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Alexandroff, S.J.; Zuschin, M.; Kroh, A.

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ORIGINAL ARTICLE

Quantitative comparison of Pleistocene and Recent coral reef habitats in the northern Red Sea (El Quseir, Egypt)

Stella Jane Alexandroff[1,2] · Martin Zuschin[1] · Andreas Kroh[3]

Abstract Fossil reefs have the potential to provide important data for studies of climate and environmental change. This is particularly true for Pleistocene-Holocene coral reefs, which predominantly consist of communities undisturbed by anthropogenic impact and therefore provide a baseline for evaluating the status of modern reefs. We used photo transects and point-counting to quantitatively compare two Pleistocene reef terraces of two Pleistocene sites, tentatively assigned to marine isotope stage 5e, with habitats (reef flat, reef edge, reef slope at 5- and 10-m water depth) of a modern reef near El Quseir, Egypt. The modern reef exhibits a clear trend of increasing taxonomic richness and diversity from the reef flat towards the reef slope at 10-m water depth. The most abundant genera are *Pocillopora*, *Acropora*, *Millepora*, and massive *Porites*, but strong differences between individual habitats were evident. The most abundant genera in the fossil reefs are massive *Porites* and *Dipsastraea*. With regard to quantitative composition, all modern reef habitats differed significantly from each other as well as from the fossil reefs. The fossil reef composition is most similar to the modern reef slope habitat at 10-m water depth. There are two conflicting hypotheses

on geodynamic processes for this area—these are tectonic uplift and tectonic stability. Considering tectonic stability, the fossil reefs would have to be interpreted as lagoonal patch reefs, for which no modern counterparts exist in the study area. However, in the case of tectonic uplift, we conclude that the fossil reefs studied were once situated at around 10-m water depth.

Keywords Taphonomy · Paleoecology · Invertebrates · Coral composition · Reefs

✉ Stella Jane Alexandroff
  s.alexandroff@bangor.ac.uk

1 Department of Palaeontology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

2 School of Ocean Sciences, Bangor University, Askew Street, Menai Bridge, Wales, UK

3 Naturhistorisches Museum Wien, Burgring 7, 1010 Vienna, Austria

Introduction

Coral reefs are geological and biological structures that preserve environmental data over thousands of years. This makes them useful proxies for sea level (Edinger et al. 2007) and climate change (e.g., Lough and Barnes 1997) and enables studying these factors on reef-coral communities in the fossil record (Pandolfi and Greenstein 2007). Comparing fossil with extant reef communities requires methods that can be employed in both settings. Here we present a case study using photo transects and point-counting of coral coverage and community composition to compare past and present reefs from the Egyptian Red Sea coast. A number of features make the Red Sea region an excellent setting for such an approach: (1) Extensive outcrops of fossil reefs occur parallel to and in close proximity of the modern coastline; (2) these are better preserved than many tropical terraces, and (3) the young age of the lowest reef terrace facilitates direct comparison with modern reef communities.

Pleistocene reef terraces of the Red Sea have been studied since the late 19th century (Walther 1888) and have been investigated over the past few decades with respect

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to sea level changes, microfacies, diagenesis, age, and faunal composition (Veeh and Giegengack 1970; Dullo 1986, 1990; Andres et al. 1988; Hoang and Taviani 1991; El Moursi et al. 1994; Gvirtzman 1994; Bosworth and Taviani 1996; Strasser and Strohmenger 1997; Taviani 1998a, b; Plaziat et al. 2008; Lambeck et al. 2011; Parker et al. 2012; Mewis and Kiessling 2013). To our knowledge, however, no study has quantitatively compared the faunal composition of modern and nearby fossil reefs in an attempt to define the original depositional water depth. This is especially worthwhile for the lowermost terraces of marine isotope stage (MIS) 5e, which show relatively minor diagenetic alteration (Gvirtzman and Friedman 1977; Dullo 1984, 1986). These reefs are the most promising target for a past-modern comparison and for evaluating community stability over geological time scales.

We therefore compare two Pleistocene reef terraces, tentatively assigned to MIS 5e, to the reef flat, reef edge, and reef slope at 5- and 10-m water depth of a modern fringing reef at the Egyptian coast of the Red Sea. An estimation of paleo-depth is a prerequisite for comparative studies because faunal composition of reefs is strongly depth controlled (e.g., Riegl and Velimirov 1994).

This work was designed to test whether the original water depth of Pleistocene reef terraces can be determined from their taxonomic composition. The main objectives were to (1) characterize the modern and fossil reef habitats regarding their taxonomic composition and diversity, to then (2) assess how similar the fossil reef terraces are to the different modern habitats.

Materials and methods

Study area

The Recent reef is located at Abu Sauatir (Fig. 1), 12 km northwest of El Quseir (26°12′25″N, 34°13′13.2″E). We divided it into four habitats: reef flat, reef edge, reef slope at a depth of 5 m, and reef slope at a depth of 10 m (Fig. 2). The reef is naturally divided into a northern and a southern part by a wadi mouth.

The fossil reef terraces are located at Abu Dabbab, 97 km southeast of El Quseir (25°19′56″N, 34°44′36″E), and at El Mohgar, 13 km southeast of El Quseir (26°0′12.3″N, 34°20′7″E). They are the lowest terraces at these sites and were studied 3–5 m above present sea level (Fig. 3a). The reef consists of coral framestones, bindstones dominated by coralline red algae or vermetid gastropods, and rud- and grainstones, consisting of coral fragments, mollusks, and echinoderm debris (Fig. 3b–f). Corresponding to ages provided for nearby terraces, the reefs are tentatively assigned

to MIS 5e (i.e., the Eemian stage) between 115 and 130 kyr before present (Plaziat et al. 2008).

