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Competition between Coral and Algae in Tertiary and Quaternary Reefs: Greenhouse to Icehouse Transitions

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Abstract

The competition between coral and algae in marine reefs is pervasive through geologic time; that competition determines the structure and composition of reef communities, which we see in the fossil record. However, the relationships between coral and calcareous algae in reefs are poorly understood. To study this relationship, several hand samples and thin sections were examined from nine different foralgal reef localities around the world. Foralgal reefs typically extend from about 20 m depth or shallower on the seaward side of the reef. The first section is Salt Mountain, Alabama, which preserves a Paleocene reef. It contains a high percentage of red coralline algae with benthic foraminifera. The second section is IDOP-U1376, IIA Limestone, it is Middle Eocene, in the form of an isolated reef sandwiched between two igneous beds. The third section is the Utoe' Limestone, New Caledonia, it is Middle Eocene in age and is composed mainly of grain-boundstone units with some igneous interlayered. The fourth section is the Darnah Formation in the West-Darnah roadcut section, Northeast Libya, it is Middle Eocene in age, it is composed of highly fossiliferous limestone (corals, red coralline algae, echinoids, mollusks, foraminifers, and bryozoans). The fifth section, the Al Bayda Formation (Algal Limestone Member) in Northeast Libya, is in the Drayanah—Al Abyar roadcut, Northeast Libya, it has several species of algae but also includes a high percentage of buildups of coral species. The sixth section is the Oligo-Miocene Al Faidiyah Formation (Al Fatayah Cement Quarry) limestone unit in Northeast Libya. The seventh section is (Core-core 20) late-early to middle Miocene Limestone Unit-Cicuco Field, NW Colombia. The eighth section is the Benghazi Formation at Benghazi Cement Quarry, in Northeast

Libya, it is fossiliferous limestone, consisting of coral, algae, mollusks, and echinoids. The ninth and tenth sections are Quaternary reefs in the Bahamas and the Florida Keys, respectively. These reefs contain a high percentage of coral, red coralline algae, echinoids, mollusks, foraminifers, and ostracods. Based on the data and static analysis results on the thin sections and hand specimens, this study determines the occurrence and outcomes of coral-algal interactions among different coral growth forms (branching, upright, massive, encrusting, plating, and solitary). The Early Paleogene (Paleocene to Eocene) has the highest percentage of algae in two forms (crustose and frondose), which is a good indicator of a warm climate. In the Middle Eocene to Late Eocene, coral replaced algae in different localities in sections of that age. This change is an indicator of climatic cooling, especially in the western Lutetian Darnah section. In the Oligocene time, high-branching corals became abundant and escaped competition with the algae due to Icehouse conditions, as shown in the Al Bayda Formation. In the Miocene, coral species started to decline because of the return to Greenhouse conditions. Coral can lose its competitive edge when chemical and physical defense systems reduce growth and production due to warming. On the other hand, crustose-form algae attract the larvae of the coral. Algae induce them to get a more highly competitive frondose form, which is useful for corals as they decrease growth and production. Algae can quickly colonize the dead reef by using the firm substrate to rebuild themselves. This research may prove valuable when predicting the response of modern coral reef systems to future climatic warming conditions and provides a model for what future reefs may look like.

Keywords

Utoe' Limestone, New Caledonia, Benghazi Formation at Benghazi Cement Quarry, Is IDOP-U1376, IIA Limestone, It Is Middle Eocene

