Discover Oceans

Review

The extreme Red Sea and its late Cenozoic shallow water benthic foraminifers

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Abstract
Semi-enclosed basins are more responsive to climate variations than the global ocean. This is true in particular for the Red Sea as a unique landlocked environment controlled by an interplay of its geographic, tectonic, and climatic features resulting in extreme salinities. Previous studies pointed to extreme salinities reaching > 53 during the low sea-level stands of glacial periods in the last 500 kyr. Yet our knowledge of the late Cenozoic evolution history of the Red Sea as a coral refuge and responses of coral reefs to these extreme salinities is scarce. Benthic foraminifers are key organisms for monitoring environmental changes in any marine setting, both shallow and deep, throughout geological times and to the present day. Here we provide a synthesis of the shallow-water benthic foraminifers that occupy the photic zones of the Red Sea environment based on the published studies, to reassess the variable saline conditions of the Red Sea across its evolution through the late Cenozoic and present-day as recorded by the shallow-water benthic foraminifer communities in association with coral reefs. Our review reveals a lack of information on shallo-water benthic foraminifers and paleoclimate data across the late Cenozoic evolution of the Red Sea encompassing climate shifts are worth being studied as analogs for modern-day and future climates; suggests a pathway to assess the salinity history of the Red Sea by using foraminiferal assemblage shifts.

Keywords Sea-level · Paleoecology · Paleoclimate · Plio-Pleistocene · Salinity · Paleoshoreline

1 Introduction

The Red Sea is a unique environment that constitutes a natural laboratory to investigate the response of a marine environment subject to abrupt climate and oceanographic shifts, strongly influenced by the shallow sill at Bab al-Mandab [24, 121], whose physiography is largely dictated by geodynamic forces [79]. All the geographic, tectonic and climatic features of the Red Sea have awarded it with a high level of marine endemism [32, 36, 128]. At the same time, the Gulf of Aqaba in the northern Red Sea has been proposed to be a climate refuge for corals during global warming and ocean

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acidification [45]. This, however, is highly debated as its land-locked nature results in extreme sensitivity to the changing environmental conditions [1, 68, 72].

Several studies documented not only the evolution of the Red Sea as a young oceanic basin [22, 46, 78, 135] but also its past climates that are archived within its deposited sediments [17, 20, 108, 120], among others). For the latter, planktic foraminifers are the most common tool to benefit from as they encapsulate the chemical properties of the ambient waters they thrive in and the climate conditions during which they secrete their calcium carbonate shells [116]. While deep water benthic foraminifers are beneficial to study long-term variation in the seawater conditions and climates as they are not prone to seasonal changes, shallow-water benthic foraminifers are among the most prolific carbonate producers in the coral reef ecosystems [33, 52, 70, 126, 77]. They are efficient tools as bioindicators to assess and monitor modern-day water quality and health of their associated coral reefs as some shallow-water benthic foraminifers (i.e., symbiont-bearing large benthic foraminifers,LBFs) thrive in similar ecological conditions as corals [15, 31, 37, 48, 96, 117]. Furthermore, changes in benthic foraminiferal assemblage can be used as an indicator of varying salinity conditions, which is especially relevant for the Red Sea due to its modern-day (e.g., [18]) and past extreme salinities (e.g., [106]).

For the above reasons, in this study, we focus on shallow-marine environmental conditions of the Red Sea across geological times as documented in studies that benefited from the shallow-water benthic foraminifers that occupy water depths less than 50 m, usually in association with coral reefs. Given that the Red Sea is a biodiversity hotspot and home to more than 300 coral species [32], there is a growing number of studies that use shallow-water benthic foraminifers as tools to monitor modern coral reefs of the Red Sea [7, 9, 18, 62, 90],among others). Natural stressors and ongoing development of ecotourism along the Red Sea coasts necessitate reviewing previous studies that focused on fossil shallow water benthic foraminifer assemblages that we can use as a reference point and benefit from to assess the modern-day and project the future conditions.

In case of future climate projections, studies worldwide that have documented past climates such as the Marine Isotope Stage (MIS) 19c (0.79–0.77 My) and mid-Pliocene Warming (3.3–3.0 My) consider those time intervals as analogues for present-day and future global climate conditions, respectively [25, 132]. Similarly, coral reef response and development linked to sea-level increase and warming in these time intervals have been discussed as analogs in various geographic regions, including Florida, the Mediterranean Sea, and Okinawa [64, 133, 137]. How the Red Sea ecosystem responded to these climate shifts and warming intervals still is not fully understood. Filling this gap is crucial for understanding the response of marine organisms across the basin to the critical environmental shifts, such as the replenishment of the basin after the Miocene salinity crisis (e.g., [66, 111]) and the transition to the glacial-interglacial fluctuations during the Quaternary. To project the future response of the Red Sea, we need to understand how its ecosystem responded to past climates that are analogs for the future. Accordingly, in this review, we aimed to reveal whether: (1) past climates as analogs for future conditions were studied in the Red Sea region; (2) we know the salinity history of the Red Sea during its evolution; (3) we can use foraminifers for a robust paleoenvironmental assessment; and (4) coral-reef associated foraminifers of the Red Sea hold potential to monitor present-day and serve as reference point for responses of corals to future climates.

2 Geological background of the region

The Red Sea is a semi-enclosed, elongated, narrow but deep basin. It is a 2000-km-long and 355-km-wide marginal sea with a maximum water depth of around 3000 m (Fig. 1) [103]. The shorelines in the northern part are only 180 km apart, but as one moves southward, the distance between shorelines is 360 km [29]. Formation of the Red Sea Basin was controlled by the divergence of the African from the Arabian plate starting during the Eocene as a tectonic spreading center, and transforming to a continental rift during the Oligocene [28, 103] During the Late Oligocene (~ 25 My), seafloor spreading started and the Gulf of Suez was opened [22, 46, 78, 135]. Progressively, the northern Red Sea was opened by the Miocene, while there is still debate on the exact timing (~ 20 My: Rasul et al. [103], or 13 My: Augustin et al. [14]). The southern portion of the Red Sea opened just about five million years ago, and it narrows to 28 km at the Bab al-Mandab Strait, which connects it to the Gulf of Aden [85, 110, 125].

