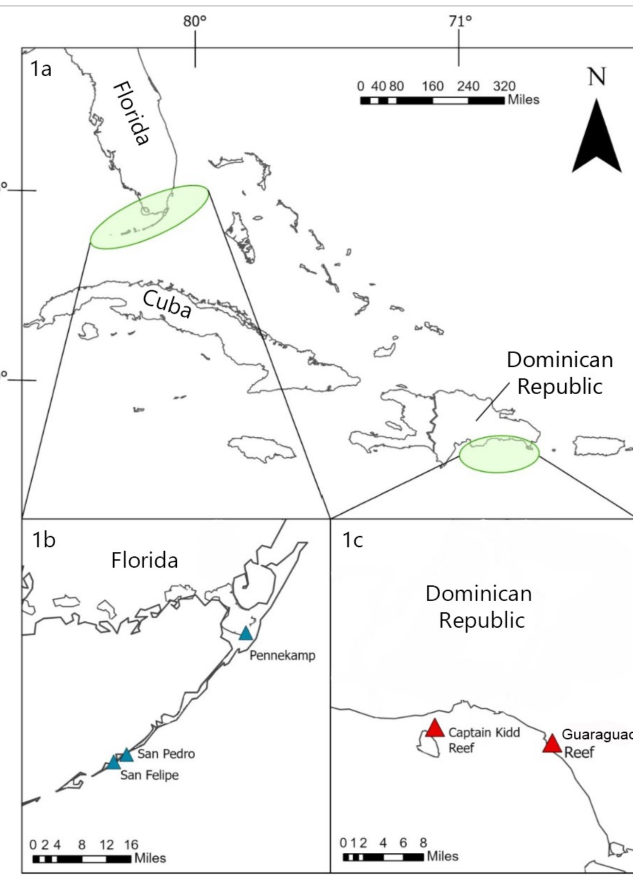


Figure 1a-c. **Study sites.** *1a: Ellipses showing the Florida Keys and Caribbean Ecoregions, 1b: Location of Pennekamp State Park, San Pedro and San Felipe shipwrecks within Florida Keys Ecoregion, 1c: Location of Captain Kidd and Guadalupe Underwater Archaeological Preserve (GUAP) shipwrecks within Caribbean Sea Region (the GUAP is located within Guaraguao reef).*

surface area, and attract fishes to consume the algae that grows on and suffocates corals. However, these shipwreck-based substrates cannot fix the widespread issues of coral bleaching and death now occurring across oceans (Olinger et al., 2019). The shipwrecks that are studied by IU provide a unique study area, as these sites are historically important and most of them are protected by laws and managed regularly, allowing for undisturbed coral growth.

To compare biodiversity between ecoregions, three comparisons were made comprising six sites in total (Figure 2). Two of the six sites are the San Felipe and San Pedro, located in the Middle Keys within the Florida Keys Ecoregion. Both shipwrecks were Spanish Galleons that wrecked in a hurricane in 1733. Their wooden hulls have deteriorated over time, but the ballast pile is still intact, providing substrate for biological growth (Beeker et al., 2018). The next site is the Captain Kidd Reef, adjacent to the Privateer Captain Kidd's ship the Quedagh Merchant in the Caribbean Sea ecoregion. This ship was scuttled and set ablaze in the La Romana River in the Dominican Republic. It drifted to sea and settled on the East coast of Catalina Island, where it sank. Today, all that remains is two concreted piles of cannons stacked neatly above the hull (Beeker & Hanselmann, 2009). The fourth site, also located in the Caribbean Sea Ecoregion (off the coast of Dominican Republic) is Guaraguao Reef, which encompasses the fifth site, the Guadalupe Underwater Archaeological Preserve (GUAP). The GUAP is a shipwreck park that utilizes features (cannons and anchor) from the Nuestra Señora de Guadalupe, a shipwreck that