1. Introduction and Settings

In the Early Paleogene Period, warming was the trend. Currently, coral, algae, and sizeable benthic foraminifera are the most important organisms for the framework reefs. Copper (1985) [1] described the phases of the reef, and how the reef organisms respond through geologic time. The Early Paleogene is known for ice-free conditions (Greenhouse) [2] (Ray, Thomas, 2007; [3] Zachos, *et al.*, 1993). Increasing temperature directly affects the distribution of organisms such as algae, coral, and large benthic foraminifera ([4] Adams *et al.*, 1990; [5] Pearson *et al.*, 2001). During the late Paleocene to early Eocene the highest concentration of CO_2 and CH_4 was present, which resulted in a decrease in the coral species and an increase in the algae ([6] Pagani *et al.*, 2006). The large benthic foraminifera, coral, and algae are significant producers of $CaCO_3$, and all these organisms are sensitive to the water quality ([7] Khameiss *et al.*, 2013; [8] 2017; [9] 2018; [10] Langer, 2008). The framework is dominated by coral species which declined during the early Paleogene and were replaced by an algal reef ([11] Geel, 2000; [12] Khameiss *et al.*, 2017; [13] 2016). In the late Eocene, coral reefs became widespread ([14] Fagerstorm, 1987; [7] Khameiss *et al.*, 2013; [15] 2014). Several coral species declined because grazers fed on them such as gastropods and echinoids; also damaging to the corals, algae hampered or prevented coral growth. Changing the framework from coral to algae reef is an obvious indicator of coral mortality. The Oligocene is well-known and studied primarily in Italy [16] (Pfister, 1980). A recent study in the Oligocene reef in eastern Libya described the species in this reef as *Antiquastrea* sp., and high crustose coralline red algae ([7] Khameiss *et al.*, 2013; [15] 2014). Both are good indicators for the falling sea level associated with the icehouse effect at this time. Oligo-Miocene reef sections come from the Al Faidiyah Formation limestone unit in the Al Fatayah Cement Quarry with two species of coral and shell fragments. Miocene reef sections are sporadic in eastern Libya. The Benghazi Formation is Upper Miocene in age; the samples came from the Benghazi Cement Quarry. In this section, only one species was found, which is *Tarbellastraea* sp., ([15] Khameiss *et al.*, 2014). It is an algal reef formation associated with a greenhouse at this time. The nine locations used in this study are identified on a modern map of the world (**Figure 1**).

All the Early Tertiary Libyan sections are from the margins of the equatorial Tethys Sea, the precursor to the Late Tertiary development of the Mediterranean Sea. The Paleocene-aged Alabama Salt Mountain reef was in a similar equatorial setting but further west. The New Caledonia section was an island complex in the Pan thalassic Ocean, the precursor to the Pacific Ocean.

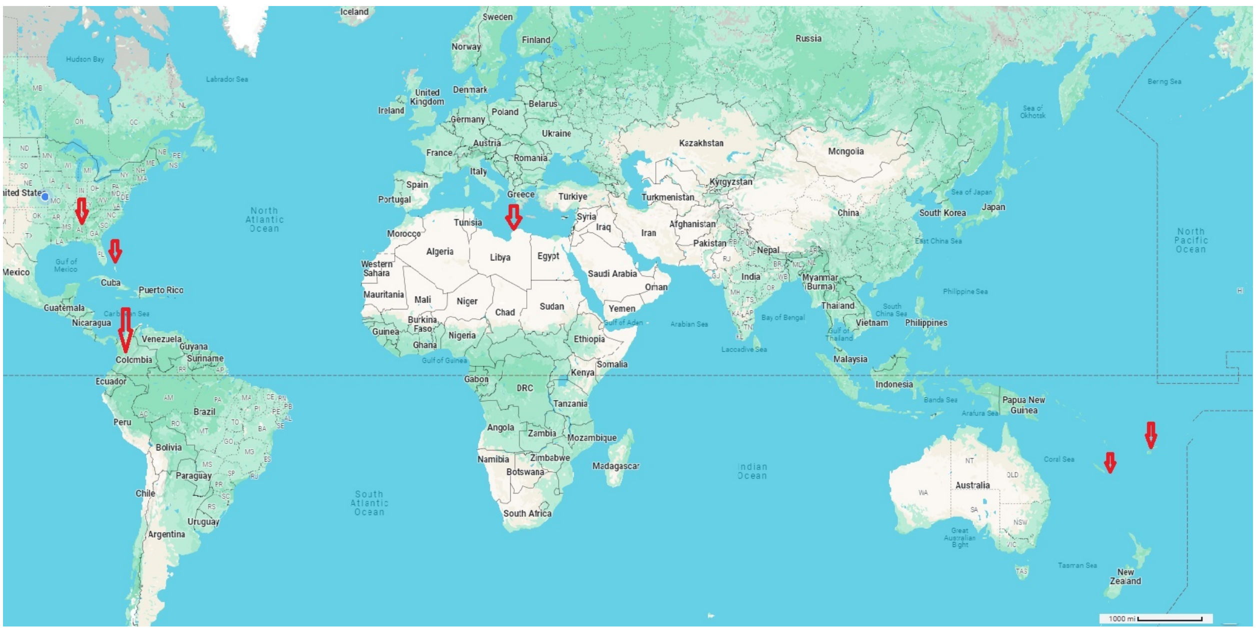

Figure 1. Shows the locations of the study areas on a world map (red arrows)[1].

