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ORIGINAL ARTICLE

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Palaeoenvironmental reconstruction based on non-geniculate coralline red algal assemblages in Miocene limestone of central Crete

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Abstract Neogene coastal sediments of the Mediterranean provide an excellent laboratory for a quantitative study of palaeoenvironmental parameters and their response to climate change. In order to examine change in environmental parameters during deposition of Tortonian limestone of southern central Crete, we use integrated field and biofacies analysis together with a detailed study of foraminfera and non-geniculate red algae. Patterns in the relative abundance of non-geniculate coralline red algae are interpreted by comparison with data from modern non-geniculate coralline red algae and with additional information from the studied sediments. Based on these integrated datasets, four red algal associations are identified: a *Lithophyllum*-dominated association restricted to the upper photic zone in warm-temperate environments, a *Lithothamnion*-dominated association found in the lower photic zone in warm-temperate environments, a *Spongites*-dominated association typical for shallow warm-temperate to tropical environments and an association with dominant *Mesophyllum* which is characteristic for the lower photic zone in warm-temperate to tropical environments. We introduce coralline red algal indices in order to quantify changes in environmental parameters. We recognise four warm intervals within a succession of the Tortonian limestones in southern central Crete. During the most extensive interval, widespread coral carpets formed under prevalent oligotrophic conditions. Analysis of the stratigraphic architecture shows that warm intervals are related to sea-level highstands and therefore may reflect global climatic processes.

Keywords Red algae · Neogene climate · Tortonian · Crete · Sequence stratigraphy · Coral carpets · Eastern Mediterranean

Introduction

The interpretation of skeletal components based on fieldwork and thin-section analysis is the classical tool for classification of carbonate sediments (Wilson 1975; Fluegel 2004). The differentiation between non-tropical and tropical carbonates is largely based on analysis of skeletal components (Lees and Buller 1972; Carannante et al. 1988; Nelson et al. 1988). Non-tropical carbonates are characterised by the absence of certain skeletal and non-skeletal grains (e.g. *Halimeda*, ooids) and framework-forming zooxanthellate corals (James 1997). Non-tropical carbonates are subdivided into warm-temperate and cool-temperate provinces (Betzler et al. 1997). The limits of the warm-temperate province are well defined with respect to temperature: Healthy coral reefs which are typical for the tropical realm are found in areas where temperatures do not fall below 18°C minimum winter sea-surface temperature (Veron 1995). The lower limit of the warm-temperate province is defined by the disappearance of symbiont-bearing larger benthic foraminifera at a minimum winter temperature of 11–12°C (Betzler et al. 1997). Other ecological factors such as water depth and nutrient flux that also control skeletal compositions in sediments and therefore the extent of faunal provinces (Hallock and Glenn 1986; Carannante et al. 1988) are less well defined. Specifically, biota commonly used for palaeoenvironmental analysis, such as benthic foraminifera, respond to a combination of several interdependent factors. Fossil non-geniculate coralline red algal associations, on the other hand, appear to vary in their composition depending on two factors: palaeo-water depth and palaeo-water temperature. The depth relationship of non-geniculate coralline red algae has been demonstrated earlier by Littler (1973a,b), Van den Hoek et al. (1975) and Adey

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et al. (1982). As for many other organisms, the apparent water depth dependency of non-geniculate coralline red algae has been interpreted to be mainly a consequence of their sensitivity to light (Adey et al. 1982; Minnery 1990). More recent studies in eastern Australia by Lund et al. (2000) and Braga and Aguirre (2004) using the revised taxonomy of Woelkerling (1988) have elaborated a depth zonation of several red algal genera. Braga and Aguirre (2001) studied non-geniculate coralline red algal assemblages in Upper Miocene carbonates in southern Spain. They found that the distribution of red algal subfamilies is not only distinct in deep and shallow-water deposits but also differs in temperate carbonate sediments from those in tropical sediments.

The abundance of non-geniculate coralline red algae in the limestones of southern central Crete offers an excellent opportunity to study palaeoenvironmental controls on coralline red algal assemblages in detail. Sedimentary successions representing the entire Tortonian interval allow us to evaluate the influence of change in ecological parameters through time. As in other parts of the Mediterranean area (Brachert et al. 1996; Esteban 1996; Braga and Aguirre 2001), Late Miocene sediments in Crete reflect deposition at the threshold between warm-temperate and tropical environments. In southern central Crete, fluctuations between warm-temperate and tropical conditions are indicated by the episodic occurrence of zooxanthellate corals and the distribution of benthic foraminifera. Successive shallowing and deepening trends are identified by stratal geometries and changes in lithology. Three-dimensional patterns of facies change and a detailed reconstruction of stratigraphic architectures allow the identification of relative sea-level changes. In this paper, relative abundances of non-geniculate coralline red algae are determined and compared to other biotic and lithological information. Based on this comparison and on recent literature data, depth and temperature-controlled coralline red algal associations are described. Relative abundances of coralline genera of the various associations are used to establish index values. This relative quantification allows palaeoenvironmental interpretation of the Tortonian limestones of southern central Crete.

Geological setting

Crete is situated in the forearc of the Hellenic subduction zone, a setting that in the Late Miocene was largely extensional (Le Pichon and Angelier 1979; Angelier et al. 1982; Fassoulas 2001). Tortonian siliciclastic fluviatile, brackish and marine sediments of the Ambelouzos Formation were deposited within extensional basins of central Crete (Meulenkamp et al. 1979a,b, 1994; Ten Veen and Postma 1999; Reuter et al. 2006); (Fig. 1). Accompanied by increasing fragmentation of the basins by normal faulting, a transition in nearshore environments from siliciclastic to carbonate sedimentation in the course of the Tortonian is observed (Meulenkamp et al. 1979a,b; Angelier et al. 1982; Postma et al. 1993; Ten Veen and Postma 1999; Reuter et al. 2006). Associated with these nearshore sediments are offshore laminated or homogeneous, light coloured marl deposits that have been termed the Varvara Formation (Meulenkamp et al. 1979a,b; Ten Veen and Postma 1999) and that are Late Tortonian to Messinian in age in the central Messara Basin (Zachariasse 1975; Hilgen et al. 1995; Krijgsman et al. 1995; Kuiper et al. 2004). In the Iraklion Basin near Agia Varvara, the boundary between the Ambelouzos and the Varvara Formation is defined by a conspicuous erosional unconformity which has been related to the Middle Tortonian 3rd order sea-level lowstand of Hardenbol et al. (1998), (Reuter et al. 2006; Fig. 1).

Carbonate sediments similar to nearshore deposits found in the Iraklion Basin are well exposed in southern central Crete over a 50 km^2 wide tableland (Figs. 2 and 3) adjacent to the Asteroussia Mountains to the east and the Messara Plain to the north (Fig. 1). The transition between Ambelouzos and Varvara Formation, however, is less well constrained in this area. Since the stratigraphic relationship is not fully resolved, we avoid a formal terminology for the sediments. The tableland, named West Asteroussia Tableland (WAT) in this paper, was mapped at a scale of 1:10000 (Fig. 2). A Tortonian age for the carbonates is indicated by ^{87}Sr/^{86}Sr ratios between 0.70884 and 0.70889 (Kroeger 2004). Carbonate sediments conformably overlie marginal

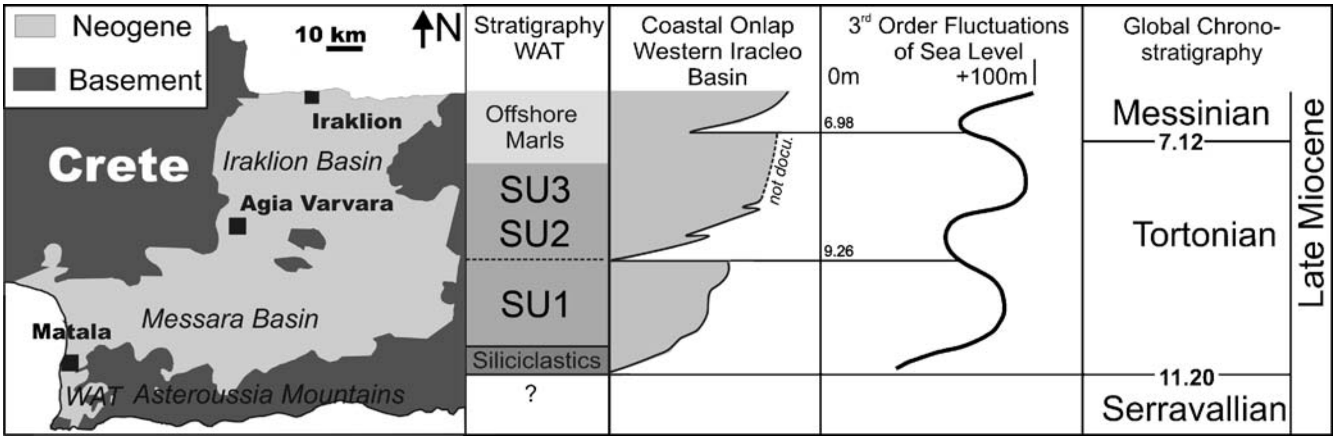


Fig. 1 Stratigraphic overview of the studied area and comparison with coastal onlap in central Crete (modified from Reuter et al. 2006 with sea-level curve after Hardenbol et al. 1998)

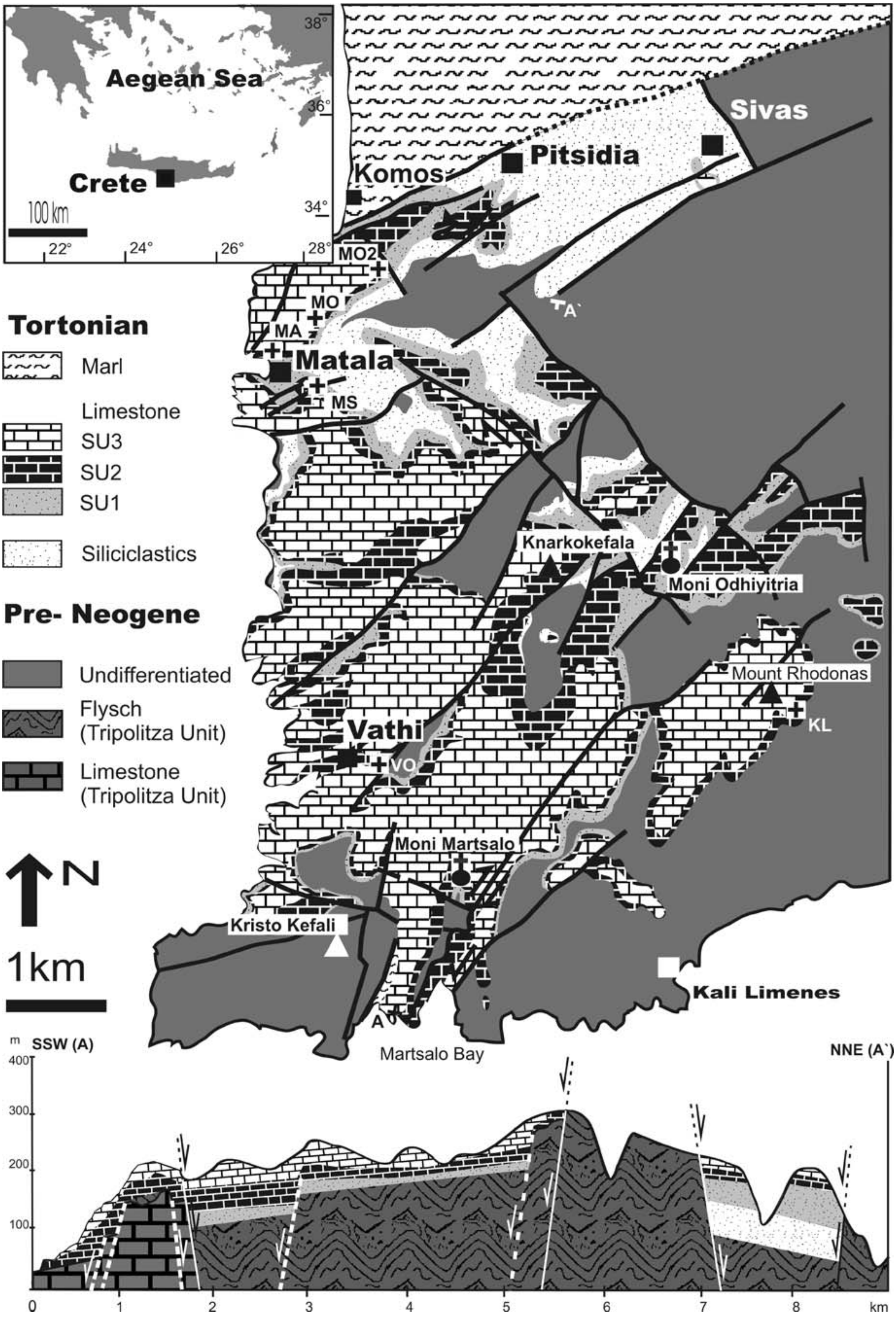


Fig. 2 Geological map and transect of the West Asteroussia Tabellands (WAT)

Fig. 3 View from Kristo Kefali (see Fig. 2 for location) to the north across the WAT. In the background is the 2500 m high Psiloritis

marine or deltaic siliciclastic deposits or unconformably overlie Mesozoic limestone and Paleogene sandstone (Flysch) of the Tripolitza Unit (Kroeger 2004). In the south of the WAT, in a small outcrop east of Mount Kristo Kefali (Fig. 2), an offshore marl overlies the limestone succession. A succession of marl deposits in the Messara Plain near Komos, 3 km northeast of Matala (Fig. 2) has been sampled. The analysis of calcareous nannoplankton suggests a middle to late Tortonian age (nannoplankton zones NN10 and 11) for the lower part of the section. Neogene sediments of the WAT are affected by a weak post-depositional tilt to the west (Fig. 3).

