Global Change Biology

WILEY

Global Change Biology

RESEARCH ARTICLE OPEN ACCESS

Late Holocene "Turn-Off" of Coral Reef Growth in the Northern Red Sea and Implications for a Sea-Level Fall

B. Feldman[1] | A. Torfstein[2,3] | M. O'Leary[4] | N. Simon Blecher[1] | R. Yam[5] | Y. Shaked[3] | A. Shemesh[5] | D. Huang[6] | O. Levy[1,3]

[1]Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat Gan, Israel | [2]The Fredy and Nadine Herrmann Institute of Earth Sciences, The Hebrew University of Jerusalem, Jerusalem, Israel | [3]Interuniversity Institute for Marine Sciences, Eilat, Israel | [4]School of Earth Sciences, University of Western Australia, Perth, Western Australia, Australia | [5]Department of Earth and Planetary Sciences, Weizmann Institute of Science, Rehovot, Israel | [6]Department of Biological Sciences, National University of Singapore, Singapore, Singapore

Correspondence: B. Feldman (barbarfel24@gmail.com) | O. Levy (oren.levy@biu.ac.il)

Received: 7 November 2024 | **Revised:** 4 January 2025 | **Accepted:** 6 January 2025

Funding: This work was supported by Israel Science Foundation (2658/17).

Keywords: coral reef community | hiatus | Holocene | Red Sea | sea-level

ABSTRACT

Coral reefs, known for their remarkable diversity, serve a pivotal function in modulating the global oceanic carbon cycle and act as natural barriers that protect coastlines from erosion and storm surges by dissipating wave energy. Despite their importance, their sensitivity to temperature fluctuations, sea-level shifts and anthropogenic changes in the future is highly unknown. In this study, we create a comprehensive documentation of coral growth, sedimentology and ecology spanning the middle to late Holocene in the Gulf of Eilat/Aqaba, northern Red Sea. We then integrate these findings with a reconstruction of the area's environmental conditions over time. The findings reveal a noticeable hiatus of reef growth between 4400 and 1000 years BP (Before Present; "present" being defined as 1950), aligning well with comparable observations made across various locations in the Southern Hemisphere. The coral diversity and abundance along the cores display surprisingly similar patterns before and after the hiatus. This implies that the distinctive coral community thriving during the initial growth phase reappeared nearly 4000 years later, presumably sourced from the deeper reefs. The results are evaluated in the context of a potential sea-level drop and the resilience of coral communities to perturbations of this magnitude. We conclude that the hiatus at this site is due to a combination of factors, including tectonic activity and glacio-eustatic sea-level changes. Our research highlights the critical importance of understanding and managing coral reef ecosystems' responses to sea-level fluctuations to mitigate future impacts on these vulnerable environments.

1 | Introduction

The biogeographic range shifts of Red Sea corals have been influenced by fluctuating sea levels and changing oceanographic conditions over glacial–interglacial climate cycles (Woodroffe and Webster 2014) During the last glacial maximum, when global sea levels were up to 120 m lower, the Red Sea experienced significant contraction in its coral reef habitats. This was due to reduced oceanic exchange between the Red Sea and Northern Indian Ocean through the shallow sill spanning Bab-el-Mandeb strait (Rohling and Zachariasse 1996), resulting in salinities as high as 57‰ in the northern and about 47‰ in the southern Red Sea (Badawi 2015). The contraction of habitats led to the isolation of coral populations or coral refugia located in the southern part of the Red Sea and/or Gulf of Aden (Montaggioni 2005). Following post glacial sea level rise (circa 18,000 years BP), corals migrated back into the Red Sea where they rapidly exploited newly available substrates along the Red Sea coast and its islands. This expansion was facilitated by the restored connectivity between the Red Sea and the Northern Indian Ocean, allowing for the exchange of coral larvae between these two regions (Kleinhaus et al. 2020).

The Red Sea is now home to an extensive coral reef system, including fringing reefs, barrier reefs, and atolls, comprising a rich coral species diversity, which extends as far north as the Gulfs of Aqaba and Suez (Loya 1972). While Red Sea reefs have shown the ability to adapt and recover on glacial–interglacial timescales, these reef systems are now under present and near-term threat from local anthropogenic impacts and climate driven increase in sea surface temperatures (Loya 2004). There is a temporal gap in our understanding of how Red Sea coral reefs responded and adapted to climate change and associated impacts across Northern Arabia during the mid-to-late Holocene period (Neugebauer et al. 2022).

The Eilat reef is situated along the seismically active Dead Sea Transform fault system, with the GoE/A representing a down-faulted block (Garfunkel et al. 1999). Uplifted late Quaternary reefs along the Aqaba coast and Sinai Peninsula (Al-Rifaiy and Cherif 1988; Gvirtzman et al. 1992; Scholz et al. 2004), as well as drowned reefs at the northwestern end of the GoE/A (Makovsky et al. 2008; Shaked et al. 2004), highlight the area's complex geological history. Holocene reef growth in the GoE/A began around ~8000 years BP, with emerged fossil Holocene reefs dated to around 5000 years BP and elevations of ~1.2 m above modern sea level, indicating a Mid-Holocene Sea-level highstand interval (Shaked et al. 2004).

The regional climate is hyper-arid (< 20 mm/y) with no significant river runoff. The main study site, the Eilat Nature Reserve Reef (NRR), is a narrow fringing reef about 20 m wide that extends for approximately 1 km along the Eilat coastline. A shallow lagoon, less than 2.5 m deep and up to 50 m wide, separates the reef edge from the shore. The history of repeated seismic down-faulting events has led to catastrophic sedimentary fluxes into the GoE/A, resulting in localized reef demise around ~4700 and ~2400 years BP (Shaked et al. 2005, 2011). Here, we report on a major hiatus in coral reef growth in the northern Red Sea. The hiatus refers to a gap or interruption in the deposition of sediments, often representing a period of non-deposition or erosion in the geological record. Hiatuses are significant as they offer valuable insights into periods when active geological processes altered or prevented sediment accumulation.

Here, we present the chronology, continuity, and community development of coral reef growth in the Gulf of Eilat/Aqaba (GoE/A), northern Red Sea, over the last ~7 years. This research is grounded in a new collection of percussion cores taken along the fringing Nature Reserve Reef (NRR) in Eilat (25.9° N 34.9° E), which is located at the northern tip of the GoE/A (Figure 1). This site represents the northernmost extension of the 2400 km-long Red Sea coral reef province. Our findings illuminate the historical response of coral ecology to environmental shifts, such as changes in sea level and temperature, offering insights into the longer-term resilience of these ecosystems. The results were obtained by integrating radiocarbon dating, coral community structure, oxygen and carbon isotopes, along with grain size and $CaCO_3$ content analyses.

2 | Results

2.1 | Geochronology

Radiocarbon dating of coral clasts collected from seven reef sediment cores taken from two locations in the Nature Reserve Reef (NRR- North and South) (Figure 1) reveals that coral growth and reef formation had initiated by at least 6700 years before present (BP), with oldest coral clast from core NR05 returning an age of 6619 ± 89 years BP (Figure 2a; Table S1). This was a phase of continuous reef growth that persisted until around 4500 years BP, as shown by dating from core NR09 at 4425 ± 92 years BP. Subsequently, an extended hiatus in reef growth, from ~4500 to ~640 years BP, is consistently detected across all sediment cores. Reef growth resumed around 640 years BP, as indicated by core NR07 (644 ± 64 years BP) and continues to the present day. Within the cores, a few age reversals were detected (older sediments were found above younger sediments in the stratigraphic sequence), notably in cores NR10, NR05, and NR07 (Figure 2a, marked in red), suggesting complex patterns of reef framework accretion and erosion. Reef vertical accretion rates were analyzed from three cores (two lagoon cores and one front reef core) that contained between 9 to 13 dated coral samples each. The vertical accretion rate from the lagoon core NR05 was 6.9 mm/year, for lagoon core NR10 the vertical accretion rate was 3.6 mm/year before the hiatus and 8.7 mm/year after the hiatus. The vertical accretion rate for the fore reef core NR07 was 9.3 mm/year before the hiatus and 4.9 mm/year afterward. Overall, the average accretion rate across the cores from Eilat was calculated to be 6.7 mm/year (Figure 2b).

