Calcareous nannofossils in extreme environments: The Messinian Salinity Crisis, Polemi Basin, Cyprus

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Abstract

The rapidly changing and extreme environmental conditions of the early Messinian Salinity Crisis are reflected in abrupt variations in nannofossil assemblages within the Messinian units (Kalavasos Formation) from the Polemi Basin. During the Messinian, sedimentary and microfossil data indicate that the Polemi Basin was a semi-enclosed, shallow water basin, subject to repeated influxes of marine and freshwater. This is supported by the absence of many open marine nannoplankton (e.g. *Discoaster*) and by the presence of neritic–littoral and freshwater diatoms. Whilst calcareous nannoplankton are known to occupy near-shore habitats, they are rarely preserved in such environments due to terrigenous and clastic influx. The shallow and eutrophic environments of the Messinian Polemi Basin therefore provide an unusual opportunity to investigate which extinct nannofossil taxa occupied marginal marine environments.

Nannoplankton diversity (3 to 11 species) is low in comparison to the open ocean, and the assemblages are extremely uneven, with high dominance. One of five species, *Reticulofenestra minuta*, *Reticulofenestra antarctica*, *Helicosphaera carteri*, *Umbilicosphaera jafari* and *Sphenolithus abies*, was observed to dominate in all of the assemblages. These were broadly distributed marine species, but capable of opportunistic behaviour. Salinity and nutrient levels are thought to be the primary factors controlling the overall nature of the nannoplankton assemblages. Using the associated diatom and sedimentological evidence we infer the palaeoecology of key nannofossil taxa and speculate on the palaeoenvironments of the Messinian Polemi Basin. *R. antarctica* is thought to have dominated in normal salinity, mesotrophic, shallow water environments; *H. carteri* in shallow, brackish, eutrophic environments; *U. jafari* in hypersaline conditions; *R. minuta* in eutrophic conditions with an abnormal salinity from brackish to hypersaline and *S. abies* in mesotrophic, deeper and normal salinity environments.
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1. Introduction

1.1. The Messinian Salinity Crisis

The Mediterranean Basin underwent dramatic changes in the Messinian (Late Miocene), when the Mediterranean Sea became isolated from the Atlantic

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at ~5.96 Ma (Krijgsman et al., 1999; Krijgsman et al., 2002) as regression in the Atlantic Ocean and shifting lithospheric plates caused the narrow connection(s) near the Straits of Gibraltar to close. The subsequent interval of evaporation, desiccation and greatly restricted circulation, termed the *Messinian Salinity Crisis* (Hsü et al., 1973, 1977), is reflected in the extensive and widespread evaporite deposits around and underlying the modern Mediterranean Sea (Hsü et al., 1973; Van Couvering et al., 1976). Astronomical chronology has revealed that the onset of major evaporite deposition was synchronous across the Mediterranean (Krijgsman et al., 2002). Pelagic oozes are found within the Messinian evaporites (Hsü et al., 1973; Di Stefano and Catalano, 1976; Rio et al., 1976), and are evidence of the intermittent flooding of marine waters into the desiccated Mediterranean Basin, indicating repeated desiccation and refilling (Hsü et al., 1973; Bandy, 1973).

In general terms the Messinian Mediterranean is adequately understood, however, many significant aspects are still outstanding, such as, the nature of the aquatic environments through the Messinian, the response of fauna and flora at this time, and whether normal marine salinities developed periodically throughout the interval. This study concentrates on the nature of the unusual environments in the Polemi Basin, Cyprus, directly prior to the major drawdown and extensive evaporite deposition of the Messinian Salinity Crisis (~6 Ma), using analysis of calcareous nannofossil assemblages. Diatom data (Burnside, 1997) and foraminifera results have also been incorporated to aid palaeoenvironmental and palaeoecological determination.

1.2. Geological setting

The south Polemi Basin, Cyprus (33°33′E, 35°00′N) (Fig. 1), is situated in a graben orientated NE–SE and bounded by steep faults (Payne and Robertson, 1995). During the Messinian, the small and elongate Polemi Basin was semi-isolated from the Mediterranean Sea by a tectonically active sill (Rouchy and Saint Martin, 1992; Roberston et al., 1995). Messinian evaporites were deposited in shallow marine environments after a lowering of sea-level and local tectonic uplift produced fault-bounded basins and gave rise to the environment required for evaporite formation (Gass and Cockbain, 1961; Robertson, 1977; Roberston et al., 1995). These sediments are known as the Kalavasos Formation and comprise gypsum and gypsiferous marls, with intercalated deposits of chalk, diatomaceous marl and claystones (Pantazis, 1978; Rouchy and Monty, 1981), which can be correlated with the extensive Messinian evaporites seen elsewhere in the Med-
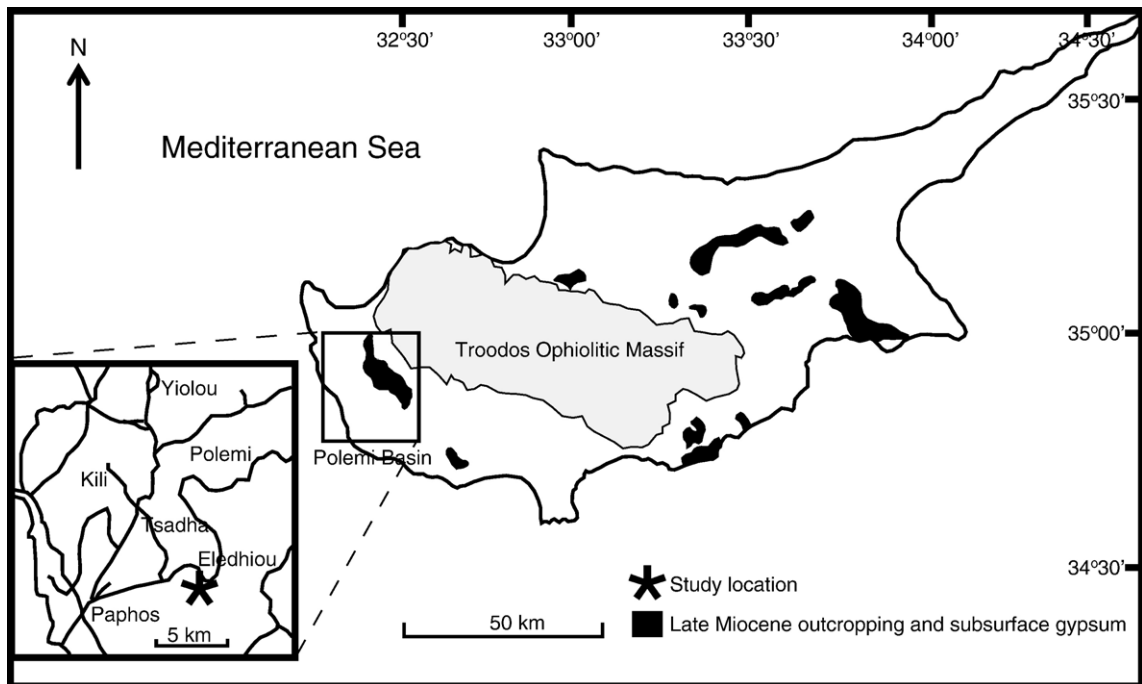

Fig. 1. Simplified map of Cyprus showing the distribution of Messinian evaporites and location of the Polemi Basin. Redrawn after Robertson (1977) and Rouchy and Monty (1981).

iterranean (Decima and Wezel, 1973; Robertson, 1977; Rouchy, 1982; Roberston et al., 1995).