Field methods

To evaluate the taxonomic composition of the modern reef habitats, 16 quadrats of 0.25 m² per habitat were photographed during snorkeling (reef flat and edge) or SCUBA diving (reef slope) along transects in April 2012. The reef edge transects were done at approx. 2-m water depth: the wave energy prohibited sampling at shallower depths in this habitat at any time of day. The starting point of each transect was chosen randomly; from there, photographs were taken at intervals between 0.5 and 2 m using a 50 × 50-cm metal frame for scaling. The reef flat was divided into a proximal and a distal transect of eight quadrats, respectively; the reef edge and the reef slope at 10-m depth were divided into northern and southern transects with eight quadrats each.

In the fossil reef, we used line transects similar to those in the Recent reef. At El Mohgar, we took photographs of 23 quadrats every 2 m along a tape measure. At Abu Dabbab, 16 quadrats were photographed without leaving a gap between the individual frames.

The modern sites were evaluated exclusively by analyzing photographs. For each quadrat, several full-view and detail images were taken. In the fossil reefs, in addition, quadrats were drafted on paper and major constituents identified directly in the field to better distinguish between in situ corals and coral rubble.

Point-counting was used to produce a quantitative dataset of the taxonomic composition. A grid with 100 intersection points was added to the best full-view image for each quadrat, resulting in 1600 data points for each of the four modern reef habitats and the fossil reef at Abu Dabbab, respectively, and in 2300 data points for El Mohgar. Using the detail-view images, the taxon under each intersection was identified and counted. Percentages of the counts were arcsine-root-transformed prior to statistical analysis to gain linear data (Legendre and Legendre 1998). Photo-quadrat (Bohnsack 1979 and references therein) and grid-point intercept sampling (e.g., Pilliod and Arkle 2013) are efficient survey methods, although there might be limitations when sampling rare taxa. The standard error of sample proportion for each taxon in the modern reef habitats (flat, edge, slope 5 m, and slope 10 m) and the fossil reef terraces was calculated using the equation $SE = \sqrt{\frac{p \times (1-p)}{n}}$ and yielded values between 0.3 and 1.2 %. It is worth noting, however, that the size of a coral colony was not always smaller than the distance between two grid points (see van der Plas and Tobi 1965).

Taxonomic richness and diversity were evaluated for each quadrat, and the arithmetic means plus 95 %
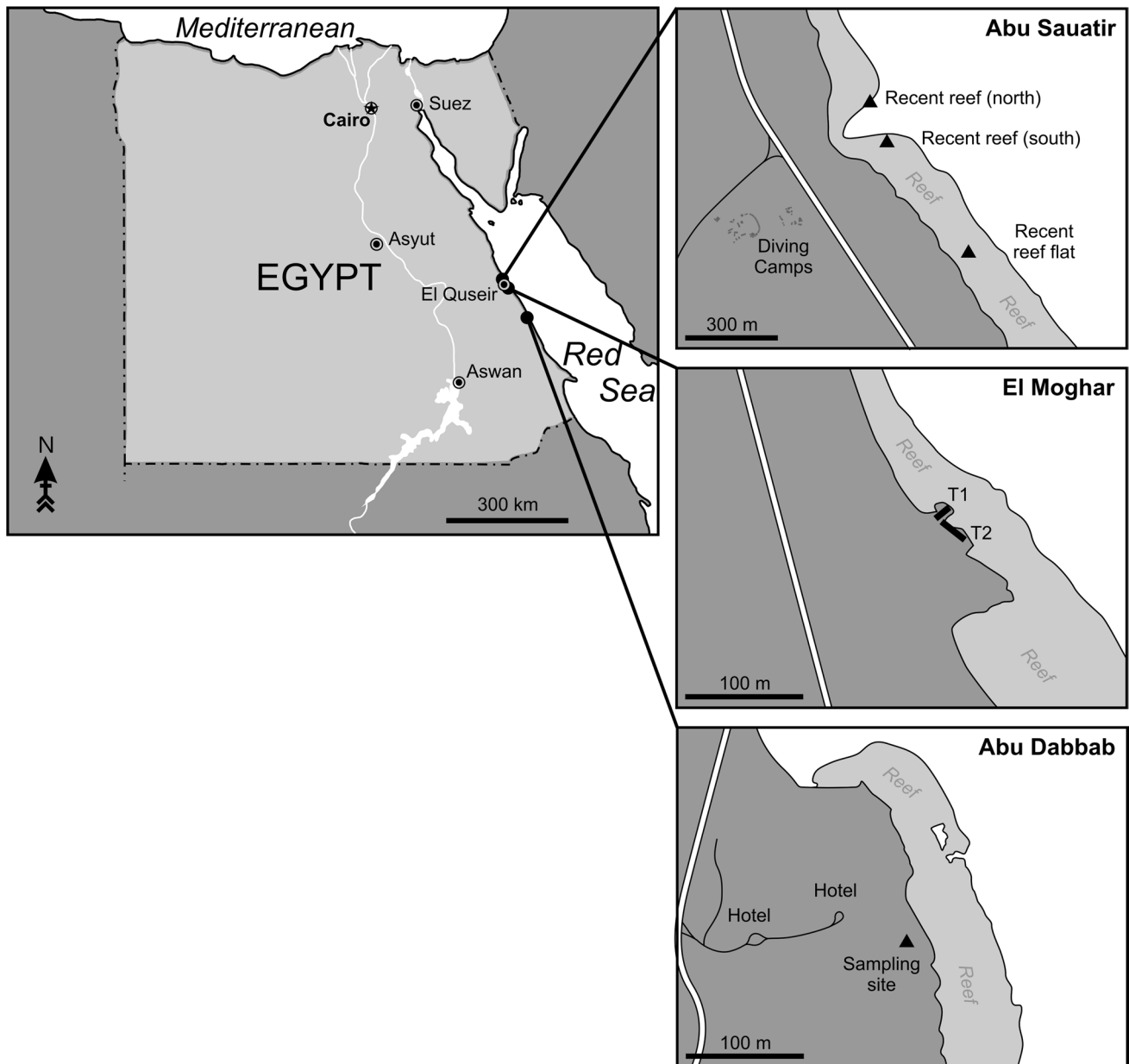
Fig. 1 Study sites of the modern reef at Abu Sauatir and the fossil reef terraces at El Mohgar and Abu Dabbab, Egypt