2.2 | Coral Community Structure

Taxonomic analysis of coral fragments contained within the NRR lagoon sediment cores reveal a diverse coral community spanning the 6600-year period of lagoon accretion, with 19 coral genera identified across all seven cores (Figure 3). This diversity mirrors findings by Perry and Smithers (2011), who reported a similar number and continuity of coral genera in Australian, Inner GBR reef cores over a 6900-year span. In the contemporary NRR lagoon, the coral community structure comprises 12 coral genera, whereas the NRR fore reef hosts 26 coral genera (NMP: Natural Monitoring Program Figure S1). Branching corals (corals distinguished by their tree-like growth forms), such as *Acropora*, *Stylophora*, *Seriatopora* (Scleractinia), and *Millepora* (Hydrozoa), have been consistently present throughout nearly the entire core record. However, there were intervals predominantly characterized by *Echinopora* (illustrated in pink in Figure 3; cores NR05, NR09, and NR10, approximately 5800–6500 years BP) or by *Pavona* (in darker pink, cores NR05 and NR10, around 6400–6600 years BP). Analysis of the Shannon index (Figure S2, Table S2) suggests that it is not possible to deduce a correlation from our data between specific time periods and the presence of certain coral genera, and so no temporal trend could be detected.

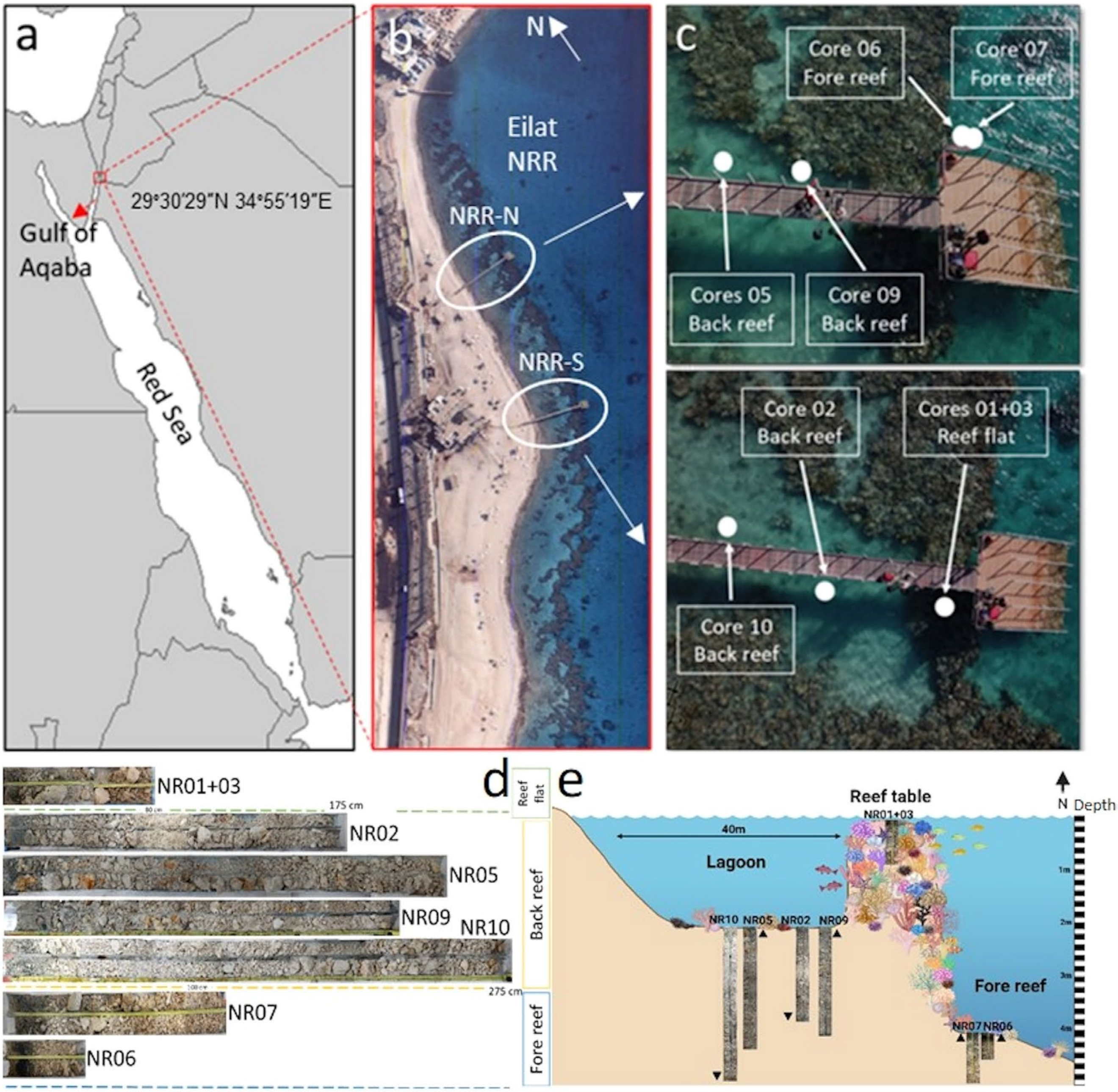

FIGURE 1 | Research location and cores. (a) A map of the Red sea and the Gulf of Eilat/Aqaba (map lines delineate study areas and do not necessarily depict accepted national boundaries) (b) Eilat Nature Reserve (NRR) (c) all coring sites at the north and south jetties in the NRR (d) Pictures of all seven cores extracted from the lagoon, reef flat and fore reef of the Nature Reserve in Eilat, and some of the coral species that have been found (e) A sketch of Eilat's Nature Reserve coral reef with all seven extracted cores and their locations. Black arrows on core's sides represent if were taken from the north (up) or south (down) jetty.

2.3 | Oxygen and Carbon Isotopes

Oxygen and carbon isotopes ($\delta^{18}O$ and $\delta^{13}C$) were obtained from *Stylophora* and *Acropora* coral samples, as detailed in Table S1. These samples were analyzed across distinct periods: 6000–7000, 4000–6000- and 0-1000-years BP, and the year 2020. The 2020 samples represent recent corals collected from the living reef of the NRR, Eilat (Figure 4). An analysis of variance (ANOVA) revealed minor differences between the periods (Figure 4; F = 7.733, p-value = 0.0002, R^2 = 0.2822). To analyze oxygen and carbon isotope values, we measured 65 samples, representing 5–7 samples per core. Specifically, δ18O values for the modern samples showed a significant decline compared to both the 0–1000-year BP and 6000–7000-year BP sample groups (Figure 4; p = 0.0385 and 0.0005, respectively; range = 2.937). Additional statistical analyses are presented in Table S3. Similarly, δ13C results from the sampled core corals, categorized into the same time periods, indicated a significant decline from the middle Holocene to recent times (Figure 4; F = 62.2, p < 0.0001, R^2 = 0.7536). Modern samples exhibited a substantial decrease in δ13C values (range = 6.183) compared to earlier Holocene samples (details in Table S3).