[1]https://gisgeography.com/high-resolution-world-map/?fbclid=IwAR0HLe6DFSz0OFHEbIVqteU4uZnrodjOYDryPURRqgaHkeCHrevD_w7mkOw.

2. Methods and Limitations

Because hand samples, thin sections, and data summaries of coral-to-algae ratios used in this study were assembled in various ways for the many worldwide localities, it is difficult to assure comparability of those ratios. Where possible, counts of species identified in multiple thin sections were used as the most reliable measure of the abundance of algae and corals. However, consistent qualitative results from these localities are clear even though quantitative results across the studied sections may be somewhat suspect. Differences in growth habit geometries between corals and algae are significant. Corals are generally cylindrical or frondose; algae are generally encrusting or tabulate/frondose. In outcrop or hand specimen scales it is difficult to precisely estimate ratios between coral and algae. On the other hand, point counts across multiple thin section fields are more precise, albeit laborious. Ratios calculated from thin section counts are the most precise.

Another limitation of this study is the fact that we have selected reefs from very different geological settings. We have not analyzed reefs based on tectonics, ecology, sedimentation, latitude, or oceanic conditions. We have only looked at coral-to-algae ratios in shallow foralgal reefs during greenhouse and icehouse times. Finally, the rapidity of Anthropocene climate warming and a variety of human-induced chemical and physical changes are substantially different now compared to the past geological record. Therefore, drawing too many predictions from our data sets may not be warranted.

3. Results and Discussion

The competition between algae and coral is one of the fundamental processes that determine the structure and composition of reefs during geological time. The change mechanism between the coral and algae is vital to understanding the phase shift [17] Littler, and Littler D. S, 1984). There is no strong evidence that simply says the coral was replaced by an overgrowth of algae because many coral reefs were killed or damaged by storms, bleaching, and eutrophication [18] [19] (Khameiss *et al.*, 2019; Khameiss, 2020). During geological time, major fluctuations of light, prey, chemistry, temperature, and sediments are the main contributors to the differences between the algal reef and coral reef [18] (Khameiss, 2019). In this paper, it is essential to fill the lack of data, especially on the Early Tertiary reef frameworks. Second, the evidence of the transition from coral to algae or vice-versa needs to be documented. Third, we wish to demonstrate the lack of data describing the interaction between species that have been ignored, such as large benthic foraminifera, algae, and coral. Finally, such analyses can aid in predicting future reef-building, using the past as a key to the present and future.

3.1. The Late Paleocene Salt Mountain Alabama

This coastal reef was constructed atop a salt dome and exhibited a thickness of

16 meters. While the physical outcrop has since vanished, preserved samples from this section find their repository within the Biostratigraphy Laboratory at Ball State University's Department of Environment, Geology, and Natural Resources. The reef's structural composition was primarily composed of red coralline algae, coral, sponges, ostracods, and foraminifers. Illustrated in **Figure 2** is the gradual replacement of coral by algae over time, marking the decline of the coral reef. The proportion of coral to algae, as derived from thin sections and rock samples, yielded the static outcomes depicted in the figure. The age of the reef was ascertained through foraminifera analysis, pinpointing it to the P4-Late Paleocene epoch (as established by Khameiss *et al.*, 2018; 2019) [9] [18].

3.2. Middle Eocene IODP-U1376, II Bed, Limestone Unit

A solitary reef stands atop a tectonically elevated platform, encompassed by two layers of igneous rock. The IODP core, sourced from the Louisville Chain within the southern Pacific Ocean, was drilled in 2013 under the aegis of the Integrated Ocean Drilling Program (at coordinates 32˚12.99'S and 171˚52.84'W). This core is replete with algae, coral, echinoids, foraminifera, and mollusks. Extracted from the 15.3-meter foralagal limestone segment, static data from 22 thin sections were employed to compute the proportions of coral and algae (refer to **Figure 3**). The age of the core was determined using its foraminifera content, revealing it to be of Middle Eocene origin (as established by Khameiss *et al.*, 2017; 2018; 2019, as well as Khameiss and Fluegeman, 2022) [8] [9] [18] [20].