In the Polemi Basin, the Kalavasos Formation locally overlies the Pakhna Formation (early–late Miocene), which is composed of pelagic and bioclastic limestones and interbedded marls (Follows et al., 1996). Field observations indicate that the top of the Pakhna Formation (~6 Ma; Krijgsman et al., 2002) is characterised by a prominent band with the large foraminifera *Discospirina*, characteristic of a warm, shallow-water environment. The change in lithology from the Pakhna to the Kalavasos Formation is thought to represent a gradual decrease in bathymetry and progressive marine isolation, resulting in the transition from shallow marginal marine to evaporite conditions (Robertson, 1977).

1.3. Calcareous nannofossils

Calcareous nannofossils are a principal component of the marine phytoplankton and comprise coccoliths and nannoliths. Cocccoliths are exoskeletal plates formed by coccolithophores, phytoplanktonic, haptophyte algae. Nannoliths are similar sized calcareous fossils which lack the characteristic features of coccoliths and so are of uncertain origin, although many are probably formed by Haptophytes (Bown and Young, 1998). Coccolithophores occupy the surface waters, and are thus affected by changes in the surface water environment, particularly temperature and nutrient availability. A number of extant species exhibit a wide range of environmental tolerances, such as *Emiliania huxleyi*, which occupies nearly all coccolithophore habitats of the marine photic zone (Brand, 1994). However, surface temperature, salinity, fertility and bathymetry restrict the distributions of many species, with the greatest diversity in low latitude, open-ocean, oligotrophic, stratified habitats (Winter et al., 1994).

In this paper, calcareous nannofossil assemblages are analysed in order to investigate the temporal palaeoenvironmental variations through the Messinian of the Polemi Basin, Cyprus. Whilst coccolithophores are known to occupy shallow water, near-shore environments (e.g. Cachao et al., 2002), their preservation in such habitats is rare due to dilution by clastic influx and increased dissolution in coarse grained sediments. The sediments of the Polemi Basin include fine-grained marls, with good nannoplankton preservation, providing an unusual snapshot of palaeoenvironments during the early Messinian Salinity Crisis and the chance to investigate which extinct species inhabited marginal marine zones. The goals of this study were to: (1)

document the nannofossil assemblages within the Messinian Polemi Basin; (2) examine the nannofossil assemblages in order to establish which taxa occupied near marginal marine and rapidly fluctuating environments; (3) combine the microfossil and sedimentological data to reconstruct environmental dynamics and surface water features in the Polemi Basin during the early Messinian Salinity Crisis.

2. Methodology

2.1. Sample collection

Sampling was focussed on the marls, chalks and claystones within the lower part of the Kalavasos Formation. Based on the astrochronology of the coeval Pissouri Section, our sequence covers a relatively short interval (~40–60 kyr) and represents the transitional interval prior to the onset of major drawdown and significant evaporite deposition (5.96 ± 0.2 kyr; Krijgsman et al., 2002). Whilst the sections are discontinuous, these sediments present a succession with which to document the short-term ecological dynamics of calcareous nannoplankton in the extreme environments of the early Messinian Salinity Crisis. Sample spacing was determined by the occurrence of favourable lithologies; breccia, sandstones and evaporite units were avoided.

Samples were taken from two sections in the southern part of the Polemi Basin, western Cyprus. Section 1a (Fig. 2) is rich in diatoms and nannofossils and is approximately 7.5 m thick. The section begins above a band of white, weathered chalk containing abundant *Discospirina* foraminifers, representing the top of the Pakhna Formation. The Kalavasos Formation consists of laminated and brecciated gypsum deposits with intercalations of chalk, and laminated green to brown diatomaceous claystones. Section 1b (Fig. 2) is located several metres to the north of Section 1a and forms part of a continuous outcrop. Close to the top of the section is a thick, fining upward sandstone unit. The sandstone body is laterally continuous from Section 1a to Section 1b (Fig. 2). From field relations and sedimentological evidence, we interpret this unit as a channel infill deposit. Samples 9 to 15 and 7, 8, 16, 17 and 18 were taken from Sections 1a and 1b, respectively. Higher resolution sampling was conducted on the claystone unit of Section 1b, using sample spacing of 10 cm (samples PB1 to PB9).