Stratigraphic units

Tortonian limestones found in the WAT are subdivided into three subunits (SU1-3) based on lithology: SU1 consists of limestone-rich in siliciclastics with intercalated calcareous sandstone (Fig. 4). A rudstone bed with quartz pebbles is

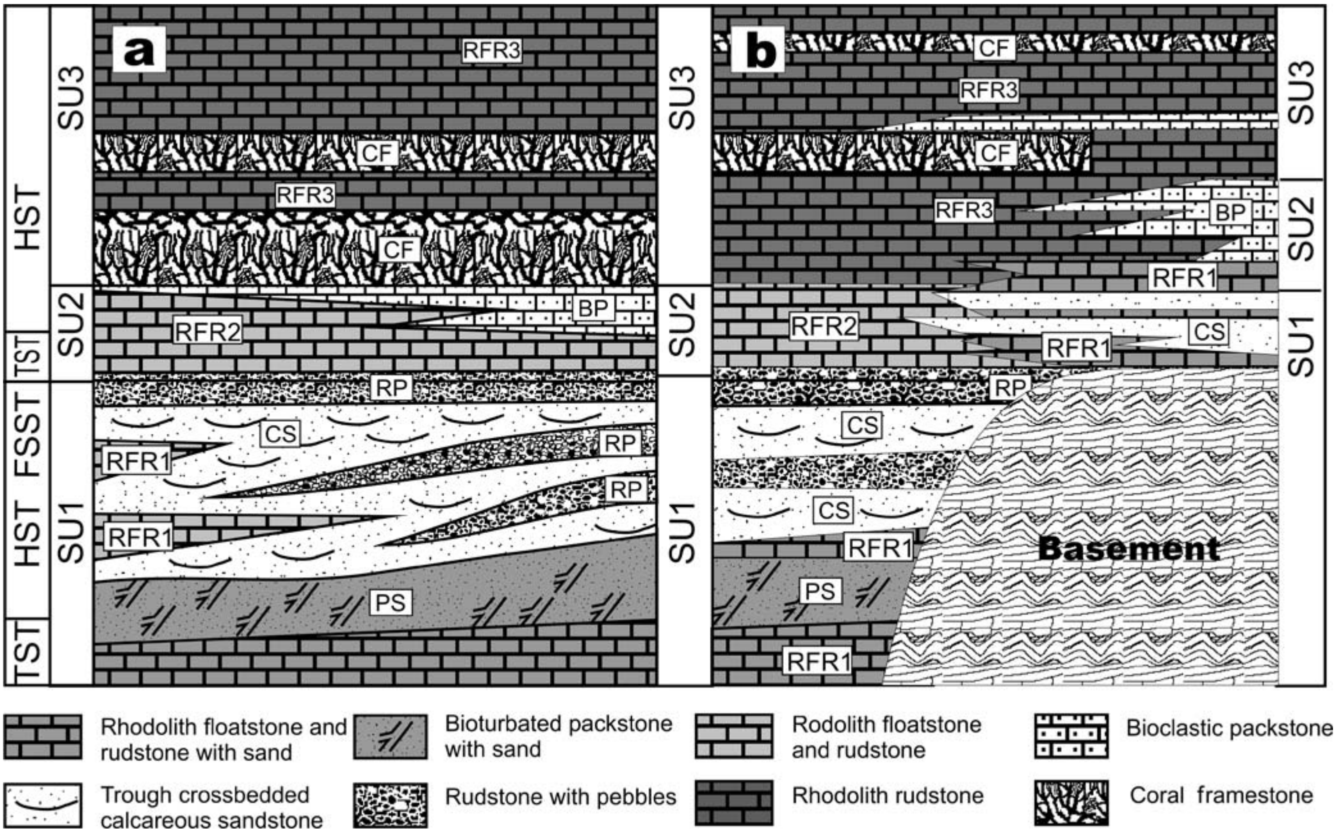


Fig. 4 Overview of the stratigraphic architecture of the West Asteroussia Tablelands with lithostratigraphic units SU1-3, the distribution of facies and sequence stratigraphic interpretation (TST: transgressive systems tract, HST: highstand systems tract, FSST: falling stage systems tract). **a** Schematic transect between sections MA and MO2 in the north of the WAT. **b** Schematic transect between sections VO and KL in the south of the WAT (see Fig. 2 for locations)

found at the top of the unit. In areas where several stacked beds of the rudstone occur, the uppermost and most extensive bed defines the upper limit of the subunit. SU1 has a maximum thickness of 40 m in the area of Matala (Fig. 2) and decreases to a thickness of 12.5 m in the south of the WAT. It is absent around Knarkokefala and east of Kristo Kefali (Fig. 2). SU1 is overlain by rhodolith rudstone to floatstone and bioclastic packstone (SU2). In general, thickness of SU2 is highest in the south of the WAT and has a maximum of 40 m east of Kristo Kefali (Fig. 2) compared to 12 m northeast of Matala. The unit thins in an eastern direction. Subunit 3 of the limestones of the WAT is formed by rhodolith rudstone and floatstone and subordinate bioclastic packstone. It is characterised by the widespread occurrence of zooxanthellate corals. Over the largest part of the WAT the base of this subunit is formed by one or two laterally extensive coral framestone horizons that weather out in the field. SU3 reaches a thickness of 25–30 m in the west of the WAT and a maximum of 50 m in the southeast (Mount Rhodonas) but decreases continuously to the east/northeast. In the Sivas area (Fig. 2), SU2 is absent and coral framestone of SU3 unconformably overlies calcareous sandstone of SU1. The thickness of the three subunits varies considerably as shown by a N–S cross-section (Fig. 2).

The subdivision of the WAT limestones based on the described lithological marker beds into units SU1-3 is straightforward in the largest part of the WAT. It is, however, more problematic, where the marker beds are absent. This is the case in the Mount Rhodonas area where a laterally continuous coral framestone interval does not occur. The identification of the base of SU3 in this case is by the presence of isolated zooxanthellate coral colonies which also occur locally in SU1 but in an arenitic matrix. Due to the absence of a discrete rudstone bed with quartz pebbles in this area that separates limestone rich in siliciclastics from overlying pure limestone elsewhere, the separation of SU1 and 2 is based mainly on siliciclastic content.

Sedimentary facies

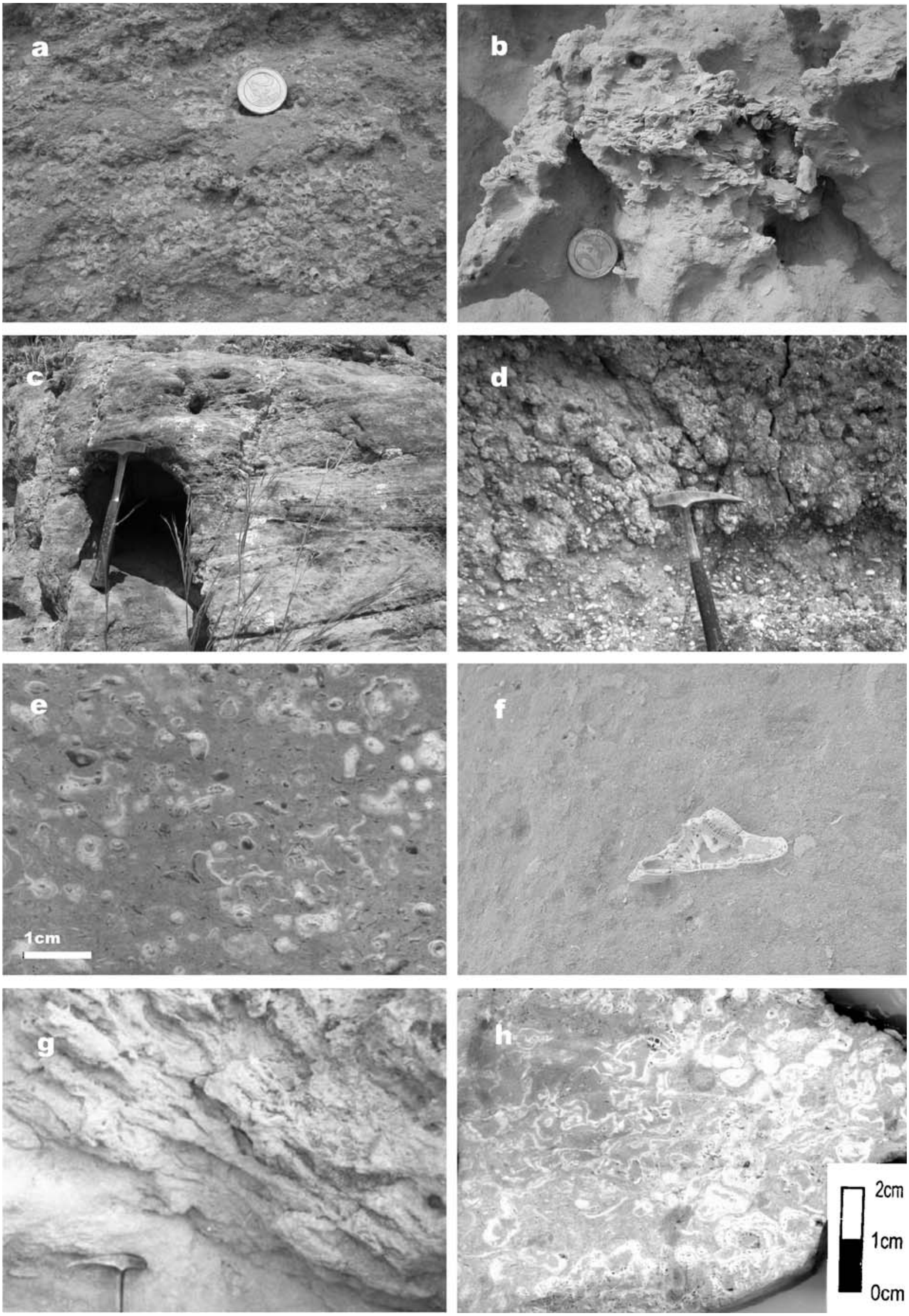
SU1

Four different facies are recognised within SU1 (Table 1; Fig. 4). At the base, rhodolith floatstone to rudstone (RFR1; Fig. 5a) with 10–50% of siliciclastic fine to medium-grained sand and well-preserved benthic foraminiferan tests occurs. Rhodoliths are ellipsoidal in shape and laminar to open-branched. In the basal bed, components of the RFR1 rhodolith floatstone to rudstone show evidence of fragmentation and abrasion. Basal rudstone is overlain by fine-grained, bioturbated packstone with sand (PS; Fig. 5b) with abundant mollusc steinkerns. On top of it, well-classified trough crossbedded calcareous sandstone (CS; Fig. 5c) with few fossils is found. At the top of SU1 and intercalated with calcareous sandstone, rudstone with siliciclastic pebbles (RP; Fig. 5d) rich in open-branched rhodoliths occurs. *Heterostegina*, celleporiform bryozoans, oysters, pectinids and *Clypeaster* are abundant. Locally, fragments of corals and isolated colonies of *Tarbellastrea* are found. The matrix consists of well-classified sand similar to the CS facies. RP beds are bioturbated at the base and grade into carbonate mud and clay-rich rhodolith floatstone (RFR2) of SU2 at the top of SU1. In many cases, the RP beds do not form a homogenous horizon but consist of several beds which differ in their biotic makeup.

The RFR1 facies forms the base of the limestone succession and is intercalated with the PS and CS facies (Figs. 4 and 6). In the area of Matala (Fig. 6), size of lithic pebbles in the RP facies increases eastward to 5 cm and RP beds intercalated into calcareous sandstone wedge out westward. Intercalated RFR1 rudstone to floatstone, on the other hand, wedges out eastward. CS–RP couplets form clinoforms with surfaces dipping in a westward direction with an angle $<2^\circ$. At Moni Odhiyitria (Fig. 2), RP rudstone eastward grades into conglomerate with a calcareous matrix and components up to 10 cm in diameter. Rhodoliths are up to 4 cm in diameter and densely branched.

Interpretation

In the RFR1 and PS facies, small size of siliciclastic components and low degrees of abrasion of skeletal components indicate deposition in a low-energy setting below storm-wave abrasion depth. The shape of rhodoliths argues against frequent turning by waves (Bosence 1976, 1991). A mechanism for the formation of low-energy rhodoliths is infrequent turning by fishes or sea urchins (Bosence and Pedley 1982; James 2000). In contrast, trough crossbedding in the CS facies indicates the formation of subaqueous dunes by frequent or permanent reworking of sediments by currents or storm waves. In the RP facies, the presence of pebble-sized lithoclasts indicates high hydraulic energy. Large biota, on the other hand, may as well be autochthonous and therefore not indicative of high hydraulic energy. However, proportions of pectinids and oysters that have the ability to attach themselves to a hard substrate, are higher in this sediment than in other lithologies. They occur together with *Clypeaster* which has been found to be common on omission surfaces (Forst 2003). *Heterostegina depressa* is also preferentially found on hard-bottom substrates in the modern Red Sea (Gulf of Aqaba; Reiss and Hottinger 1984 and Bay of Safaga; Piller 1994) and on coarse skeletal debris (Hottinger 1977). On the other hand, the presence of a relatively fine-grained sandy matrix, openly branched rhodoliths and the preservation of celleporiform bryozoans sensitive to abrasion (Smith and Nelson 1996) indicates quiescent periods. An event condensation process that leads to the amalgamation of two communities, one associated with periods of hard substratum created by storm events and the other associated with soft substratum conditions during quiet intervals has been described by Seilacher (1984) and Kidwell and Aigner (1985). They have shown that condensation down to one initial event deposit can operate in geologic time scales and that, depending on the frequency of storm events, the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degree of fragmentation and abrasion of biota is not necessarily high. The association with the CS facies suggests a genetic relationship: The accumulation of sandstone is interpreted to be the result of winnowing out of this material from the RP facies that formed a facies belt shoreward of the CS facies. The storm-influenced RP facies, according to the definition of Burchette and Wright (1992), is interpreted to have been deposited in a mid ramp setting and the CS facies in a mid to outer ramp setting. Similar mid and outer ramp cross-bedded sandstone has been described by Pomar et al. (2002) from the Upper Miocene of Menorca. Inner ramp sediments are represented by conglomerate found in the Moni Odhiyitria area. Rhodolith rudstone to floatstone (RFR1) was deposited on the outer ramp oceanward of the CS facies. Seaward displacement of facies belts is reflected by the superposition of moderate to high-energy facies (CS, RP) over the low-energy outer ramp PS facies. Clinoforms formed by CS–RP couplets indicate progradation which reaches a maximum at the top of SU1. Thus SU1 represents, after initial transgression of the RFR1 facies, an over-all upward shallowing succession with CS–RP couplets reflecting a high frequency change in relative sea level.

SU2

Content in siliciclastic components decreases markedly at the top of the uppermost RP bed of SU1 (Fig. 4). The RP facies is overlain by massive (*sensu* Ingram 1954) rhodolith floatstone to rudstone (RFR2; Fig. 5e) with openly branched and laminar rhodoliths and minor amounts of unattached branches. The matrix consists of marly limestone (wackestone or packstone) and contains unclassified intact skeletons and bioclasts. The degree of fragmentation of skeletal elements in the matrix increases upsection. Intercalated into the RFR2 facies are beds of bioclastic packstone and subordinate wackestone (BP; Fig. 5f) with horizontally-oriented, abraded, fragmented and micritized bioclasts. In the upper part of SU2, sand-sized coral fragments occur in the packstone. The BP facies increases in thickness eastward (Fig. 6) and replaces the RFR2 facies. At basement highs, where SU1 is not present, SU2 onlaps basement, for example around Kristo Kefali and Knarkokefala (Fig. 2). At these locations, conglomerate underlies the RFR2 and BP facies.

In the Mount Rhodonas area (Fig. 2), a westward transition from RFR1 to RFR2 is observed as a consequence of decreasing siliciclastic contents. Beds of the CS facies wedge out westward or merge with the BP facies of SU2. This lateral facies change and the transition from SU1 to SU2 as sketched in Fig. 4b, however, is not as well documented in outcrop as in the Matala area (Figs. 4a and 6).

◀ **Fig. 5** Field aspects of facies found in limestone of the WAT. **a** Detail of RFR1 rhodolith rudstone with open branched rhodoliths. **b** Pocket with abundant *Heterostegina* in packstone with sand (PS facies). **c** Crossbedded calcareous sandstone (CS facies). **d** Rudstone with quartz pebbles at the base (RP facies). **e** Polished rock surface of RFR2 rhodolith rudstone. **f** Bioclastic packstone with *Clypeaster*, approximately 12 cm in diameter (BP facies). **g** Coral framestone in widespread coral carpets (CF facies) with columnar *Porites*. **h** Polished rock slab of RFR3 rhodolith rudstone showing boxwork rhodolith largely composed of foliose coralline red algae

Interpretation

Similar as the RFR1 facies, rhodolith floatstone to rudstone of SU2 is interpreted to represent a low-energy outer ramp facies, as evidenced by abundant open-branched rhodoliths and a fine-grained matrix. The bioclastic packstone facies (BP), similar to the calcareous sandstone of SU1, is interpreted to represent a high-energy facies that formed shoreward of the RFR2 facies. The presence of coral fragments in the BP facies suggests that shoreward situated parts of the BP facies not represented in outcrop contained coral buildups predating the widespread occurrence of coral carpets in SU3.

The transgression of the RFR2 facies at the top of SU1 (Figs. 4 and 6) indicates relative rise in sea level. The multipartite character of the uppermost RP bed of SU1 suggests that the upper part represents a transgressional lag. The upward increasing content of fragmented bioclasts in the RFR2 facies indicates shallowing that is also reflected by progradation of the high-energy BP packstone. The transition from the low-energy RFR2 facies to the prograding high-energy BP facies indicates that similar as SU1, SU2 represents an overall shallowing-upward succession.