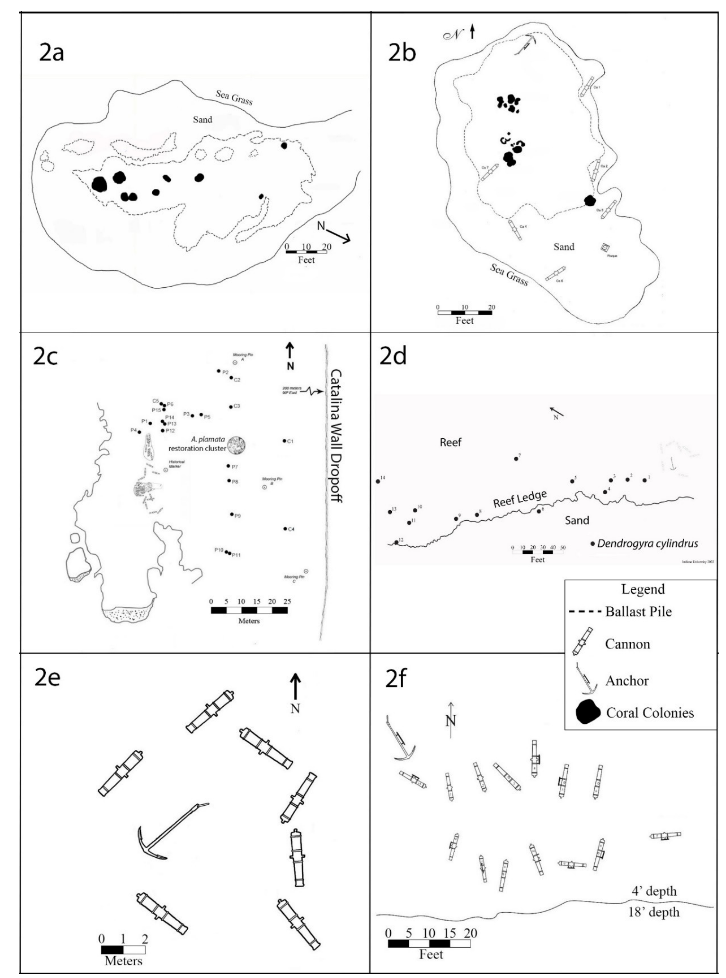


Figure 2a-f: **Site plans of selected sites.** *2a: San Felipe, 2b: San Pedro, 2c: Captain Kidd Reef, 2d: Guaraguao Reef, 2e: GUAP, 2f: Pennekamp State Park. See Table 1 for area calculations for each site.*

was lost to a hurricane in 1724 off the Northeast coast of Dominican Republic (Simonelli, 2008). Site six is another park, John Pennekamp State Park located in Key Largo, Florida (Florida Keys Ecoregion). The features of this park (anchors and cannons) were also from a Spanish galleon that wrecked in 1715 (Beeker & Hanselmann, 2008).

The Florida Keys and Dominican Republic ecoregions were analyzed for coral biodiversity in order to examine and understand differences in biodiversity. In this research, two main hypotheses were investigated. The dispersal of biota on surface currents hypothesis suggests that differences in biodiversity could be attributed to surface currents pushing coral larvae to different ecoregions throughout the Caribbean Sea. The historical legacy hypothesis suggests that biodiversity in each ecoregion is attributed to dominant reef building species colonizing reefs over time to shape the biology of the reef-scape in each ecoregion. Data were collected to test each hypothesis and were analyzed to evaluate biodiversity differences. The results in this study serve to summarize and reflect upon the coral-reef-specific data gathered since the inception of the program in each ecoregion.

METHODS AND MATERIALS

Field Collection

Data collection has been conducted by graduate and undergraduate students from IU on yearly field schools. Data were collected in various formats, including lists of unique coral species identified at each site, and photographic, video, and photogrammetric images. Photogrammetric data consist of highly precise, large area images created from a series of overlapping photos that are stitched together. They are commonly used for monitoring marine benthic ecosystems and archaeological sites over time. Photogrammetric data were processed into an orthomosaic model which was used for measuring the geographic area of some of the sites in this study. The data collected on yearly field schools culminated in the creation of Rapid Assessment Reports for every site surveyed. Rapid Assessment Reports include a discussion on the archaeological and biological integrity of the site, and the identification of coral species growing on shipwreck and natural reef sites. This database of sites in the Florida Keys and Dominican Republic is presented as a cumulative study.

Laboratory Data Processing

Coral presence-absence data were collected for a total of nine sites throughout the Florida Keys and Dominican Republic using past Rapid Assessment Reports created by IU. A database indicating the presence or absence of a species for each year was created for each site. Presence-absence data have been shown to be "the only functional diversity index," (Loiseau, 2015, p. 4022) due to its ability to take species function into account as well as the degrees of difference between species.

Each site studied required an independent geographic area analysis (Table 1). Geographic area calculations of the *San Felipe* and *San Pedro* shipwrecks used an area of an oval equation, (a)(b)(π). This equation was chosen due to the ships being undisturbed during the wrecking process, allowing the ballast stones to concrete together in the relatively ovular shape similar to how they were held in the hull. The rectangle formula (a=(l)(w)) was utilized to calculate the area of both the Captain Kidd Reef and Guaraguao Reef due to the shape of the orthomosaic models for these sites, which were rectangular. These orthomosaic models encompassed all necessary components of each site, and thus the full extent of the model was used in the size comparison. The area of the GUAP and Pennekamp State Park sites was limited to the area of the cannons and anchors upon which coral grew. Thus, the formula used for the cannons was the area of a cylinder (2πrh)+(2πr²). That area was then halved to account for the fact that half of the cannon is in direct contact with bottom substrate and cannot support biotic growth. For the anchors, the sum of the area of the shaft using the cylinder formula, and the sum of the area of each fluke, also using the cylinder formula, were calculated.