confidence intervals were calculated for each habitat. Richness was measured as the total number of genera and diversity was measured with the Shannon–Wiener index (Shannon 1948). The Margalef index (Margalef 1958) and Simpson index (Simpson 1949) showed similar trends as the Shannon–Wiener index and are therefore not shown here. The Mann–Whitney U test (Mann and Whitney 1947) was used to compare the northern and the southern transects of the reef edge and the slope.

We evaluated the difference between all modern reef habitats and the fossil reefs using one-way analysis of similarity (ANOSIM; Clarke and Warwick 1994). Pairwise comparisons yielding R values above 0.75 (well separated), above 0.5 (overlap, but clearly separated), above 0.25 (stronger overlap, poorly separated) or under 0.25 (negligible separation) display the degree of separation between habitats (Clarke and Gorley 2006). Non-metric multidimensional scaling (MDS; Kruskal 1964) was used to visualize the differences among all habitats. The Bray-Curtis similarity index (Bray and Curtis 1957) was chosen as distance measure. The distances between two points represent the ranks of dissimilarity (Clarke and Gorley 2006). Similarity percentages (SIMPER; Clarke and Warwick 1994) were calculated to evaluate which taxa primarily contributed to
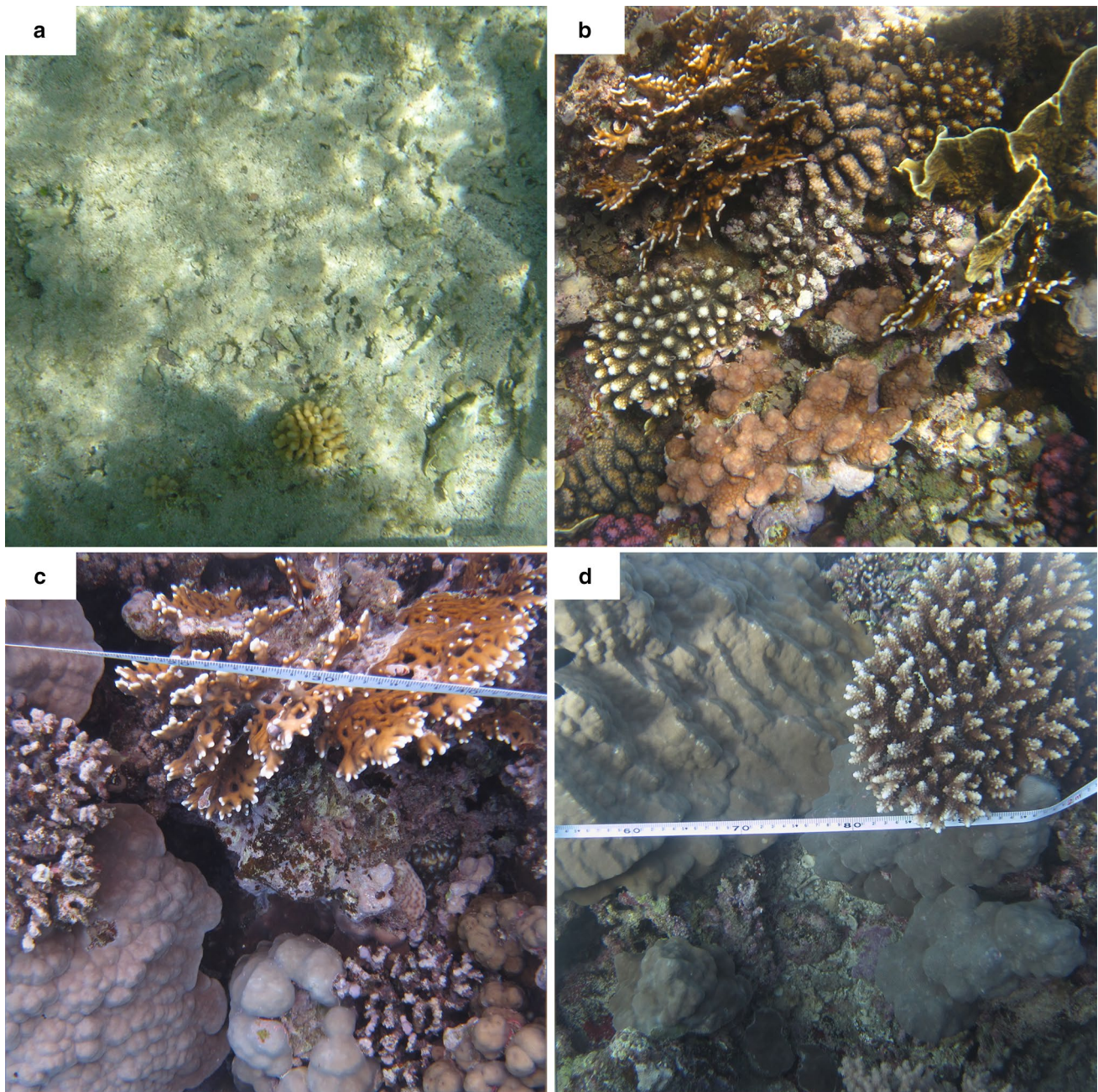
Fig. 2 Modern reef habitats: transect pictures of the **a** reef flat with *Stylophora*; **b** reef edge with *Acropora*, *Millepora*, *Pocillopora*, and others; **c** reef slope in 5-m depth with *Porites*, *Millepora*, and others; and **d** reef slope in 10-m depth with *Porites* and *Acropora*, and others

dissimilarities between the habitats. These analyses were done using the software package PAST (Hammer et al. 2001) and PRIMER 6 (Clarke and Gorley 2006).