SU3

The base of SU3 is defined by the presence of 1–5 m thick coral carpets (CF facies; Fig. 5g) which occur in the largest part of the WAT (Fig. 7) and single *Tarbellastrea* colonies overlying rhodolith rudstone or bioclastic packstone of SU2 (Figs. 4 and 6). Framework builders in coral carpets are *Porites* and *Tarbellastrea* with rare *Acanthastrea*. Common growth forms of *Porites* are 1–4 cm thick branches or columns that are up to 1 m high and, more rarely, massive encrustations. Columns may be stabilised by lateral bridges. *Tarbellastrea* forms tabular to globular colonies that are usually 5–10 cm in diameter. Lateral or vertical zonation in terms of growth forms and relative abundance of coral taxa is not observed. Framework density is estimated to reach 50–70%. Intraframework sediments are mudstone or packstone but growth framework porosity may also be filled by skeletal rudstone. In situ-framework laterally passes into intervals with massive coral debris (coral rudstone) or debris floating in a fine-grained and locally marly wackestone to packstone matrix. Carpets wedge out to the west (Fig. 6). Their eastern limits are not well defined but it appears that carpets become patchier and are replaced by bioclastic packstone (BP). This lithology is similar to the BP facies of SU2 but is attributed to SU3 where it is overlying coral carpets (Figs. 4 and 6).

In the area of Matala, the lower carpet interval is overlain by red algal bindstone. Otherwise, sediments intercalated between coral carpet intervals and overlying coral

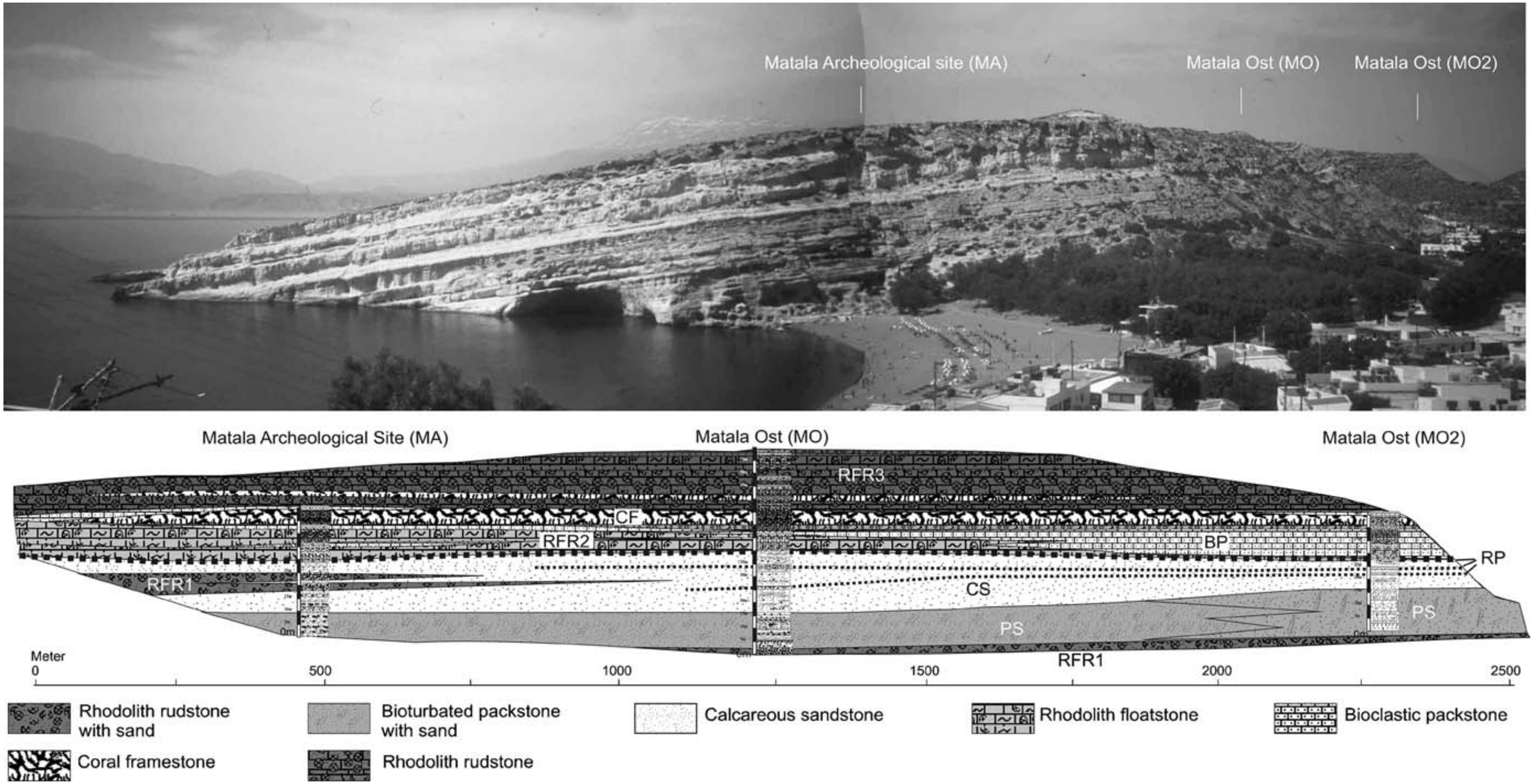


Fig. 6 Transect at the village of Matala showing the laterally persistent character of facies. Note clinoforms formed by couplets of RP rudstone beds (*dashed line*) and CS sandstone. See Fig. 2 for location of sections

Table 1 Facies attributes and interpretation

Stratigraphic unit	Facies	Macrofossils	Petrology	Sedimentary structures and bioturbation	Max. thickness of beds	Taphonomy	Interpretation
SU1	RFR1 (rhodolith floatstone to rudstone with quartz sand)	Ellipsoidal and laminar to open-branched or columnar rhodoliths, ϕ 1–8 cm and fewer unattached 1.5–4 mm thick branches; oysters, *Pecten* spp., celleporiform bryozoans	*Matrix:* mud-rich packstone with 10–50% of fine to medium-grained siliciclastic (mainly quartz) sand	No sedimentary structures	4 m	Low fragmentation and abrasion except at the base of SU1	Low-energy outer ramp and basal transgressive facies of SU1, large components autochthonous, rhodoliths turned by organisms
SU1	PS (packstone with sand)	*Heterostegina,* infaunal echinoids (*Schizaster* sp.), various bivalves (*Pecten* spp.*, Chlamys* spp.*,* oysters*, Cardium* sp.*, Panopea* sp.), gastropods (*Turritella* sp.*, Conus* sp.*, Strombus* sp.), open-branched rhodoliths, more rarely occurring celleporiform bryozoans; *Turritella* sp. is especially abundant west of Pitsidia	*Components:* poorly rounded moderately-classified micritized carbonate grains and 10–40% silt to medium sand-sized siliciclastics (dominantly quartz) *Matrix:* clay and carbonate mud	Bioturbation (*Thalassinoides*), accumulations of *Heterostegina* in pockets	4 m	Gastropods preserved as steinkerns, little abrasion and fragmentation of skeletal elements, some of the thin-shelled echinoids wholly preserved	Low-energy outer ramp environment with soft substratum, possibly with sea grass
SU1	CS (calcareous sandstone)	Rare rhodoliths, *Heterostegina* sp.*,* large pectinids and celleporiform bryozoans	*Components:* well-classified angular, fine to medium sand with 40–70% siliciclastic grains (predominantly quartz); poorly cemented and low matrix content	Decimeterscale to meterscale low angle (usually $<10°$) trough crossbedding; usually not bioturbated	2 m	Macrofossil components little fragmented	Moderate-energy mid ramp environment with submarine dunes
SU1	RP (rudstone with pebbles)	Densely to open-branched rhodoliths, celleporiform bryozoans, pectinids, oysters, *Clypeaster* sp. and *Heterostegina* sp	*Components:* well-rounded quartz pebbles increasing in size to the east of the WAT *Matrix:* well classified angular fine to coarse-grained sand with 40–70% siliciclastic grains; little silt and clay	Bioturbation common	2 m	Pectinid and oyster shells are extensively bored by sponges, degree of fragmentation and abrasion is variable	Amalgamated facies deposited in a mid to inner ramp setting and episodically affected by high energy conditions; top of uppermost RP horizon represents transgressional lag
SU2	RFR2 (rhodolith floatstone to rudstone)	Open-branched or elliptical, laminar rhodoliths up to 7 cm in diameter and minor amounts of unattached branches; rare *Pecten* spp.*, Clypeaster* sp. and bryozoans	*Matrix:* marly wackestone or packstone with low (<5%) and upward decreasing content of siliciclastic silt and fine sand; unsorted carbonate grains, bioclasts and intact skeletons	No sedimentary structures except hardgrounds of limited extent	12 m	Skeletal elements mostly intact at the base of SU2; proportion of fragmented bioclasts increases upsection	Low-energy outer ramp and basal transgressive facies of SU2, large components autochthonous, rhodoliths turned by organisms
SU2	BP (bioclastic packstone)	*Heterostegina* sp. and *Clypeaster* sp	Packstone and subordinate wackestone with mainly fine to medium sand-sized (0.1–0.3 mm in diameter) bioclasts and micritized grains (peloids) *Matrix:* mottled texture that results from partially decomposed and micritized bioclasts and silt-sized peloids; mud content is variable	Horizontal orientation of components	4 m	Skeletal elements strongly abraded, fragmented and micritized	Moderate to high- energy mid ramp facies deposited landward of the outer ramp rhodolith rudstone facies or adjacent to coral carpets and patches

Table 1 Facies attributes and interpretation

Stratigraphic unit	Facies	Macrofossils	Petrology	Sedimentary structures and bioturbation	Max. thickness of beds	Taphonomy	Interpretation
SU3	CF (coral framestone)	Frameworks and coral detritus composed chiefly of branching and columnar *Porites, Tarbellastrea* and rare *Acanthastrea*; corals may be encrusted by red algae, bryozoans and foraminifera; crustacean carapaces and rare gastropods occur in intraframework sediment	*Matrix and intraframework sediments:* micritized carbonate grains and bioclasts of variable grainsize (mudstone to packstone)	Coral rudstone often characterised by horizontal orientation of coral detritus	5 m	Original mineralogy of coral skeletons not preserved, some gastropod moulds are preserved by micrite rims	Laterally extensive coral carpets restricted to relatively short time intervals
SU3	RFR3 (rhodolith floatstone to rudstone)	Openly branched rhodoliths, foliose red algae and large boxwork rhodoliths up to 10 cm in diameter; celleporiform and massive branching bryozoans, *Pecten* spp., *Clypeaster* sp., *Heterostegina* sp. and single colonies of *Tarbellastrea*	*Matrix:* mud- to wackestone and packstone, poorly to well-classified with medium grain sizes around 0.5–1 mm, mottled due to partially decomposed and desintegrated grains	No macroscopic sedimentary structures; horizontal orientation of components in intervals and formation of microhardgrounds	4 m	Skeletal components in intervals strongly fragmented, ripped-off foliose red algae and fragmented echinoids common	Mostly low but episodically elevated energy conditions mid to outer ramp

carpets are rhodolith floatstones to rudstones (RFR3; Fig. 5h) which differ from other RFR sediments by a larger degree of fragmentation of bioclasts, a more foliose character of red algal thalli and the occurrence of boxwork rhodoliths. Skeletal elements in many cases show evidence of reworking. Ripped-off foliose thalli of red algae, fragments of echinoids and fragmented *Heterostegina* are common. Large funnel-shaped *Tarbellastrea* colonies, up to 200 cm in diameter occur in intervals, and in the south of the WAT (Vathi, Mount Rhodonas), an additional coral carpet interval is present. In the upper part of the succession, the matrix of RFR3 deposits becomes increasingly marly.

Interpretation

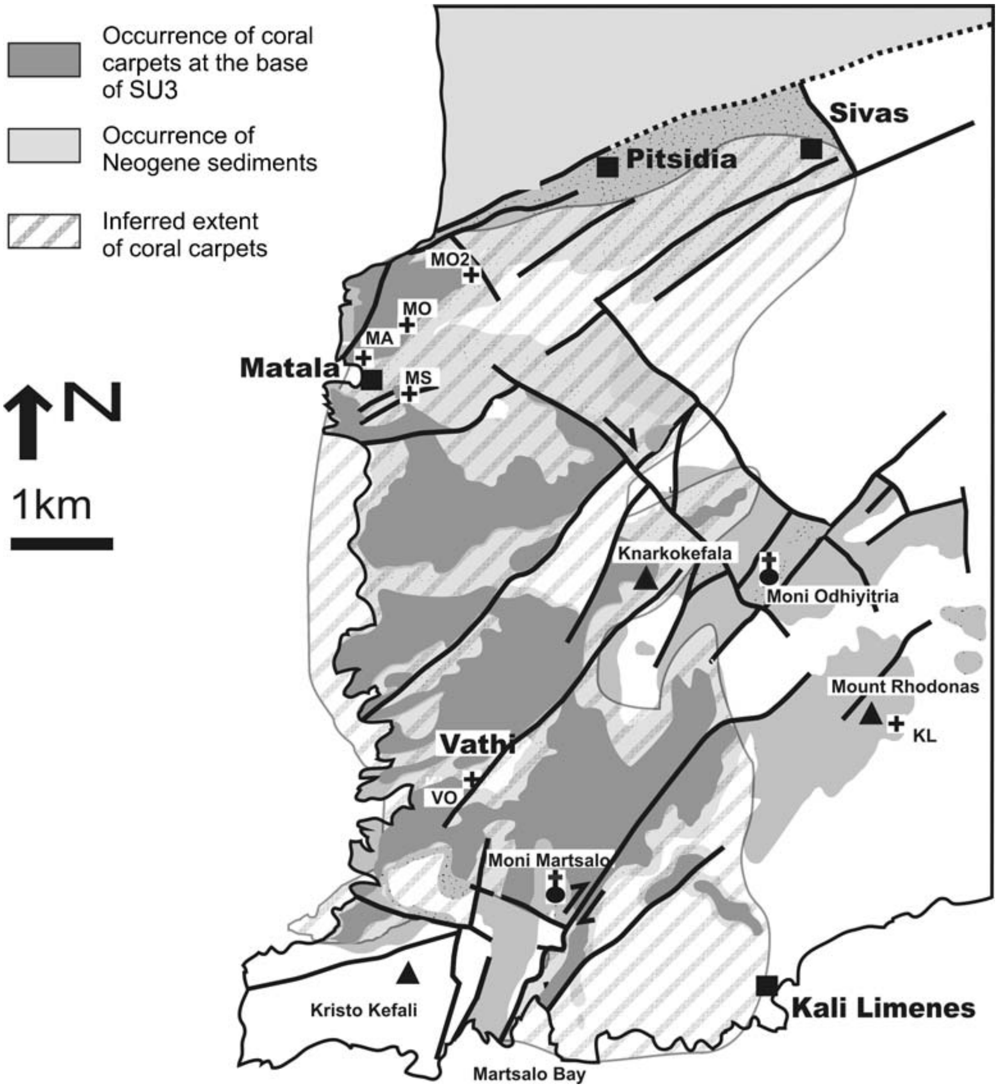
Coral carpets have been studied in detail in the modern Red Sea by Riegl and Piller (1997) and (1999): Coral carpets occur in areas with no pronounced seafloor relief and/or low-hydraulic gradients. In that area, carpets formed chiefly by *Porites* as framework constructor are found in water depths between 5 and 25 m.

RFR3 rhodolith rudstone shows, compared to RFR1 and 2, relatively high degrees of reworking and therefore reflects relatively shallow water within storm-wave abrasion. Boxwork rhodoliths, on the other hand, have been interpreted to reflect relatively low-energy conditions (Basso 1998; Rasser and Piller 2004), indicating rapid deepening after formation of coral carpets. Deepening is also indicated by upward increasing proportions of clay in the matrix.