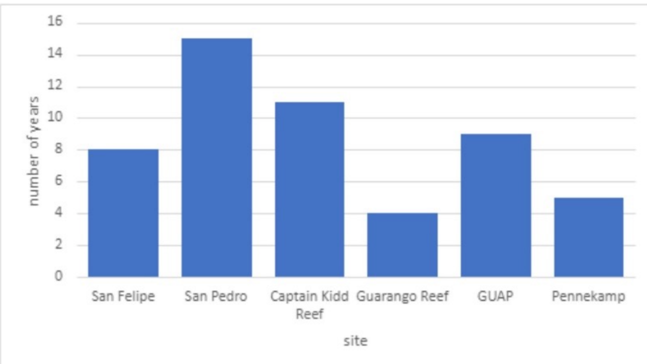


Figure 3: **Number of years of data collected at each site from 1988 through 2021.**

The number of years of data collected on the six sites since IU first began its underwater biological and archaeological documentation are shown in Figure 3. Data were collected initially in 1988 and continued through 2021 apart from fieldwork suspended in 2020 due to the COVID-19 Pandemic. Data were not collected consistently at each site for each year. IU research projects, interests, and needs varied throughout the years, leading to other sites being investigated, but not included in this work.

The metrics used to choose each site were amount of data present through the years, geographic area of the site, natural versus artificial reef, and protection status. It was decided based on these metrics to analyze the *San Pedro, San Felipe*, Captain Kidd Reef, Guaraguao Reef, the GUAP, and Pennekamp State Park. Three analyses of two sites compared biological diversity for each of the metrics. Comparative sites were the *San Felipe* and *San Pedro*, the Captain Kidd Reef and Guaraguao Reef, and the GUAP and Pennekamp State Park. Once the data were consolidated into six sites of interest in the three comparisons, coral species diversity from all sites and all years was graphed (Figure 4), and ecological analysis of the coral data for each site began. Alpha, beta, and gamma species richness indices were calculated on Microsoft Excel for diversity within, between, and among sites. Alpha richness is a measure of the number of unique species present on a site. Beta species richness is the number of unique species between two sites. Gamma species richness is the total number of unique species present for all sites being surveyed.

Analysis and creation of a surface current map showing trends in the Caribbean Sea and Florida Keys ecoregions were done by combining data from historic and recent surface current maps. These sites include NOAA buoy data and Earth Nullschool interactive map with data from OSCAR Earth & Space Research. By combining data from these sources, a simplified general current flow map was created (Figure 5) that encompasses trends from all sources.

Phylogenetic data were obtained via a literature review using two databases. The World Register of Marine Species (WoRMS) was utilized to determine the taxonomic families for each of the coral species examined in this paper. The Paleobiology Database lists the timing and distribution of each coral family, so this database was used to determine when on the geologic time scale each coral family first occurred in both Florida and the Dominican Republic.

RESULTS

Geographic area calculations of the GUAP and Pennekamp State Park were limited to the areas of the cannons and anchors upon which coral grew. The GUAP geographic area totaled 17.03 m². The 25.40 cm diameter of the GUAP's cannon bore was estimated using the size of the corresponding ammunition (a 10.16 cm diameter cannon ball size and 7.62 cm for each side wall). The length of the cannon (2.60 m) was input to calculate an area of 2.2 m² per cannon. That area was then halved to account for the fact that half of the cannon is in direct contact with the bottom substrate and cannot support biotic growth; total area for all 7 cannons= 15.26 m². The length of an anchor from a Rapid Assessment archaeology report (3.63 m) and estimated diameter of the shaft (15.24 cm) were used for shank dimensions. The length of each fluke is 1.81 m, and diameter was the same as the shank. Area of a cylinder calculations were done for the full length of the shank and flukes and was summed, totaling 1.77 m².

Pennekamp State Park total geographic area was 35.65 m². The diameter of the cannon barrel was estimated to be 25.40 cm using the size of the ammunition used by the Spanish in the 18th century (10.16 cm cannon ball diameter and 7.62 cm side walls). Other measurements of the Pennekamp cannons were listed in a thesis written on the development of the site (Lane, 2011), giving the total area of one cannon = 1.88 m². That area was then halved to account for the fact that half of the cannon is in direct contact with bottom substrate and cannot support biotic growth. The anchor area was calculated, beginning with the length of the shaft (3.28 m), the estimated diameter of shaft (15.24 cm) and the estimated length of each fluke (1.64 m).

For the remaining sites, the total geographic area varied considerably. The *San Felipe* (area of an oval calculation) was 638 m², the *San Pedro* (area of an oval calculation) was 687 m². The geographic area of the Captain Kidd Reef (area of a rectangle) was 120 m², while the area of Guaraguao Reef was the largest area at 3396.77 m² (Table 1).