Section 2 (Fig. 2) consists of massive and selenitic gypsum interbedded with white to green laminated marls and clays. Seven samples (20, 21, 22, 24, 26,
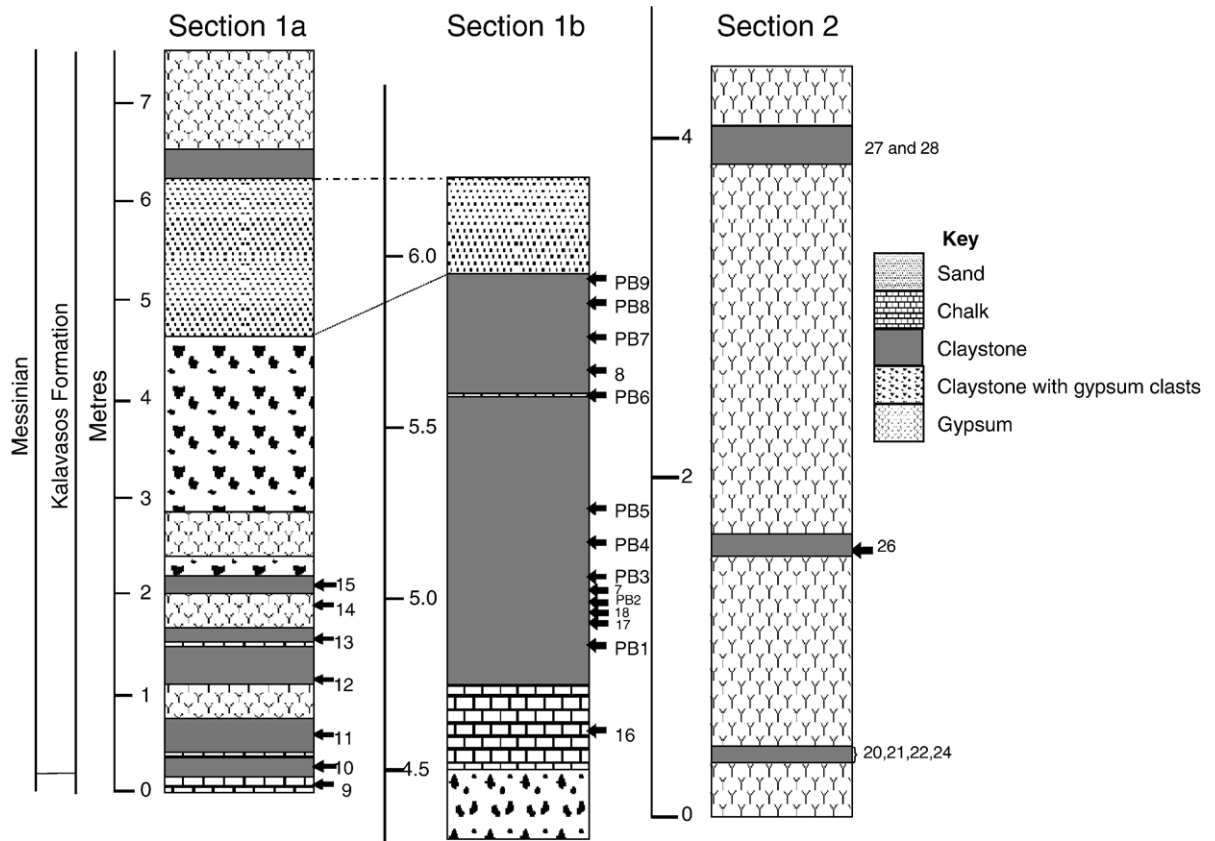
Fig. 2. Stratigraphic Sections 1 and 2, Kalavasos Formation, showing the position of samples studied and laterally continuous sandstone body, note changes in scale from section to section.
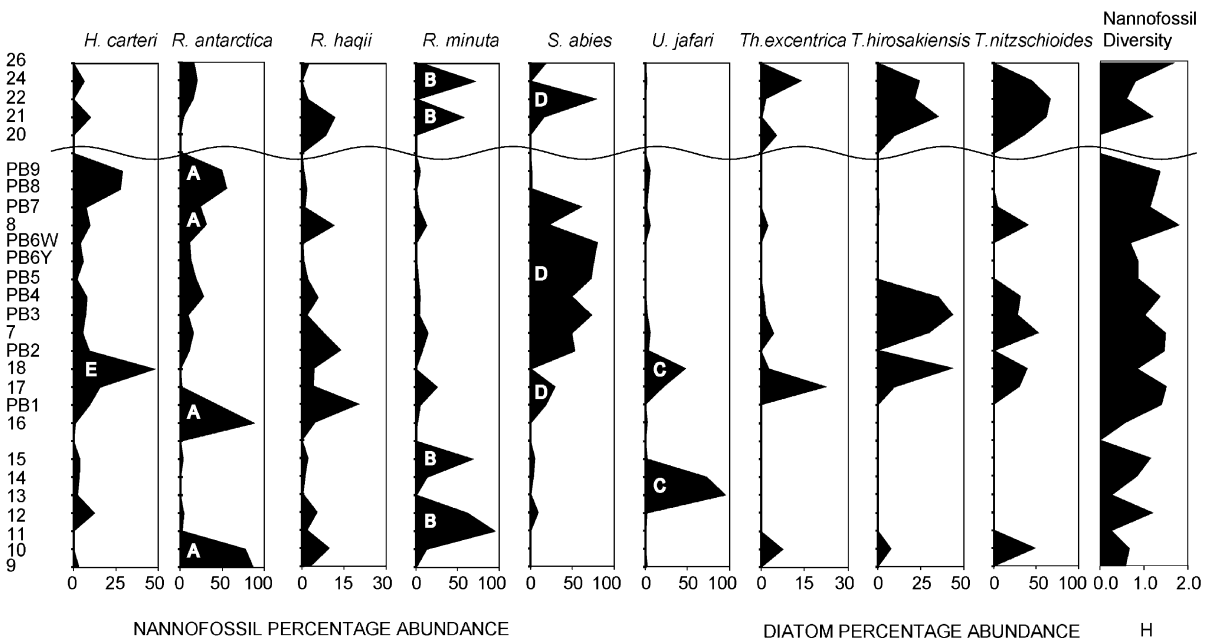

Fig. 3. Percentage distribution of dominant nannofossil taxa and selected diatom taxa. Note changes in scale. Letters denote dominant assemblages discussed in the text, (A) *R. antarctica*; (B) *R. minuta*; (C) *U. jafari*; (D) *S. abies*; (E) *H. carteri*.

Table 1
Nannofossil assemblage data for the south Polemi Basin, Cyprus

Species/sample	9	10	11	12	13	14	15	16	17	18	7	8	20	21	22	24	26	PB1	PB2	PB3	PB4	PB5	6Y	6W	PB7	PB8	PB 9
A. primus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
C. leptoporus	9	–	–	4	–	–	14	3	–	–	3	4	–	–	–	–	7	3	3	2	1	–	6	3	–	8	10
C. macintyrei	–	–	–	–	–	–	1	1	–	–	–	–	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cc. pelagicus	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–
D. variabilis	–	–	–	–	–	–	–	–	–	–	–	–	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–
H. carteri	9	–	–	37	7	10	11	3	47	143	16	29	–	30	–	19	–	28	28	21	24	6	17	12	22	83	87
P. discopora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	4	2	–	2	–	–	–	–
P. multipora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–
Pontosphaera spp.	3	–	–	2	3	–	7	2	–	–	2	–	–	–	–	–	–	–	–	–	3	–	–	3	–	1	1
R. antarctica	261	233	7	12	–	–	10	263	6	–	46	93	–	12	47	60	49	134	31	27	83	56	38	33	70	166	149
R. haqii	9	29	5	16	1	3	6	14	12	13	22	34	25	35	6	–	7	60	41	5	17	6	2	1	3	5	2
R. minuta	2	38	284	186	2	40	204	6	76	–	44	38	–	172	5	214	21	16	22	12	15	8	4	2	10	3	15
R. pseudoumbilicus	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Reticulofenestra spp.	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rh. claviger	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–
Rhabdosphaera spp.	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–
S. abies	–	–	2	27	2	10	15	1	88	1	148	66	–	48	234	1	56	55	159	219	149	218	228	239	182	5	6
T. striatus	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
U. jafari	7	–	1	5	285	218	7	7	65	143	18	18	–	–	–	6	–	3	10	7	2	2	2	–	6	11	18
Un. placolith	–	–	–	–	–	–	–	–	–	–	–	–	17	–	–	–	–	6	1	1	–	3	2	1	6	17	12
Unidentified	–	–	–	8	–	7	–	–	–	–	–	–	25	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Reworked	–	–	1	–	–	6	15	–	6	–	1	–	212	2	8	–	133	–	–	2	1	1	–	6	–	–	–
Total	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300
Diversity (H)	0.60	0.68	0.26	1.22	0.27	0.86	1.18	0.59	1.55	0.86	1.53	1.84	–	1.24	0.62	0.83	–	1.44	1.51	1.04	1.40	0.89	0.89	0.71	1.17	1.29	1.40