Stratigraphic architecture

Tortonian limestone deposits of the WAT are correlated by lithological marker horizons. According to the wide lateral extent of the uppermost RP horizon and its interpretation to represent a minimum in sea level, the base of the transgressional lag which is part of the RP facies at the top of SU1 represents a correlative conformity. Stratigraphic architecture is characterised by parallel to subparallel bedding planes with a westward inclination of <2° prior to tilting resulting in a layer cake pattern. With exception of the BP facies, facies are restricted to either one of subunits SU1-3. Vertical facies change is much more apparent than lateral facies change and presumably reflects change in environmental conditions through time. The extent of facies reflecting changes in water depth in the entire carbonate ramp system of the WAT suggests control by change in relative sea level. Relative tectonic movements did not significantly overprint this signal, although differences in relative thickness of sedimentary packages between the north and south of the WAT can be attributed to differential subsidence. In addition to comparatively high rates of subsidence, high siliciclastic sediment input and carbonate production has played a role in the Rhodonas area, where SU3 is relatively thick and where vertical facies change is less pronounced. Also, due to high siliciclastic sediment

Fig. 7 Map of the WAT showing the distribution of coral carpets at the base of SU3 mapped in the field and their inferred original extent into areas where SU3 is eroded and beyond the modern coastline



input, SU1 replaces and interfingers with SU2 in this area (Fig. 4b). To a much smaller extent, beds of calcareous sandstone (CS facies) are also found in the lower part of SU3 (section KL).

The carbonate succession of the WAT can be subdivided into two sedimentary sequences separated by the correlative conformity within the uppermost RP bed (Fig. 4). The transgressive systems tract (TST) of the older sequence is formed by RFR1 rhodolith rudstone at the base of the succession. The overlying PS and CS sediments represent the highstand (HST) and falling stage systems tracts (FSST). The latter is characterised by a relatively small seaward shift of coastal onlap and no significant erosion. This is interpreted to be a consequence of high tectonic subsidence of the entire area. The TST of the overlying sequence is formed by RFR2 rhodolith floatstone, or in the Rhodonas area, where the older sequence is not present, by RFR1 rhodolith rudstone. The HST is represented by prograding bioclastic packstone (PS) and coral framestone (CF). Upward deepening towards the top of the succession as indicated by increasingly clay-rich sediments is interpreted to be a consequence of a gradual increase in subsidence of the WAT region.

We propose that in addition to observed change in water depth in consequence of sedimentation lagging behind sea-level change, other factors such as water temperature and nutrients also played a role in controlling the vertical facies change. This is indicated by the restriction of framework-forming corals to certain stratigraphic intervals within SU3 as will be discussed below. Controlling factors on biotic communities will be evaluated in the following by biofacies analysis and analysis of foraminiferal and red algal associations.

Biofacies analysis

Methodology

In order to evaluate the influence of environmental parameters on facies change, a semiquantitative biofacies analysis was carried out for facies units described above. Four representative sections in three areas of the WAT (Matala

– section MO and MS; Vathi – section VO and Mount Rhodonas – section KL; Fig. 1) that were accessible for continuous sampling and measuring were chosen. Samples were picked randomly from each bed and in intervals of 50 to 200 cm. Skeletal components were quantified in thin-section using classes of relative abundance (common 3/6, 50%; uncommon 2/6, 33.3% and rare 1/6, 16.7%). In the case of dominance of one type of components in a sample, classes were modified to dominant (3/4; 75%), rare (1/6; 16.7%) and very rare (1/12; 8.3%).

Results

The most common skeletal components in limestones of the WAT are non-geniculate coralline red algae and foraminifera, whereas echinoids, bryozoans and bivalve components are less common (Fig. 8). Rare components are serpulids and crustacean elements. Colonial corals represent the main component (45%) in the CF facies but are only minor constituents in the BP, RP and RFR3 facies and are absent in all other facies. Non-geniculate coralline red algae reach an average proportion between 50 and 70% of skeletal elements total in the three RFR facies and between 10 and 30% in all other types. Inversely, the proportion of foraminifera is highest (between 45 and 60%) in the CS and BP facies which are composed of sand-sized components. Echinoid, bryozoan and bivalve components together contribute 30% in the PS facies and less than that in all other facies.

Interpretation

Biotic associations, based on the quantification of skeletal elements can be described to be relatively uniform. Most variation results from the considerable change in relative abundance of non-geniculate coralline red algae and corals. However, abundant steinkerns of bivalves and gastropods in the PS facies suggest that there is a significant taphonomic bias due to the low degree of cementation typical for non-tropical carbonates and high dissolution loss of aragonite components during early diagenesis (Brachert et al. 2002). This results in a bias between living and fossil associations, and an over-representation of calcite skeletons in fossil material. Taking into account this bias, the PS facies is interpreted to represent a biotic association rich in molluscs which therefore is closest to the classical foramol association defined by Lees and Buller (1972). This association commonly has been related to temperate or cool-water conditions. The other facies can be classified as molechfor, rodalgal, chlorozoan and rhodozoan as described by Lees and Buller (1972), Carannante et al. (1988) and Halfar et al. (2000) and are typical for a variety

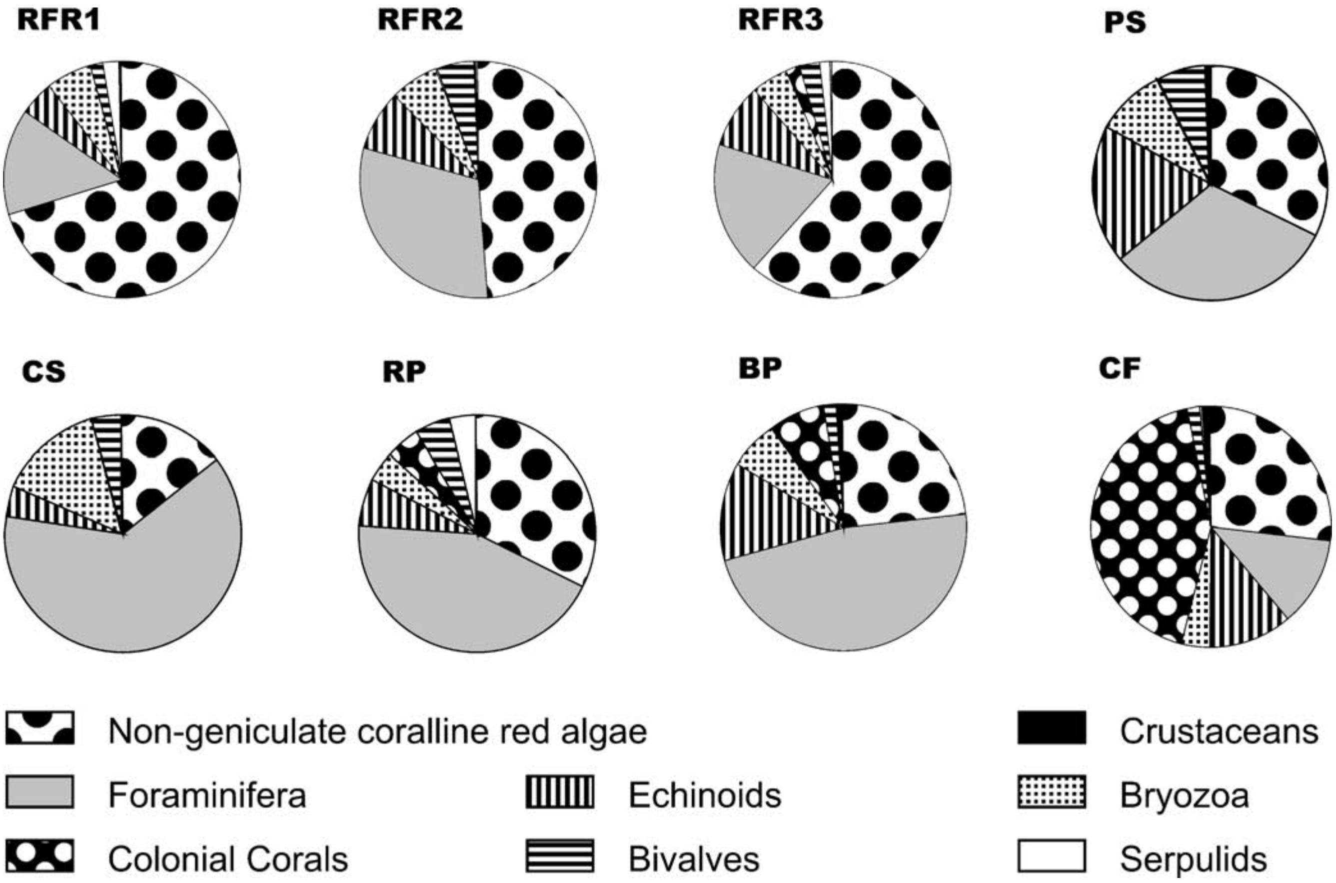


Fig. 8 Results of biofacies analysis shown separately for each facies. Pie diagrams represent 100% volume percent of identifiable skeletal components

of cool to warm shallow-water environments. Lees and Buller (1972), Lees (1975), Carannante et al. (1988) and Hallock and Schlager (1986) have concluded, that factors such as water depth, nutrients and salinity additionally influence biotic associations. Consequently, a certain biotic association may exist in various environments. For example, while the abundance of bryozoans in most studies is observed to increase with depth (James et al. 2001; Brachert et al. 2003; Forst 2003) and foraminifera and red algae dominate in shallower waters (Piller 1994; Halfar et al. 2000), bryozoans may also be the dominant skeletal element in sediments shallower 25 m water depth in enclosed bays (Upper Miocene of southern Spain, Martin et al. 1996). Therefore, to minimize the interplay of different ecological factors reflected in skeletal associations, it is necessary to find and to study groups of fossils that have a relatively simple response to a limited number of ecological factors.

Foraminifera

Distribution

A semiquantitative analysis of the distribution of foraminifera in the four sections MO, MS, VO and KL was carried out using the same approach as for quantification of skeletal elements. Quantification on genus level has only been possible for genera which are easily identified in thin-section such as *Amphistegina, Elphidium, Heterostegina, Ammonia* and *Borelis*. Groups of genera whose quantitative differentiation in thin-section is uncertain have been given descriptive names. Most abundant are benthic rotaliid taxa such as *Amphistegina, Elphidium, Heterostegina, Ammonia* and cibicidids, including also fixosessile forms such as *Victoriella* and *Homotrema*. Other fixosessile forms such as *Acervulina* were not identified without doubt. Milioliids are locally abundant, mostly represented by *Quinqueloculina* and triloculine forms as well as *Borelis*. Agglutinating foraminifera are represented by textulariid forms. They are widely distributed but occur in relatively small numbers. Planktonic foraminifera (mostly globigerinids) are abundant in the upper 10 m of section MO and in the PS facies 5 m above the base (Fig. 9).

Of the benthic foraminifera, *Amphistegina* is most abundant. It is dominant in most samples of the sections at Mount Rhodonas (KL; Fig. 9) and Vathi (VO). In the area of Matala (sections MO, MS), *Amphistegina* is common in the middle part of the succession (25–65 m of section MO, top 25 m of section MS). In section MO, it is, however, uncommon in the PS facies. The number also decreases significantly towards the top of the section.

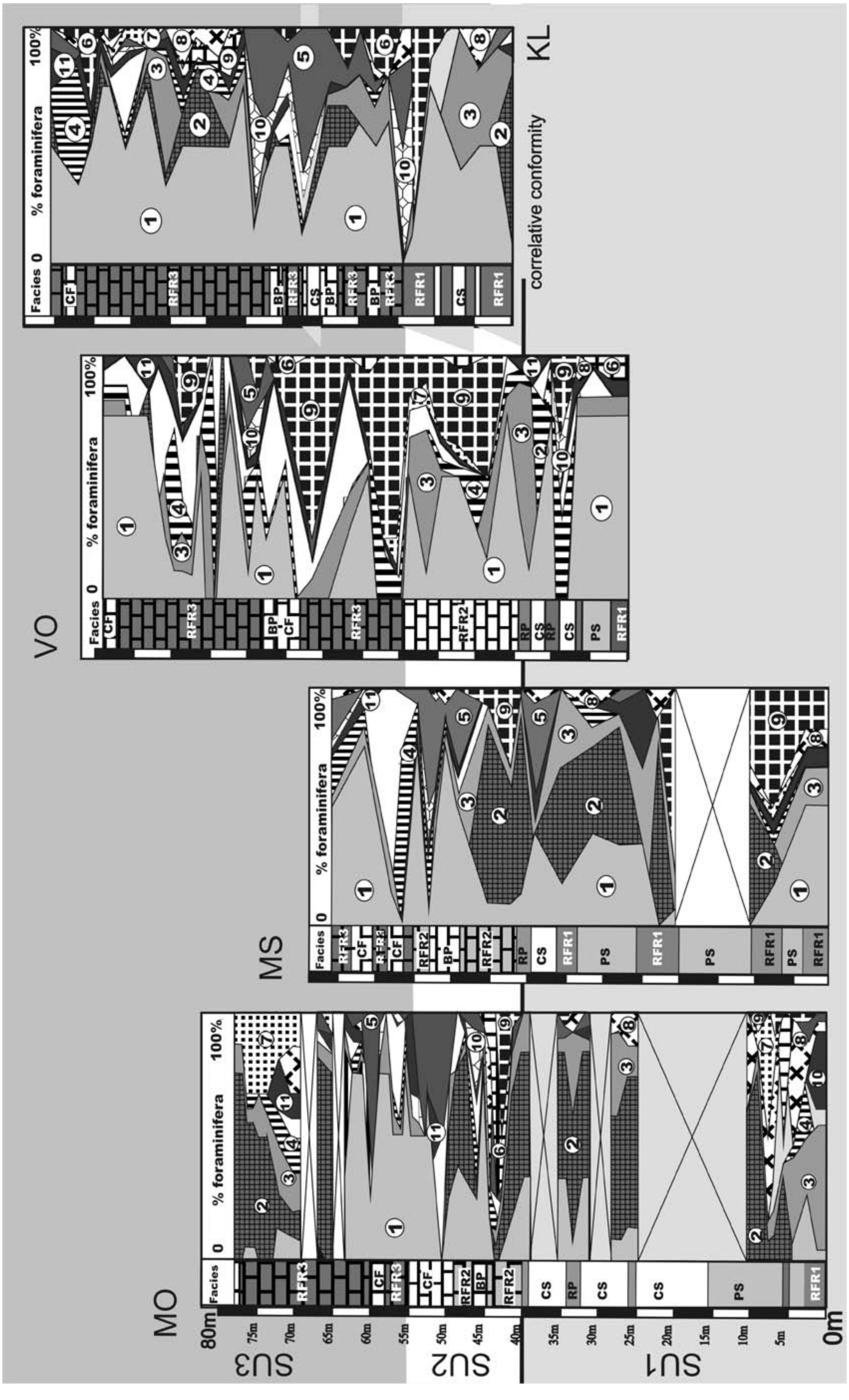
Amphistegina is represented by dominant *A. lobifera* and *A. lessonii*, which can be separated in thin-section by their characteristic outline and test organisation: *A. lessonii* is characterised by its bulging shape and ventrally thickened umbo with characteristically laminated, thick test wall. It is also characterised by a comparatively large main chamber in the ultimate whorl. Because of the size of the chamber and the strongly backward bent main septum, in many cases not only two adjacent main chambers are cut in section but also the stellar chamberlet formed by the folded umbilical plate. In contrast, *A. lobifera* is characterised by its subglobular shape and thick, perforate tests (compare Hottinger et al. 1993). Of the two species of *Amphistegina*, *A. lobifera* is most common in RFR1. *A. lessonii* is more common in SU2 and 3 than *A. lobifera* and dominates in the RP and BP facies.