3.3. Middle Eocene New Caledonia, Utoe' Limestone

Presented here is a remarkable depiction of a foram-algal reef and its current correlation with volcanic activity, situated at coordinates 21˚48.4'S/166˚03.7'E. All calculations are rooted in thin sections, precisely nine in number, hailing from a combined thickness of 34 meters. These sections reveal an abundance of algae, coral, foraminifera, mollusks, and sponges within the outcrop (**Figure 4**). Through analysis of foraminifera, the age was determined to be Middle Eocene, as established by [21] Micheal *et al.*, 2011; [22] Fluegeman, and Nicholson, 2017; [9] [18] Khameiss *et al.*, 2018; 2019).

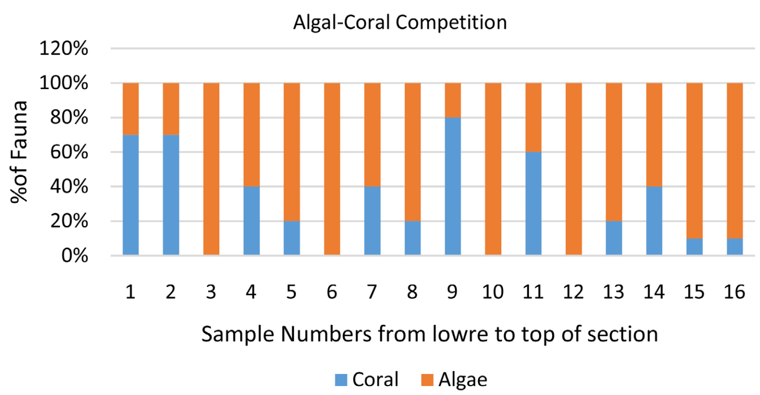

Figure 2. Shows the framework of the late Paleocene Salt Mountain, Alabama.

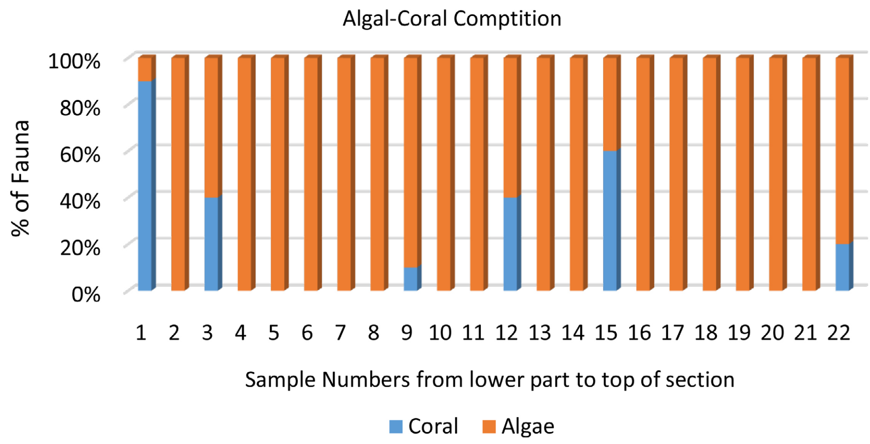

Figure 3. Shows the framework of the middle Eocene IODP-U1376, II Bed, Limestone unit.

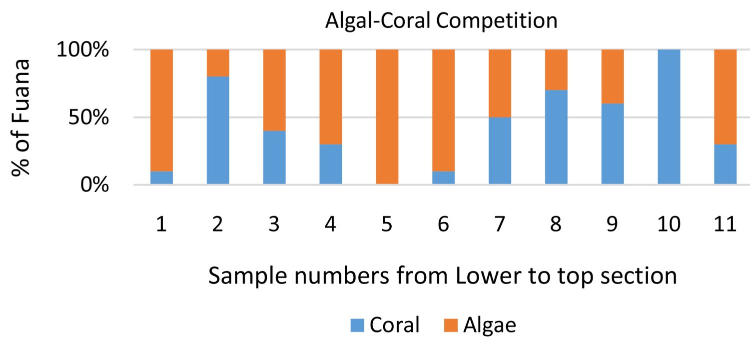

Figure 4. Shows the framework of the middle Eocene New Caledonia.