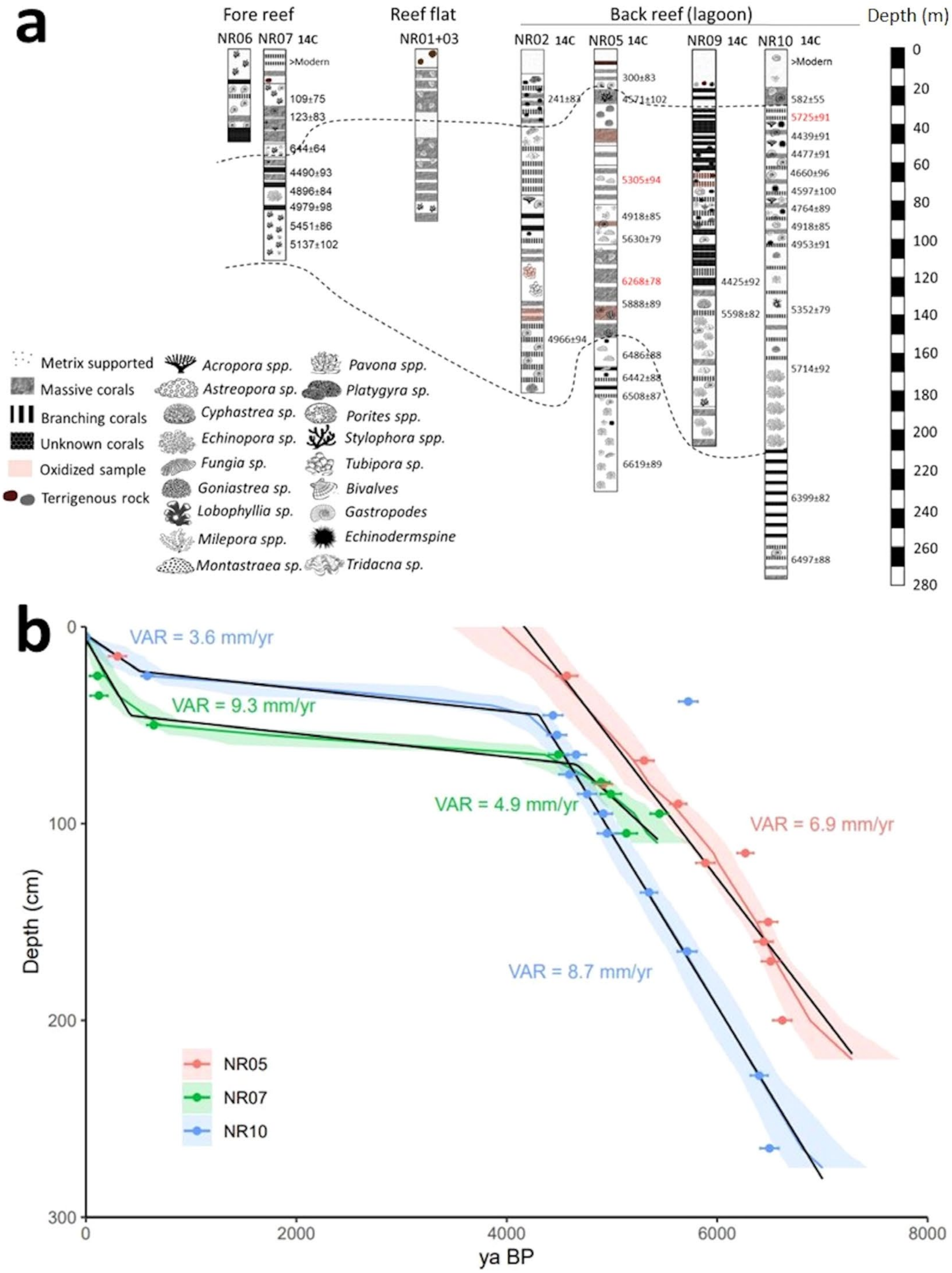

FIGURE 2 | (a) Core lithology and coarse coral community structure of all seven cores from the Nature Reserve Eilat. ^{14}C dates (calibrates year BP) as well as U-Th dates are presented at the right side of each core. Dates in red represent age reversals. The upper dashed line separate between recent samples and 4000 yr. dated samples. The middle part separates the 4000 yr. dates and the 5000 yr. samples. Everything beneath the lower line is 6000 yr. and older. (b) Age depth model for cores NR05, NR07 and NR10. Measured ages are marked by colored symbols and error bars (dR = −8 and uncertainty = 33). The model is the black line with error in matching color. Accordingly, the hiatus spans between ~4400 y cal BP and ~700 y cal BP.

2.4 | Sediment Grain Size and $CaCO_3$ Content

The results for the < 63 mm fraction exhibit a general trend of decreasing relative weight from the mid-Holocene to recent sediment samples across all three cores (Figure S3). In the NR05 lagoon core, weights are significantly different across all periods (ANOVA; $F = 15.04$, p-value < 0.0001, $R^2 = 0.75562$, with Tukey's multiple comparison results presented in Table S4). The NR10 lagoon core weights also show significant differences, particularly between the 0–1000-year samples and other periods (ANOVA; $F = 7.018$, p-value $= 0.0033$, $R^2 = 0.3262$, with Tukey's multiple comparison results in Table S4). For the NR07 fore reef core, which lacks results for the 6000–7000-year BP period, a t-test was conducted between the two available periods. A significant difference was observed between the 0–1000- and 4000-6000-year periods

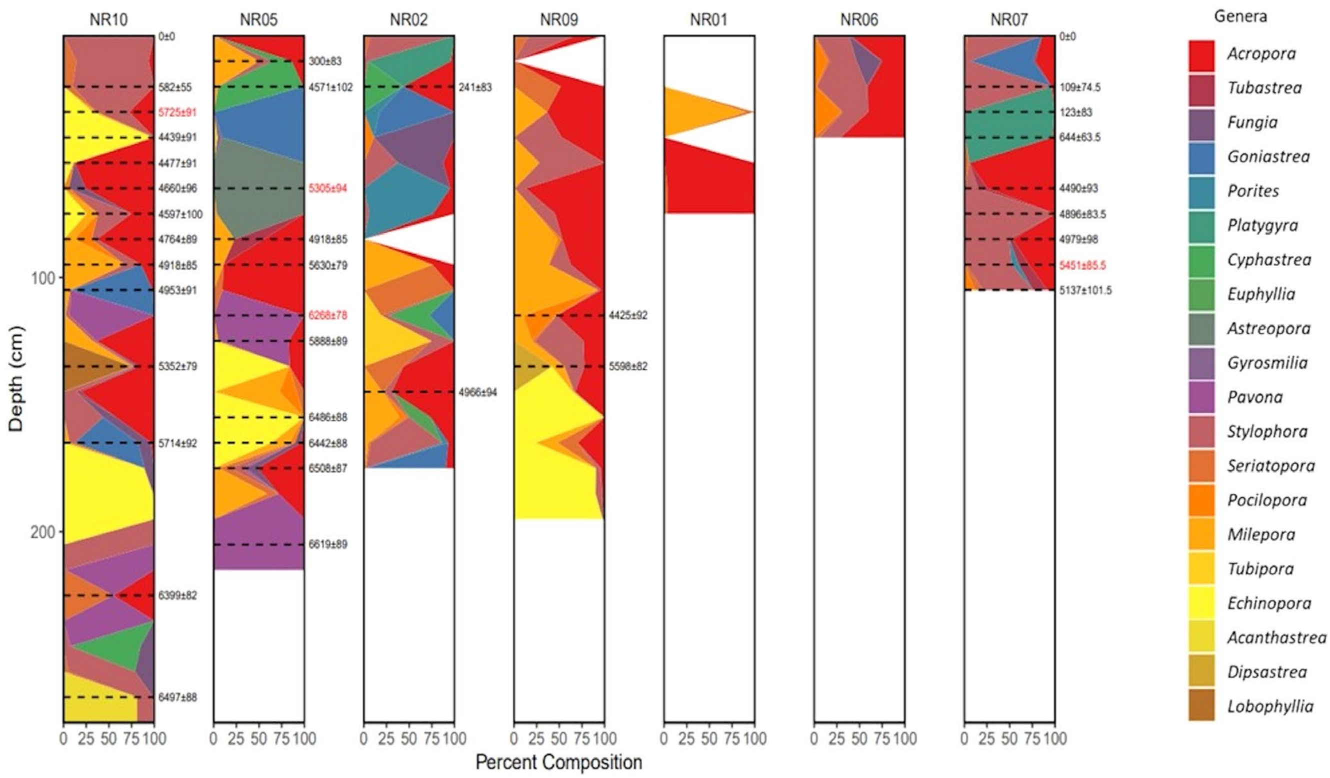

FIGURE 3 | Detailed coral community structure of all Eilat cores Percent hard coral (Scleractinia and Millepora) composition of the seven cores of NRR. At the right side of each core the ^{14}C radiocarbon dates are presented with error as years before present (BP) ± 2SD error. Age reversals are depicted in red.