Heterostegina is also very common: it occurs in great numbers in the RP facies. In the Matala area, *Heterostegina* is common in the PS, RFR1 and RFR2 facies. In the latter facies, it decreases in abundance upsection but dominates in the RFR3 facies at the top of section MO. *Elphidium* is a minor constituent in most samples and occurs commonly together with *Amphistegina* and/or *Heterostegina* as well as in the PS facies together with *Ammonia*. Cibicidids usually are minor components but locally abundant in the PS facies (section MO) and in the RFR3 facies in the upper part of sections VO and KL. *Ammonia* is abundant in the PS facies in section MO but is uncommon elsewhere. Of the miliolid foraminifera, quinqueloculine forms are most abundant in the PS facies and the CS facies (section MS) and in the upper part of coral framestone units (section MO). *Borelis* is also most abundant in the BP facies but occurs as well within coral framestone and in rhodolith rudstone overlying coral framestone. Of fixosessile or incrusting foraminifera, the homotrematid forms are most common. They are mostly found on or intergrown with rhodoliths. Planktonic foraminifera are common in section MO in the middle part the PS facies and at the top of the section in the RFR3 facies.

Palaeoecological implications

Most foraminifera found in great number in Neogene deposits of the WAT belong to the group commonly called “larger benthic foraminifera”. A significant property of this group of foraminifera is their housing of algal symbionts that, in turn strongly influence the specific needs of the foraminifer (Lee and Anderson 1991).

The distribution of species of *Amphistegina* in dependence of water depth and temperature is especially well known from the modern Mediterranean and the Red Sea. The absolute abundance of *Amphistegina* is greatest between 50 and 70 m in the Red Sea (Hansen and Buchardt 1977; Haunold et al. 1998). The maximum depth where *A. lobifera* is found is less than 60 m while *A. lessonii* occurs down to 80 m (Hottinger 1977; Hollaus and Hottinger 1997; Haunold et al. 1998). In other areas, the depth range, especially of *A. lessonii* is considerably lower (down to no more than 50 m at Okinawa Island south of Japan; Hohenegger 1994, 1995). A pronounced increase in abundance of *A. lessonii* at the base of SU2 is in accordance with the interpretation of increasing water depth. However, Hansen and Buchardt (1977) have shown that substratum strongly influences the occurrence of *Amphistegina* spp.


SU3
SU2
SU1
MO
MS
VO
KL
80m
75m
70m
65m
60m
55m
50m
45m
40m
35m
30m
25m
20m
15m
10m
5m
0m
Facies
% foraminifera
0
100%
RFR3
CF
RFR2
BP
CS
RP
PS
RFR1
1
2
3
4
5
6
7
8
9
10
11
correlative conformity

Amphistegina is also common in the Bay of Safaga on rocky surfaces with thin sand veneers and on a macroid facies (Haunold et al. 1997). This observation is in agreement with the abundance of *A. lessonii* in the RFR facies. Hohenegger et al. (1999) found that on the Island of Okinawa an umbiliconvex form of *A. lessonii* prefers soft substrates, whereas the biconvex form that is more similar to the forms found in the WAT prefers firm substrates. This could explain the rarity of *A. lessonii* in the fine-grained PS facies.

Heterostegina is most abundant in three distinct facies not associated with each other: the amalgamated RP facies, the fine-grained PS facies and the RFR3 facies at the top of section MO. The RP facies is interpreted to represent a mid ramp to inner ramp setting that was frequently affected by storm reworking while both other facies are interpreted to represent comparatively low-energy mid to outer ramp settings. The occurrence of planktonic foraminifera and increasing mud content indicate deepening in the upper part of the RFR3 facies. In this part, *Heterostegina* gradually replaces *Amphistegina*. The wide range of facies occupied by *Heterostegina* is in accordance with the depth range (20–120 m) of *Heterostegina* and abundance in either hard or soft substratum in modern environments (Hottinger 1977; Hohenegger 1994, 1995; Hohenegger et al. 1999).

Quinqueloculina spp. and *Triloculina* spp., often with *Borelis*, are especially common in sandy sediments (BP and to a lesser degree CS facies). This is in agreement with the observations of Haunold et al. (1997) in the Gulf of Safaga, where species of *Quinqueloculina* dominate on shallow (<35 m water depth) sand bottoms. There they often live epiphytic on sea grass or occur in sand patches between coral carpets where they are associated with *Borelis*. The latter observation corroborates the assumption, that some of the BP facies is connected to coral carpets or coral fringes not preserved in outcrop.

In conclusion, the depth distribution of foraminifera in many cases is strongly controlled by substratum but nevertheless supports deepening and shallowing trends indicated by lithological change (Fig. 4). Important reworking and basinward transport of benthic foraminifer tests is observed neither in the modern Red Sea (Hansen and Buchardt 1977) nor in Oligo-Miocene ramp environments (Pedley 1998). Transport from the higher energy RP, CS and BP facies to adjacent lower energy facies is therefore regarded to be of little impact on the distribution of foraminifera.

Foraminifera are also commonly used as indicators of water temperature (Betzler et al. 1997; Hollaus and Hottinger 1997; Langer and Hottinger 2000). The biogeographic distribution of larger foraminifera allows conclusions concerning minimum temperatures (Langer and Hottinger 2000): *Amphistegina* occurs in regions with minimum winter sea-surface temperatures of 14°C. *Heterostegina depressa* is limited to areas with minimum winter sea-surface temperatures of 18°C and *Borelis schlumbergeri* in regions with a 21°C minimum. Thus, foraminiferal associations indicate deposition of the limestone units under temperature conditions typical for the warm-temperate realm and typical for the tropical faunal province in intervals where *Borelis* occurs and micritised peloids are abundant (BP and CF facies).

The occurrence of larger benthic foraminifera is not only limited by the annual minimum temperature but also by nutrient contents: very much like zooxanthellate corals, larger benthic foraminifera are usually restricted to oligotrophic environments, so called blue deserts (Langer and Hottinger 2000). On the other hand, certain species of *Elphidium* and *Ammonia* may expel their symbionts and adopt heterotrophic feeding strategies in order to adapt to high nutrient levels (Jorissen 1988). High numbers of *Ammonia* and *Elphidium* are therefore found in areas with fresh water input or high content of organic matter (Jorissen 1988; Langer and Lipps 2003). Both genera display a characteristic inflation of chambers with increasing trophic levels (Jorissen 1988). In sections in the WAT, inflated forms of *Ammonia* but not of *Elphidium* occur. Large numbers of *Ammonia* are found in the PS facies in section MO, thus indicating increased nutrient input. They are associated with *Heterostegina* that also has been attributed relatively high ecological tolerances compared to other larger benthic foraminifera (Langer and Hottinger 2000) and with high numbers of planktonic foraminifera that may represent plankton blooms in consequence of increased nutrient input. Increased amounts of nutrients in the lower part of SU1 in the area of Matala are also indicated by the abundance of turritellid gastropods in the most shoreward part of the PS facies: turritellid gastropods are suspension feeders that are especially abundant in non-tropical high productivity environments (Allmon 1988; Lukasik et al. 2000).

While high nutrient contents promote planktonic foraminiferal blooms, their number is also limited by water depth since zooplankton layers migrate down to 40–50 m below sea level in the modern Red Sea during the day (Reiss and Hottinger 1984). The abundance of planktonic foraminifera in the PS and upper RFR3 facies is thus in accordance with a deposition in an outer ramp environment.

Non-geniculate coralline red algae

Methodology

Analysis of red algal associations was carried out semiquantitatively, using abundance classes (common: 3/6; 50%; uncommon: 2/6; 33.3% and rare: 1/6; 16.7%) similar to the method applied for biofacies analysis. Red algae were identified according to the classification of Woelkerling (1988) and its application to fossil material by Bosence (1991), Braga et al. (1993), Braga and Aguirre (1995) and Rasser and Piller (1999). Samples

◀ **Fig. 9** Distribution of foraminifera in sections MO (Matala East), MS (Matala South), VO (Vathi) and KL (Mount Rhodonas). Shown foraminifera are 1: *Amphistegina*, 2: *Heterostegina*, 3: *Elphidium*, 4: cibicidids, 5: quinqueloculine and triloculine miliolids, 6: *Victoriella*, 7: globigerinids, 8: *Ammonia*, 9: *Homotrema*, 10: *Borelis*, 11: textulariine forms. *White fields* represent unidentified taxa. See Fig. 2 for location of sections

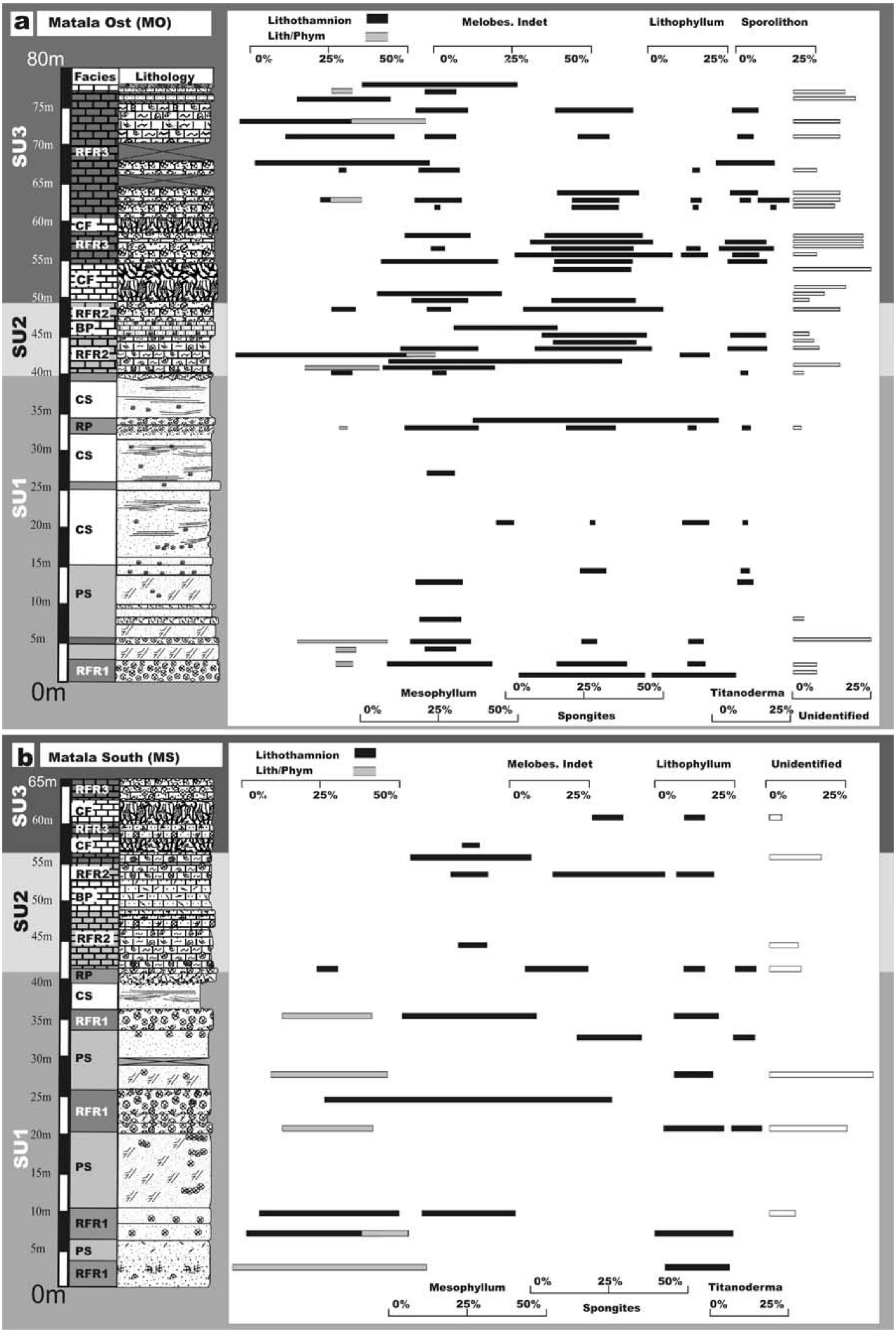


Fig. 10 Abundance of coralline red algal genera in sections **a** Matala East, **b** Matala South, **c** Vathi and **d** Rhodonas in volume percent of skeletal components total. See Fig. 6 for explanation of signatures