Scleractinians and *Millepora* were identified to genus level because species identification based on photographs alone was not consistently possible. Genus data, however, are considered sufficient for the purpose of this study because, based on an extensive data set, Pandolfi (2001) concluded that analyses of Quaternary coral communities

are robust to taxonomic scale between species and genus level. Sessile mollusks were identified to genus level but later pooled due to low numbers. Other biota categories included Porifera, octocorals and non-coralline algae. Coral rubble, dead corals, sand and coralline algae could not be consistently distinguished and were therefore combined for the analyses (category "coral rubble/coralline red algae").

In addition, data of the northern and southern reef edge as well as reef slope transects were pooled, as there were no
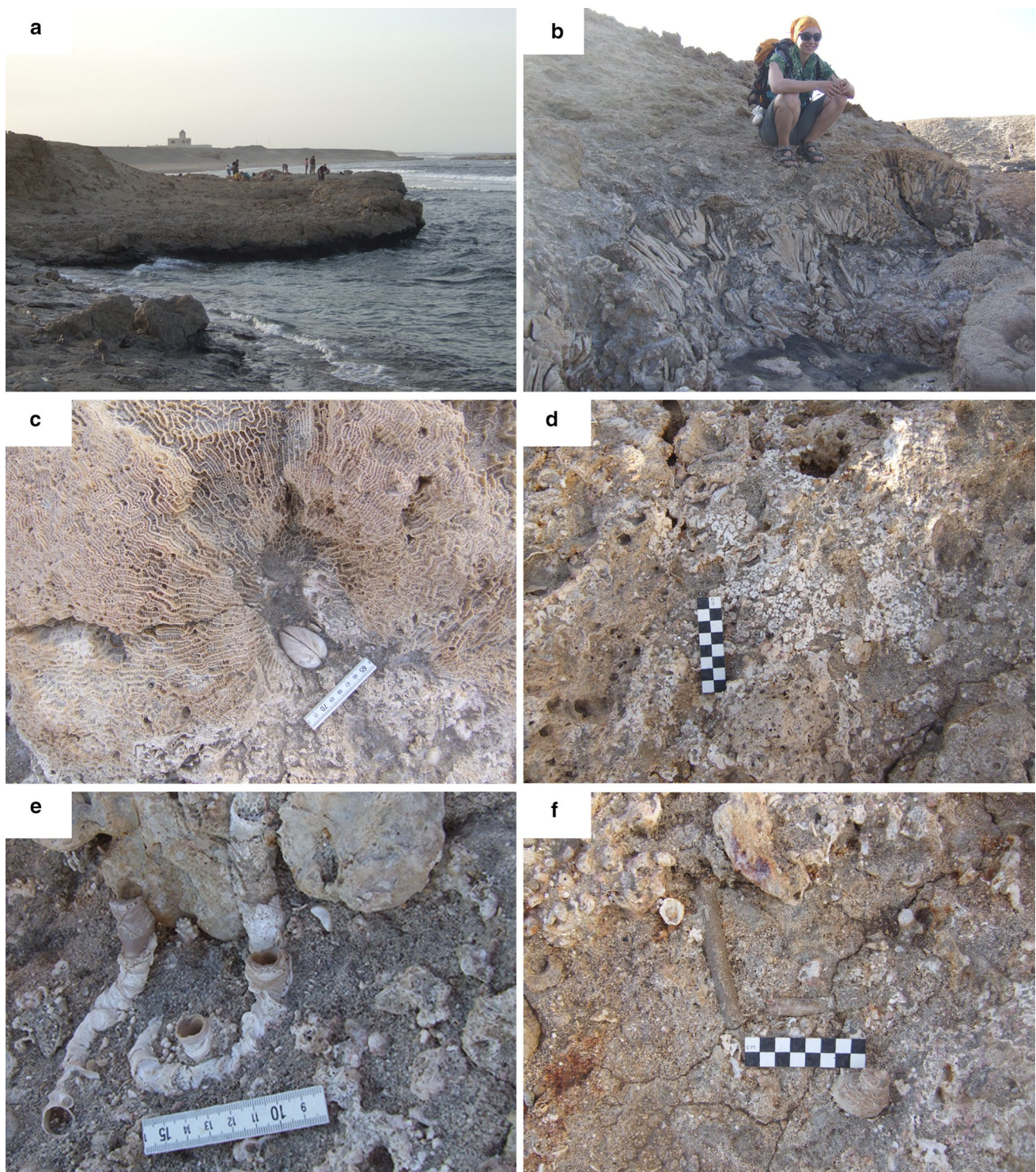
Fig. 3 Fossil reef terraces: **a** the studied terraces at El Mohgar, **b** framestone of *Lobophyllia* patch reef at Abu Dabbab, **c** framestone with coral *Leptoria* and venerid bivalve *Periglypta* at Abu Dabbab, **d** bindstone with coralline red algae at El Mohgar, **e** bindstone with the vermetid gastropod *Dendropoma maxima* and coralline red algae at El Mohgar, **f** rudstone with spines of *Heterocentrotus mamilatus* and gastropod *Turbo radiatus* at El Mohgar