Data collected from IU research projects and field schools span over three decades for the longest studied site, the *San Pedro*, and as little as four years for the least studied site, Guaraguao Reef (Figure 3). Data collection began in 1979 and continues to the present day, with varying sites becoming the focus based on the year. Pairing these sites for comparisons, the *San Pedro* had 7 more years of data collection than the *San Felipe* (15 and 8, respectively). Captain Kidd Reef had 11 years of data collection, while Guaraguao Reef had 4, giving a difference of 7. Lastly the GUAP and Pennekamp State Park had a difference of 4 years (9 and 5, respectively).

Given the multiple decades of data collection, and the fact that presence-absence data were used and not abundance of corals, the study proceeded with comparing geographic areas. There was a wealth of data on coral diversity at each of these sites. Forty-one total coral species were identified among all sites and were ordered based on their frequency of occurrence on all six sites across all years (Figure 4). Of those species, the five corals most frequently seen in both Ecoregions were *Siderastrea siderea, Diploria labyrinthiformis, Meandrina meandrites, Pseudodiploria strigosa,* and *Montastraea cavernosa*. The alpha richness measurements for all sites were relatively similar, with one outlier being Pennekamp State Park (Table 2). The *San Felipe* site had an alpha richness value of 20, while the *San Pedro* had a value of 28. Captain Kidd Reef had an alpha richness of 23, and Guaraguao Reef had an alpha richness value of 30, the highest value for all sites. The GUAP had an alpha richness value of 20, while Pennekamp State

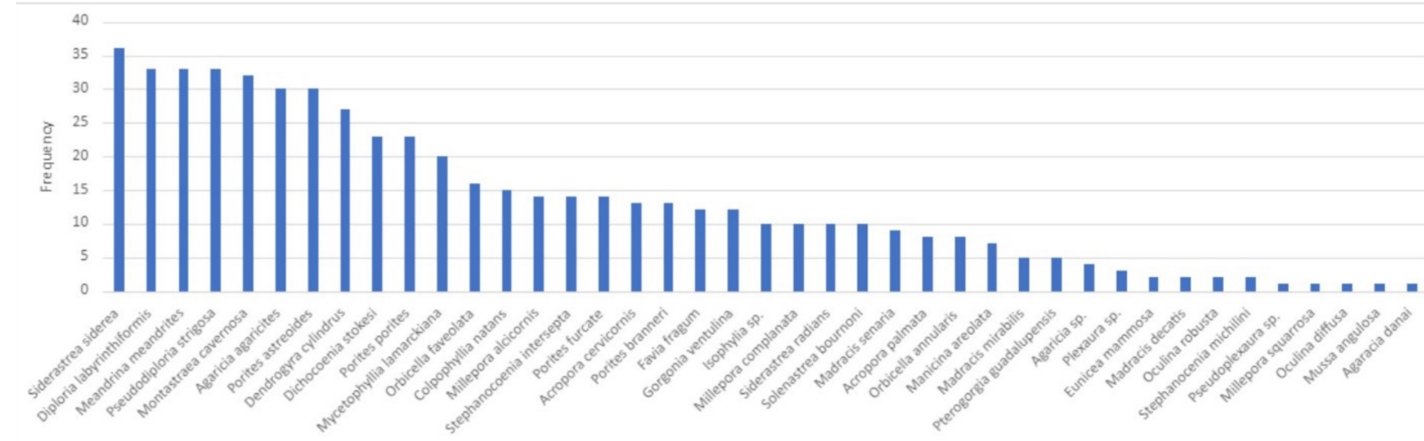


Figure 4: **Coral species diversity tallied from all sites across all years.**

Figure 5: **Surface current flow in the Caribbean Sea, spanning both Ecoregions of interest (Caribbean Sea and Florida Keys).**

Park had a value of 3. This alpha richness value is representative of a diverse coral species ecosystem and is a unique count of every species seen at a site for all years of data.

Beta richness is the sum of the unique species between two separate sites; it is a measure of how different sites are from one another. The comparison between the *San Felipe* and *San Pedro*, both sites within the Florida Keys Ecoregion, returned a beta richness value of 14 (Table 3). Of the Captain Kidd and Guaraguao Reef comparison, both in the Caribbean Sea Ecoregion, the beta richness was 16, slightly higher than the Florida Keys Ecoregion comparison (Table 3). Lastly, the GUAP and Pennekamp State Park comparison returned a beta richness value of 19. The last comparison was between Ecoregions, as the GUAP is in the Caribbean Sea, while Pennekamp is in the Florida Keys. In order to compare these three beta richness values to one another, the standardized beta richness was found by dividing each beta richness value by 41, the total number of corals identified across all sites and years, i.e. the gamma richness. The standardized beta richness value for the *San Felipe* and *San Pedro* was 0.34. For the Captain Kidd Reef and Guaraguao Reef comparison, standardized beta richness was 0.39. Lastly, the GUAP and Pennekamp State Park comparison returned a standardized beta richness value of 0.46 (Table 3).