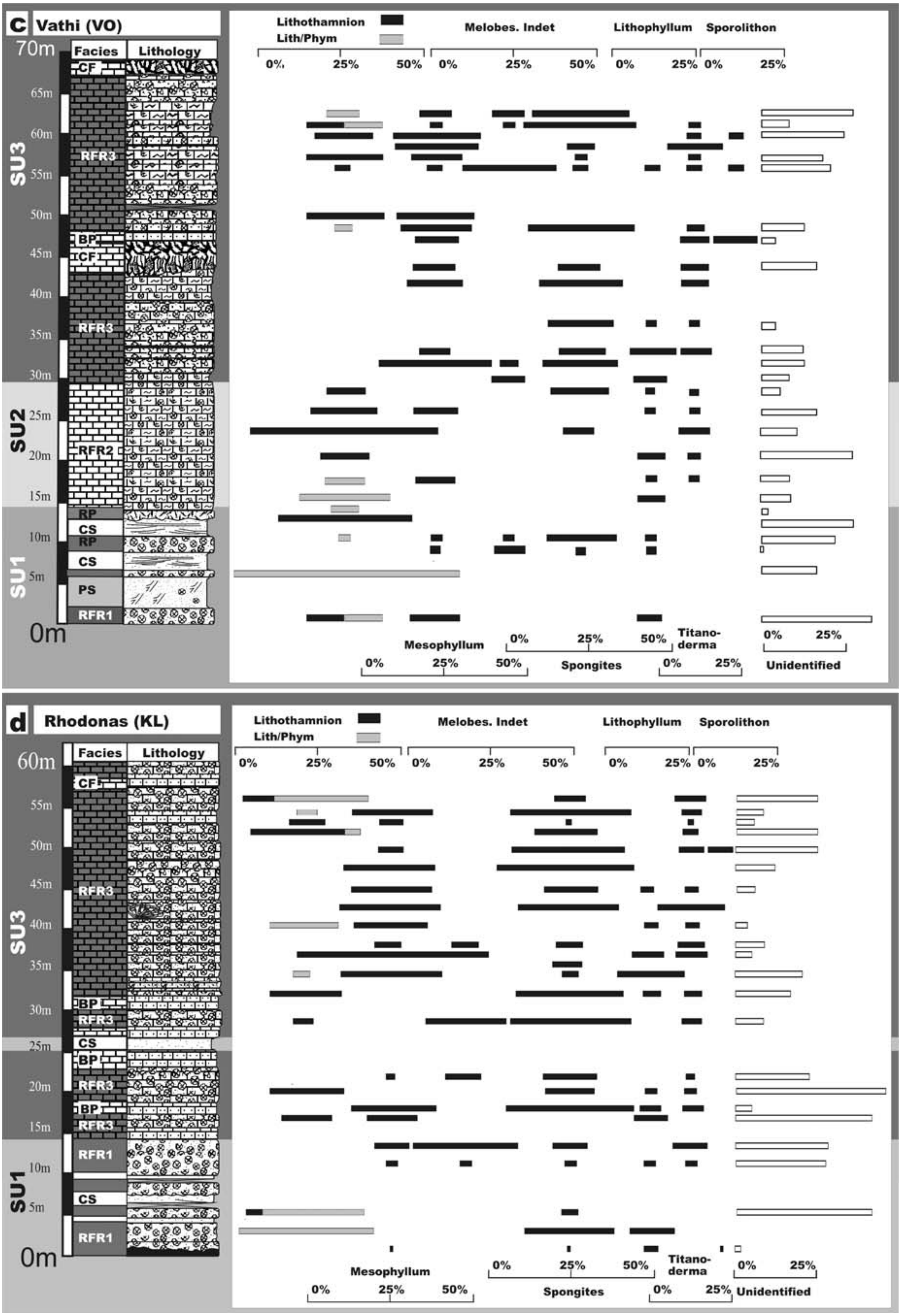
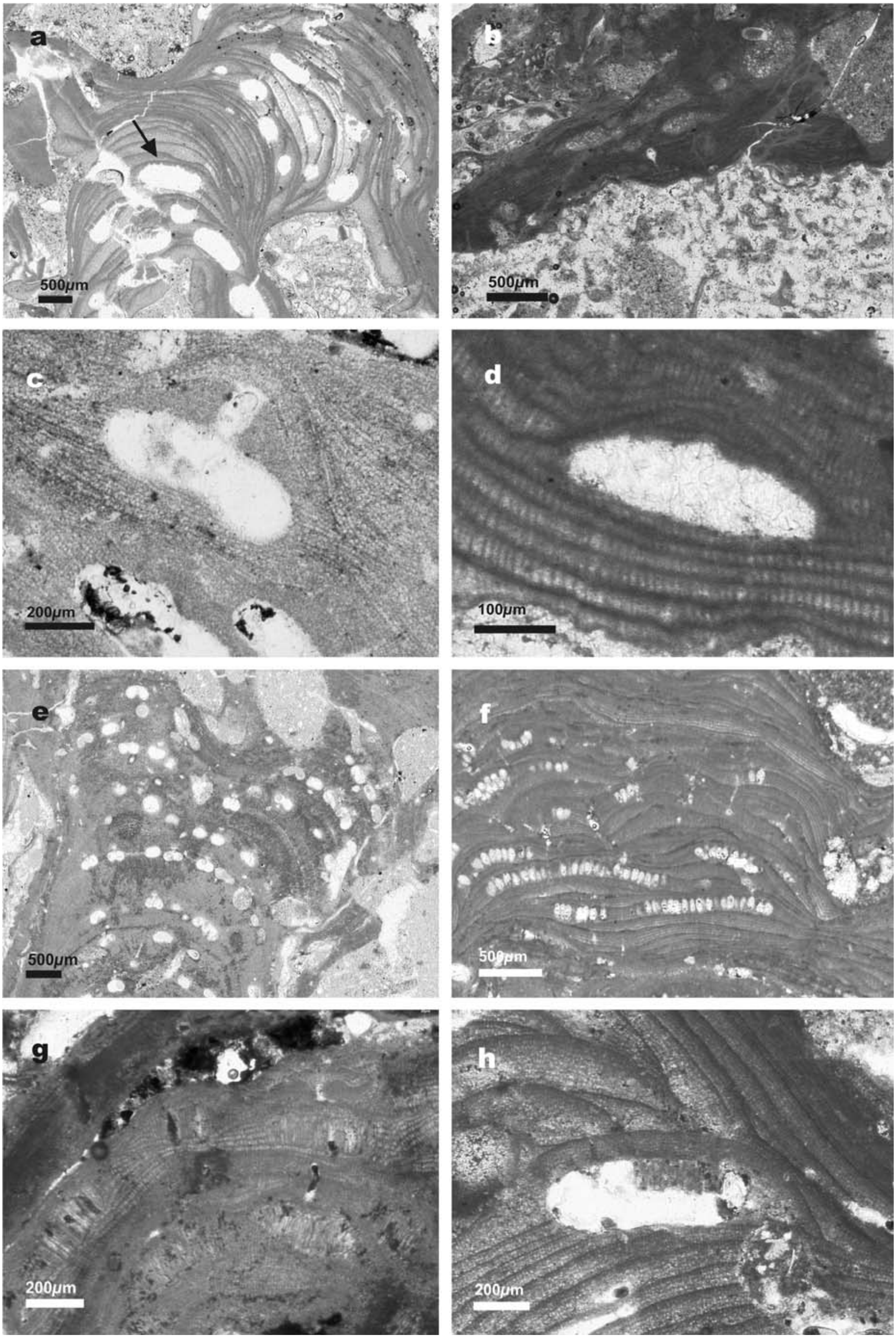


Fig. 10 Continued


a
500μm
b
500μm
c
200μm
d
100μm
e
500μm
f
500μm
g
200μm
h
200μm

were analysed in thin-section. See Kroeger (2004) for a taxonomic assessment. Results are given as a percentage of total skeletal components (Fig. 10).

Results

In four sections (MO, MS, VO, KL; Fig. 10), the distribution of non-geniculate coralline red algae was investigated in detail. Assemblages are dominated by the taxa of subfamilies Melobesioideae (*Lithothamnion, Phymatolithon, Mesophyllum*; Fig. 11a, b), Mastophoroideae (*Spongites*; Fig. 11c) and Lithophylloideae (*Lithophyllum, Titanoderma*; Fig. 11d, e). Additionally, rare *Sporolithon* (Fig. 11f) occurs. The identification of the different genera of the Melobesioideae proved to be problematic since many characteristics relate to features with a low potential for fossilization. Therefore, separation between *Lithothamnion* and *Phymatolithon* in many cases was not possible. Only two species, *L. ramosissimum* (Fig. 11g) and an informal species 1 of *Lithothamnion* (Fig. 11h) could be identified without doubt and separated from *Phymatolithon* (Kroeger 2004). Identification of *Mesophyllum* in many cases was limited to samples containing core elements of the thallus. Following Irvine and Chamberlain (1994), *Titanoderma* is treated as a separate genus of the Lithophylloideae.

All identified species that could not be related to taxa described in the literature were treated as informal species. The number of identified taxa is highest in *Mesophyllum* (*M. curtum, M. sancti-dionysii* and two informal species). In addition to the two identified species of *Lithothamnion,* one species that either belongs to *Lithothamnion* or *Phymatolithon* was found. In addition, three species of *Lithophyllum* (*L. dentatum, L. incrustans* and *L. nitorum*), two of *Spongites* (*S. albanensis* and one informal species), two informal species of *Sporolithon* and one species of *Titanoderma* (*T. pustulatum*) occur. *Spongites albanensis* is the dominant species of *Spongites* (Kroeger 2004).

In all sections, conspicuous patterns in the distribution of non-geniculate coralline red algae are observed: melobesioid red algae dominate in the lower part of sections MO, MS, VO and KL in the RFR1 facies, in the PS facies and in the RFR2 facies. An exception to this is the RFR1 rhodolith rudstone at the base of section MO that shows evidence of elevated hydraulic energy. Here, *Spongites* and *Lithophyllum* are dominant. *Spongites* also increases in abundance in the upper part of the massive rhodolith unit (RFR2 facies). In the RFR3 facies both *Spongites* and various melobesioid forms are abundant. Among melobesioid genera, *Mesophyllum* is more abundant in the part of sections where coral framestone and single colonies of zooxanthellate corals occur (SU3): in intervals with corals both *Mesophyllum* and *Spongites* are common. Among *Mesophyllum* in these intervals, *M. sancti-dionysii* is especially abundant and is often found to encrust corals. The abundance of *Lithophyllum* is generally low and it rarely occurs together with corals. It is also mostly absent in the upper 20–30 m of all sections except section MS. *Titanoderma pustulatum* generally is a minor but common constituent in all sections. It is, however, uncommon in sediments with high siliciclastic contents, especially in the PS facies. *Sporolithon* is very uncommon and occurrences are mostly near the top of sections.

In samples of the RP facies, a high number of different species is found. In the lower RP horizons mostly *Spongites* and to a lesser degree *Lithophyllum* are dominant. In the uppermost RP horizon, where red algae occur only in samples from the top, *Lithothamnion*/*Phymatolithon* and *Mesophyllum* are more common. In a sample from the uppermost RP horizon east of section MO, however, *Spongites* dominates with additional *Lithophyllum nitorum, Mesophyllum* sp. and *Titanoderma pustulatum.*

Palaeoecological implications

The above described patterns, which are apparent in Fig. 10 can be interpreted according to published data on modern and fossil red algae: In the Miocene of southern Spain (Braga and Aguirre 2001), *Lithophyllum* occurs mainly in temperate environments that are defined by the absence of tropical foraminifera and zooxanthellate coral reefs (Betzler et al. 1997). It is also the most common genus in modern temperate shallow-water environments in the northern and western Mediterranean (Adey 1986; di Geronimo et al. 1993) down to 20 m water depth (Bosence 1991), as well as southern Australia (James et al. 1992) and the Gulf of California (Rosmena-Rodriguez et al. 1999). Mastophoroids such as *Spongites* are commonly found in shallow tropical environments (Adey et al. 1982; Bosence 1985; Braga and Aguirre 2001, 2004). This corresponds to the abundance of *Spongites* in intervals with zooxanthellate corals and *Borelis* in SU3, and to the rarity of *Lithophyllum* in these intervals. Along with the Sporolithaceae, the melobesioids are observed to be the deepest taxa in recent and Neogene environments, occurring down to 110–120 m water depth (Adey et al. 1982; Lund et al. 2000; Braga and Aguirre 2001, 2004). This is in accordance with the dominance of melobesioid taxa in the RFR facies which is interpreted to represent low to moderate energy mid-ramp to outer-ramp deposits. The dominance of melobesioids is most evident in the widespread massive RFR2 unit that reflects low-energy conditions and therefore an increase in water depth after deposition of the RP facies. Similarly,

◀ **Fig. 11** Thin section photographs of analysed coralline red algae. **a** Fruticose melobesioid plant with large multiporate conceptacles (arrow); section KL, sample K21. **b** *Mesophyllum sancti-dionysii* encrusting *Porites*; section Vathi, sample VO14. **c** Bean shaped uniporate tetra-/bisporangial conceptacle of *Spongites albanensis*; section KL, sample K16. **d** Conceptacle of *Titanoderma pustulatum*; note comparably large size of cells and absence of cell fusions; sample MD14. **e** Swollen, bifurcated protuberance of *Lithophyllum incrustans*. Note horizontal alignment of uniporate conceptacles, sample MD14. **f** Warty banded thallus of *Sporolithon* sp.1 with tetrasporangial conceptacles arranged in sori, section KL, sample K27. **g** Multiporate tetra-/bisporangial conceptacles of *Lithothamnion ramosissimum* that are filled with prematurely calcified filaments, section KL, sample K28. **h** Large multiporate tetra-/bisporangial conceptacle of *Lithothamnion* sp.1 that is incised into the underlying thallus. Note considerable roof thickness, sample MO26c melobesioid genera dominate in the uppermost 25 m of section MO, where overall deepening is indicated by an increasing clay content and abundant planktonic foraminifera. Of the melobesioids, *Phymatolithon* (Adey et al. 1982; Irvine and Chamberlain 1994) and *Lithothamnion* (Freiwald and Henrich 1994; Henrich et al. 1995) are commonly associated with modern arctic to warm-temperate environments. This is in accordance with the abundance of *Lithothamnion*/*Phymatolithon* in the lower part of sections (RFR1 and 2 and PS facies) where corals and foraminifera susceptible to winter sea-surface temperatures below 18°C occur only locally. *Mesophyllum* on the other hand rarely occurs in cold environments. In the British Islands, for example, the occurrence of *Mesophyllum* is reduced to one species, *Mesophyllum lichenoides* (Irvine and Chamberlain 1994) which is not identified in the material from Crete. The preferred occurrence of *Mesophyllum* together with other melobesioids in clay-rich deeper water sediments and on corals indicates that *Mesophyllum* occurs in relatively warm water as well as in relatively deep environments.

The heterogeneous red algal composition in the RP facies indicates reworking and redeposition of red algal components and reflects the amalgamated nature of the deposit. The dominance of melobesioids at the top of the uppermost condensed horizon indicates that the top represents a lag. Condensation at the top occurred in consequence of sediment starvation through relative sea-level rise. A larger proportion of shallow-water non-geniculate coralline red algae in the same bed along the Matala transect (Fig. 6) to the east indicates shallower water to the east in accordance with an eastward (shoreward) increase in pebble size.

The dominance of larger benthic foraminifera indicates prevalent oligotrophic conditions (Langer and Hottinger 2000) and consequently, nutrients can be excluded as a main controlling factor on coralline red algal assemblages. The prevalence of *Ammonia* in the PS facies however indicates temporarily increased nutrient levels. *Titanoderma* is absent in intervals with abundant *Ammonia* and is therefore interpreted to be especially susceptible to increased nutrient input. Alternatively, the general rarity of *Titanoderma* in SU1 can be interpreted as a consequence of high terrigenous influx.

Water depth and temperature indices based on non-geniculate coralline red algal assemblages

We demonstrated above that certain red algae are linked to certain facies. Based on lithology and foraminiferal distributions these facies were shown to reflect different water depth and temperature. In order to obtain standardised values between 0 and 1 for these parameters, a temperature index with *Spongites* and *Mesophyllum* as warm-water taxa and *Lithophyllum* and *Lithothamnion* + *Phymatolithon* as cool-water taxa has been defined:

$$T = \frac{a + d}{a + b + d + g}$$

An analogous water depth index incorporates melobesioids and *Sporolithon* as deep-water taxa and the mastophoroids and *Lithophyllum* as shallow-water taxa:

$$D = \frac{a + b + c + f}{a + b + c + d + e + f}$$

In both equations a is the percentage of *Mesophyllum* of total red algal content in each sample, b of *Lithothamnion* + *Phymatolithon*, c of Melobesioideae indet., d of *Spongites*, e of *Lithophyllum* and f of *Sporolithon*.

No discrimination is made between *Lithothamnion* and *Phymatolithon* since their separation in thin-section is often problematic and no differences in preferences regarding water temperature or water depth are known or apparent from the material from Crete. *Titanoderma* does not appear in the index because it shows no preferences in terms of water depth and water temperature and *Sporolithon* is not used in the temperature index since its preferences in terms of water temperature are not known.

Coralline red algal index values correspond to the distribution of foraminifera and of zooxanthellate corals (Fig. 12): Warm shallow-water is indicated in the part of section MO where coral carpets and tropical foraminifera occur. At the top of the upper reef unit, increasing water depth index values indicate deepening. The distribution of zooxanthellate corals and tropical foraminifera can also be linked with temperature index values in all other examined sections. In these sections, where coral carpets are absent or not as well developed as in the Matala area, water depth index values are higher than in section MO. Intervals with dominant *Heterostegina* and planktonic foraminifera that have been interpreted to represent outer ramp deposits show a high water depth index. The change in lithology from mid ramp RP facies to outer ramp RFR2 facies that indicates deepening is also characterised by an increase to maximal water depth index values. Few data are present for the BP facies but they largely result in low water depth index values in accordance with the mid-ramp to inner-ramp setting of this facies. The picture is more complex in the RP facies since red algal proportions reflect both, shallow conditions and reworking in the lower RP horizons and increasing water depth and formation of a lag deposit at the top of the uppermost condensed horizon.

Relationships between water depth and temperature indices

It is reasonable to expect a decrease in water temperature index values with increasing water depth. However, no covariance emerges between both datasets (Fig. 13). This implies that non-geniculate coralline red algae, as a consequence of their sensitivity to light, are restricted to certain depth intervals within the photic zone. In particular, melobesioid taxa will not become more abundant in shallow-water if water temperature decreases and lithophylloid taxa will not be more common in deeper water if temperature increases. This assumption is corroborated by the observation that, although in recent environments of Brittany, Great Britain and Norway, *Phymatolithon* and *Lithothamnion* are found mostly in water depths shallower than 20 m (Irvine and Chamberlain 1994; Henrich et al. 1995), specimens of *Phymatolithon* depend on shading to survive in shallow water (Figueiredo et al. 1992). Similarly, Adey et al. (1982) describe the occurrence of deep-water taxa in shaded settings. The observation in the material from Crete that *Mesophyllum sancti-dionysii* commonly encrusts corals in the CF facies also suggests a preference of shaded settings. Accordingly, in the material from the WAT it is not observed that *Mesophyllum*, which is interpreted to occur in deep water in areas with high surface temperatures, is found together with *Lithophyllum* in shallow cold environments.