Fig. 4 a Taxonomic richness measured as average number of genera and **b** Shannon–Wiener index for each habitat. *Error bars* represent 95 % confidence intervals

significant differences between the two sites (Mann–Whitney test; $U = 401.5$; $p = 0.3812$, $U = 447$; $p = 0.9667$, respectively).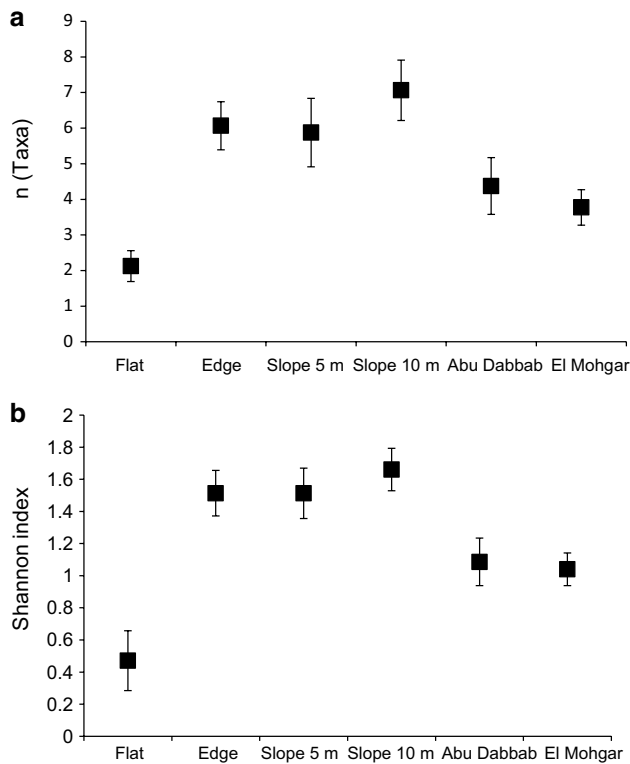 Three samples (one modern, two fossil) were dominated by single taxa and excluded from statistical analysis because they were outliers in all statistical analyses.

Results

Abundance and diversity of the modern reef

Taxonomic richness and diversity increase from the reef flat towards the reef slope, with a small drop on the reef slope at 5-m depth (Fig. 4). *Stylophora* is the only coral genus found on the reef flat; the reef edge holds 10, the reef slope at 5-m depth 16, and the slope at 10-m depth 17 genera of stony corals (Table 1). *Acropora* and *Pocillopora* are the most abundant hexacorals on the reef edge; *Pocillopora* is also dominant at 5-m depth (Table 1; Figs. 5, 6). *Porites* is the dominant genus at 10-m depth, followed by *Acropora* (Table 1; Figs. 5, 6).

Abundance and diversity of the fossil reefs

The fossil reefs in El Mohgar and Abu Dabbab have similar compositions (Table 1; Fig. 7): Coral rubble, sand and coralline algae account for 67 and 73 %, respectively, and *Porites* is the most abundant coral genus. However, *Dipsastraea* makes up 13 % of total coverage in El Mohgar, but is rare (3 %) in Abu Dabbab). *Leptoria* is exclusively found in Abu Dabbab. Overall, nine taxa were found in Abu Dabbab and El Mohgar, respectively (Table 1).

Species richness and diversity are lower at the fossil sites than on the modern reef edge and slope, but considerably higher than on the reef flat. The Shannon-Wiener index is marginally lower in El Mohgar ($H = 1.040$) than in Abu Dabbab ($H = 1.086$; Fig. 4).

Modern reef habitats in comparison

Most modern reef habitats and the two fossil sites are well separated from each other. Among the modern habitats, however, the reef slope at 5-m water depth differs only slightly from the reef edge and the slope at 10-m depth (Table 2). The reef flat is the most distinct modern reef habitat, as is also shown by ordination (Fig. 8). The other three modern reef habitats overlap partially.

Coral rubble/coralline algae is the most important category in all habitats. On the reef flat, this category contributed almost 90 % to average similarity (see Electronic Supplementary Material, S1). On the reef edge, coral rubble/coralline algae (64 %) and *Pocillopora* (16.6 %) are important. The reef slope in 5-m depth is similar to the reef edge: four groups contribute 94 % to average similarity; coral rubble/coralline algae (53 %) is followed by *Pocillopora* (24 %) and *Millepora* (13 %). In 10-m depth, five groups contribute 93 %; most important are coral rubble/coralline algae (56 %), *Acropora* (15 %), and *Porites* (15 %).

Coral rubble/coralline algae is also the largest contributor to the average dissimilarity between the reef flat and all other modern reef habitats (see Electronic Supplementary Material, S2). The reef flat is best distinguished from the reef edge and reef slope at 5-m water depth by *Pocillopora*, and from the reef slope at 10-m depth by *Porites*, *Acropora*, and coral rubble/coralline algae. *Millepora*, *Pocillopora*, and coral rubble discriminate the best between the reef edge and the reef slope in 5 m, and *Porites*, *Acropora*, and *Pocillopora* between the reef edge and the reef slope at 10 m. The two reef slope habitats are best distinguished by *Pocillopora*, (highly abundant at 5-m depth), followed by *Millepora*, *Porites*, and *Acropora*.