3.4. West-Darnah Roadcut Section-Darnah Formation, Northeast Libya

The geographical coordinates for this section are 32˚53'00''N, 21˚55'01''E. Within this location, a profusion of large benthic foraminifera, algae, coral, mollusks, and echinoids is evident. The comprehensive analysis, drawn from 15 collected samples during this interval, readily unveils the intricate composition of coral and algae, as depicted in Figure 5. Although two species are referenced within this section, their nomenclature remains pending as further statistical scrutiny is essential for future research endeavors. Among these species, *Caulastrea* sp., takes precedence over *Stylophora* sp., due to its more rapid colony growth, as observed in the dominance of the former [13] (Khameiss *et al*., 2016).

3.5. Daryanah-Alabyar Roadcut Section—Al Bayda Formation Northeast Libya

Situated at a latitude of 32˚37'60''N and a longitude of 20˚36'98''E, this section is positioned approximately 60 km east of Benghazi City. The formation's aggregate thickness spans 28 meters and is classified as an Algal Limestone member, signifying its Lower Oligocene origin [23] (Abdulsamad, E. O., 1999a). Within this member, a profusion of *Nummulites fichteli* and *N. vascus*, algae, bivalves, and echinoid species thrive. Among the coral species documented in this section is *Antiquastrea* sp., Notably, the lower segment of this formation, constituting the algal limestone member, harbors a cave and karstic feature in Northeast Libya [24] (Khameiss *et al.*, 2012; [7] 2013; [25] El Sakran *et al.*, 2016). The most prevalent coralline red algae featured in this section is *Lithothamnion* sp., as detailed in the study by Hassan, and Ghosh, 2003 [26]. **Figure 6** visually displays the coral-to-algae ratios for the nine samples.

3.6. Oligo-Miocene Al Faidiyah Formation—Al Fatayah Cement Quarry

Located approximately 27 kilometers east of Darnah City, this exposed rock formation can be pinpointed at latitude 32˚35'46"N and longitude 22˚43'21". Its total thickness measures 10 meters, and the bed's distinctive feature is the presence of white limestone. The outcrop is characterized by the prevalence of significant benthic foraminifera such as nummulites, algae, echinoids, and bryozoans. Among the coral species observed are *Cyphastrea* sp., and *Aleveopera* sp., as documented by [27] El Ebaidi, 2000; [28] [29] Khameiss, 2008; 2007; [7] Khameiss *et al.*, 2013. Utilizing the data extracted from the thin sections, the timeline of coral emergence and the subsequent replacement of algal reefs during the icehouse period can be readily deduced (refer to **Figure 7**).

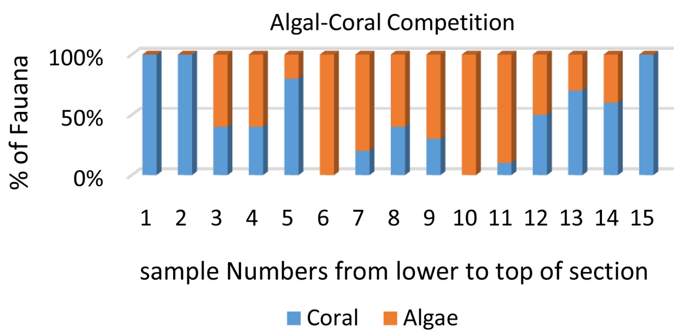

Figure 5. Shows Darnah Formation, West-Darnah Road cut section, Northeast Libya.