To test the hypothesis of whether corals are dispersed throughout each ecoregion or have a historical legacy, data were analyzed for surface current trends in the Caribbean Sea. In addition, phylogenetic data evaluated the evolution of coral species, and species' ages were matched to ecoregion. Shown in Figure 5, surface current patterns in the Caribbean Sea sweep clockwise from Southeast to Northwest, flowing from the Caribbean Sea Ecoregion where the Dominican Republic sites are located, to the Florida Keys Ecoregion. The phylogenetic data in Table 4 show the age of each coral species on a geologic time scale as well as when each species was first present in the ecoregions.

DISCUSSION

Sample sizes across geographic areas for comparative sites are unequal, as some corals were recorded growing on natural calcium carbonate substrates, while others were recorded on cannons and anchors. In order to reduce the variation of unequal sample size, comparisons of coral diversity were made between sites with similar areas. Overall, the goal of this paper is to determine the differences in coral species biodiversity between the Florida Keys and Dominican Republic and assess if these differences were attributable to coral larval dispersal or a historical legacy of species at each site.

The *San Felipe* and *San Pedro* sites were comparable because both sites are shipwrecks that are now present as ballast stones that corals have colonized. The geographic areas of the *San Felipe* and *San Pedro* are represented as ovals and are approximately equal: 638 m² and 687 m², respectively (Table 1). Given the similarities between these two sites (location within the Florida Keys Ecoregion, geographic area, and type of wreck) their standardized beta richness was 0.34. For a comparison within the same ecoregion, the beta diversity was expected to be low, since these two sites are extremely similar in both surface area, wreck topography, and location. This standardized beta value was the lowest beta value for each of the three comparisons, indicating that of the three comparisons made, these two sites were the most similar in coral diversity.

For the Captain Kidd Reef and Guaraguao Reef sites corals growing on a natural calcium carbonate substrate, outside of shipwreck features, were compared (Table 1). This comparison had the second highest beta richness at 16 unique species for both sites (Table 3). This standardized beta richness value is 0.39, slightly higher than the *San Felipe* and *San Pedro* comparison. This value was expected, as these sites differ in geographic area by a large amount and are farther away from each other. However, when comparing the beta richness between the Florida Keys sites (*San Pedro* and *San Felipe)* and the Dominican Republic sites (Captain Kidd Reef and Guaraguao Reef) they are similar, (0.34 and 0.39, respectively) indicating that the coral species diversity of each ecoregion is similar throughout the geographic area.

Comparisons between GUAP features and Pennekamp shipwreck parks represent artificial substrates raised above natural sea floor (i.e. cannons and anchors) (Table 1). This comparison returned a beta richness value of 19, the highest value for each of the comparisons (Table 3). The standardized beta richness value was 0.46; almost half of all coral species recorded at both sites were unique to one site or the other. This indicates that the coral diversity between ecoregions is more different than the diversity within ecoregions.

In the Florida Keys ecoregion, the most common corals (*Porites astreoides, Siderastrea siderea, Favia fragum*) were first identified in the Oligocene geologic period or Oligocene and Miocene (Table 4). The most common corals in the Dominican Republic in the Caribbean Ecoregion (*Meandrina meandrites, Siderastrea siderea, Diploria labyrinthiformis*) were also found in the Oligocene or Miocene geologic periods. Since the most common corals at each site were first found during the same time periods, there is reason to believe that the diversity of corals at each ecoregion is due to a historical legacy of coral species that evolved and continued to dominate coral reefs at each location.

Surface ocean currents in the Caribbean Sea sweep from the Lesser Antilles to the Gulf of Mexico, then join the Gulf Stream (Figure 5). In relation to the biodiversity data and the species most frequently cited at each site, it appears dispersal on surface currents could be a viable method for explaining the differences in coral species distribution in the two ecoregions.

In summary, based on biodiversity data, surface current analysis, and evolutionary historical data, contributions to modern day differences in biodiversity among sites can be attributed to both an historical legacy stemming from the rock record and the larval dispersal of species. Further, the difference in beta diversity between the Florida Keys ecoregion and the Dominican Republic in the Caribbean Sea ecoregion could be analyzed in future studies to include more modern factors, such as regional coral diseases that target specific corals, and environmental factors including rising sea surface temperatures and ocean acidification.

CONCLUSION

Coral reef ecosystems are under increasingly higher levels of stress due to anthropogenic influences such as increased sea surface temperatures, decreasing ocean pH causing ocean acidification, and increased pollution (Hughes et al., 2003). Therefore, it is becoming more important to identify hotspots of coral biodiversity to aid in understanding the environmental conditions that harbored such high biodiversity and to focus management and restoration efforts in that area. Studies have shown that coral colonies have a better chance of survival when proper marine management practices are in place. As mentioned in Favoretto et al. (2020), coral reefs studied off the Yucatan Peninsula that were isolated and protected under federal laws had a higher coral count and coral recruitment count than reefs that were unprotected. This study suggests that the impact of proper management practices could have had an effect on the difference in alpha diversity of the *San Pedro* and *San Felipe* comparison. While both sites are located within the Florida Keys National Marine Sanctuary, the *San Pedro* is recognized as a state park, and thus has proper management practices in place to ensure the integrity of archaeological features. This indirectly improves the biological health of the site, as there is a mooring system for boats, archaeological teams come out regularly to service the sites, and there are anti-fishing and anti-collection laws in place at the site.