Restricted marginal marine conditions of the Red Sea from the late Oligocene until the transgression in the early Miocene (Burdigalian) that resulted in the first coral bioherms [39, 61, 97] in tandem with the global formation of carbonate platforms [21]. These restricted conditions were followed by again restricted conditions during the middle Miocene that lasted until the earliest Pliocene and resulted in the development of carbonates interlayering with thick evaporites in the basin [59–61, 85, 99]. In the Red Sea Basin, this restriction occurred in an interplay with global sea-level variations

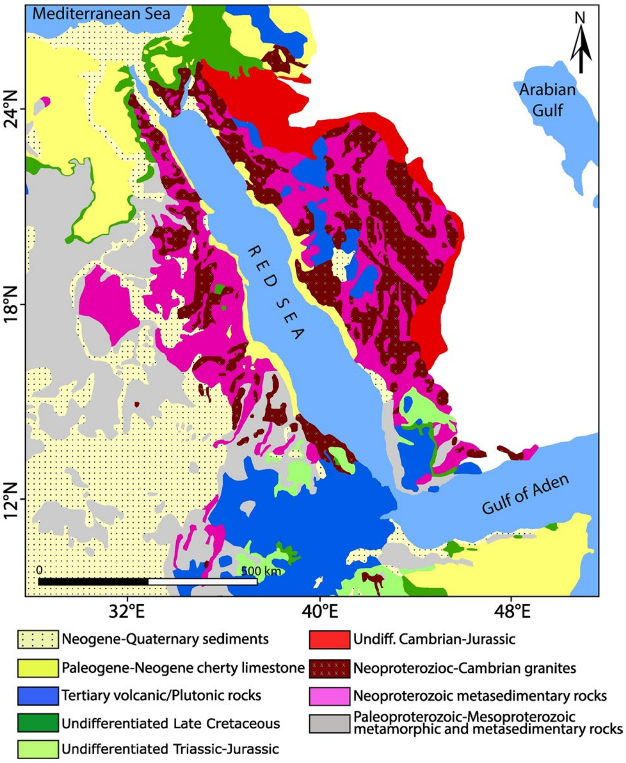

Fig. 1 Simplified general geological map of the Red Sea area (after Mohriak & Leroy [86])

and regional tectonics [65, 94, 101, 102]. During that time, the Red Sea was still disconnected from the Indian Ocean, but connected to the Mediterranean Sea as suggested by the Mediterranean coral species [94, 97] and nannoplankton assemblages [75] in the northern Red Sea rock record. The later evaporite basin is expressed in seismic reflection profiles [110, 125].

The evaporite deposition started as early as the Langhian, just after the coral intermezzo [97], and points to a pronounced sea-level drop during the Tortonian that lasted through the Messinian until the second marine incursion ~ 6–5 My ago (Fig. 2,[89, 118]). This second large marine incursion of the Red Sea Basin, this time through the Bab-al-Mandab in the south, established a connection to the Indian Ocean, and normal marine conditions were restored (Fig. 2,[60, 71, 125]).

Through the Plio-Pleistocene, intervals of connection to the Mediterranean Sea are thought to have happened during the high sea-level stands of the interglacial warm periods [23, 82, 99]. Mediterranean shallow-water foraminiferal affinities in the northern Egyptian Red Sea [115] are thought to reflect these repetitive sporadic connections via the Gulf of Aqaba along the Dead Sea Fault Zone [80], although a potential connection via the Gulf of Suez was discussed [111]. Mediterranean bivalve affinities found in the Late Pliocene sediments of the Egyptian Red Sea are assumed to agree with foraminifer findings (Fig. 2,[66]). On the other hand, especially in the southern and central Red Sea, deep-sea planktic foraminifers are in parallel to the Indian Ocean affinities [4], suggesting that the main connection was to the Indian Ocean (Fig. 2).

3 Shallow water benthic foraminifers of the Red Sea

The Red Sea has been at the center of interest of researchers studying foraminifers since the eighteenth century. The first mentions of benthic foraminifers of the region were mainly taxonomic descriptions and include those of von Fichtel & von Moll [134], d'Orbigny [34], Parker & Jones [92], Gräffe [49], and Heron-Allen & Earland [56], which largely focused on species descriptions. To provide nomenclatural consistency among the analyzed literature, in this present study, we update all foraminiferal taxa according to the World Register of Marine Species (WoRMS) database. We further report the number of studies conducted in the Red Sea region that concentrated on the benthic foraminifers and their use in marine ecology and climate interpretations (Fig. 3,*Supplementary Information*, *SI*). Our review shows that despite numerous studies concentrated on the recent shallow-water foraminifers in the Red Sea, there are only a handful of studies that report fossil foraminifers that we can benefit from to understand past