(p-value = 0.0003, t = 4, df = 14). The weights of $CaCO_3$ primarily show a reduction from the 4000–6000 to the 0–1000-year periods (Figure S4), with ANOVA and Tukey's multiple comparison results detailed in Table S5.

3 | Discussion

3.1 | Eilat Reef Growth Over the Holocene

The new radiocarbon ages provide fundamental insights into the chronology of coral reef development in the northernmost extension of the Red Sea reef system. The oldest coral sample was dated to 6619 ± 89 years BP. However, it does not appear that the reef cores captured a complete depositional sequence, as the earliest known age for reef initiation at Eilat is approximately 8000 years BP (Shaked et al. 2011). This timeline for reef initiation at Eilat aligns well with that of other Indo-Pacific fringing reefs, where reef initiation commenced between approximately 8500–7000 years BP as observed in Australia (Dechnik et al. 2015; Leonard et al. 2020; Perry and Smithers 2011), the Pacific Ocean (Cabioch et al. 1995; Hamanaka et al. 2012), the Caribbean (Gischler and Hudson 2004), and the Red Sea (Makovsky et al. 2008; Shaked et al. 2011).

However, a significant distinction here is the initial source of coral larval recruitment at Eilat, would have been located in the Gulf of Aden, approximately 2400 km to the south (Abelson et al. 2005; Dibattista et al. 2016). This suggests that corals rapidly recruited newly available substrate and migrated along 2400 km of the Red Sea coast as the glacial age meta to hypersaline conditions ameliorated following post glacial sea level rise

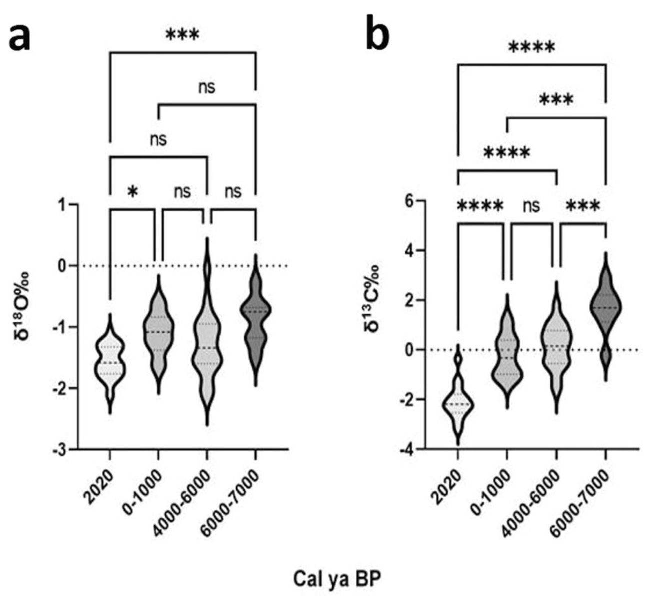

FIGURE 4 | Coral skeleton δ18O (a) and δ13C (b) composition. Samples from the presented periods have been pooled, illustrating temporal trends across the Holocene (Cal ya BP: Calibrated years ago before present). Statistical analysis (Table S3) was performed using one-way ANOVA followed by Tukey's multiple comparisons test, (Significance values indicate $*p \leq 0.05$, $***p \leq 0.001$), ($N = 15$ replicates per period).

and the deepening of the Bab-el-Mandeb Strait which separates the Red Sea from the Gulf of Aden (Clark et al. 2009).

The first phase of reef growth captured in our Eilat reef cores shows 2600 years of continuous coral growth between ~7000 years BP and ~ 4400 years BP (Figure 2; NR09), which is the period leading into the mid-Holocene highstand and prior to the mid to late Holocene Sea level regression (Mayewski et al. 2004; Shaked et al. 2004). While the paleoclimate of the Gulf of Eilat/Aqaba (GoE/A) is considered to have been mostly arid with low precipitation, the region has been subject to wetter climate phases as recorded in multiproxy analyses of sediment (Edelman-furstenberg and Almogi-labin 2009). High nutrient levels, indicating a wetter climate, were documented from 5700 to approximately 4400 years BP (Sansoleimani et al. 2022), and may have facilitated increased sediment runoff in the GoE/A and a local increase in turbidity (Edelman-furstenberg and Almogi-labin 2009). This period of reef growth ended ~4500 years BP and was followed by an extended growth hiatus lasting approximately 3800 years. The climate during the hiatus was relatively arid from 4400 to approximately 3300 years BP and had a less arid phase from 3300 to approximately 2000 years BP (Albert et al. 2007). The re-initiation of reef growth started around 700 years BP (Figure 2; NR07) and is still ongoing today, as indicated by the flourishing coral reef communities of Eilat. Edelman-Furstenberg and Almogi-labin (2009) suggest that from 2000 to approximately 700 years BP, the climate returned to be relatively more arid. The final shift, between 700 years BP and present, is marked by less mixing of the water column, suggesting a climate less dominated by aridity.

The only other continuous record of Holocene reef growth from the Red Sea is located at the IUI, Eilat (Shaked et al. 2011), approximately 2 km south of the NRR. The IUI reef's first initiation window was 6750 ± 80 years BP until 4685 ± 125 years BP. The hiatus observed here is slightly shorter than at the NRR and lasted only ~2000 years. Re-initiation reef growth started 2610 years BP in the reef front. Samples dated to 2600–1690 years BP were observed (Shaked et al. 2011) at depth suggesting that while a reef growth hiatus similarly began at both locations at approximately the same time, it appears that coral growth reinitiated first in deeper forereef areas of the NRR before the shallower reef crest and flat areas.

Fringing reefs typically grow vertically until they reach sea level, after which they expand seaward. In Eilat, however, this natural progression is restricted both vertically and horizontally. Vertically, the reefs have reached sea level, limiting further upward growth. Horizontally, the steeply sloping inner shelf inhibits seaward expansion, resulting in a relatively narrow fringing reef system, with widths ranging from 20 to 50 m (Shaked et al. 2005). The observed hiatus in reef growth after 4000 years may represent the Eilat reefs reaching a senile phase in their development, with limited vertical accommodation space and restricted seaward substrate availability, preventing a positive reef accretionary budget. The initiation of fringing reef growth at 650 years BP likely occurred when additional accommodation space became available for reef expansion. While there is no evidence of a eustatic sea level rise event during this period, a more plausible explanation is a local relative sea level rise event, which created the necessary conditions to reinitiate reef growth on the sea level-constrained reef flats. One possible scenario is a tectonic event causing land subsidence along the Eilat coast. This hypothesis aligns well with records of previous downfaulting in the area, which created the submerged reef (Shaked et al. 2004).

A study of four map zones along the GBR shelf, indicates that the central zone of the GBR has been subject to increased subsidence during the Holocene (Sansoleimani et al. 2022). This subsidence resulted in less mature reef growth stages, the occurrence of lower antecedent platform and more continuous growth through an interval where other offshore reefs were 'turned off' (Gischler and Hudson 2004). Conversely, tectonic uplift, exemplified by a recent earthquake in the Solomon Islands 2007, can have detrimental effects, raising reefs 1–3 m above the high-water mark leading to significant die-off (Albert et al. 2007). Such findings highlight the intricate interplay between tectonic movements and coral reef ecosystems, revealing that these geological processes can profoundly influence reef development and sustainability. Shaked et al. (2004) found indications for an earthquake that displaced the Holocene fringing reef of the NRR to several meters below its original position, some 2300 years BP. Our results support this hypothesis as the unconformity lines show a clear drop between the fore and back reef (see Figures 1d and 2a).

Accretion rates across two lagoon cores (NR05 and NR10) and one front reef core (NR07) showed no significant variation, with an average rate of 6.7 mm per year measured across all three cores (Figure 2b). The rate of reef accretion can be indicative of construction activities by reef builders, such as Scleractinian corals, coralline algae, tridacnid clams, and foraminifera, as well as consolidation or erosion caused by biological and physical impacts, including bioerosion and storms (Neo et al. 2015; Yamano et al. 2000). In addition, the reef area in Eilat was subjected to several down-faulting events, leading to sediment fluxes to the reef (Shaked et al. 2004, 2011). Thus, it is consistent with our findings that accretion rates are in line with those observed in other sediment-dominated reefs (Perry et al. 2012) or lagoon reefs (Gischler et al. 2008). Furthermore, the accretion rate remained constant during the re-initiation period following the 3800-year hiatus.