Abbreviations: *A.*=*Amaurolithus*, *C.*=*Calcidiscus*, *Cc.*=*Coccolithus*, *D.*=*Discoaster*, *H.*=*Helicosphaera*, *P.*=*Pontosphaera*, *R.*=*Reticulofenestra*, *Rh.*=*Rhabdosphaera*, *S.*=*Sphenolithus*, *T.*=*Triquetrorhabdulus*, *U.*=*Umbi-licopshaera*, Un.=unidentified.

27 and 28) were collected from this section. A reconnaissance study of samples 27 and 28 revealed that the nannofossil abundances of these samples were insufficient to undertake an accurate quantitative study.

2.2. Sample preparation

For detailed calcareous nannofossil examination, simple smear slides were prepared using standard procedures (Bown and Young, 1998). To maintain the original sediment composition, no concentration of the material was employed. For quantitative analysis 300 nannofossil specimens were counted per slide.

Standard techniques were used in diatom preparation and analysis (Battarbee, 1986), with 300 specimens counted per slide. Samples were also washed over a 63 μm sieve and qualitatively examined for their foraminiferal and ostracod content.

2.3. Taxonomic discussion of the genus *Reticulofenestra*

The taxonomy of the reticulofenestrid group is rather poorly constrained (see Young (1998) for discussion of reticulofenestrid morphology and taxonomy). The taxonomy used here is summarised as follows.
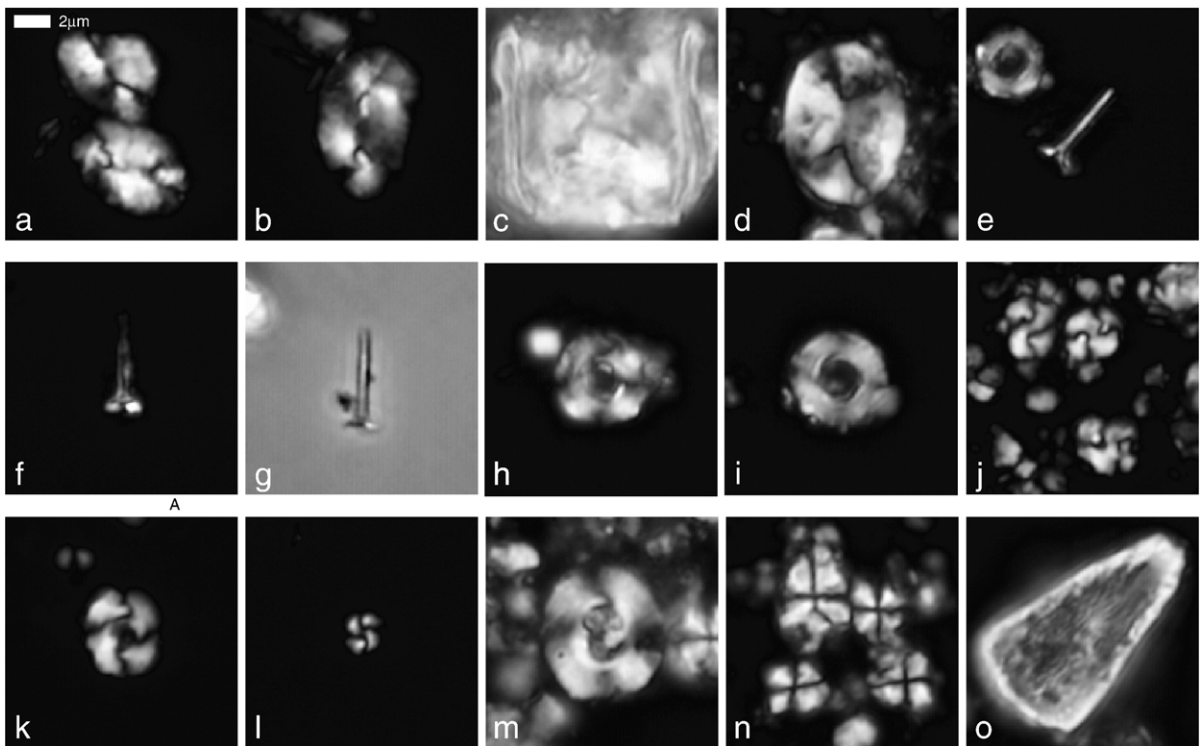

Plate I. Calcareous nannoplankton from the Polemi Basin. All images in crossed nicols except where indicated otherwise.

a)   *Helicosphaera carteri*, sample 18.
b)   *Helicosphaera carteri*, sample 21.
c)   *Scyphosphaera ? pulcherrima*, sample PB6Y.
d)   *Pontosphaera japonica*, sample PB6Y.
e)   *Rhabdosphaera clavigera*, sample 18.
f)   *Rhabdosphaera* spp., sample 18.
g)   *Rhabdosphaera clavigera*, sample 18 (transmitted light).
h)   *Umbilicosphaera jafari*, sample 13.
i)   *Umbilicosphaera jafari*, sample 13.
j)   *Reticulofenestra antarctica*, sample 16.
k)   *Reticulofenestra haqii*, sample PB6Y.
l)   *Reticulofenestra minuta*, sample 21.
m)   *Reticulofenestra pseudoumbilicus*, sample PB6Y.
n)   *Sphenolithus abies*, sample 22.
o)   *Ascidian spicule*, sample 18.