In addition to management practices playing a role in coral diversity across sites, there are also impacts from evolutionary and abiotic factors that facilitate coral diversity. It was shown that the most common corals at each ecoregion appeared during the same geologic epoch, and larval dispersal could explain the patterns of coral distributions. Therefore, more research is needed in order to identify biotic and abiotic drivers of differences in biodiversity between the Florida Keys and Caribbean Sea ecoregions. Other metrics, such as species genetic diversity, larval recruitment, growth rate, nitrogen and phosphorus content, and other biotic and abiotic variables could better inform this study on the specific drivers of biodiversity difference between sites and across ecoregions.

APPENDIX

Site	Calculations Used	Geographic Area (m²)
San Felipe	Area of an Oval: (a)(b)pi	638
San Pedro	Area of an Oval: (a)(b)pi	687
Captain Kidd Reef	Area of a Rectangle: (l*w)	120
Guaraguao Reef	Area of a Rectangle: (l*w)	3396.77
GUAP	Cannons: Area of a cylinder divided by 2: $(2\pi rh+2\pi r^2)/2$ Anchor: Area of a cylinder divided by 2: $(2\pi rh+2\pi r^2)/2$	17.03
Pennekamp	Cannons: Area of a cylinder divided by 2: $(2\pi rh+2\pi r^2)/2$ Anchor: Area of a cylinder divided by 2: $(2\pi rh+2\pi r^2)/2$	35.65

Table 1: **Calculations used for determining area of the features on which corals grew (i.e., cannons, anchor) or geographic area of the site (m²).**

	San Felipe	*San Pedro*	Captain Kidd Reef	Guaraguao Reef	GUAP	Pennekamp
Alpha Richness:	20	28	23	30	20	3

Table 2: **Alpha Richness metrics for each site, representing the unique count of coral species present for all years of data collected.**

	San Felipe & San Pedro	Captain Kidd Reef & Guaraguao Reef	GUAP & Pennekamp
Beta Richness	14	16	19
Standardized Beta Richness	0.34	0.39	0.46
Gamma Richness	41		

Table 3: **Beta Richness values and corresponding standardized beta richness values on a 0-1 scale for all three comparisons.**

Species	Family[1]	Age[2]
Millepora complanata	Milleporidae	Panama: Pliestocene[3]
Millepora alcicornis		
Millepora squarrosa		
Agaricia agaricites	Agariciidae	Florida: Pliocene DR: Miocene
Agaricia sp.		
Agaracia danai		
Dichocoenia stokesi	Meandrinidae	
Meandrina meandrites		
Stephanocoenia intersepta	Astrocoeniidae	Florida: Miocene DR: Oligocene
Stephanocenia michilini		
Isophylia sp.	Faviidae Subfamily: Mussidae	Florida: Oligocene-Miocene DR: Oligocene
Mussa angulosa		
Mycetophyllia lamarckiana		
Pseudodiploria strigosa	Faviidae	
Colpophyllia natans		
Solenastrea bournoni		
Diploria labyrinthiformis		
Favia fragum		
Manicina areolata		
Siderastrea siderea	Siderastreidae	
Siderastrea radians		
Acropora cervicornis	Acroporidae	
Acropora palmata		
Madracis mirabilis	Pocilloporidae	Florida: Oligocene DR: Oligocene
Madracis senaria		
Madracis decatis		
Porites porites	Poritidae	
Porites astreoides		
Porites branneri		
Porites furcate		
Eunicea mammosa	Plexauridae	
Plexaura sp.		
Dendrogyra cylindrus	Merulinidae	
Orbicella faveolata		
Orbicella annularis		
Montastraea cavernosa	Montastraeidae	
Oculina robusta	Oculinidae	Florida: Eocene DR: Quaternary
Oculina diffusa		
Gorgonia ventulina	Gorgoniidae	??
Pterogorgia guadalupensis		

Table 4: **Phylogeny of all coral species discussed in paper, arranged by family and first recorded appearance in the geologic time scale.**