3.2 | Hiatus

A hiatus in coral growth and/or reef development can result from multiple causes, involving various processes. Dechnik et al. (2017) examined available data on reef flat hiatuses at the Great Barrier Reef (GBR) and suggested that a relative fall of approximately 0.5 m in sea level was responsible for the cessation of reef growth between 3900 and 1500 years BP. Hamanaka et al. (2012) speculated that oceanographic factors, such as the weakening of the Kuroshio Current, or climatic changes, like the strengthening of the Asian monsoons, could explain the hiatus in reef growth they documented between 4400 and 4000 years BP in the northwestern Pacific. In Brazil, reef growth continued until approximately 3700 years BP and then abruptly ceased, likely due to reduced accommodation space as a result of falling sea levels (Dechnik et al. 2019). At the IUI shore of Eilat, Shaked et al. (2011) discovered that an influx of clastic sediments ca. 4700 years BP, possibly triggered by down-faulting at the site, covered the IUI reef, causing a hiatus of 1700 years. In this study, we propose not just a local sea level condition causing specific reef turn-offs or hiatuses, but rather a global phenomenon of sea level fall. In light of our findings from Eilat and examining the reports from different locations around the globe (discussed above), we identify a global hiatus in reef growth between approximately 4000 and 2300 years BP (Figure 5). The available studies found almost no fossil corals dated to this time interval at sites across the Atlantic, Indian, and Pacific Oceans (Cortes et al. 1994; Dechnik et al. 2019; Gischler et al. 2008; Perry and Smithers 2011; Shaked et al. 2004, 2005, 2011; Toth et al. 2012), with all localities experiencing similar timelines of reef demise and re-initiation (Toth et al. 2012).

3.3 | Community Structure

Comparison of Holocene coral community structures with those of modern communities from the same locations can shed light on long-term reef ecological pathways, which may be obscured by short-term changes (Jackson 1992). Our work, which includes reef cores from all parts of the fringing reef in Eilat (lagoon, table, and fore reef) spanning a long period, allows us to explore coral community structure on both temporal and spatial scales (Figure 3). All 18 coral genera found in the Eilat NRR cores were also recorded in surveys of the modern reef (NMP: Natural Monitoring Program, Figure S1). This suggests that the unique coral community that was established during the initial Holocene growth period re-established almost 4000 years later, following a period of no-growth. Upon examining the modern mesophotic coral reef of Eilat, we found that most species are common to both shallow and mesophotic reefs (Table S6). Thus, we propose that the upper and lower mesophotic reefs, characterized by the structural complexity and diverse habitats described in Weinstein et al. (2020), which host depth-generalist corals, may have acted as a refuge for the reef during the hiatus (Eyal et al. 2022).

Research conducted in the Red Sea (Hammerman et al. 2022), Australia (Roff 2020), and the Pacific Ocean (Edinger et al. 2001) has shown shifts in coral community structure due to climate change, sea level changes, and anthropogenic impacts. Fine et al. (2013) suggested that corals at the northern tip of the Red Sea have undergone millennia of natural selection due to a thermal barrier at the southernmost end of the Red Sea, hence exhibiting greater resilience. Thus, even if a thermal event occurred (i.e., significant climate shift toward warmer environment) at the Eilat reef, the corals likely possessed the genetic pool necessary to overcome it. We have found that coral genera such as *Lobophyllia*, *Echinopora*, *Pavona*, *Gyrosmilia*, *Euphyllia*, and *Tubastraea* were common in our lagoon cores (NR10, NR05, NR02, and NR09). Data from the National Monitoring Program in Eilat (NMP, Figure S1) show that these coral genera are not currently observed in the lagoon area of the reef, although they are quite common at the reef front. This observation may suggest two possibilities: (1) coral samples from the lagoon cores were transported into the lagoon from another reef zone, or (2) there was a change in the former position of the lagoon when the sea level rose from 0 to +2 m during the mid-Holocene Sea level rise (Shaked et al. 2004). At the early stage of that rise, the modern reef flat had not yet formed (Shaked et al. 2011), and thus the modern lagoon was merely a continuous slope under the rising sea level. Eilat has been, and remains, rich and diverse in Scleractinia corals (Loya 1972), despite being on the northern limit of global reef occurrence (29.5100° N, 34.9224° E). Even after the temporary hiatus in reef growth, it re-established with a highly diverse coral community.

3.4 | Oxygen and Carbon Isotopes

The $\delta^{18}O$ values in the GoE/A did not exhibit drastic changes across the hiatus period (i.e., between 4000 and 6000 years BP and 0–1000 years BP, Figure 4). Salinity and temperature are the two primary factors affecting oxygen isotope fractionation in corals. Salinity may increase due to the evaporation of

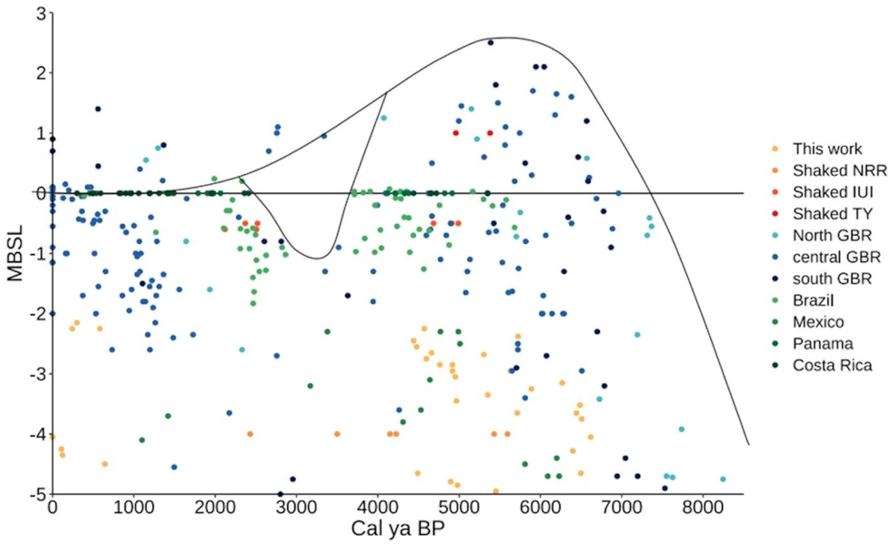

FIGURE 5 | Reconstruction of global sea level—Compilation of radiocarbon dates from seven sites vs. mean below sea level (MBSL). Possible global sea level curve is presented with demonstrated fall between ~4000–2300 years BP.

seawater or decrease through freshwater runoff (Beck 1998). High temperatures and low salinity result in lighter $\delta^{18}O$ values and vice versa (Epstein et al. 1970; Johnsen et al. 1972). Moustafá et al. (2000) reported higher seasonal $\delta^{18}O$ amplitude in Holocene GoE/A coral samples compared to modern samples, suggesting stronger seasonality of sea surface temperatures and changes in the precipitation and evaporation regime during the mid-Holocene, when summer monsoon rains reached the northern end of the Red Sea. Arz et al. (2003) suggested that a reduction of 3‰ in surface water salinity between 9250 and 7250 years ago at the GoE/A was caused by substantially higher rainfall and freshwater runoff, likely due to early Holocene Arctic Oscillation and regional monsoon-type circulation. Although salinity might have been lower in the mid-Holocene compared to now (a fact that would result in lighter $\delta^{18}O$ values in mid-Holocene samples), our results indicate no significant change in $\delta^{18}O$ values between 4000 and 6000 years ago and recent samples. Hence, we suggest that sea surface temperatures were likely stable over the last 6000 years at the Gulf (Figure 4a), allowing the coral community structure to remain consistent over this period (Figure 3). Contrary to the $\delta^{18}O$ results, $\delta^{13}C$ analyses show a negative trend of lighter skeletal $\delta^{13}C$ values from the mid-Holocene to present (Figure 4b). The reasons for this trend are varied and may include rising sea levels leading to a deeper environment, increased cloud cover which impact the photosynthesis and metabolic performances, or a shift in the coral community toward more heterotrophy-dependent species. It is important to note that $\delta^{13}C$ results before and after the hiatus (i.e., 4000–6000 and 0–1000 years ago) did not significantly differ, suggesting that environmental factors influencing $\delta^{13}C$ remained unchanged during this period. Results from modern (2020) coral samples showed significantly lighter skeletal $\delta^{13}C$ values (Figure 4), associated with the "Suess Effect" (Swart et al. 2010), reflecting changes in the $\delta^{13}C$ of dissolved inorganic carbon in ambient seawater due to the addition of anthropogenically derived CO_2 (13C-depleted) to the atmospheric carbon reservoir (Dassié et al. 2013).