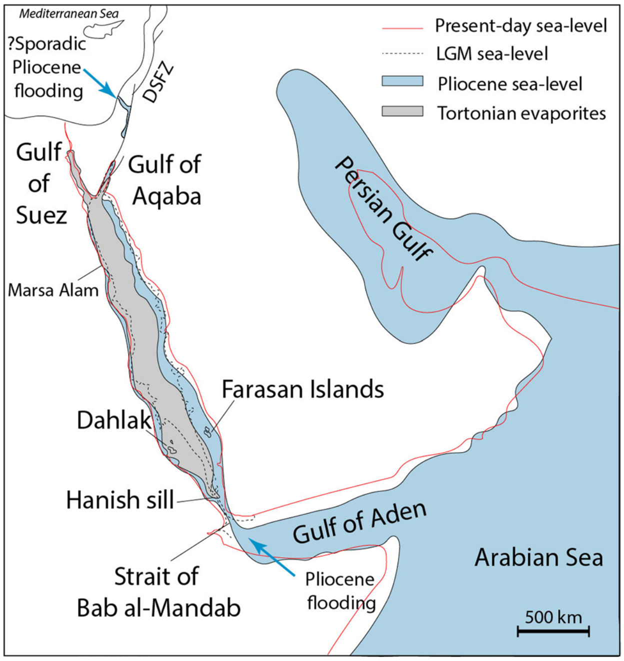

Fig. 2 Map showing present day, Last Glacial Maximum (LGM), and Pliocene coastlines and Tortonian evaporites as comparison for the basin shrinking/expanding related to the pronounced sea-level changes. Present-day contour (red) adapted from GeoMapApp; LGM contour (dashed) for the Red Sea is redrawn after Bailey et al. [19], Pliocene extent of marine waters (blue) and Tortonian desiccation evaporites (gray) are redrawn after Segev et al. [118]

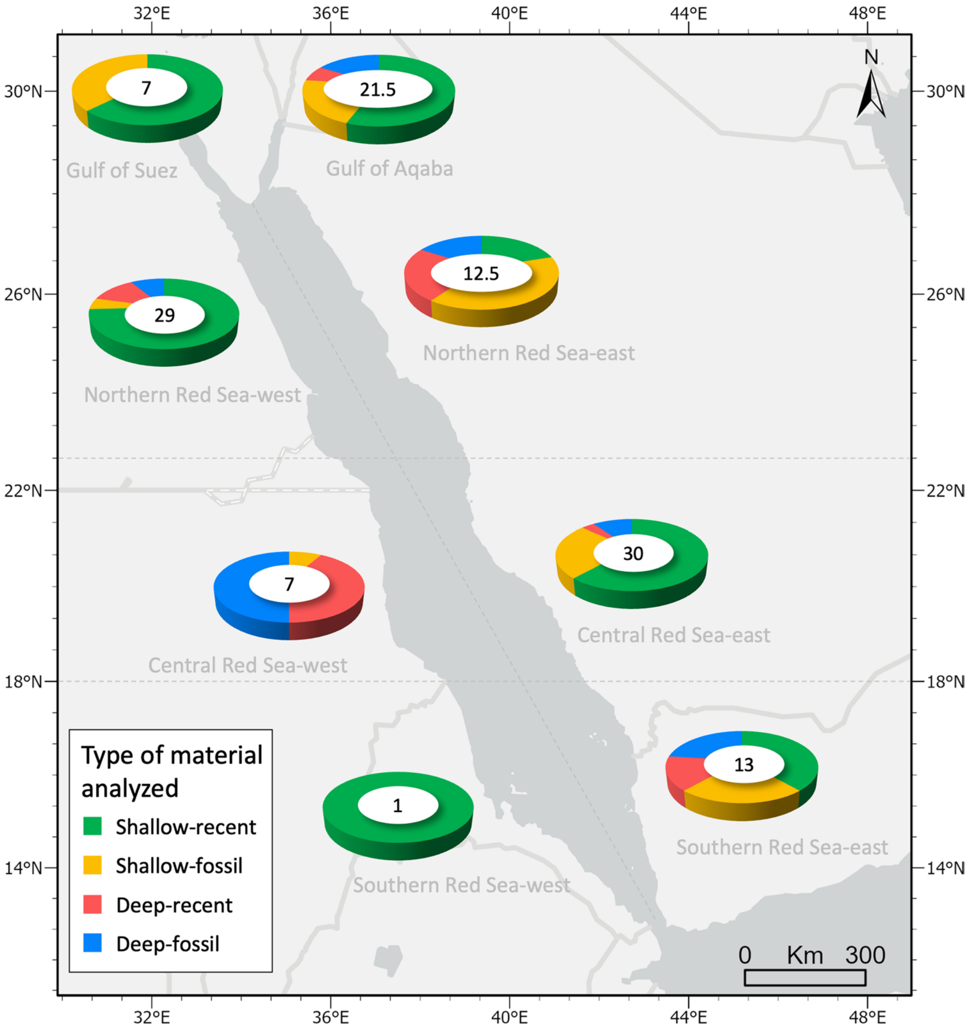

Fig. 3 Number of benthic foraminifer studies in eight areas as Gulf of Suez, Gulf of Aqaba, northern Red Sea-east, northern Red Sea-west, central Red Sea-east, central Red Sea-west, southern Red Sea-east, southern Red Sea-west, as per the concentration of the studies that used foraminifers for ecology and climate interpretations, are shown as pie-charts. Studies were considered under four categories as shallow-recent, shallow-fossil, deep-recent, and deep-fossil. Pie-charts were generated according to the location and type of material used in the respective studies. Non-integer counts are due to the studies that use a combination of materials

shallow-water environments and their associated corals (*SI*, Table S1, Fig. 3). In this section, we document the studies that concentrated on fossil shallow water benthic foraminifers and recent shallow water benthic foraminifers in chronological order. We concentrate on studies using foraminifers specifically for paleoenvironmental interpretation, and we have intentionally excluded studies that incidentally reported foraminifers without making use of them for detailed interpretations on the ecology, environment, and climate conditions.