[1]*World Register of Marine Species*

[2]*Paleobiology Database*

[3]*Dubé et al., 2019*

AUTHOR INFORMATION

All correspondence should be sent to the first author:
hlaml001@fiu.edu

ACKNOWLEDGEMENTS

The authors would like to acknowledge Dr. Claudia C Johnson, professor of Earth and Atmospheric Sciences and associate director of the Center for Underwater Science, for her generosity in presenting this research opportunity to the authors, for sharing her extensive knowledge of coral reef ecosystems, and for guidance throughout the research process. The authors gratefully acknowledge Charles D. Beeker, professor in the department of Kinesiology, director of the Academic Diving Program, founding director of the Center for Underwater Science, and principal investigator on the Florida and Dominican Republic projects, for providing opportunities for countless undergraduates to participate in underwater research encompassing shipwrecks, cultural, historical, and biological resources. We thank Dr. Alex Zimmerman, Earth and Atmospheric Sciences, for guidance on research design and statistical methods, Sam Haskell, assistant director, Center for Underwater Science, for editorial assistance, Anupama Chandroth, Ph.D. student in Earth and Atmospheric Sciences, for research guidance, Tori Galloway for guidance in data acquisition and database management, and undergraduate Sam Arvin for data collection. Funding to support data compilation and analysis and manuscript development was provided by an anonymous donor to CCJ. Through the generosity of these individuals, we were able to take the biological resources and analyze and evaluate them in this research paper for the benefit of future generations. The authors also acknowledge the support they gained in obtaining scientific diving skills and experience in IU's Academic Diving Program.

BIBLIOGRAPHY

Ammar, M. S. A. (2009). Coral reef restoration and artificial reef management, future and economic. *The Open Environmental Engineering Journal, 2*(1) 37-49.

Beeker, C. D., & Hanselmann, F. H. (2008). *John Pennekamp Coral Reef State Park Assessment: Mock 1715 Spanish Shipwreck.* Available upon request.

Beeker, C. D., & Hanselmann, F. H. (2009). The wreck of the Cara Merchant: Investigations of Captain Kidd's lost ship. *ACUA Underwater Archaeology Proceedings*, 223–230.

Beeker, C. D., Hawley, K., Galloway, T., Haskell, S., Johnson, C., & Lagunas, A. (2018). *Photogrammetric Assessment of 1733 San Pedro Underwater Archaeological Preserve and 1733 San Felipe Shipwreck Sites following Hurricane Irma (FKNMS-2018-040).* Available upon request.

Dubé, C. E., Bourmaud, C. A., Mercière, A., Planes, S., & Boissin, E. (2019). Ecology, biology and genetics of Millepora hydrocorals on coral reefs. *Invertebrates-Ecophysiology and Management,* 15-50.

Earth: A global map of wind, weather, and ocean conditions. (n.d.). https://earth.nullschool.net

Favoretto, F., Mascareñas-Osorio, I., León-Deniz, L., González-Salas, C., Pérez-España, H., Rivera-Higueras, M., Ruiz-Zárate, M.-Á., Vega-Zepeda, A., Villegas-Hernández, H., & Aburto-Oropeza, O. (2020). Being Isolated and Protected Is Better Than Just Being Isolated: A Case Study From the Alacranes Reef, Mexico. *Frontiers in Marine Science*, 7, 1-13. https://www.frontiersin.org/article/10.3389/fmars.2020.583056

Gardner Toby A., Côté Isabelle M., Gill Jennifer A., Grant Alastair, & Watkinson Andrew R. (2003). Long-Term Region-Wide Declines in Caribbean Corals. *Science, 301*(5635), 958–960. https://doi.org/10.1126/science.1086050

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J., Lough, J. M., Marshall, P., Nystrom, M., Palumbi, S. R., Pandolfi, J. M., Rosen, B., & Roughgarden, J. (2003). Climate Change, Human Impacts, and the Resilence of Coral Reefs. *Science, 301*, 929–933. https://doi.org/10.1126/science.1085046

Lane, J. (2011). *Mock Spanish Shipwreck Project John pennekamp Coral Reef State Park; Key Largo, Florida.* Indiana University Individualized Major Program Final Project Submission. Available upon request.

Loiseau, N. Gaertner, J.C. (2015). Indices for Assessing Coral Reef Fish Biodiversity: The Need for Change in Habits. *Ecology and Evolution.* 5(18), 4018-4027.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics, 29*(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Olinger, L. K., Scott, A. R., McMurray, S. E., & Pawlik, J. R. (2019). Growth estimates of Caribbean reef sponges on a shipwreck using 3D photogrammetry. *Scientific Reports, 9*(1), 1–12.

PBDB - Paleobiology Database. (n.d.). Taxonomic name search. https://paleobiodb.org/classic/beginTaxonInfo

Rohwer, F., Youle, M., & Vosten, D. (2010). *Coral Reefs in the Microbial Seas.* Plaid Press. https://books.google.com/books?id=C1GVSQAACAAJ

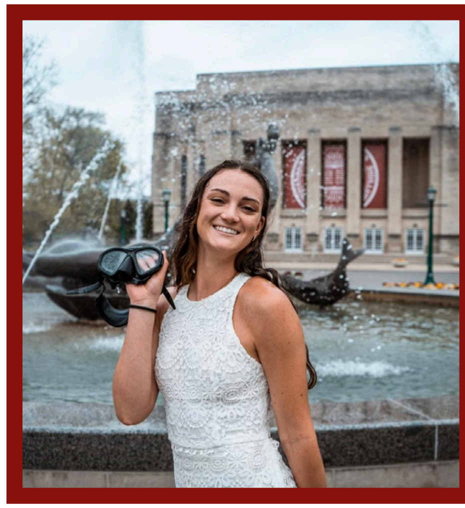
Simonelli, I. (2008). *1724 Guadalupe Underwater Archaeological Preserve 2007—2008.* Indiana University Individualized Major Program Final Project Submission. Available upon request.