Coralline red algal associations

Four coralline red algal associations are identified (Fig. 14): a *Lithophyllum*-dominated association in shallow "cool" environments, a *Spongites*-dominated association in shal-

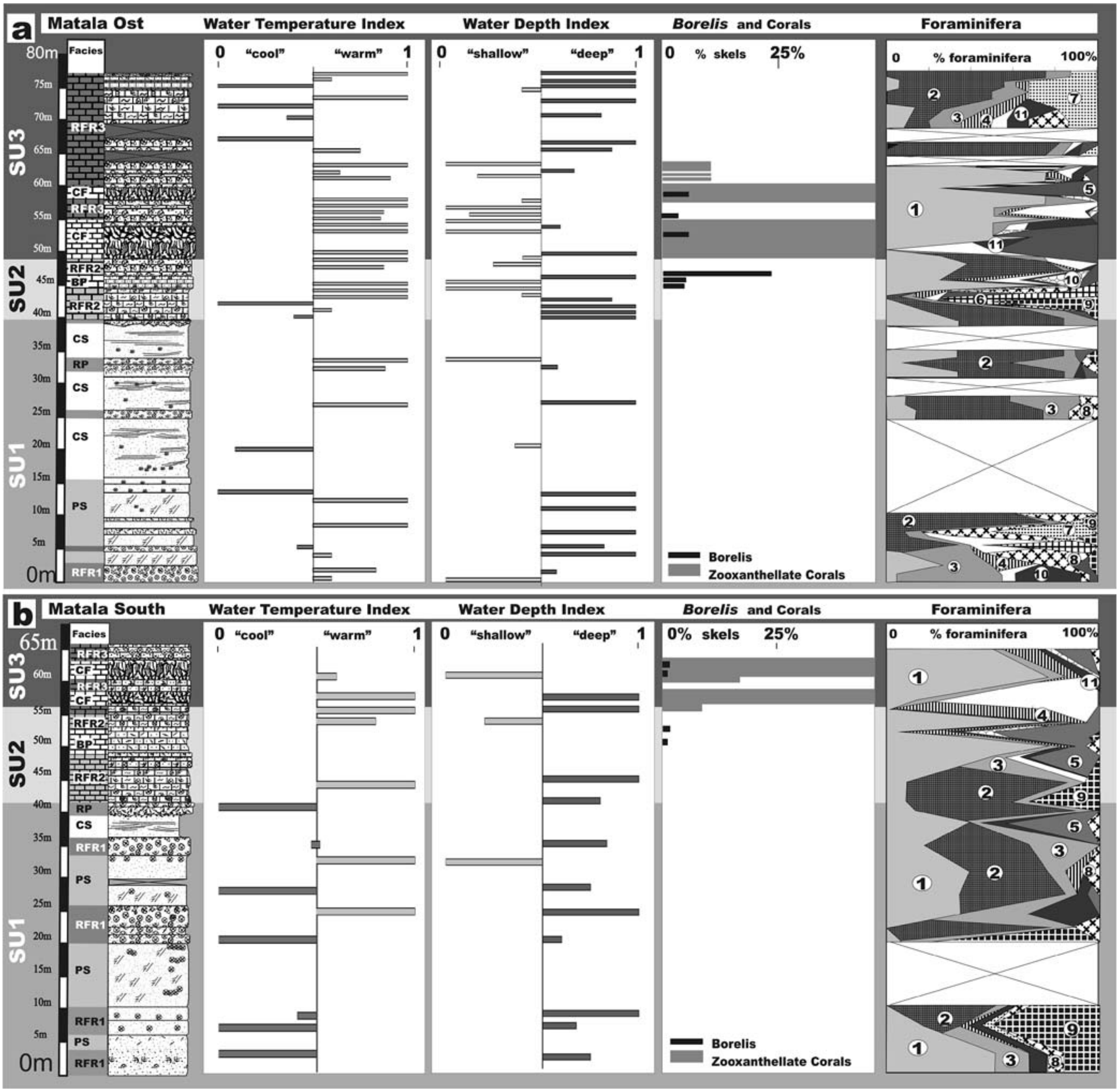


Fig. 12 Comparison of water depth and temperature index values calculated from abundances of coralline red algal genera with occurrence of corals and the tropical foraminifer *Borelis* and the distribution of foraminifera as shown in Fig. 9. Representation of red algal indices with *bars* originating at 0.5 was chosen to show values of zero. Values of 0.5 are represented by short *centred bars*

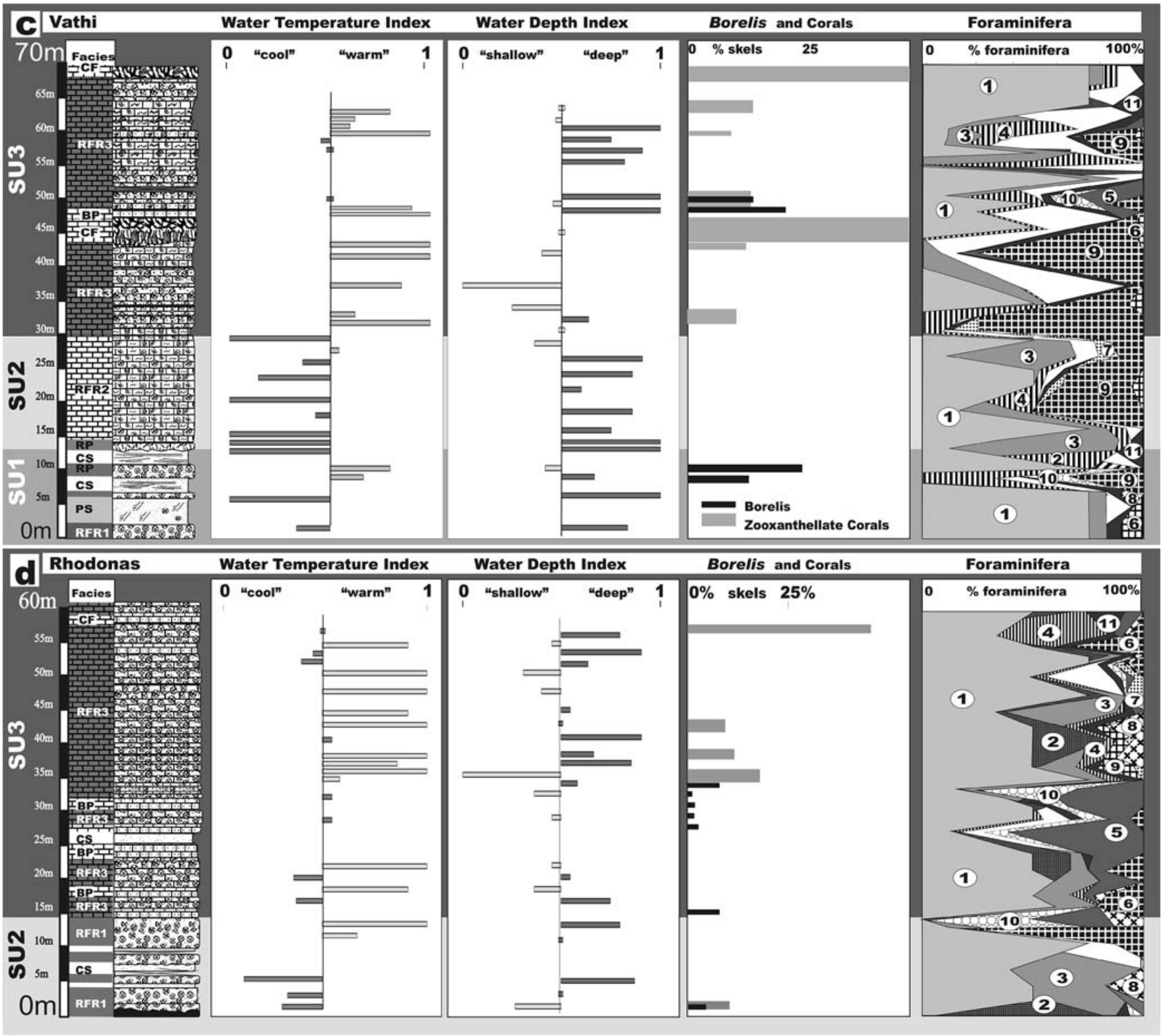


Fig. 12 Continued

low "warm" environments, an association characterised by dominant *Lithothamnion* in deep "cool" environments and a *Mesophyllum*-dominated association in "warm" deep environments. In consequence of the temperature dependency of coralline red algal associations and the different limitation in terms of light intensity of most red algal taxa, the shallow temperate association is not found in tropical deep water. Instead the deep temperate association is replaced by an entirely different association during climatic warming (Fig. 14). These associations can be identified in fossil material and used for palaeoclimatic reconstruction.

Palaeoecological interpretation

Based on stratigraphic analysis, facies analysis and analysis of foraminiferal and red algal associations, three ecological parameters, temperature, water depth and nutrients will be discussed in detail below. Other parameters such as light intensity, sediment input, turbulence and hydraulic energy are linked to these parameters.

The absence of typical brackish or hypersaline associations in limestones of the WAT suggests that salinity was normal marine. Other influences such as biotic interactions are hard to evaluate but important regarding the effects of shading or for epiphytic organisms and therefore potentially influence the distribution of certain foraminifera and non-geniculate coralline red algae.

Nutrients

Rhodalgal or foramol sediments with larger benthic foraminifera are common in the Miocene of the Mediter-

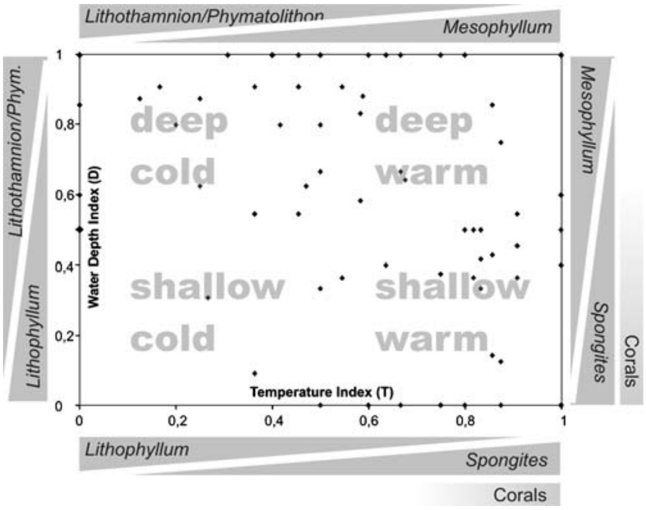
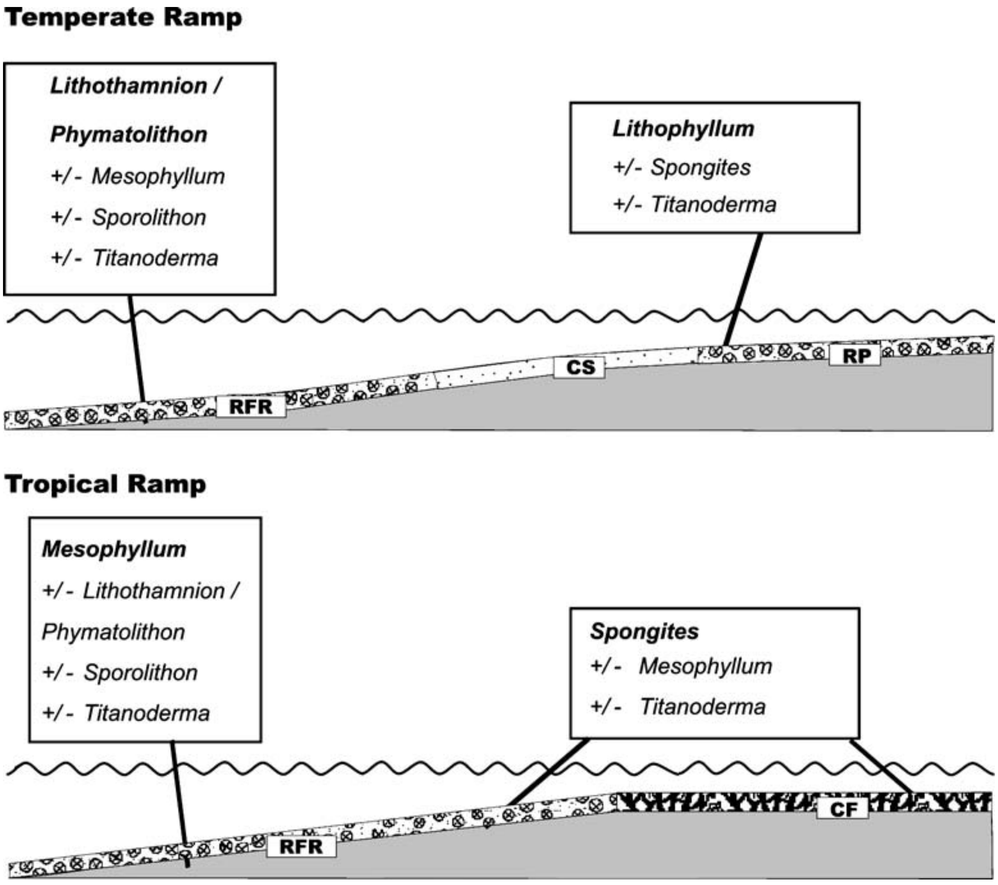


Fig. 13 Relationship between water depth and temperature index values and relative change in abundance of relevant coralline red algal genera; absence of trends indicates independence of both index values

ranean. Since most larger benthic foraminifera occur only in oligotrophic environments (Langer and Hottinger 2000), most Mediterranean sediments are not likely to have been deposited under high nutrient conditions. Little is known about the trophic tolerances of non-geniculate coralline red algae. A lower proportion of red algae in the PS facies, where increased nutrient input is indicated by foraminiferal associations and the abundance of *Turritella*, suggests that non-geniculate coralline red algae are generally susceptible to nutrient input. *Titanoderma pustulatum* appears to be sensitive even to small increases in nutrients. It is also unlikely that the slow growing red algae (on average 1 mm/year; Freiwald and Henrich 1994) profit from high nutrient input, which promotes fast growing organisms in competition for space. Nevertheless, data of Halfar et al. (2004) suggest that non-geniculate coralline red algae tolerate short periods of annual eutrophication as a consequence of upwelling. It is also noteworthy that, in contrast to non-geniculate coralline red algae, geniculate red algae tolerate eutrophical conditions as well as variable salinities (Johansen 1981). Therefore, environmental preferences of non-geniculate and geniculate coralline families are not to be mixed up in palaeoenvironmental reconstructions.

Besides upwelling, the sources of nutrients in seawater are mainly continental runoff and advection (Hallock and Schlager 1986). Upwelling as a source of nutrients depends on the availability of cold, nutrient-rich deep waters. In the modern Mediterranean, the availability of nutrients in deep water is limited by the Mediterranean circulation pattern (anti-estuarine circulation, Seibold 1970): Relatively warm and nutrient-poor Atlantic surface water enters the Strait of Gibraltar sinks and forms Mediterranean deep water. Modelling by Meijer et al. (2004) suggests similar circulation patterns for the Tortonian. Therefore, a general eutrophication of the Mediterranean appears to be unlikely. Nutrient

Fig. 14 Coralline red algal associations in warm-temperate and tropical environments and their occurrence on schematic Tortonian ramp profiles



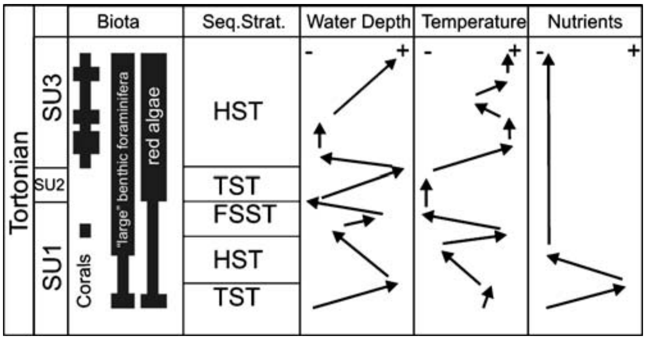


Fig. 15 Occurrence of most important biota and sequence stratigraphy of the Tortonian limestone succession of the WAT with trends in water depth and temperature based on coralline red algal indices and nutrient input inferred from biotic associations

input by continental runoff, on the other hand, may have played an important role, especially if increased by mountain uplift or high precipitation.