Table 2
Siliceous microfossil assemblage data from the Messinian Polemi Basin (Burnside, 1997)

Species/sample	9	10	11	12	13	14	15	16	17	18	7	8	20	21	22	24	26	PB1	PB2	PB3	PB4	PB5	6Y	6W	PB7	PB8	PB 9
Achnanthes dimbriate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
Actinoptychus spp.	–	–	–	–	–	–	–	–	–	–	–	36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Actinocyclus curvatulus	–	–	–	–	–	–	–	–	–	–	16	–	–	–	11	11	–	–	–	–	–	–	–	–	–	–	–
Amphora spp.	–	–	–	–	–	–	–	–	–	2	1	–	1	–	–	4	–	–	–	2	–	–	–	–	3	–	–
Archaeomonos japonica	–	–	–	–	–	–	–	–	14	1	–	7	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Asterolampra acutiloba	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum cososum	–	11	–	–	–	–	–	–	10	–	–	57	1	–	–	–	–	–	–	1	2	–	–	–	6	–	–
Chaetoceros spores	–	–	–	–	–	–	–	–	–	–	3	14	1	–	1	3	–	–	–	13	22	–	–	–	177	–	–
Cocconeis placentula	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2	2	–	–	–	2	–	–
Cocconeis scutellum	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	1	–	–	–	15	17	–	–	–	6	–	–
Cocconeis spp.	–	–	–	–	–	–	–	–	–	5	2	–	–	–	–	3	–	–	–	–	–	–	–	–	3	–	–
Coscinodiscus hustedii	–	–	–	–	–	–	–	–	5	–	–	–	2	4	–	7	–	–	–	–	–	–	–	–	–	–	–
Denticula spp.	–	11	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Epithemia spp.	–	–	–	–	–	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fragilaria inflata	–	–	–	–	–	–	–	–	10	–	1	–	–	3	–	–	–	–	–	–	–	–	–	–	1	–	–
Grammatophora oceanica	–	–	–	–	–	–	–	–	5	1	1	–	73	–	–	–	–	–	–	9	3	–	–	–	61	–	–
Grammatophora spp.	–	–	–	–	–	–	–	–	14	4	2	7	40	–	–	1	–	–	–	2	–	–	–	–	10	–	–
Mastoiglia braunii	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melosira spp.	–	56	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Nitzschia marina	–	11	–	–	–	–	–	–	–	–	–	–	–	–	5	5	–	–	–	–	1	–	–	–	–	–	–
Nitzschia spp.	–	–	–	–	–	–	–	–	19	7	–	–	5	–	4	4	–	–	–	1	6	–	–	–	1	–	–
Pseudopodosira westii	–	–	–	–	–	–	–	–	10	–	–	–	21	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Rhisosolenia spp.	–	–	–	–	–	–	–	–	–	–	7	–	10	–	–	7	–	–	–	31	36	–	–	–	1	–	–
Synedra undulata	–	–	–	–	–	–	–	–	–	7	–	–	–	–	2	1	–	–	–	–	–	–	–	–	1	–	–
T. hirosakiensis	–	22	–	–	–	–	–	–	29	129	89	–	29	105	64	73	–	–	–	130	107	–	–	–	2	–	–
T. nitzschioides	–	144	–	–	–	–	–	–	91	118	157	122	109	186	199	134	–	–	–	84	94	–	–	–	14	–	–
Thalassiosira eccentrica	–	22	–	–	–	–	–	–	67	8	13	7	16	1	5	41	–	–	–	5	3	–	–	–	–	–	–
Unidentified	–	23	–	–	–	–	–	–	26	9	5	29	12	0	5	5	–	–	–	4	6	–	–	–	12	–	–
Total	–	300	–	–	–	–	–	–	300	300	300	300	300	300	300	300	–	–	–	300	300	–	–	–	300	–	–

Abbreviation: *T.=Thalassionema.*

Reticulofenestra minuta = all reticulofenestrids <3 μm in length.

Reticulofenestra antarctica = reticulofenestrids 3–5 μm in length, with a closed central area.

Reticulofenestra haqii = reticulofenestrids between 3 and 5 μm with an open central area.

Reticulofenestra pseudoumbilicus = all reticulofenestrids larger than 5 μm.

3. Results

3.1. Nannofossils

Calcareous nannofossils are found in all the sections studied, and show variations in abundance, degree of preservation and assemblage composition. All assemblages are dominated by one of five species: *Helicosphaera carteri*, *R. antarctica*, *R. minuta*, *Sphenolithus abies* and *Umbilicosphaera jafari* (Fig. 3). The most abundant species was *S. abies*, but they were not found in all the samples. In contrast *R. minuta* was slightly less common, but present in almost every sample. *Reticulofenestra haqii* was present in most samples (up to 20%), but did not dominate any assemblage. The species *Calcidiscus leptoporus*, *Calcidiscus macintyrei*, *Coccolithus pelagicus*, *Pontosphaera* spp., *Scyphosphaera* spp., and *Rhabdosphaera* spp. were also present, typically occurring at abundances >1% and never more than 9%. Reworked components were identified in a number of samples, and the significance of these observations are discussed below. Relative abundances of the dominant nannofossils are plotted in Fig. 3, with data counts presented in Table 1. Species are listed alphabetically in Appendix A, with polarised and transmitted light images in Plate I.

Shannon's index (H′) was utilised to quantify the diversity (species richness and the evenness) of nannoplankton for each sample (Shannon and Weaver, 1949). The results range from 0.26 (sample 11) to 1.84 (sample 18), and are plotted with nannofossil assemblage data (Fig. 3). Low numbers indicate a reduced species richness and high dominance.

3.2. Diatoms

Thirteen of the samples studied contained diatoms abundant enough for quantitative analysis (Burnside, 1997). Marine planktonic species were dominant, with abundant *Thalassionema nitzschioides* and *T. hirosakiensis* (up to 66%). *Thalassiosira eccentrica* was also common with 22% in sample 17. Other diatom species included *Actinoptychus* spp., *Bacteriastrum comosum*,

Grammatophora oceanica and *Rhisosolenia* spp. (Burnside, 1997) (Table 2). Plots of diatom abundance were restricted to *T. nitzschioides*, *T. hirosakiensis* and *T. eccentrica*, as these species exceeded abundances of 15% and were considered of environmental significance within the samples studied for nannofossil assemblages (Fig. 3).

3.3. Foraminifera

Benthic foraminifera within the sequence include *Triloculina* spp. (sample 9), *Cibicidoides* spp. (sample 11), *Bulimina aculeata*, *Elphidium* spp. (sample 15) and *Bolivina spathulata* (samples 21, 22 and 24). Planktonic foraminifera were rare or absent. Additionally, small bivalves and echinoid spines were present in sample 9 and 11. Sample 15 contained sponge spicules, fish teeth, gastropods and ostracods (*Bythocypris* spp. and *Hemicythere* spp.).