To summarize, the Holocene development and evolution of the coral reef community in Eilat, northern Red Sea, provides a longer-term perspective, and understanding of reef connectivity at both regional and hyperlocal scales, and insights into the ecological responses to reef geomorphic and environmental change.

A global hiatus in coral reef development, that was largely driven by eustatic sea level drop during the late Holocene and caused a lack of vertical accommodation space is clearly captured in Eilat Reefs. Despite relatively stable environmental conditions across the Holocene at Eilat, a reduction in accommodation space through receding sea levels resulted in mass mortality or sea level constrained corals.

Around 700 years BP, a tectonic event caused the subsidence of the Eilat reef flat, creating new substrate with sufficient accommodation space for corals to recolonize (Bar et al. 2018; Shaked et al. 2002). Upper or lower mesophotic corals likely acted as a key larval source for the reef flats and may serve as important refugia if shallow reef systems become more heavily impacted by future climate change. As a result, and despite an extended hiatus in reef growth, the coral community structure has shown remarkable resilience, persisting over millennia. Future sea level rise could provide additional accommodation space for currently sea level-constrained reef systems, potentially leading to a significant increase in coral cover. However, the ecological, sedimentological, and hydrodynamic impacts of this "reef turn-on" on broader ecosystem functions remain unclear.

The study highlights the adaptability of coral reefs to past climate variations and suggests that if aided by effective conservation strategies, coral reefs may have a chance of surviving the current and projected future environmental challenges Understanding the past responses of coral reefs to environmental changes is crucial for developing informed approaches to protect these vital ecosystems in an era of rapid climate change and anthropogenic impacts. Coral reefs that recovered from the growth-hiatus event, such as the NRR reef of Eilat, should be investigated alongside other reefs that did not survive such events, to help identify the mitigating factors.

4 | Methods

4.1 | Sampling

A total of seven cores were extracted from the back reef, reef flat and fore reef of the Nature Reserve fringing reef of Eilat, Gulf of Aqaba during a drilling campaign in January 2019 (Figure 1). The cores were extracted using standard manual percussion coring. Four cores were extracted from the NRR lagoon (cores NR02, NR05, NR09, and NR10), one core (NR01 + 03; 2 continuous cores, will hereafter be referred to as NR01) was extracted from the NR reef flat and two cores (NR06 and NR07) were extracted from the NR reef front. Cores NR04 and NR08 were extracted from the reef flat; however, due to incomplete retrieval, they were excluded from this study. Cores were then sectioned lengthways using a circular saw, photographed (Figure 1c), and coarse coral and sedimentary identification were logged at 10 cm intervals. Half of each core was archived at 4°C and the other half was used for further compositional and geochemical analyses.

4.2 | Coral Community Structure

All seven cores from the Eilat NRR were wet-sieved through a 2 mm mesh at 10 cm intervals. Coral material larger than 2 mm was categorized based on overall and corallite morphology. When possible, corals were identified to the genus level following current taxonomic classifications (Veron 2000; Veron and Pichon 1980; World Register of Marine Species 2021). Additionally, all rock material and other invertebrates (e.g., echinoderms, gastropods, and bivalves) were sorted. The contribution of each coral genus to the total weight of identified corals within each 10 cm interval was plotted. The correlation between the depth (and age) of each core and coral community structure was assessed using the Shannon index calculated at each 10 cm interval.

4.3 | Radiocarbon Dating and Stable Isotopic Analyses

Throughout five selected cores (NR02, NR05, N507, NR09, and NR10), samples of *Stylophora* and *Acropora* (mainly-detailed in Table S1) were selected for radiocarbon dating haphazardly (i.e., with no bias for the taphonomic state of fragments). These species were selected due to their high frequency of occurrence across all cores. This choice was made to ensure uniformity and minimize variables during this type of analysis. Each coral sample was cut to 2–3 g sub-sample, cleaned, using a dental driller (head FG 171), for removing big sediment particles and live tissue, and then crushed to small fragments using a hammer. Coral fragments were then bath-sonicated in three rounds: (1) 20 min in DDW (2) 15 min in H_2O_2 10% (3) 15 min in H_2O_2 5% (4) 15 min in DDW. Following overnight drying at 50°C, the samples were crushed to a homogenic powder using 250 μm grain size sieve. The powder was weighed and divided into three 1.5 mL tubes for two purposes: (a) ^{14}C dating at NOSAMS, WHOI (Woods Hole Oceanographic Institution), and (b) Isotopic composition of $d^{18}O$ and $d^{13}C$ analyses at Weizmann Institution. All ^{14}C ages were calibrated using the Marine20 calibration curve using CALIB 8.2 with $dR = -8$ and uncertainty = 33 (Stuvier et al. 1993). Age-depth models were established using rbacon v2.4.1 R package (Blaauw et al. 2022).

4.4 | Sediment Grain Size and $CaCO_3$ Content

The fine-grained matrix surrounding the coral fragments within cores NR05, NR07, and NR10 was sampled at 5 cm intervals (up to a depth of 50 cm) and at 10 cm intervals (from 50 cm to the end of each core). These three cores contain the highest number of dated samples among the seven analyzed, so we selected them exclusively for this analysis. Samples were oven-dried at 60°C overnight and then weighed. All samples were treated with 1% Calgon solution to facilitate sediment granule breakdown, vortexed, and allowed to settle for an hour. Subsequently, the samples were wet sieved using four sieve fractions (63 μm, 250 μm, and 1 mm). The fractions smaller than 63 μm were centrifuged at 3000 rpm for 5 min to consolidate all suspended sediment. Each fraction (< 63 μm, 63–250 μm, 250–1 mm, and > 1 mm) was then oven-dried overnight at 60°C, weighed, and the relative proportion of the < 63 μm fraction was analyzed. The $CaCO_3$ content was determined on the < 63 μm fraction using a calcimeter; 20 mL of HCl were injected into the chamber, and the gas released (as per the equation: $CaCO_3(s) + 2\ HCl(aq) \rightarrow CaCl_2(aq) + CO_2(g) + H_2O(l)$) was recorded after 30 s. Following calibration with $CaCO_3$ powder and a blank 20 mL HCl sample, the $CaCO_3$ weights were calculated and normalized to the dry sample weight.

4.5 | Statistics

Isotopic signatures parameters ($\delta^{13}C$, $\delta^{18}O$) were evaluated using one-way ANOVA with the GraphPad Prism 10 program. If indicated, ANOVA was followed by post hoc Tukey's test. Homogeneity of variances and data normality were checked prior to the analysis using Levene and Shapiro–Wilk tests, respectively. Data were log-transformed to meet ANOVA assumptions when necessary. In all cases, the significance level adopted was 95% ($\alpha = 0.05$). Results were expressed as mean ± SE.

Author Contributions

B. Feldman: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **A. Torfstein:** conceptualization, data curation, formal analysis, methodology, project administration, supervision, writing – original draft, writing – review and editing. **M. O'Leary:** conceptualization, data curation, methodology, writing – original draft, writing – review and editing. **N. Simon Blecher:** methodology, writing – original draft. **R. Yam:** data curation, methodology, validation, writing – original draft. **Y. Shaked:** formal analysis, methodology, writing – original draft. **A. Shemesh:** data curation, formal analysis, methodology, project administration, resources, validation, writing – original draft. **D. Huang:** conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, writing – original draft, writing – review and editing. **O. Levy:** conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, validation, visualization, writing – original draft, writing – review and editing.