In the WAT, increased nutrient input from the hinterland is indicated only for the lower part of SU1 (PS facies; Fig. 15), where *Ammonia* and turritellid gastropods are abundant and *Titanoderma* is absent. A decrease in siliciclastic input observed in the WAT and elsewhere on Crete (Meulenkamp et al. 1979a,b) in the course of the Tortonian reflects a change from humid to arid climatic conditions (Reuter et al. 2006).

In conclusion, biotic associations, circulation patterns and increasingly arid conditions suggest deposition under oligotrophic conditions for the largest part of the limestone succession of the WAT (Fig. 15).

Temperature

Since the recognition of non-tropical carbonates in modern and ancient settings (Lees and Buller 1972; Carannante et al. 1988; Nelson et al. 1988; Brachert et al. 1993), temperature is known to be a key factor controlling the character of carbonate sedimentation. For many reasons, however, it is difficult to relate changes in sedimentary environments and skeletal associations to absolute temperature values. As discussed before, the best approach is to use the appearance or disappearance of certain temperature-sensitive biota in a sedimentary succession as an indication that water temperature rose above or fell below a critical threshold temperature. However, these biotic markers should be interpreted carefully for the following reasons:

1. Temperature thresholds usually relate to surface temperatures, whereas the critical organisms may live at various water depths and water temperature may not gradually decrease with water depth (thermoclines).
2. While threshold temperatures usually are given in minimum winter temperature it may also be seasonality or summer maximum temperature that is controlling the occurrence of critical biota.
3. The minimum temperature at which the organisms thrive may depend on various ecological factors other than water depth.

As discussed before, using non-geniculate coralline red algal associations for the calculation of a water temperature index largely eliminates the influence of other ecological factors such as water depth and nutrients. Water depth and temperature are limiting factors on the occurrence of both, zooxanthellate corals and non-geniculate coralline red algae. Increased nutrient and siliciclastic sediment input however may have prevented coral reef formation despite otherwise favourable conditions in the lower part of the limestone unit (SU1; Fig. 15). A red algal index >0.5 correlates with the occurrence of zooxanthellate corals and foraminifera indicative of elevated minimum temperatures. High indices, however, are also found in sediments deposited under oligotrophic conditions without zooxanthellate corals (Figs. 12 and 15). In this case the absence of corals is related either to higher water depth or to a threshold temperature which is lower for the occurrence of "warm" red algal associations (*Mesophyllum* and *Spongites* associations; Fig. 14) than for the formation of zooxanthellate coral frameworks (Fig. 15). Therefore, high temperature index values may indicate both, warm-temperate and tropical conditions. "Shallow" warm-temperate associations that are close to the threshold of the tropical biotic association correspond to the rhodozoan association of Halfar et al. (2000) wherein red algae are abundant together with non-framework-forming zooxanthellate corals. Index values between 0 and 0.5 in intervals with abundant large benthic foraminifera but without zooxanthellate corals (Fig. 12) are also indicative of warm-temperate environments. Thus, the index based on non-geniculate coralline red algae is a high resolution palaeo-thermometer for warm-temperate environments.

Due to annual variability of surface water temperatures and non-linear temperature profiles in the water column, the index can be only an approximation for surface temperatures: According to the data from Crete, the transition between the *Lithophyllum*/*Lithothamnion* associations and the *Spongites*/*Mesophyllum* associations occurs at an annual minimum surface temperature of between 14 and 18°C as defined by the presence of *Amphistegina* and absence of zooxanthellate corals in shallow oligotrophic water (Fig. 16). The threshold between "cold" and "warm" coralline red algal associations therefore is concluded to be around 16°C, reflected by index values intermediate between 0 and 1. Accordingly, a water temperature index of 0 indicates temperatures of less than 16°C and a temperature index of 1 temperatures of more than 16°C.

Water depth

As recognised by Lees and Buller (1972) and Carannante et al. (1988), tropical deep-water sediments may resemble non-tropical shallow-water sediments in their biotic makeup. To draw a conclusion on climate, it is therefore necessary to know the depositional depth of the analysed sediments. As discussed before, the red algal association in deep warm environments differs from the association in cold shallow environments and a specific association is

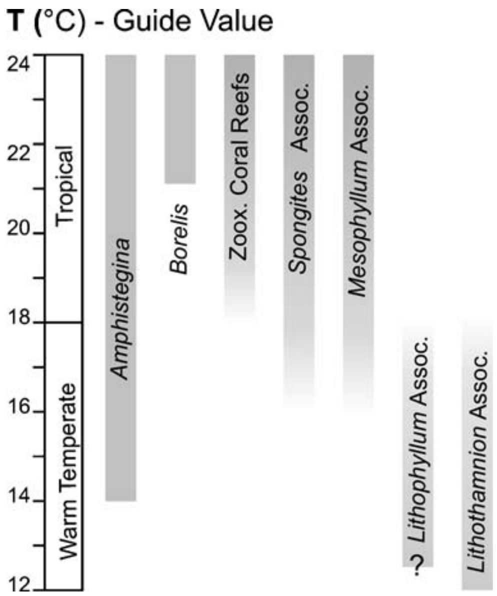


Fig. 16 Temperature range for the occurrence of selected biota in comparison with red algal associations. All temperatures are winter minimum sea-surface temperatures. Note that absolute temperatures are only guide values that may be modified by other environmental parameters

therefore indicative for both water depth and temperature. Therefore, the water depth index can be regarded independently from the temperature index. Though similar as for water temperature it is, however, difficult to draw quantitative conclusions on water depth. Since the required or tolerated amount of light is the controlling factor on red algae and other biotic water depth indicators, various factors influence the water depth in which a certain association is found, water turbidity is most important but shading by other organisms or reflectivity of the sea-floor are also key factors.

Nevertheless, by comparison with recent occurrences of the analysed red algae, water depth ranges can be defined; data from eastern Australia (Lund et al. 2000) suggest that *Lithothamnion* and *Mesophyllum*, which are the most important "deep-water" genera in the analysed material from the WAT, are most abundant at water depths below 40 m. This is in agreement with the abundance of *Amphistegina lessonii* in sediments of the WAT with high water depth index values. It also agrees with the hydrodynamic interpretation that sediments with high water depth indices are relatively low-energy outer ramp deposits: The upper limit of the outer ramp is defined by the position of the storm-wave base (Burchette and Wright 1992) which is at 30–40 m water depth in the modern Mediterranean (Betzler et al. 1997). Water depth index values between 0 and 0.5 are typical for the CF facies (Fig. 12), which represents a similar environment to *Porites* carpets as reported from water depths of no more than 25 m in the modern Red Sea (Riegl and Piller 1997, 1999). Occasional high water depth index values in the coral horizons in section MO are a consequence of the occurrence of *Mesophyllum sanctidionysii* in shaded environments within the carpet. Single tabular coral colonies occur in intervals with intermediate water depth index values. These intervals therefore can be linked to the most shoreward reaches of RFR3 facies and may thus correspond to a water depth between 25 and 40 m.

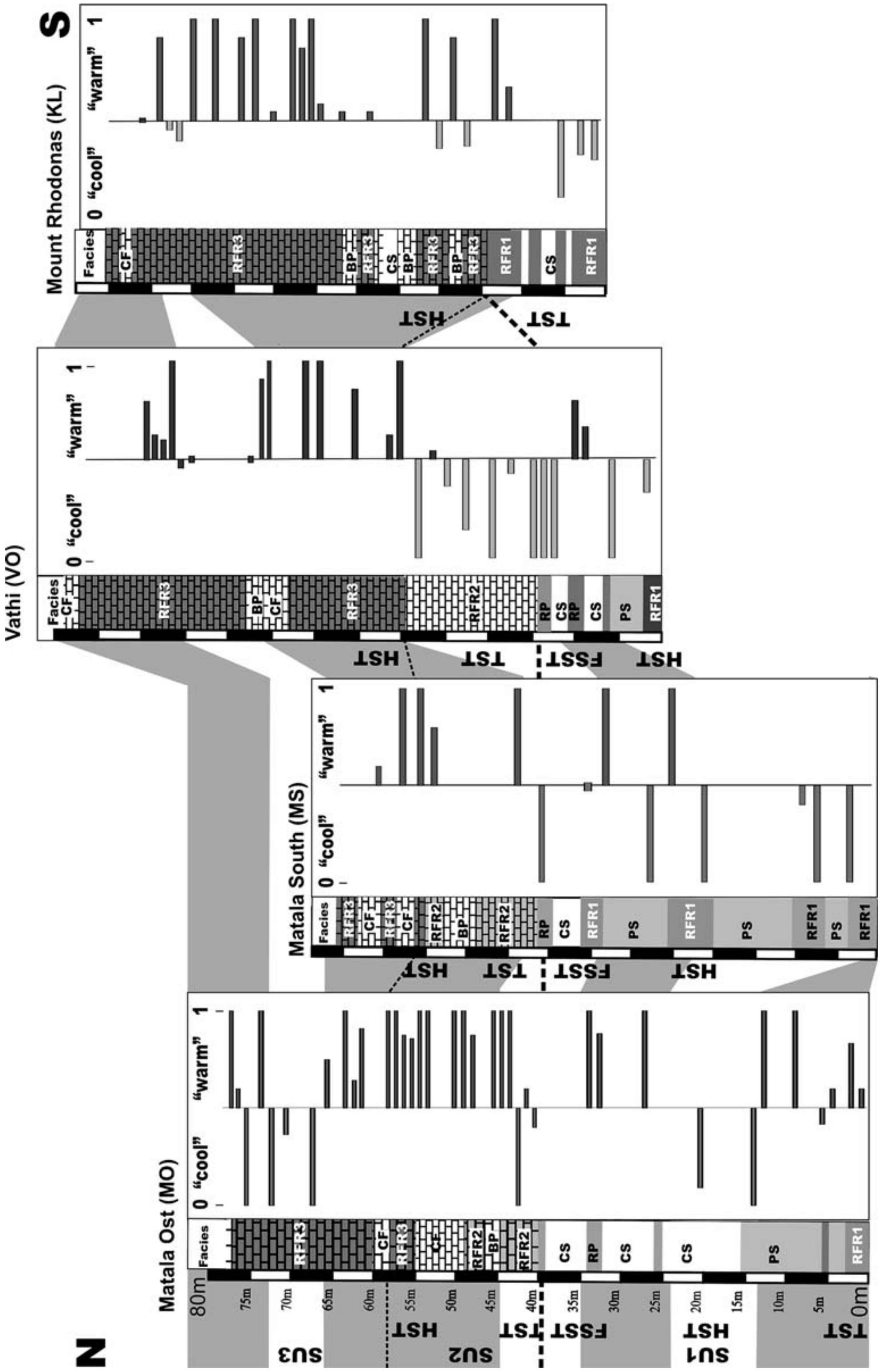
Climate change

Changes in non-geniculate coralline red algal associations were controlled by ecological change which can be related to climatic change and relative sea-level fluctuations. A total of four warm intervals are recognised in the limestone succession of southern central Crete (Fig. 17): the oldest during transgression and early highstand as observed at the base of SU1 in the area of Matala (section MO), a second interval related to late highstand deposits within SU1, a third interval that resulted in widespread coral carpet formation or growth of coral colonies and a fourth interval at the top of sections during which patchy coral carpets formed in the southern part of the WAT. The two younger intervals fall into the highstand that is represented by the up to 50 m thick limestone succession of SU3. Its thickness can be attributed to strong subsidence that caused the overall deepening trend at the top of the limestone succession in the WAT, when, eventually, sedimentation could not keep up with relative sea-level rise.

Separation of sedimentary units in the field was based strictly on lithologic criteria. At the boundary between SU2 and 3 that has been defined on the basis of the occurrence of zooxanthellate corals lithostratigraphic units also have a climate stratigraphic aspect. This boundary reflects a transition from cooler to warmer water temperatures which is also indicated by the change in non-geniculate coralline red algal associations. However, since the warm red algal association occurs at lower temperatures than framework-forming zooxanthellate corals, the change in coralline red algal associations occurs below the SU2/SU3 boundary. Because red algal associations have a larger depth range than zooxanthellate corals, red algal associations as a stratigraphic marker are less affected by local variation in water depth. We therefore suggest that coralline red algal associations can be used in climate stratigraphy to fine-tune chronostratigraphic frameworks similar to the approach used by Brachert et al. (2001) in Miocene carbonates of southern Spain.

Climate stratigraphy implies a relationship to regional or global climatic processes. The data presented here are not sufficient to correlate the warm intervals globally. However, warm intervals found in the WAT are related to times of relative sea-level highstand (Fig. 17). The two sequences are separated by a correlative surface (type II sequence boundary) which is recognised in the largest part of the WAT and, where present, also forms the boundary between SU1 and 2. Since, in sequence stratigraphy, sediments underlying a sequence boundary are always older than sediments above it, and since there is no visible erosional event between deposition of both sequences in the largest part of the WAT, observed changes in water depth are concluded to be approximately contemporaneous and a reflection of relative sea-level change.

Fig. 17 Comparison of temperature indices in the measured sections calculated from abundances of coralline red algal genera and sequence stratigraphic interpretation. Warm intervals are shaded *grey*. Note that intervals with high temperature indices fall into the highstand systems tract (HST)



Contemporaneous sea-level change within the WAT alone does not necessarily indicate a relationship to eustatic change. However, we interpret the connection of warm intervals to highstands to reflect a response to global climate change.

Conclusions

Data from Crete show that it is possible to use results based on coralline red algal assemblages as an approximation of water temperature and water depth. In Tortonian limestone of Crete, four non-geniculate coralline red algal associations indicative of specific conditions in terms of water depth and water temperature are found:

1. (1) The *Lithophyllum* association which is typical for warm-temperate conditions with annual minimum seawater surface temperatures well below 18°C and a maximum abundance in the upper photic zone shallower than approximately 40 m, depending on turbidity.
2. (2) The *Lithothamnion* association occur at surface temperature conditions similar to those that favour the *Lithophyllum* association but is restricted to the lower photic zone and shaded environments.
3. (3) The *Spongites* association which is dominant under warm-temperate conditions if annual minimum surface temperature does not fall under a minimum value of approximately 16°C (Fig. 16) and which is also typical for the tropical faunal province in the upper photic zone shallower than ~40 m.
4. (4) The *Mesophyllum* association which dominates the lower part of the photic zone and in shaded environments under similar conditions as the *Spongites* association.

The temperature limits between the described non-geniculate coralline red algal associations lie within the warm-temperate realm and therefore they can be used most efficiently to analyse warm-temperate sediments. However, to assign absolute values to the four associations with a high level of confidence more detailed studies of modern non-geniculate coralline red algae are necessary. Nevertheless, we propose that the indices presented here can be used in Miocene sediments of the Mediterranean and are transferable into other regions. We also suggest that at this stage, the utilisation of coralline red algal indices should be supported by analysis of as many other data as possible.

Biotic assemblages found in Tortonian limestone of southern central Crete suggest prevailing oligotrophic conditions of deposition, especially in the upper parts of the limestone succession. This is in accordance with an upward decrease in continental input and an increasing aridity in the Mediterranean region. It is also in accordance with the nutrient budget of the Mediterranean that is chiefly controlled by input from continental sources, not by upwelling.

Our data show that among the remaining factors, change in water temperature and water depth are most important in controlling biotic associations and character of facies. The application of non-geniculate coralline red algae as palaeoenvironmental indicators allows for the separation of effects of change in water depth and water temperature. Temperature and water depth indices based on coralline red algal associations thus are important proxies for the identification of changes in climate.

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