4. Discussion

4.1. Diatom analysis

Diatoms are sensitive to salinity and the majority of species recorded here are marine in origin. However, brackish to freshwater species (e.g. *Melosira*) are also present, indicating freshwater input into the Messinian Polemi Basin (Burnside, 1997). The basin was probably subject to fluctuations in salinity with shifts from brackish water conditions to hypersaline environments immediately prior to gypsum deposition.

The presence of diatoms in the sections indicates highly productive environments. The samples are dominated by *T. nitzschioides*, a eutrophic species (Schuette and Schrader, 1979) that has previously been noted for its abundance in assemblages of other Late Miocene sections (e.g. Jurkschat et al., 2000; Bellanca et al., 2001; Blanc-Valleron et al., 2002; Pestrea et al., 2002). A eutrophic environment is also indicated by abundant *Chaetoceros* resting spores (59%, sample PB7), which are indicative of high productivity environments (Jurkschat et al., 2000). Nutrients were probably sourced from fresh-water runoff or river input, as attested by the presence of freshwater diatoms.

4.2. Reworking and preservation

The majority of samples yield well preserved, stratigraphically consistent nannofossil assemblages, however, two samples within and directly above the massive gypsum deposits (samples 20 and 26) included

reworked Cretaceous to Miocene specimens (71% in sample 20). Sample 14 was taken from the laminated gypsum itself, and although the assemblage was consistent with a Messinian age, all specimens are thought to be reworked due to the poor preservation. A small number of reworked specimens occur in other samples, but these were not in large enough quantities to impede environmental analysis.

Modification of assemblages by dissolution can alter the composition of coccolith assemblages (Roth, 1994) leading to low diversity. Although some etching and overgrowth was observed, the variability of the assemblages, the abundant presence of small and delicate coccoliths, and the absence of solution-resistant discoasters, indicates that the compositions are primary. The assemblages reveal striking abundance variations that cannot be explained by reworking, transportation, dissolution or diagenesis, and are thought to reflect palaeoecological responses to fluctuations in the physical and chemical environment, not a preservational artefact.

4.3. Nannofossil diversity

Many of the nannofossil species encountered in this study are extinct. Palaeoecological data for these species are limited, and therefore the Messinian coccolith assemblages are interpreted by analogy to modern environments, peri-tethyan nannofossil data and Messinian assemblages elsewhere.

One of the most striking features of these assemblages is the extremely low diversity (species richness) (Fig. 3), which is considerably lower than coeval open ocean assemblages. Excluding any reworked components, the samples contained between 3 and 11 species (Table 1). In modern nannoplankton assemblages, diversity is strongly correlated with environmental stability. High diversity assemblages are characteristic of stable, oligotrophic, mid ocean gyre habitats, whereas a decreased diversity is typical of highly fluctuating, eutrophic, unstable environments with extreme ecological conditions (Sanders, 1969; Aubry, 1992; Bollmann et al., 1993; Brand, 1994; Roth, 1994). The low diversities recorded here clearly indicate extreme palaeoenvironments.

4.4. Dominance

Dominance is a typical characteristic of disturbed and sub-optimal ecological conditions and is a feature of almost all the samples here. In the study sections the dominant species change over a very short sampling interval (Fig. 3), indicating a strongly and rapidly fluctuating environment. The highest dominance was observed in samples 11 and 12, with 95% *R. minuta* and 95% *U. jafari*, respectively (Fig. 3). The rapidity and magnitude of the shifting dominance may represent a good index for eutrophy and/or instability of the environment.

The variations in lithology, presence of diatom rich intervals and very low nannofossil diversities (H'= 0.26—sample 11; 1.84—sample 8) indicate very unusual environmental conditions (Fig. 3). Whilst temperature may influence species abundance, it is unlikely that such large variations would take place over these timescales. Changes in nutrient and salinity are far more likely to have shifted rapidly, and thus to have been the major control over the microfossil assemblages.

4.5. Comparison with open ocean settings

Species-restricted fossil assemblages are common in the Messinian Mediterranean and open marine species are frequently absent (e.g., Cita, 1973; Selli, 1973; Rouchy and Monty, 1981). A better understanding of the nutrient and salinity instability in the Polemi Basin can be gained from looking at the Messinian nannofossil species that were absent or rare in the studied interval. These include species of the genera *Discoaster*, *Ceratolithus*, *Amaurolithus* and *Triquetrorhabdulus* that are indicative of open-ocean, warm water conditions, and evidently were excluded by the unusual environments of the Messinian Polemi Basin. Ellis and Lohman (1979) found a rapid increase in these genera following the Pliocene marine transgression at Capo Rossello, Sicily and Deep Sea Drilling Project (DSDP) Leg 42, Sites 375/376 (Florence Rise, west of Cyprus) confirming that they were excluded from the Mediterranean area by ecological controls.

Discoasters are one of the key taxonomic groups absent from the assemblages. Discoasters were a diverse, k-selected group, common in oligotrophic, warm, deep water, stable environments (Haq, 1980; Lohmann and Carlson, 1981; Flores and Sierro, 1987; Chepstow-Lusty et al., 1989, 1992; Aubry, 1992; Young, 1998), but rare or absent at high fertility equatorial sites (Chepstow-Lusty et al., 1989; Chapman and Chepstow-Lusty, 1997) and in marginal seas (Perch-Nielsen, 1985). The exclusion of discoasters was therefore probably a function of environmental instability, particularly salinity and nutrient fluctuations.

Braarudosphaera is a long-ranging taxon with a curious palaeoecology, often suggested to be a neritic opportunist, capable of attaining high abundances in

periods of eutrophication and environmental stress, including reduced surface water salinity (Gran and Braarud, 1935; Takayama, 1972; Bukry, 1974). The absence of *Braarudosphaera* from the Kalavasos sequence is thus surprising. *Braarudosphaera* spp. were however present in the qualitative analysis of the underlying Pakhna Formation, which although not fully open marine in origin, and relatively shallow (50–200 m), probably did not experience the large fluctuations in salinity experienced during the Messinian Salinity Crisis. *Braarudosphaera,* though common in modern neritic environments, are not present in those with high salinity (e.g. Red Sea, Bukry, 1974). They may therefore have been excluded from the Polemi Basin by the extreme fluctuations in salinity and hypersaline conditions that directly preceded gypsum deposition. The absence of *Braarudosphaera* in near-shore environments has also been reported by Bybell and Self-Trail (1997).

Other absent or rare species include *C. pelagicus* and *C. leptoporus*. *C. pelagicus* is abundant in open ocean upper Miocene sediments and common in low salinity waters (~34‰) (McIntyre and Bé, 1967). Hypersaline environments may also have excluded these species.