First Pliocene shallow-water benthic foraminifers, including the genus *Borelis* were identified by Cox [30] in association with Ostreidae and Pectinidae. Later, *Robulus* sp., *Rotalia* sp., and *Cymbaloporetta* were documented by Stainforth [124] from sediment overlying Miocene evaporites, recovered from boreholes in the Gulf of Suez. Although the depositional water-depth (i.e., less or more than 50 m as per the scope of this study) of these Pliocene sediments is not stated, the foraminiferal fauna was considered of Indian Ocean origin, linked to the connection of the Red Sea to the open ocean settings [124]. From the Pliocene-aged marly limestone deposits in Helwan, Egypt, Said [115] identified 40 benthic foraminifer species. Although this specific locality is next to the modern Nile River and thus not at the Red Sea coast, it is important to note that the presence of some species identified there necessarily requires a connection between the Mediterranean and the Red Sea during the Plio-Pleistocene times, given that the sediments were deposited along a narrow Mediterranean branch incised the Nile Valley. Said [115] noted that these specific species (i.e., *Anomalina gibbosa* and *Hanzawaia rhodiensis*) were found in the recent Red Sea fauna and the Lower Pleistocene of Rhodes Island in the Mediterranean Sea [83]. Yet again, the depositional depth hosting these species was not discussed. Along the Egyptian Red Sea coast in Qoseir, Souaya [122] detailed the foraminifer content of fossiliferous (marly) limestone and limegrits. He identified 31 genera and 47 Plio-Pleistocene species and subspecies of shallow water benthic foraminifers and three biostratigraphic units, which are Pliocene *Archaias angulatus*, Pliocene *Borelis* cf. *B. pygmaeus*, and Pleistocene *Borelis schlumbergeri* [122]. Felesteen et al. [42], instead, assigned *A. angulatus* to the Miocene, and identified *Asterigerina* Zone for the Pliocene with associated foraminifers *Pleurostomella tenuis, Quinqueloculina costata, Triloculina angulatus, Turitellalla sprianus, Nonionella auris, Amphistegina lessonii, A. madagascariensis,* and *Lenticulina alatolimbata*. It is worth noting, however, that *Turitellalla sprianus* does not appear in any other literature or WoRMS database.

The literature is also rich in studies of modern shallow water benthic foraminifers focusing on species distribution and ecology (e.g., [2, 5, 54, 81, 88, 104], among others), and more recently on pollution (e.g., [3, 138, 139], among others) (Fig. 3, Table S1). The first study on recent benthic foraminifers was undertaken by Marie [76], and was followed by studies of [112–114]. Reiss and his colleagues focused on recent LBF of the Gulf of Aqaba [104, 105]. Some researchers dealt with Red Sea (mainly the northern part) shallow-water benthic foraminifers in case studies (e.g., [41, 93], among others). Recently, several studies emerged focusing on sediment transport mechanisms in the shelf zones of the Red Sea using LBFs as indicators [11–13, 127].

One of the most extensive studies on recent benthic foraminifer assemblages of the Red Sea was published by Hottinger et al. [58] focusing on the northern Red Sea, while not considering foraminifer suborders and species that can be found only in small size fractions [69]. Nonetheless, they have identified 337 species and subspecies of recent benthic foraminifers. Among others, Haunold et al. [54] reported shallow water (0–70 m) benthic associations from the northern Red Sea coasts of Egypt. They listed 13 associations, which are: 1) *Quinqueloculina mosharrafai-Borelis schlumbergeri-Bolivina* (*Brizalina*) *simpsoni*, 2)*Heterostegina depressa-Amphistegina lessonii/bicirculata*, 3)Cibicidids-*Rosalina-Amphistegina lobifera-Pseudoschlumbergerina ovata*, 4)*Peneroplis planatus*; 5) *P. planatus-Varidentella neostriatula*, 6) *P. planatus-Coscinospira hemprichii-V. neostriatula*; 7) *Quinqueloculina* spp.; 8) *Pseudohauerina diversa-Sorites orbiculus*; 9) *Verneuilina* sp.-*Articulina pacifica- Fijiella simplex;* 10) *Textularia agglutinans/rugulosa-Bolivina variabilis;* 11) *T. agglutinans-Ammonia bradyi-Elphidium fichtelianum* (syn. *E. jenseni*)*/Haynesina depressula* subsp. *simplex* (syn. *E. simplex*)*;* 12) *Operculina ammonoides-Adelosina laevigata-Bolivina striatula/subspathulata*; and, 13) *B. variabilis-Miliolinella-Nonion faba- Haynesina depressula* subsp. *simplex*. They distinguish four different types of substrate associated with these benthic foraminifer communities providing clues also for interpreting past ecological settings. Accordingly, associations 1, 2, and 3 represent hardgrounds; associations 4 to 8 sandy bottoms (with or without seagrass and/or corals); associations 9 to 12 represent firmgrounds; and lastly association 13 represents soft bottom environments. Madkour [74] contributed with findings from shallow water benthic foraminifers of the Egyptian Red Sea coast by documenting species that occupy calm shallow waters as reflected by abundant Soritacea and Miliolacea, and, to a lesser extent, Rotaliacea.

4 Foraminifers associated with coral reefs of the Red Sea

Our understanding of the Pleistocene benthic foraminifer fauna in the Red Sea was significantly expanded through the research conducted by Kora et al. [67] along the coastal plain of Marsa Alam on the Egyptian Red Sea coast. These authors studied raised beach deposits and coral reefs, and their foraminifer contents, that according to U/Th datings by El-Moursi et al. [38] cover the three interglacial stages MIS 5 (130 – 80 kyr), MIS 7 (~ 243 kyr), and MIS 9 (~ 337 kyr). In those deposits, Kora et al. [67] identified several benthic foraminiferal genera representative of shallow marine environments including *Amphistegina*, *Sorites*, *Borelis*, *Pyrgo* and miliolids (e.g., *Triloculina*, *Quinqueloculina*).