US Department of Commerce, N. O. and A. A. (n.d.). *The Global Conveyor Belt—Currents.* https://oceanservice.noaa.gov/education/tutorial_currents/05conveyor2.html

Wilkinson T., E. Wiken, J. Bezaury-Creel, T. Hourigan, T. Agardy, H. Herrmann, L. Janishevski, C. Madden, L. Morgan, M. Padilla. (2009). *Marine Ecoregions of North America.* Commission for Environmental Cooperation. Montreal, Canada. 200 pp.

WoRMS - World Register of Marine Species. (n.d.). Taxa search. https://www.marinespecies.org/aphia.php?p=search

ABOUT THE AUTHORS



hlaml001@fiu.edu

Hannah-Marie Lamle

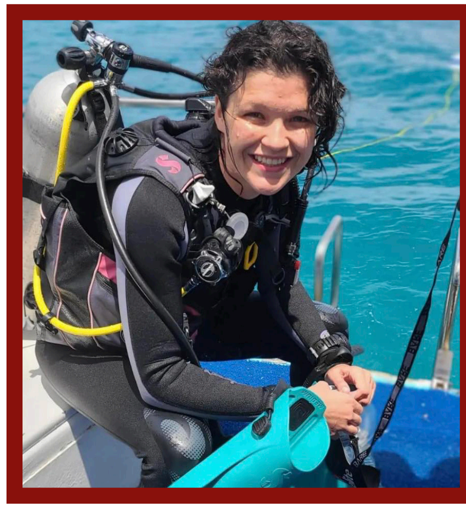
Hannah-Marie graduated from Indiana University in 2022 with a B.S. in Environmental Science, a certificate in Underwater Resource Management, in addition to obtaining her PADI Dive Master certification. She worked in the Center for Underwater Science under Professor Beeker and the Geology of Invertebrates Lab under Dr. Johnson gaining valuable research skills. After graduation she was hired on with the Center for Underwater Science as a Visiting Lecturer and Research Associate, where she taught the Open Water Scuba classes and assisted with ongoing research. Specifically, she was interested in how archaeological sites and features create suitable habitat for coral recruitment and survival, taking a spatial ecology approach to understanding patterns related to coral settlement on vs off archaeological features. She is currently a Ph.D. Candidate in the Santos Seascape Ecology Lab at Florida International University studying the function and response of coral communities to environmental gradients using functional traits.

ABOUT THE AUTHORS

smmucker@iu.edu

Sarah Muckerheide

Sarah Muckerheide graduated Indiana University with degrees in Underwater Archaeology and Anthropology, along with minors in Spanish and Biology, and a certificate in Underwater Resource Management. Through her underwater archaeological work and mentorship from Dr. Claudia Johnson, she came to have an acute appreciation and research concern for coral reef ecosystems in the Caribbean. As an undergraduate, she had the privilege to see endangered Caribbean corals first hand and use scuba to document coral on the majority of the sites discussed in this paper. Sarah is currently a PADI Scuba Instructor teaching classes within the IU Academic Diving Program. She is also the Laboratory Coordinator for the IU Center for Underwater Science.



jbaelz@iu.edu

Jenna Baelz

Jenna is a marine conservation specialist with a lifelong connection to aquatic environments. She earned an undergraduate degree in Marine Conservation and a certificate in Underwater Resource Management from Indiana University. Her hands-on experience includes an internship at Quiescence Diving Services in Key Largo, Florida, as well as attending various field schools with IU in the Dominican Republic, Florida Keys, Lake Michigan, and Indiana local waters. Her work focuses on dive training, equipment safety, and underwater site management. She specializes in the establishment of underwater parks and the protection and preservation of submerged biological and cultural resources. Jenna now serves as an Adjunct Instructor, Scuba Equipment Technician, and Assistant Diving Safety Officer at Indiana University where she is committed to advancing sustainable diving practices and safeguarding underwater heritage for future generations.

carley.divish@maritime archaeologytrust.org

Carley Divish

Carley graduated from Indiana University in 2022 with degrees in Anthropology, Underwater Archaeology, and Classical Civilizations, a minor in Environment and Sustainability Studies, and a Certificate in Underwater Resource Management. She worked with the Center for Underwater Science and the Department of Geology doing research in multiple areas of study. After her time at IU, she attended the University of Southampton for an MA in Maritime Archaeology, completed in 2023 on lithics found in secondary context. She completed each degree with honors. Currently, Carley works at the Maritime Archaeology Trust, focusing on prehistory, lithics, and community outreach.