4.6. Messinian nannofossil palaeoecologies

4.6.1. Reticulofenestra minuta

In samples 11, 12, 15, 21 and 24, more than 50% of the assemblage consists of *R. minuta* (Plate Il) with maximum values observed in sample 11 (95%) (Fig. 3). *H. carteri* accounts for up to 11% here and *S. abies* and *R. haqii* were also present in varying abundances.

Small reticulofenestrids such as *R. minuta* were documented to dominate the nannoflora along continental margins (Haq, 1980). These are usually eutrophic environments due to continental runoff and/or river input, and *R. minuta* are thus considered hardy, opportunistic taxa with wide ecological tolerance but capable of flourishing in nutrient-rich conditions (Aubry, 1992; Flores et al., 1995). The assemblages dominated by *R. minuta* are therefore thought to reflect eutrophic environments.

R. minuta may also have been able to withstand intervals of high environmental stress, respond quickly to changes within that environment and dominate in conditions where other nannofossil species cannot compete. *R. minuta* tend to dominate assemblages immediately prior to and following evaporite deposition. These are likely to be the most extreme shallow eutrophic environments with large salinity fluctuations.

Abundant *R. minuta* are associated with the diatom species *T. eccentrica* at some levels, with both of these species having elevated abundances in samples 17, 7 and 8 (Fig. 3). *T. eccentrica* is a brackish water diatom, associated with river mouths, with a preferred salinity range of 0.2–10‰ (Hajós, 1973). Enhanced river input and continental runoff may have resulted in the periodic development of eutrophic, brackish surface waters and the observed increase in *T. eccentrica* and *R. minuta*. It can therefore be inferred that *R. minuta* may have tolerated the brackish to hypersaline, high productivity environments, which prevailed immediately before and after the evaporite deposition. Anomalous assemblages of small reticulofenestrids were also documented from Messinian sediments of the DSDP Site 372 (Balaeric Sea) (Müller, 1985).

4.6.2. Helicosphaera carteri

H. carteri (Plate Ia and b) is one of the five dominant species here, but typically formed a minor component of the assemblages. *H. carteri* is a cosmopolitan species, which occupies both neritic and oceanic environments and is a dominant species in the Mediterranean today (Ziveri et al., 2000). An abundance increase in *H. carteri* in sample 18 (Fig. 3) is accompanied by a decrease in many other species, *R. antarctica* and *R. minuta* were absent, and *R. haqii* and *S. abies* were rare. *Helicosphaera* species appear to be able to thrive in shallow, eutrophic environments, with enhanced abundances in hemipelagic, near-continental environments (Perch-Nielsen, 1985), upwelling regions, and gyre margin waters with a higher fertility (Schmidt, 1978; Giraudeau, 1992). *H. carteri* has also been documented in eutrophic, hyposaline waters (Giraudeau, 1992) and estuarine environments (Cros, 2002; Cachao et al., 2002), and its presence in the Black Sea is further evidence for a capability to withstand salinity fluctuations. The increase in the abundance of *H. carteri* here, along with the presence of diatoms and low nannofossil diversity, may thus represent a shift to a brackish, eutrophic, shallow water environment.

4.6.3. Umbilicosphaera jafari

U. jafari (Plate Ih and i) dominates sample 13 (95%) and is an important component of sample 18, comprising 48% of the assemblage (Fig. 3). Nannofossil diversity is very low in these samples, with *R. antarctica* absent, and *R. minuta* and *S. abies* minor components. Modern species of *Umbilicosphaera* have been reported from a range of environments (Roth and Berger, 1975; Okada and McIntyre, 1979; Giraudeau, 1992), Ziveri et al. (2004) suggest that *U. sibogae* is an

oligotrophic species whilst *U. foliosa* is mesotrophic. Little is known about the palaeoecology of *U. jafari*, it has a widespread distribution in the fossil record occurring in virtually all Neogene samples, with elevated abundances in restricted, near-shore marine environments (e.g., the Paratethys and here), but there is also evidence for a high salinity environment here. Diatoms were absent from sample 13 indicating that the abundance of *U. jafari* was not a response to increased nutrients. This sample may reflect a very shallow, high salinity environment (>35 ppt) that developed immediately antecedent to gypsum deposition. The enhanced abundance of and dominance of *U. jafari* may thus reflect an ability to flourish in shallow water, hypersaline environments.

4.6.4. Sphenolithus abies

S. abies (Plate In) was present in almost all samples studied, and dominated most of Section 1b (29–80%) (Fig. 3, Plate II). Sphenoliths have been thought to share the same environmental niche as discoasters (k-selected), being common in warm water, oligotrophic, stable environments (e.g. Haq and Lohmann, 1976; Haq, 1980; Lohmann and Carlson, 1981; Perch-Nielsen, 1985; Aubry, 1992). However, the high abundance and almost monospecific assemblages of sphenoliths in these extreme and diatom-rich environments (Plate IIc) would suggest otherwise. The data here indicate that *S. abies*, whilst usually present in oligotrophic open-ocean habitats was also capable of opportunistic behaviour and of attaining high abundances in unusual environments. High abundances of *Sphenolithus* spp. have also been documented in Messinian sediments from Ocean Drilling Program Leg 160, Site 967 (Castradori, 1998), the Tripoli Formation, Sicily (Blanc-Valleron et al., 2002), Pissouri Section, Cyprus (Kouwenhoven et al., 2004), Morocco and DSDP Site 372 (Müller, 1985). Sphenoliths therefore appear to have been an opportunistic taxon that were capable of occupying a wide range of environments including restricted mesotrophic waters.