Table 1 Percentage cover of all taxa and taxonomic groups found in the modern and fossil reefs

|	Reef flat	Reef edge	Reef slope 5 m	Reef slope 10 m	El Mohgar	Abu Dabbab
CR/CA	85	56	51	56	67	73
Stylophora	<1	2	<1	1	1	
Pocillopora		9	18	2		<1
Porites		<1	5	15	16	
Montipora		<1	2	3		
Acropora		7	3	10	<1	<1
Millepora		9	15	2	<1	<1
Goniastrea		4	<1	1		
Octocorals			3	6		
Sessile molluscs	<1	<1			<1	<1
Non-coralline algae	14	7	1	1		
Porifera	<1	<1	1	<1		
Dipsastraea		1	<1	1	13	3
Favites		1	<1	<1	1	<1
Leptoria		1	<1			4
Hydnophora		<1	<1	<1		
Coscinaraea			<1			
Tubastrea				<1		
Astreopora				1		
Psammocora				<1		
Pavona				1		
Leptoseris			1	<1		
Cyphastrea				<1		
Pachyseris				<1		
Gardineroseris			<1	1		
Echinopora		<1	<1			
Turbinaria			<1			
Siderastrea			<1			
Galaxea					1	1
Lobophyllia					<1	<1
Total (*n*)	5	16	21	22	10	10

CR/CA Coral rubble/Coralline algae
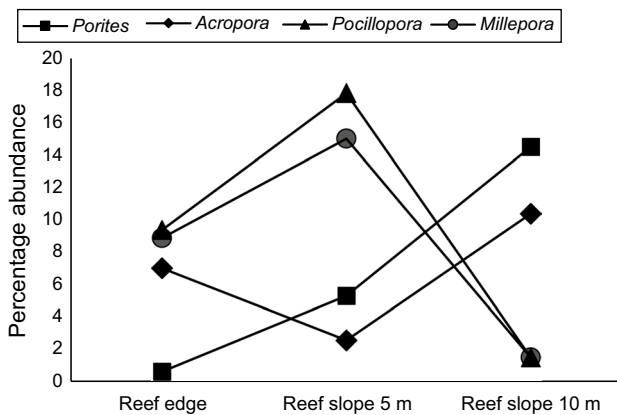
Fig. 5 Percentage per habitat of most abundant corals in the modern reef (excluding reef flat as none of these genera can be found there)

Modern versus fossil reefs

Results of ANOSIM indicate a very high similarity between the two fossil sites, however, both are well separated from all modern habitats (Table 2). The reef slope at 10-m depth is the most similar to the fossil sites (*R* values < 0.6) of all habitats in the Recent reef. These results are reflected in the MDS (Fig. 8), where the reef slope at 10 m and the two fossil sites plot relatively close to each other.

Coral rubble/coralline algae and *Porites* contribute more than 90 % to the average similarity in Abu Dabbab and El Mohgar (see Electronic Supplementary Material, S1). Fifteen and fourteen taxa contribute over 90 % to the average dissimilarity between Abu Dabbab/El Mohgar and the reef slope at 10-m depth, respectively (see Electronic Supplementary Material, S2). *Acropora*, coral rubble/coralline
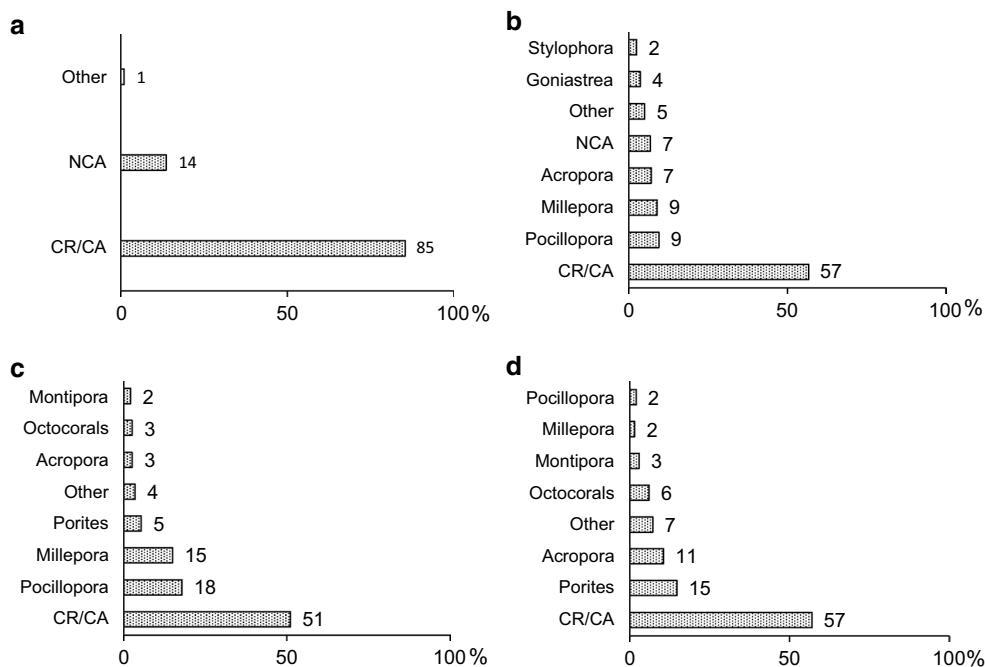
a