Dullo [35] documented Pleistocene scleractinian coral reefs along the Saudi Arabian Red Sea coast and their associated foraminifers. He reported 14 foraminifer genera and displayed their common occurrences in lateral reef zonation (Fig. 4). Along the Saudi Arabian side of the Gulf of Aqaba, Taviani et al. [130] reported Pleistocene (MIS5e, ~ 130–115 kyr) coral-reef associated foraminifers that included smaller miliolid taxa (e.g., *Quinqueloculina*) and large foraminifers such as *Sorites, Heterostegina, Peneroplis, Amphisorus, Amphistegina,* and *Averculina*. They also noted epipelagic foraminifers (e.g., *Globigerinoides ruber*, *Orbulina universa*) along with pteropods, suggesting fringing reef size decline during MIS5e. Parker et al. [91] conducted a quantitative study on the Pleistocene and modern foraminifer and coral communities of the coral reef environments in southern Sinai. They reported 182 fossil and 95 modern species of shallow water benthic foraminifers. Moreover, the relative abundance of skeletal grains indicated that shallow-water benthic foraminifers are the predominant group in the seagrass zone, accounting for 22% of the components, whereas corals constitute only

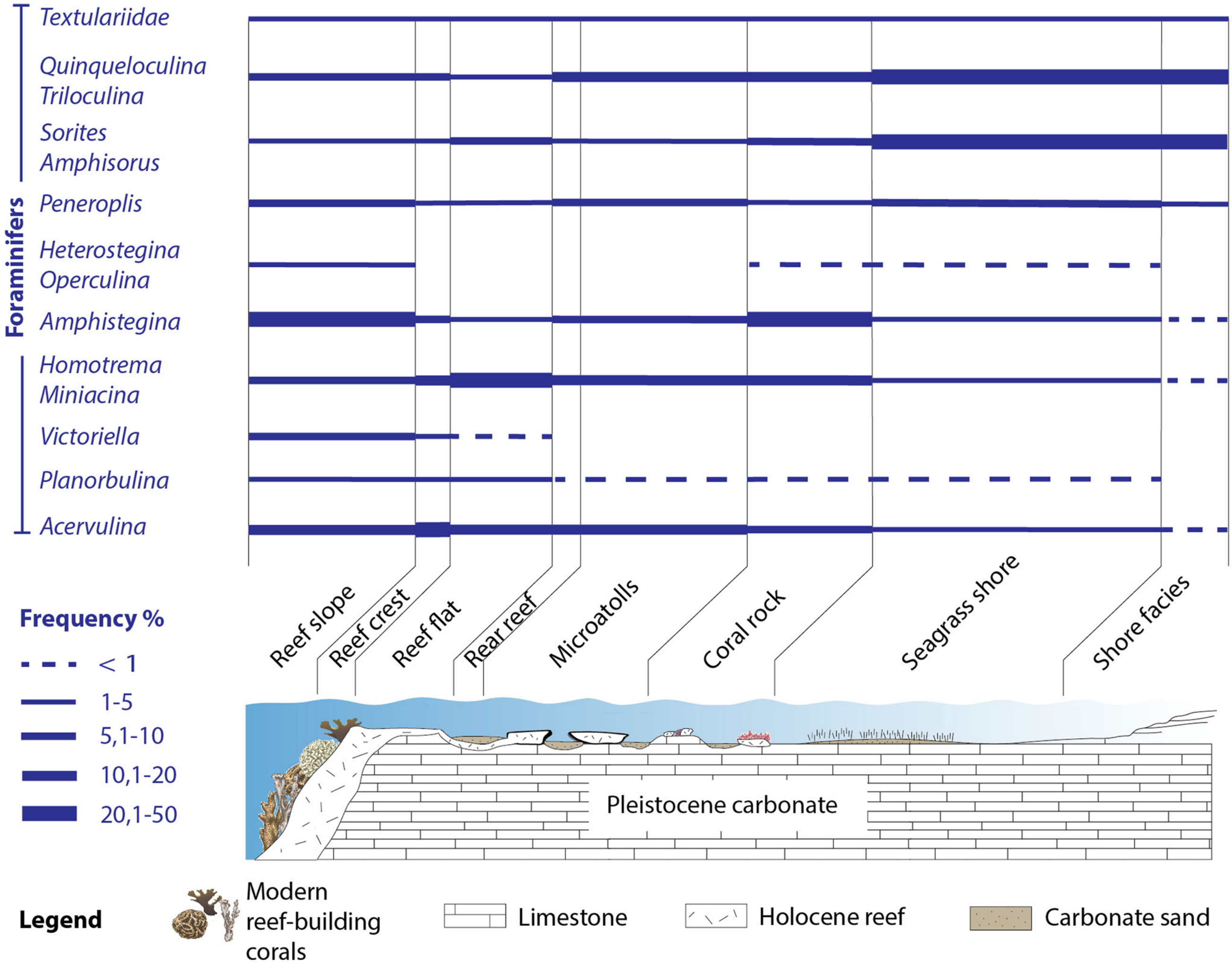

Fig. 4 Schematic display of lateral facies of a recent fringing reef of the Red Sea and associated foraminifers (modified after [35])

10% of the assemblage. Later, El-Sorogy et al. [40] provided an extensive list of coral communities and their associated foraminifer species of a late Pleistocene coral reef, located along the northern Saudi Arabian Red Sea coast. They reported 24 foraminifer and 67 coral species from the northern Red Sea, thus adding to the list of Dullo [35] foraminiferal genera such as *Clavulina*, *Sahulia, Coscinospira, Epistomaroides, Neorotalia, Elphidium*, and *Flintina*; however, they did not conduct a quantitative study on the foraminiferal abundances in the different reef zonations.