Acknowledgments

We thank the Interuniversity Institute for Marine Sciences at Eilat (IUI) for the logistical support. We are indebted to A. Zvifler and B. Yarden for their help with the fieldwork, G. Eyal, H. Rapuano and R. Tamir with coral skeleton identifications, J. Roff with data assessments and J. Benichou with statistical analyses. This study was supported by the Israel Science Foundation (ISF) No. 2658/17. We thank the Israel Nature and Parks Authority for cooperation and assistance in the field work.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in Zenodo at https://doi.org/10.5281/zenodo.14751913.

References

Abelson, A., R. Olinky, and S. Gaines. 2005. "Coral Recruitment to the Reefs of Eilat Red Sea: Temporal and Spatial Variation and Possible Effects of Anthropogenic Disturbances." *Marine Pollution Bulletin* 50, no. 5: 576–582. https://doi.org/10.1016/j.marpolbul.2005.02.021.

Albert, S., J. Udy, G. Baines, and D. McDougall. 2007. "Dramatic Tectonic Uplift of Fringing Reefs on Ranongga Is., Solomon Islands." *Coral Reefs* 26, no. 4: 983. https://doi.org/10.1007/s00338-007-0307-x.

Al-Rifaiy, I. A., and O. H. Cherif. 1988. "The Fossil Coral Reefs of al-Aqaba, Jordan." *Facies* 18, no. 1: 219–229. https://doi.org/10.1007/BF02536801.

Arz, H. W., F. Lamy, J. Patzold, P. J. Mu¨ller, and M. Prins. 2003. "Mediterranean Moisture Source for an Early-Holocene Humid Period in the Northern Red Sea." *Science* 300: 118–121.

Badawi, A.. 2015. "Late Quaternary Glacial/Interglacial Cyclicity Models of the Red Sea." *Environmental Earth Sciences* 73, no. 3: 961–977. https://doi.org/10.1007/s12665-014-3446-8.

Bar, N., A. Agnon, M. Yehudai, B. Lazar, Y. Shaked, and M. Stein. 2018. "Last Interglacial Sea Levels and Regional Tectonics From Fossil Coral Reefs in the Northeast Gulf of Aqaba." *Quaternary Science Reviews* 191: 41–56. https://doi.org/10.1016/j.quascirev.2018.04.031.

Beck, W. 1998. "No Warmer and Wetter 6000 Years Ago?" *Science* 279, no. 5353: 1003–1004.

Blaauw, M., J. A. Christen, M. A. A. Lopez, et al. 2022. "Package 'rbacon'."

Cabioch, G., L. F. Montaggioni, and G. Faure. 1995. "Holocene Initiation and Development of New Caledonian Fringing Reefs, SW Pacific." *Coral Reefs* 14, no. 3: 131–140. https://doi.org/10.1007/BF00367230.

Clark, P. U., A. S. Dyke, J. D. Shakun, et al. 2009. "The Last Glacial Maximum." *Science* 325, no. 5941: 710–714. https://doi.org/10.1126/science.1172873.

Cortes, J., I. G. Macintyre, and P. W. Glynn. 1994. "Holocene Growth History of an Eastern Pacific Fringing Reef, Punta Islotes, Costa Rica." *Coral Reefs* 13: 65–73.

Dassié, E. P., G. M. Lemley, and B. K. Linsley. 2013. "The Suess Effect in Fiji Coral δ 13 C and Its Potential as a Tracer of Anthropogenic CO 2 Uptake." *Palaeogeography, Palaeoclimatology, Palaeoecology* 370: 30–40. https://doi.org/10.1016/j.palaeo.2012.11.012.

Dechnik, B., A. C. Bastos, L. S. Vieira, et al. 2019. "Holocene Reef Growth in the Tropical Southwestern Atlantic: Evidence for Sea Level and Climate Instability." *Quaternary Science Reviews* 218: 365–377. https://doi.org/10.1016/j.quascirev.2019.06.039.

Dechnik, B., J. M. Webster, P. J. Davies, J. C. Braga, and P. J. Reimer. 2015. "Holocene "Turn-On" and Evolution of the Southern Great Barrier Reef: Revisiting Reef Cores From the Capricorn Bunker Group." *Marine Geology* 363: 174–190. https://doi.org/10.1016/j.margeo.2015.02.014.

Dechnik, B., J. M. Webster, G. E. Webb, L. Nothdurft, and J. x. Zhao. 2017. "Successive Phases of Holocene Reef Flat Development: Evidence From the Mid- To Outer Great Barrier Reef." *Palaeogeography, Palaeoclimatology, Palaeoecology* 466: 221–230. https://doi.org/10.1016/j.palaeo.2016.11.030.

Dibattista, J. D., M. B. Roberts, J. Bouwmeester, et al. 2016. "A Review of Contemporary Patterns of Endemism for Shallow Water Reef Fauna in the Red Sea." *Journal of Biogeography* 43, no. 3: 423–439. https://doi.org/10.1111/jbi.12649.

Edelman-furstenberg, Y., A. Almogi-labin, and C. Hemleben. 2009. "Palaeoceanographic Evolution of the Central Red Sea During the Late Holocene." *Holocene* 19, no. 1: 117–127. https://doi.org/10.1177/0959683608098955.

Edinger, E. N., J. M. Pandolfi, and R. A. Kelley. 2001. "Community Structure of Quaternary Coral Reefs Compared With Recent Life and Death Assemblages." *Paleobiology* 27, no. 4: 669–694. https://doi.org/10.1666/0094-8373(2001)027<0669:csoqcr>2.0.co;2.

Epstein, S., R. P. Sharp, and A. J. Gow. 1970. "Antarctic Ice Sheet: Stable Isotope Analyses of Byrd Station Cores and Interhemispheric Climatic Implications." *Science* 168, no. 3939: 1570–1572. https://doi.org/10.1126/science.168.3939.1570.

Eyal, G., J. H. Laverick, O. Ben-Zvi, et al. 2022. "Selective Deep Water Coral Bleaching Occurs Through Depth Isolation." *Science of the Total Environment* 844: 157180. https://doi.org/10.1016/j.scitotenv.2022.157180.

Fine, M., H. Gildor, and A. Genin. 2013. "A Coral Reef Refuge in the Red Sea." *Global Change Biology* 19, no. 12: 3640–3647. https://doi.org/10.1111/gcb.12356.

Garfunkel, Z., Y. Eyal, M. Eyal, et al. 1999. "Geological Map of the Northern Gulf of Elat Area." *Geological Map of the Northern Gulf of Elat Area* 48, no. 3–4: 133–134.

Gischler, E., and J. H. Hudson. 2004. "Holocene Development of the Belize Barrier Reef." *Sedimentary Geology* 164, no. 3–4: 223–236. https://doi.org/10.1016/j.sedgeo.2003.10.006.

Gischler, E., J. H. Hudson, and A. Pisera. 2008. "Late Quaternary Reef Growth and Sea Level in the Maldives (Indian Ocean)." *Marine Geology* 250, no. 1–2: 104–113. https://doi.org/10.1016/j.margeo.2008.01.004.

Gvirtzman, G., J. Kronfeld, and B. Buchbinder. 1992. "Dated Coral Reefs of Southern Sinai (Red Sea) and Their Implication to Late Quaternary Sea Levels." *Marine Geology* 108, no. 1: 29–37. https://doi.org/10.1016/0025-3227(92)90211-Y.

Hamanaka, N., H. Kan, Y. Yokoyama, T. Okamoto, Y. Nakashima, and T. Kawana. 2012. "Disturbances With Hiatuses in High-Latitude Coral Reef Growth During the Holocene: Correlation With Millennial-Scale Global Climate Change." *Global and Planetary Change* 80: 21–35. https://doi.org/10.1016/j.gloplacha.2011.10.004.

Hammerman, N. M., G. Roff, A. Rodriguez-Ramirez, et al. 2022. "Reef Accumulation Is Decoupled From Recent Degradation in the Central and Southern Red Sea." *Science of the Total Environment* 809: 151176. https://doi.org/10.1016/j.scitotenv.2021.151176.