b

c

d

Fig. 6 Coverage of the four studied habitats of the Recent reef: **a** reef flat, **b** reef edge, **c** reef slope 5 m, **d** reef slope 10 m. *CR/CA* Coral rubble/Coralline algae, *NCA* non-coralline algae. All taxa accounting for less than 2 % were pooled as "other". Standard errors of sample proportion are too small (0.3–1.2 %) to be presented here
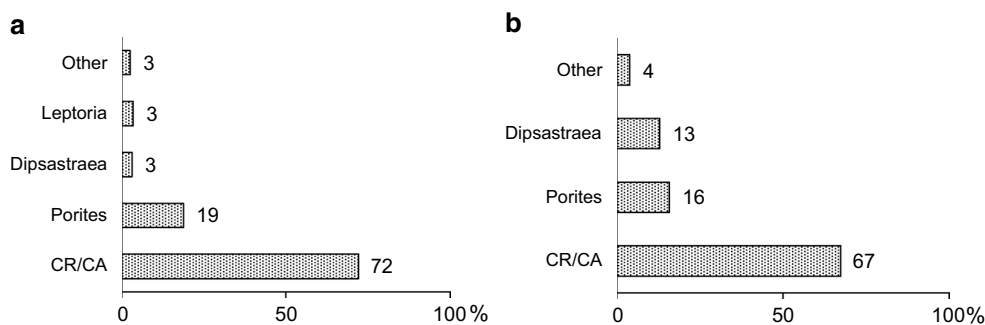
a

b

Fig. 7 Coverage of the two fossil reefs at **a** Abu Dabbab and **b** El Mohgar. *CR/CA* Coral rubble/Coralline algae. All taxa accounting for less than 2 % were pooled as "other". Standard errors of sample proportion are too small (0.4–1 %) to be presented here

Table 2 R values (*bottom left*) and Bonferroni-corrected p values (*top right*) of the pairwise comparisons between the different habitats of the modern reef and the fossil reefs in Abu Dabbab and El Mohgar with one-way ANOSIM (distance measure: Bray–Curtis similarity index)

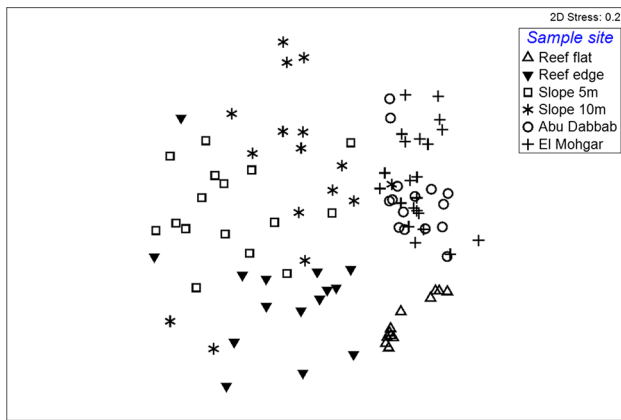|	Reef edge	Reef flat	Slope 5 m	Slope 10 m	Abu Dabbab	El Mohgar
Reef edge		0.0015	0.0030	0.0015	0.0015	0.0015
Reef flat	0.5129		0.0015	0.0015	0.0015	0.0015
Slope 5 m	0.3067	0.9515		0.0015	0.0015	0.0015
Slope 10 m	0.4515	0.8006	0.4832		0.0015	0.0015
Abu Dabbab	0.6814	0.6859	0.8361	0.5175		0.9975
El Mohgar	0.7795	0.6903	0.8588	0.6020	0.07889	

R overall = 0.6065; p = 0.0001

Fig. 8 MDS plot of all reef habitats (distance measure: Bray–Curtis similarity index)

algae, and *Porites* (with decreasing contribution) are the three most discriminating taxa between the reef slope at 10 m and the Pleistocene assemblage of Abu Dabbab, whereas for El Mohgar these are *Acropora*, *Porites*, *Dipsastraea*, and coral rubble/coralline algae.

Discussion

Although we found a significant difference between all modern predefined reef habitats, the degree of separation varies considerably. The reef edge and the reef slope at 5-m depth are the least separated, probably because the difference in water depth is small. Including images from the most wave-exposed part, on the actual reef crest, would probably have led to slightly different results, but this was not possible during our fieldwork.

The Abu Sauatir reef shows the assemblages typical for wind-exposed settings with a steep relief as described by Riegl and Velimirov (1994) from the northern Red Sea. A relatively high abundance of *Millepora* on the reef edge and the upper reef slope has also been documented for other localities in the northern Red Sea (e.g., Loya and Slobodkin 1971; Riegl and Velimirov 1994) and indicates the exposition to currents (Riegl and Piller 1997).

A comparison of coral coverage data of the modern reef suggests similarities in mean values and trends with water depth with nearby localities: At Abu Sauatir (this paper), coral cover is the highest at 10-m depth, nearly as high at 5 m and at the reef edge, and clearly the lowest on the reef flat. The drop in diversity from reef edge to reef slope at 5-m depth can be attributed to the dominance of *Millepora* and *Pocillopora* at 5 m. The sites examined by Riegl and Velimirov (1994) at Hurghada had similarly high coral coverage, with values ranging from 36 to 82 % (plus considerable soft coral cover at some of their sites). Stony

coral coverage was not significantly different between the sheltered, semi-exposed, and exposed sites, and the sheltered group of reefs included both the highest and lowest coral cover observed by Riegl and Velimirov (1994). Riegl and Piller (2000) compared live coral coverage in different reef habitats at Safaga in the northern Red Sea and also found uniformly high coverage ranging from 43 to 59 % in reef crest, reef edge, reef slope and slope base habitats of exposed and semi-exposed sites. Sheltered localities, however, had strongly variable coverage ranging from 24 to 26 % on the reef crest and slope base sites, respectively, to 68 % on the reef edge and even 85 % on the slope and in and low-relief areas. Alter (2004) surveyed the species composition, zonation and diversity patterns of reef-building coral communities in the Gulf of Aqaba. In contrast to our study, he found coral cover to be the highest (36.5 %) on the upper reef slope at 0.5–3 m-depth, and it decreased with increasing depth to 20 % (3–7 m) and 13.4 % (8–12 m). With the exception of the reef flat (11.1 %), those coverage values are lower than on the modern reef in Abu Sauatir. Loya (1972) reported a higher mean coverage from Eilat, but the overall trend of decreasing coverage from the reef edge to the reef slope was the same.