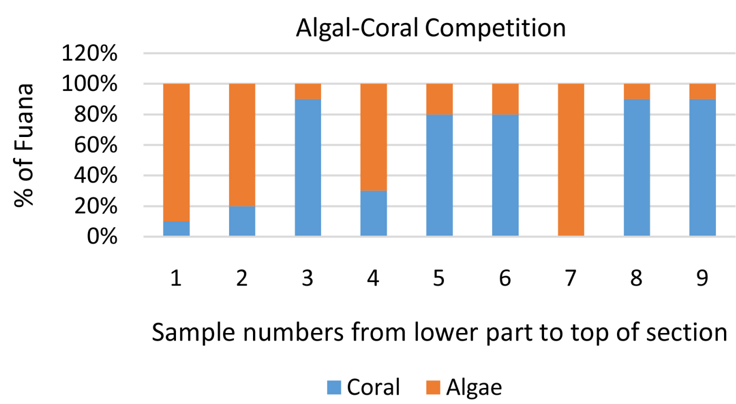

Figure 6. Shows the framework of the Al Bayda Formation—Daryanah-Alabyar roadcut, Northeast Libya.

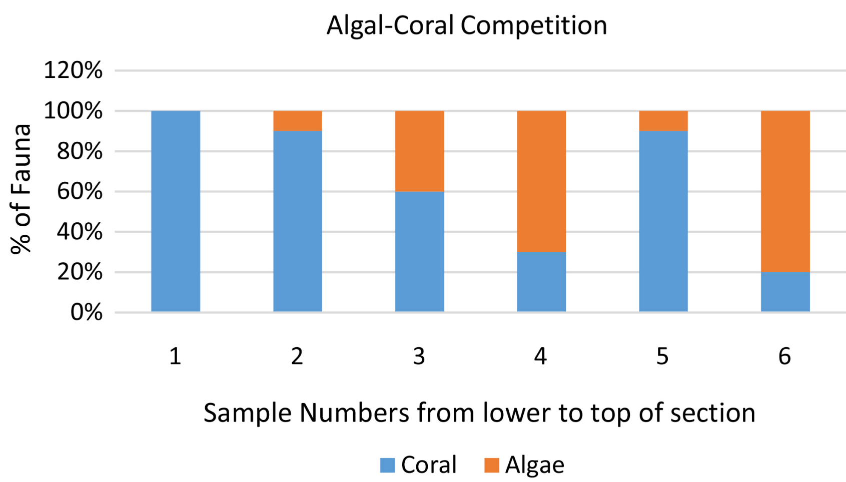

Figure 7. Shows the framework of the Al Faidiyah Formation—Al Fatayah cement quarry.

3.7. Late-Early to Middle Miocene-Limestone Unit-Cicuco Field, NW Colombia

This core 20 came from Cicuco Field, NW Colombia southwest of and may be found between latitude 9˚16'N and longitude 74˚39'W. The total thickness is 29 m, and the white limestone in this bed is distinctive. The Formation contains foraminifera, algae, echinoids, bryozoan, and coral, Mollusk, Khameiss *et al.*, 2023 [30]. Based on the static data from the eleven thin sections, it is simple to determine when the coral began to appear and when the algal reefs were replaced during the icehouse period (**Figure 8**). Utilizing the static data extracted from the 11 thin sections, it becomes straightforward to ascertain the onset of coral emergence and the subsequent replacement of algal reefs throughout the icehouse period.

3.8. Late Miocene Benghazi Formation in Benghazi Cement Quarry

Positioned approximately 18 kilometers southwest of Benghazi City, this exposed rock formation is situated between the coordinates of latitude 75˚31'59"N and longitude 73˚32'00"E. Spanning a total thickness of 35 meters, the bed is characterized by its distinctive white limestone. Originally, these sizeable fossiliferous limestones from the Middle Miocene were designated the "Benghazi limestone" by Gregory, in 1911 [31]. Subsequently, [32] Klein, 1974 bestowed the formal name "Ar Rajmah Formation" upon this limestone. Within this formation, a diverse array of significant benthic foraminifera, including *Nummulites*, as well as algae, echinoids, bryozoans, and corals such as *Cyphastrea* sp., and *Aleveopera* sp., have been documented [27] (El Ebaidi, 2000; [29] Khameiss; 2007; [7] 2013). By harnessing the static data gleaned from the seven thin sections, it becomes uncomplicated to discern the chronological progression of coral emergence and the subsequent replacement of algal reefs during the icehouse period (refer to **Figure 9**).