Jackson, J. B. C. 1992. "Pleistocene Perspectives on Coral Reef Community Structure." *Integrative and Comparative Biology* 32, no. 6: 719–731. https://doi.org/10.1093/icb/32.6.719.

Johnsen, S. J., W. Dansgaard, H. B. Clausen, and C. C. Langway. 1972. "Oxygen Isotope Profiles Through the Antarctic and Greenland Ice Sheets." *Nature* 235, no. 5339: 429–434. https://doi.org/10.1038/235429a0.

Kleinhaus, K., A. Al-Sawalmih, D. J. Barshis, et al. 2020. "Science, Diplomacy, and the Red Sea's Unique Coral Reef: It's Time for Action." *Frontiers in Marine Science* 7: 1–9. https://doi.org/10.3389/fmars.2020.00090.

Leonard, N. D., M. L. Lepore, J. x. Zhao, et al. 2020. "Re-Evaluating Mid-Holocene Reef "Turn-Off" on the Inshore Southern Great Barrier Reef." *Quaternary Science Reviews* 244, no. 244: 106518. https://doi.org/10.1016/j.quascirev.2020.106518.

Loya, Y. 1972. "Community Structure and Species Diversity of Hermatypic Corals at Eilat, Red Sea." *Marine Biology* 13, no. 2: 100–123. https://doi.org/10.1007/BF00366561.

Loya, Y. 2004. "The Coral Reefs of Eilat — Past, Present and Future: Three Decades of Coral Community Structure Studies." *Coral Health and Disease*: 1–34. https://doi.org/10.1007/978-3-662-06414-6_1.

Makovsky, Y., A. Wunch, R. Ariely, et al. 2008. "Quaternary Transform Kinematics Constrained by Sequence Stratigraphy and Submerged Coastline Features: The Gulf of Aqaba." *Earth and Planetary Science Letters* 271, no. 1–4: 109–122. https://doi.org/10.1016/j.epsl.2008.03.057.

Mayewski, P. A., E. E. Rohling, J. C. Stager, et al. 2004. "Holocene climate variability." *Quaternary Research* 62, no. 3: 243–255. https://doi.org/10.1016/j.yqres.2004.07.001.

Montaggioni, L. F. 2005. "History of Indo-Pacific Coral Reef Systems Since the Last Glaciation: Development Patterns and Controlling Factors." *Earth-Science Reviews* 71, no. 1–2: 1–75. https://doi.org/10.1016/j.earscirev.2005.01.002.

Moustafá, J., Y. A. Pätzold, and Y. G. Loyá Wefer. 2000. "Mid-Holocene Stable Isotope Record of Corals From the Northern Red Sea." *International Journal of Earth Sciences* 88: 742–751.

Neo, M. L., W. Eckman, K. Vicentuan, S. L. M. Teo, and P. A. Todd. 2015. "The Ecological Significance of Giant Clams in Coral Reef Ecosystems." *Biological Conservation* 181: 111–123. https://doi.org/10.1016/j.biocon.2014.11.004.

Neugebauer, I., M. Dinies, B. Plessen, et al. 2022. "The Unexpectedly Short Holocene Humid Period in Northern Arabia." *Communications Earth & Environment* 3, no. 1: 47. https://doi.org/10.1038/s43247-022-00368-y.

Perry, C. T., S. G. Smithers, P. Gulliver, and N. K. Browne. 2012. "Evidence of Very Rapid Reef Accretion and Reef Growth Under High Turbidity and Terrigenous Sedimentation." *Geology* 40, no. 8: 719–722. https://doi.org/10.1130/G33261.1.

Perry, C. T., and S. G. Smithers. 2011. "Cycles of Coral Reef "Turn-On", Rapid Growth and "Turn-Off" Over the Past 8500 Years: A Context for Understanding Modern Ecological States and Trajectories." *Global Change Biology* 17, no. 1: 76–86. https://doi.org/10.1111/j.1365-2486.2010.02181.x.

Roff, G. 2020. "Reef Accretion and Coral Growth Rates Are Decoupled in Holocene Reef Frameworks." *Marine Geology* 419, no. 2019: 106065. https://doi.org/10.1016/j.margeo.2019.106065.

Rohling, E. J., and W. J. Zachariasse. 1996. "Red sea outflow during the last glacial maximum." *Quaternary International* 31, no. 95: 77–83.

Sansoleimani, A., G. E. Webb, D. Harris, S. Phinn, and C. Roelfsema. 2022. "Antecedent Topography and Active Tectonic Controls on Holocene Reef Geomorphology in the Great Barrier Reef." *Geomorphology* 413: 108354. https://doi.org/10.1016/j.geomorph.2022.108354.

Scholz, D., A. Mangini, and T. Felis. 2004. "U-Series Dating of Diagenetically Altered Fossil Reef Corals." *Earth and Planetary Science Letters* 218, no. 1–2: 163–178. https://doi.org/10.1016/S0012-821X(03)00647-2.

Shaked, Y., A. Agnon, B. Lazar, S. Marco, U. Avner, and M. Stein. 2004. "Large Earthquakes Kill Coral Reefs at the North-West Gulf Af Aqaba." *Terra Nova* 16, no. 3: 133–138. https://doi.org/10.1111/j.1365-3121.2004.00541.x.

Shaked, Y., S. Marco, B. Lazar, et al. 2002. "Late Holocene Shorelines at the Gulf of Aqaba: Migrating Shorelines Under Conditions of Tectonic and Sea Level Stability." *EGU Stephan Mueller Special Publication Series* 2, 105–111.

Shaked, Y., B. Lazar, S. Marco, M. Stein, and A. Agnon. 2011. "Late Holocene Events That Shaped the Shoreline at the Northern Gulf of Aqaba Recorded by a Buried Fossil Reef." *Israel Journal of Earth Sciences* 58, no. 3–4: 355–368. https://doi.org/10.1560/IJES.58.3-4.355.

Shaked, Y., B. Lazar, S. Marco, M. Stein, D. Tchernov, and A. Agnon. 2005. "Evolution of Fringing Reefs: Space and Time Constraints From the Gulf of Aqaba." *Coral Reefs* 24, no. 1: 165–172. https://doi.org/10.1007/s00338-004-0454-2.

Stuvier, M., and P. J. Reimer. 1993. "Extended 14C Data Base and Revised CALIB 3.0 14C Age Calibration Program." *Radiocarbon* 35, no. 1: 215–230.

Swart, P. K., L. Greer, B. E. Rosenheim, et al. 2010. "The 13 C Suess Effect in Scleractinian Corals Mirror Changes in the Anthropogenic CO_2 Inventory of the Surface Oceans." *Geophysical Research Letters* 37: 1–5. https://doi.org/10.1029/2009GL041397.

Toth, L. T., R. B. Aronson, S. V. Vollmer, et al. 2012. "ENSO Drove 2500-Year Collapse of Eastern Pacific Coral Reefs." *Science* 336, no. 6090: 81–84. https://doi.org/10.1126/science.1221168.

Veron, J. E. N. 2000. *Corals of the World*. Australian Institute of Marine Science.

Veron, J. E. N., and M. Pichon. 1980. *Scleractinia of Eastern Australia. Part 3. Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae*. Australian National University Press for the Australian Institute of Marine Science.

Weinstein, D. K., R. Tamir, N. Kramer, et al. 2020. "Mesophotic Reef Geomorphology Categorization, Habitat Identification, and Relationships With Surface Cover and Terrace Formation in the Gulf of Aqaba." *Geomorphology* 379: 107548. https://doi.org/10.1016/j.geomorph.2020.107548.

Woodroffe, C. D., and J. M. Webster. 2014. "Coral Reefs and Sea-Level Change." *Marine Geology* 352: 248–267. https://doi.org/10.1016/j.margeo.2013.12.006.

World Register of Marine Species. 2021. "WoRMS Editorial Board."

Yamano, H., T. Miyajima, and I. Koike. 2000. "Importance of Foraminifera for the Formation and Maintenance of a Coral Sand Cay: Green Island, Australia." *Coral Reefs* 19, no. 1: 51–58. https://doi.org/10.1007/s003380050226.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.