These studies yielded that the corals are most abundant in the fore-reef (reef slope) environment with 46–47% of the sedimentary components, whereas foraminifers only represent between 3 and 7%. The modern *vs.* fossil (i.e., Pleistocene) comparison based on the relative abundance of foraminifers revealed that, while the modern reef flats and fore-reefs are dominated by *Sorites orbiculus* (dominant) and *Peneroplis pertusus*, in the back-reef (e.g., lagoon) the relationship between these two species is reversed. Conversely, fossil reef flats and fore-reefs were dominated by *Amphistegina lessonii*. Consistently, Dullo [35] reported *Sorites* and *Peneroplis* as common genera for the back-reef environment in agreement with Parker et al. [91], while *Amphistegina* was found in both back-reef and fore-reef environments (Fig. 4).

Contrary to the extensive knowledge of Pleistocene corals and their associated foraminifers, the Pliocene remains largely understudied. During the Pliocene, the Red Sea became a permanent marine environment with the connection to the Indian Ocean with the submergence of the Bab al-Mandab Strait [23, 118] as shown by sedimentary and micropaleontological data [4, 44, 109, 125]. Until this southern connection became permanent, the Red Sea is thought to have had some sporadic connection to the Mediterranean Sea in the north as suggested by foraminifer and bivalve findings (Fig. 2, [80, 115]). The Early Pliocene mixed mollusk fauna of the north central Red Sea coasts along Egypt were representative of Mediterranean and Indo-Pacific affinities correlated with the Early Pliocene foraminiferal zones, *A. angulatus* of Souaya [122] and the *Asterigerina* Zone of Felesteen et al. [42], and the Late Pliocene Zone of *Borelis* cf. *B. pygmaeus* of Souaya [122], which were later dominated by the Indo-Pacific affinities of the fauna in the late Pliocene and were correlated with Zone of *Borelis schlumbergeri* of Souaya [122] [66].

5 Foraminifers for coral health assessment in the Red Sea

In 2003, Hallock et al. [53] introduced an innovative and practical method for monitoring the health of coral reefs, called the FoRAM (Foraminifera in Reef Assessment and Monitoring) Index and later it was revisited by Prazeres et al. [100] who introduced a standardized protocol. This method is based on the relative abundance of the three main ecological groups within foraminiferal assemblages: large benthic and symbiont-bearing taxa, small heterotrophic species, and opportunistic taxa. Large benthic, symbiont-bearing foraminifers (e.g., *Amphistegina*, *Heterostegina*, *Borelis*, *Sorites*, *Marginopora*, *Amphisorus* and *Alveolinella*) that thrive in coral reefs possess similar environmental requirements, including water quality. Their shorter lifespan makes them ideal tools to monitoring any environmental change that may cause a decline in long-living coral communities. Their abundance within marine ecosystems ensures statistically robust results, and the minimal impact of collecting foraminifers on corals further enhances their suitability as indicators for assessing reef health.

The FoRAM Index calculated from living foraminiferal assemblages in the Al Bawadi Islands of the southern Red Sea, yielded values indicating a favorable environment for reef growth [18]. Similar results were also recently reported from the northeastern Red Sea, specifically to provide a baseline for ecological conditions in an area (NEOM) exposed to intensive construction activities [90]. However, some localities exhibited adverse changes in environmental quality in central Saudi Arabian coasts [8, 47] and southern Sinai Peninsula in the northern Red Sea [18]. This underscores the effectiveness of the method in the Red Sea for assessing coral health. Additionally, the genera used for the FoRAM Index [53] correspond to those identified in a Pleistocene-aged coral reef in the Red Sea (Fig. 4, [35]) and modern-day carbonate platforms located along the Saudi Arabian Red Sea coastline (F. Giovenzana, unpublished data, Fig. 5). It has been also proposed that Pleistocene reef zones bear similarity to their modern counterparts [6, 26]. If this holds true, fossil foraminifers can be used for comparison with contemporary foraminifers, serving as a reference point for future assessments of coral health.

6 Red Sea as an extreme environment

Throughout its evolution history, the Red Sea has experienced severe sea-level variations (Fig. 2). Since the early Tortonian (~8 My), the basin was almost desiccated, leading to voluminous evaporite deposition [89, 118]. The start of the Pliocene (~5.2 My) was marked by a refill event with the opening of Strait of Bab-al-Mandab that led to the modern-day-like conditions in the Red Sea environment [60, 71, 85, 125].