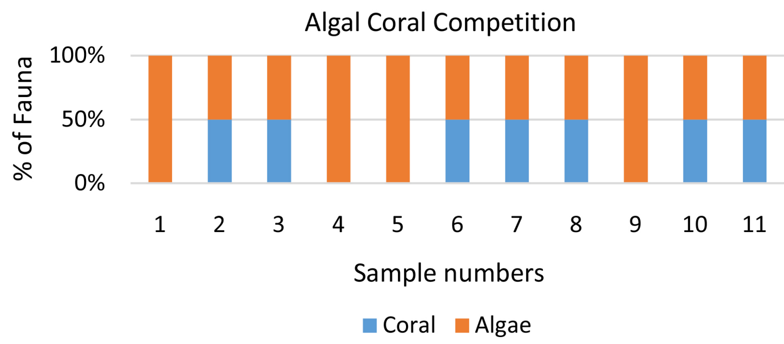

Figure 8. Shows the Framework of the Limestone Unit—Cicuco Field, NW Colombia.

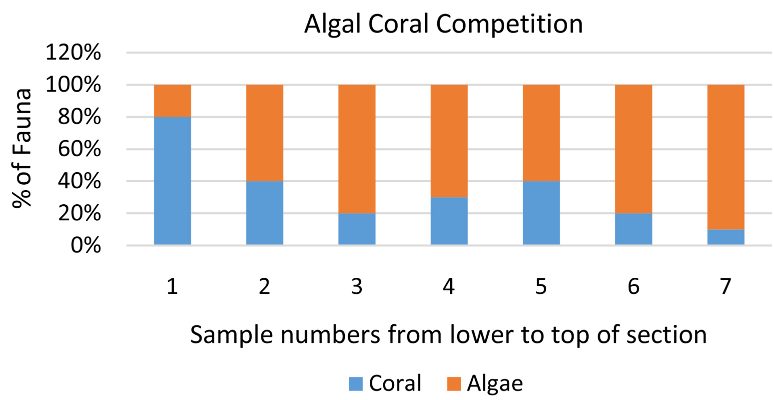

Figure 9. Shows the framework of the Benghazi Formation in Benghazi cement quarry.

3.9. Quaternary Reefs

The Bahamas occupies the expanse between 72˚ and 80˚ west longitude and 20˚ and 28˚ north latitude. This intricate reef complex materialized during the final stages of the ice age, fashioned by the collaborative efforts of coral, algae, foraminifera, echinoids, and mollusks [33] [34] (Lessos, 1988; Hirschfield *et al.*, 1968). Within this geographical scope, the taxonomy of coral species is delineated by *Acropora palmata*, *A. cervicornis*, *Acroporid* sp., and *Pterois* sp., as documented by Deleveaux *et al.*, 2001; 2013 [35] [36], and Precht and Hoyt, 1987 [37]. Amidst this region's vibrant tapestry, the red coralline algae, *Millepora* sp., finds itself amidst an assortment of coral species such as *Dendrogyra cylinders* and *Eusimilina fastigiata*.

A perceptible transformation has befallen this coral reef during the Anthropocene, an epoch influenced by human activity. Karmer Pr., 2008 [38]; Karmar, Karmer P. R., 2010 [39], observe a discernible decline, sparking a direct impact on trophic levels and community systems. The intricate interplay among sessile invertebrates within the reef undergoes alteration in the face of human-induced phenomena, including elevated temperatures, overfishing, heightened nutrient levels, ocean acidification, and oil contamination. As a result, many coral species suffer decline and eventual demise in response to climate change driven by human actions, whereas algae assert their resilience and flourish. Notably, a drop in fish populations has engendered the proliferation of echinoids like *Diadema an-*

tillarum. The foremost algae taking root is the crustose variety, indicating a habitat situated within shallow marine environs. As exemplified in **Figure 10**, an evident dominance of corals is exhibited, yet it is foreseeable that algal reefs will emerge as the prevailing norm in the times ahead.

3.10. The Florida Keys Coral Reef

The formation of this reef complex mirrors the Bahamas' coral structures in both manner and pattern. Among the species present are *Montastrea annularis*, *millepora hydrocorals*, *Octocorallia* sp., along with foraminifera like *Amphistegina* sp., and various forms of marine life including red coralline algae such as *Dictyota pulchella*, green algae exemplified by *Halimeda* sp., worms, and mollusks. Human activities, particularly fishing, have triggered a decline in the coral species populating this region, as evidenced by the research conducted by Jennings and Pluming (1996) [40]. The reduction in coral populations is a primary outcome of these anthropogenic influences on the reef's ecosystem by Hughes, 1994 [41]. Paralleling the trends observed in the Bahamas, the Florida Keys' coral decline and subsequent algal proliferation follow an analogous trajectory, as illustrated in **Figure 11**.