The quantitative composition of the fossil assemblages at the two sites was compared to the modern habitats in order to estimate their depositional water depth. At large spatial scale by-occurrence subsampling leads to interpretable results (Kiessling et al. 2012). However, we did not subsample our data due to low numbers of quadrats (16 per modern reef habitat, 39 in the fossil reefs) and genera (only nine genera of stony corals were found in the fossil reefs). The fossil reefs are most similar to—but still significantly different from—the modern reef slope at 10-m water depth. There are two possible interpretations: (1) the fossil terraces belong to quiet-water conditions of a lagoon, which would also show a similar species composition, or (2) the fossil terraces belong to a reef slope at about 10-m water depth and differences to the modern reef at this depth reflect taphonomic bias, and/or natural temporal and spatial variability of coral communities.

Porites is among the dominant taxa at both fossil localities. Modern communities dominated by massive *Porites* are either taken as an indicator for shallow reef environments with moderate wave energy such as back-reef margins or lagoons (Riegl and Velimorov 1994; Veron 2000; Montaggioni 2005; Gischler et al. 2008; Hongo and Kayanne 2011) or may indicate low-energy environments at depths of 10–15 m (Done 1982; Riegl and Velimorov 1994; Riegl and Piller 1999; Grossman and Fletcher 2004; Montaggioni 2005). At our modern study site, massive *Porites* increased with water depth, being the dominant genus in 10-m depth. Back-reef zones are absent in the modern reef we studied and could thus not be used for comparison to

the fossil reefs. However, the mean sea level was higher during the Eemian, and back-reef deposits are present in MIS 5e reefs at Quseir el Qadim (Plaziat et al. 1998; Taviani 1998a). It is therefore possible that the *Porites*- and merulinid-dominated coral communities of the fossil reef terraces were once situated in a lagoonal back-reef habitat. The idea of tectonic uplift in this area has been rejected in numerous publications (e.g., Hoang and Taviani 1991; Bosworth and Taviani 1996; Plaziat et al. 1998, 2008), which supports the interpretation of the fossil terraces as back-reefs rather than reef slopes. However, in a study that takes glacio-hydro-isostatic processes into account, Lambeck et al. (2011) conclude that long-term tectonic uplift along the northern and central sides of the Red Sea is more likely than tectonic stability. The uplift rate for Quseir el Qadim is stated as 0.057 mm per year and the observed Last Interglacial sea level as 7 m higher than today (Plaziat et al. 2008; Lambeck et al. 2011). Thus, the MIS 5e fossil reef terraces that are situated 3–5 m above sea level today could have been reef slopes at around 10-m depth or deeper.

Arborescent corals and most notably Milleporidae, which are abundant in certain zones of the studied modern reefs, were absent or underrepresented in the fossil reefs studied here. This difference could result from the fossil sites representing a lagoonal habitat that is not present in the modern reef we studied. Another possible reason for this discrepancy, however, is taphonomic bias because life and death assemblages of coral reefs typically differ significantly (Greenstein and Pandolfi 1997; Pandolfi and Greenstein 1997a, b; Edinger et al. 2001). These differences are mostly attributed to growth form biases, typically towards arborescent growth forms in death assemblages, but are also influenced by the environment (Greenstein and Pandolfi 2003).

Finally, the differences between the fossil sites studied and any of our studied modern habitats could reflect the natural spatial and temporal variability observed in the modern Red Sea. The modern reef was 25 and 110 km away from the fossil reef terraces in El Mohgar and Abu Dabbab, respectively. Thus, differences between modern and fossil reefs could be partly caused by such local effects. In the northern Red Sea, however, differences between coral communities at different localities and water depths are mostly due to hydrodynamic exposure, with massive *Porites* always being characteristic for sheltered conditions (Riegl and Velimirov 1994). Moreover, coral coverage may differ widely in the northern Red Sea as outlined above, but coral zonation is very conservative (e.g., Riegl and Velimirov 1994; Riegl and Piller 1997). In a survey that spanned 20 years, a trend towards increasing community homogenization and decreasing average size of coral colonies in the Red Sea was found and related to the impact of climate change (Riegl et al. 2012). These trends, however, are subtle compared to the strong differences between the modern and fossil reefs in our study. We are therefore confident that these differences reflect either different habitats or taphonomic bias and not natural spatial or temporal variability of coral communities in the northern Red Sea.

Conclusions

This is one of the few attempts to evaluate the depositional water depth of late Pleistocene reef terraces (here tentatively assigned to MIS 5e) at the Red Sea by quantitative analysis of coral coverage and taxonomic composition (see also Mewis and Kiessling 2013). The studied modern reef at Abu Sauatir shows the assemblages of wind-exposed settings with a steep relief that are typical for the northern Red Sea. Live coral coverage is similar to values reported from other localities in the region but differs strongly from those reported from the Gulf of Aqaba. Except for the reef flat, the fossil reefs studied at Abu Dabbab and El Mohgar were less diverse and less rich in taxa than the modern reef habitats. Considering tectonic activity and sea-level change, the fossil reefs must have been situated at 10-m depth or deeper. This is corroborated by statistical analysis: While the fossil reef terraces are significantly different from all modern habitats, they are most similar to the modern reef slope at 10-m depth. We attribute differences to the modern reef slope mainly to selective loss of arborescent and branching corals during fossilization and mixing of life and death assemblages in the fossil reef. However, should the hypothesis of tectonic stability be correct, a second way to interpret the data is that the fossil reefs belonged to a back-reef lagoon, which is absent in the modern reef.

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