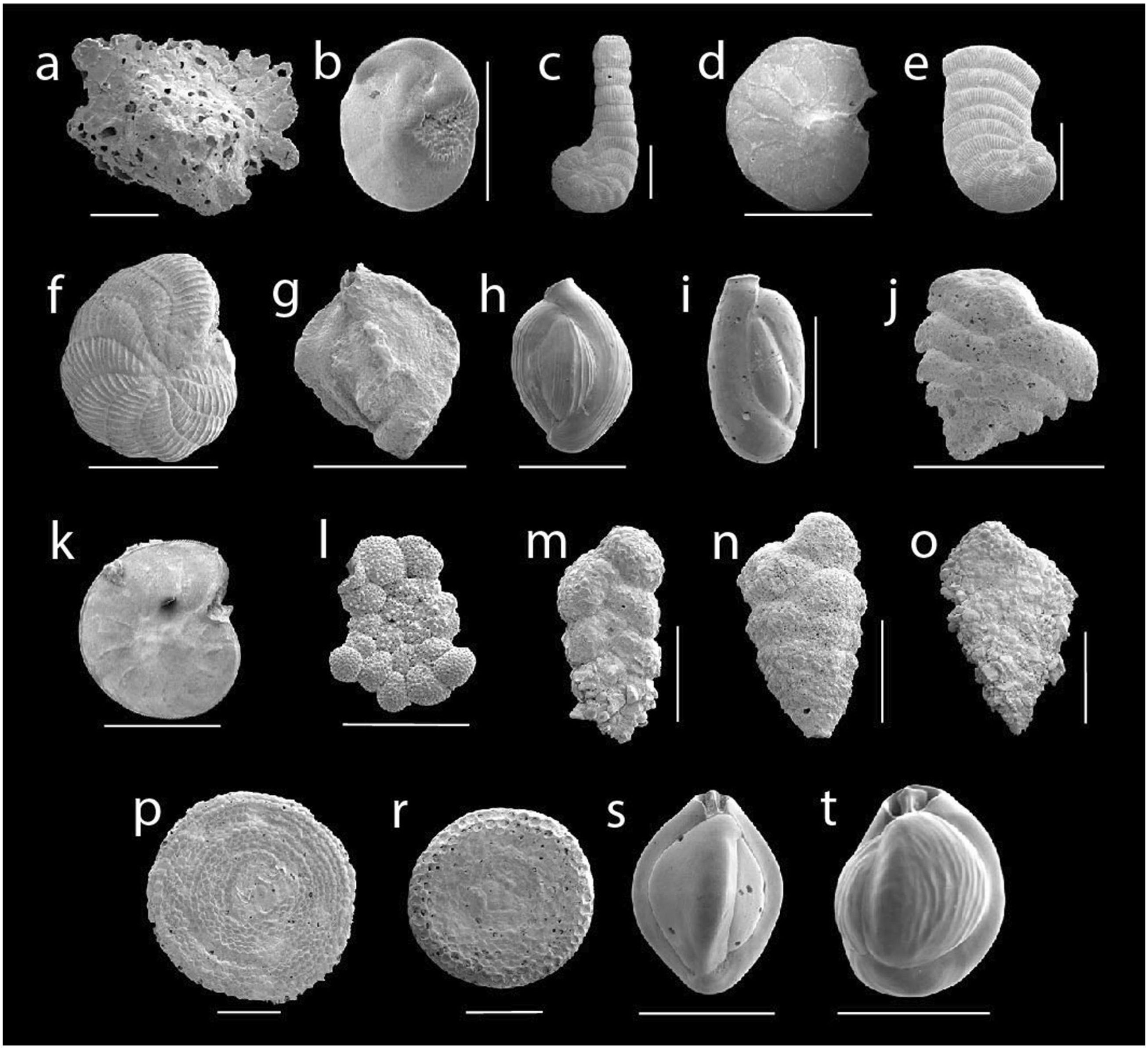

Fig. 5 SEM photos of selected benthic foraminifer species from modern-day fringing reef of Al-Wajh carbonate platform located in northwest Saudia Arabia. a. *Acervulina* sp.; b. *Amphistegina lessonii*; c. *Coscinospira hemprichii*; d. *Heterostegina depressa*; e. *Peneroplis planatus*; f. *Peneroplis pertusus;* g. *Quinqueloculina contorta*; h. *Quinqueloculina boueana*; i. *Quinqueloculina* cf. *laevigata* j. *Sahulia kerimbaensis*; k. *Operculina ammonoides*; l. *Planorbulina* sp.; m. *Textularia agglutinans*; n. *Textularia communis*; o. *Textularia foliacea occidentalis*; p. *Sorites* sp.; r. *Sorites orbiculus*; s. *Triloculina tricarinata*; t. *Triloculina* sp. (F. Giovenzana, unpublished data). Scale bars = 500 µm

The Early Pliocene marine refill was noted by Kora and Abdel-Fattah [66] who reported data from the Egyptian Red Sea on the rare presence of the Early Pliocene corals of Indo-Pacific affinities linked to this marine excursion. Despite the importance of the Pliocene times in the Red Sea realm, to our knowledge, the literature lacks documentation of the Pliocene sea-level variations recorded in the Red Sea, except for the paleogeographical reconstructions [118]. The recent study of Mitchell et al. [84] from contourite-like deposits suggests that during the Early Pliocene times, the Red Sea might have had lower sea-level stand and intermittent brackish conditions, which align well with the diatom findings from the Gulf of Suez that are suggestive of shallow water, freshwater, and brackish water conditions [131]. The possible causes of such conditions could be related to monsoon/rainfall dynamics and wetter climate as it was in the Mediterranean Sea [50, 73] or a change in the source of the great Nile River [10]. However, the role of Nile River and the Mediterranean inflow in the replenishment of the Red Sea temporally and spatially are less known. Indeed, spatial variation in micropaleontological findings from the Pliocene sediments were noted by Pocknall et al. [98] who stated that while in the Gulf of Suez they recorded palynomorphs indicators of wet and warm climates and, as per the dinoflagellates, varying salinity conditions, DSDP sites covering the central and southern Red Sea were barren of palynomorphs. Despite the brackish conditions in the Red Sea could be considered the lower end of the extreme salinity spectrum and benthic foraminifers could be used to reveal varying salinity conditions (as discussed below), until further research, we lack foraminiferal data to discuss this issue for the Pliocene times at the moment. Therefore, we focus on the sea-level variations that occurred in the Red Sea during the last 500 kyr [51, 106] and their responses as salinity extremities recorded by the marine fauna (Fig. 6).

The extreme saline conditions of the Red Sea are recorded in deep-sea fauna of the last 500 kyr [106]. Sediment archives from the deep Red Sea registered aplanktic zones, where planktic foraminifers disappeared due to extreme salinities [43, 55, 106]. During the last 500 kyr, three distinct aplanktic zones were recorded: MIS 12 (~470 kyr), MIS 6 (~130 kyr, and MIS 2, in other words the Last Glacial Maximum (LGM; 23–19 kyr) (Fig. 6). The LGM resulted in extreme salinities reaching > 53 due to drastic global sea-level drop (by ~120 m) that severed marine fauna [55, 119] (Fig. 6), but a new study displayed deep-water corals and benthic foraminifers survived this salinity extremity [27] contrary to the previous findings [129]. This new finding aligns well with the earlier findings of Rohling et al. [106] (Fig. 6) and Winter et al. [136] who recorded the high-salinity resistant deep-sea miliolid taxa with increased abundance corresponding to aplanktic zones during the low sea-level stands. The resilience of miliolids as salinity tolerant taxa was noted also by Parker et al. [91] who discussed that miliolids might have survived in the Red Sea during the Holocene after the LGM, given some modern reef taxa were not encountered in the uplifted Pleistocene reef terraces (e.g., *Coscinospira hemprichii, Monalysidium acicularis, Elphidium craticulatum, E. striatopunctatum, Quinqueloculina mosharrafai,* among others); however, we lack studies to accurately reach this information for specific extreme salinity intervals during glacial low sea-level stands such as MIS 16, MIS 6, and MIS 2 (Fig. 6) from uplifted deposits.