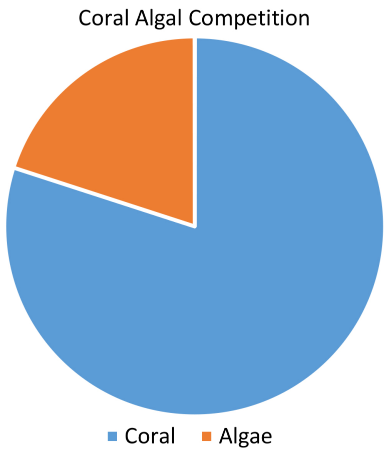

Figure 10. Shows the framework of the Bahamas.

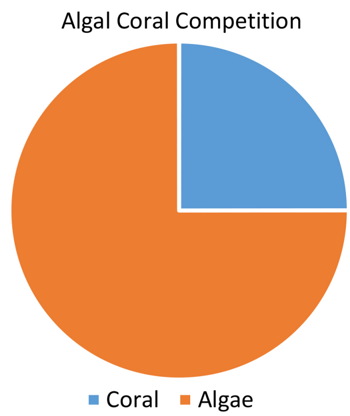

Figure 11. Shows the framework of the Florida Keys coral reef.

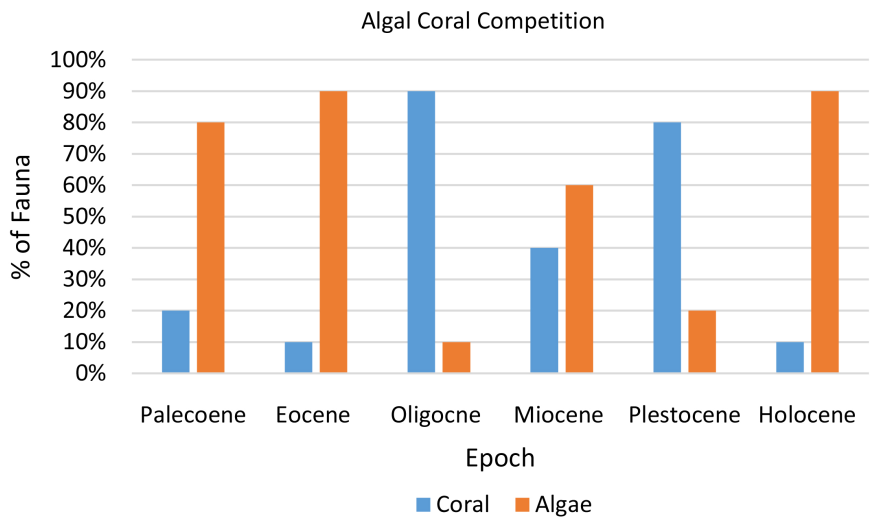

Figure 12. Shows the framework of reefs during the Cenozoic Era.

4. Conclusions

The geological and environmental data depicted in **Figure 12** reveal the significant changes that have occurred in reef communities and their underlying framework during the Tertiary and Quaternary periods. These changes are closely associated with various factors, including geological and chemical dynamics, and are intricately interwoven with shifts in climate. The prevalence of coral or algae in these reef communities, and the transition between them, are distinctly influenced by these climatic alterations.

The prevalence of coral within this locale stands as a telltale sign of colder conditions, characterized by ice sheets enshrouding high-latitude terrains. Such conditions are accompanied by diminished atmospheric CO_2 levels and a reduced incidence of volcanic activity, which collectively result in cooler water temperatures. Conversely, instances of escalated CO_2 levels over geological time correspond to heightened algal presence, commonly referred to as an "algal bloom". Simultaneously, tectonic activities linked to continental adjustments correlate with rising sea levels. The phenomenon of bleaching, a consequence of changing ocean salinity and coral species, portends significant repercussions for future reefs and reef communities. This bleaching process triggers the degeneration of coral cells and precipitates the disintegration of coral reef structures.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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