Indeed, using foraminiferal assemblage shifts in the Red Sea has the potential to be a strong approach to document the salinity history of the Red Sea across geological timescales. Miliolids from shallow and deep-sea basins are used as indicators of varying salinity conditions of restricted basins [16, 43, 106]. Assemblage shifts between hyaline Rotaliida and porcelaneous Miliolida [18, 63, 95] can be used to reveal salinity evolution of the Red Sea both from shallow water and deep-water (e.g., Fig. 6 for the last 500 kyr,[106]) settings providing information on how this extreme environment formed and started to host its endemic species and corals.

7 Final remarks and future research directions

This review study focused on the previous studies that used shallow water benthic foraminifers to evaluate the Red Sea paleoecology and paleoclimate, and their link to coral health assessment.

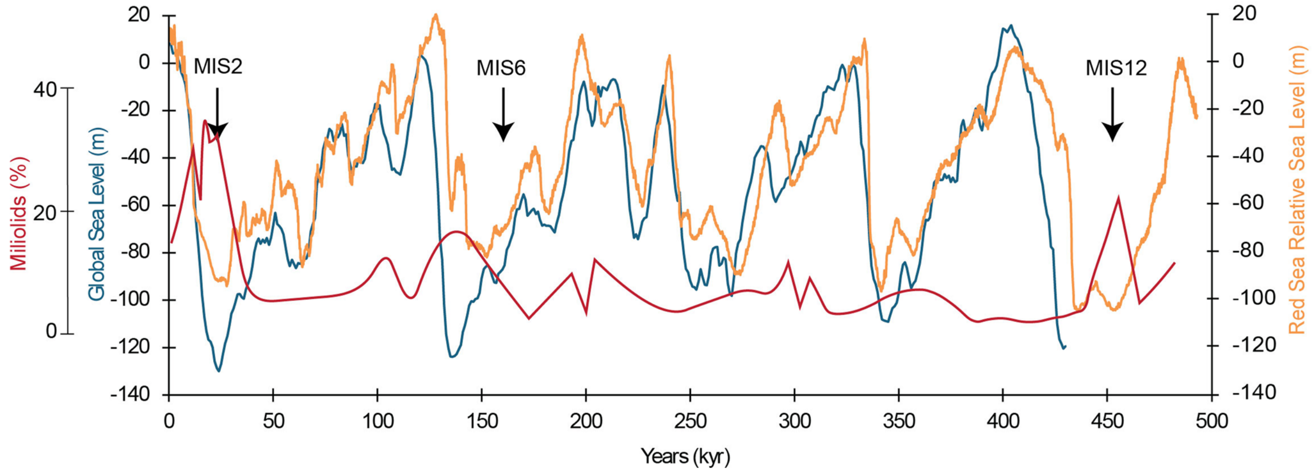

Fig. 6 Benthic foraminifer $\delta^{18}O$ global sea-level stack in dark blue (after [123]), Red Sea relative sea-level estimations in orange derived from planktic foraminifer *Globigerinoides ruber* and bulk sediment $\delta^{18}O$ (after [51, 107]), and relative abundance of deep-sea miliolids as indicator of salinity changes in red [106] covering the last ~500 kyr. Black arrows correspond to Marine Isotope Stages with extreme salinity events recorded as aplanktic zones in the Red Sea during sea-level low stands of glacials with salinities reaching > 53 [55, 106]

Our study pointed to significant gaps in our understanding of the evolution of the Red Sea as a young ocean. Despite the rich late Quaternary studies in the Red Sea region, a considerable gap in the Pliocene and Early-Middle Pleistocene climates, especially intervals of present and future climate analogues, stands out. A better understanding of the past response of the Red Sea to climate shifts is crucial to projecting its present-day and future response to ongoing climate warming. Furthermore, for a sound assessment of coral reef health by benefitting from the reef-associated foraminifers to monitor and protect the marine biodiversity and environment of the Red Sea, these analogues play an important role. As a future roadmap, to better understand the Red Sea as a coral refuge under the global warming scenarios, our findings point to the following thoughts as imperative future research directions:

1) Tandem analysis of shallow-water and deep-sea benthic foraminifers along the Red Sea, focusing on assemblage shifts, would reveal salinity evolution of the Red Sea Basin;
2) Fossil shallow water benthic foraminifers associated with coral reefs can be used as a reference to study modern-day reef environments and ecological variations;
3) Pliocene-aged shallow environments can be used as a guide to better establish paleoshorelines of the Red Sea;
4) Pliocene and Pleistocene climates as analogs for present-day and future climates can be used as references to assess the Red Sea as a climate refuge in future climate conditions.

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Author contributions NÖ and HW conceptualized the study. NÖ wrote the main manuscript text and prepared Figs. 2, 4, 5 and 6. AK prepared Fig. 1. FG prepared Supplementary Information, Fig. 3, and prepared SEM photos for Fig. 5. NÖ, HW, FG, AK, and GMV reviewed and contributed to the discussion and the revised version of the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate Not applicable.

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Competing interests Authors declare a potential conflict of interest as HW is a Guest Editor of the Special Issue and a co-author of this paper. HW was not involved in the peer-review process and editorial handling of this paper. Editorial process was handled independently by another editor with no conflict.

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