Diversity is slightly higher in samples rich in *S. abies* (mean H'=1.13) and *R. antarctica*, *H. carteri*, *R. minuta*, *U. jafari* and *R. haqii* are also usually present (Fig. 3). This may indicate the temporary re-establishment of deeper marine conditions (~100 m) and that the Polemi Basin was open to the Mediterranean for short intervals, resulting in normal marine salinity in the surface waters. These samples are also rich in diatoms, suggesting a eutrophic environment, and *S. abies* may have thrived when water fertility had declined, following a diatom bloom. The controlling
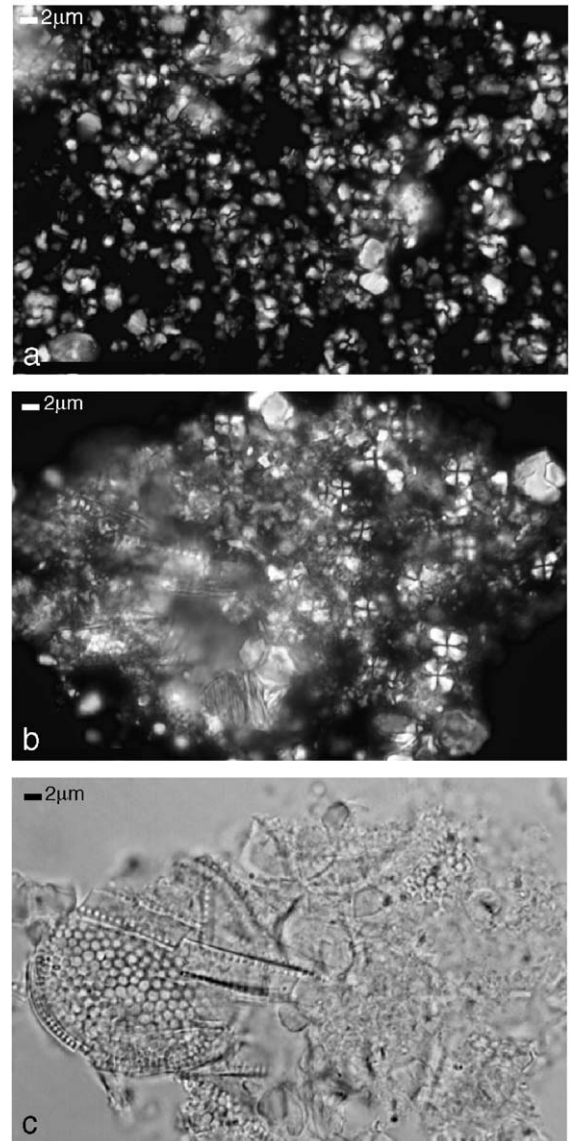

Plate II. Calcareous nannoplankton assemblages from the Polemi Basin.

a)   Monospecific assemblage of *Reticulofenestra antarctica*, from sample 16.
b)   Image of sample PB6Y in crossed nicols showing monospecific assemblage of *Spenolithus abies*.
c)   Image of sample PB6Y as in (b) but in transmitted light, showing the presence of diatoms in samples rich in *Spenolithus abies*.

factor for *S. abies* may therefore have been marine, mesotrophic waters.

4.6.5. Reticulofenestra antarctica

Samples 9, 10, 16, PB1, PB8 and PB9 are dominated by *R. antarctica* (31 - 87%) (Plate II), and are very

similar in composition, with *S. abies*, *U. jafari* and *R. minuta* low in abundance and *H. carteri* and *R. haqii* (Plate Ik) normally present, and accounting for up to 29% and 20%, respectively. Reticulofenestrids with closed central areas were documented by Krhovsky et al. (1992) from diatom-rich Oligocene sediments from the Czech Republic, suggesting a palaeoecology related to eutrophic environments with brackish to normal marine salinity.

In all samples, an inverse relationship was found between *S. abies* and *R. antarctica* (Fig. 4). As there appears to be no such relationship with diatom distributions this is most likely a result of fluctuations in salinity or water depth rather than productivity. *R. antarctica* dominated in shallow water environments whilst *S. abies* increased during periods of marine influx and deeper marine conditions.

In summary, *H. carteri*, *U. jafari*, *R. antarctica*, *R. minuta* and *S. abies* were all widely distributed marine species, but evidently were also able to flourish in these rapidly fluctuating environments that excluded most other open ocean taxa. These species can therefore be considered to be opportunists, capable of reproducing quickly and tolerant of a wide range of ecological conditions. A schematic representation of the possible controlling environmental factors for each nannoplankton species is illustrated in Fig. 5. This is a tentative

model based on the limited paleoecological data for each species. The water depth is not thought to have been greater than 200 m for any of the samples. We suggest that changes in the fertility, salinity and bathymetry of the Polemi Basin surface waters resulted in the succession of taxa seen here: *R. antarctica* is thought to have dominated in normal salinity, mesotrophic, shallow water environments; *H. carteri* in shallow, eutrophic environments; *U. jafari* in hypersaline conditions; *R. minuta* in eutrophic conditions with an abnormal salinity from brackish to hypersaline; and *S. abies* in mesotrophic, deeper and normal salinity environments (Fig. 5). Most of the species found in the assemblages are cosmopolitan, long-ranging taxa, which provide further indication that these species have broad environmental tolerances. The complex and rapid changes in nannofossil assemblage composition reflects a widely fluctuating environment and a range of r-selected strategies and adaptations to extreme conditions.

4.7. Environments of the Messinian Polemi Basin

Microfossil assemblage data and sedimentological evidence provide insights into palaeoenvironmental variations within the Messinian Polemi Basin and for the Mediterranean as a whole at that time. Like the Messinian Mediterranean, the Polemi Basin was restricted by a tectonically active sill, which segregated the basin partly, or periodically even completely, from the Mediterranean Sea (Roberston et al., 1995). The combination of regional and local tectonics in addition to sea-level fluctuations resulting from the Messinian Salinity Crisis and global eustacy gave rise to large fluctuations in the bathymetry of the Polemi Basin (Roberston et al., 1995) as documented by the gypsum deposits and neritic–littoral diatom species. The massive gypsum units of Section 2 indicate the continued separation and restriction of the basin. Stromatolitic limestones were also noted from this interval and within the nearby Psematismenos Basin, providing further evidence for extreme shallow water conditions. As sea-level fell within the basin during the onset of the Messinian Salinity Crisis, the environment became increasingly hypersaline. However, diatoms also provide evidence for brackish water conditions. The salinity decreases are thought to reflect increased fluvial discharge or runoff into the basin, which resulted in the development of eutrophic environments and the deposition of diatomaceous rich marls. The environment therefore experienced extreme changes in nutrients and salinity and shifts from hypo- to hypersaline con-
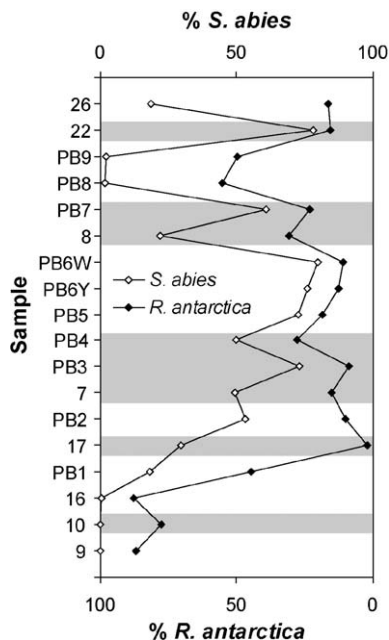

Fig. 4. Relationship between *S. abies* and *R. antarctica* in samples dominated by these taxa. Assemblages dominated by *R. minuta*, *H. carteri* and *U. jafari* have been excluded. Shaded areas indicate samples rich in diatoms.
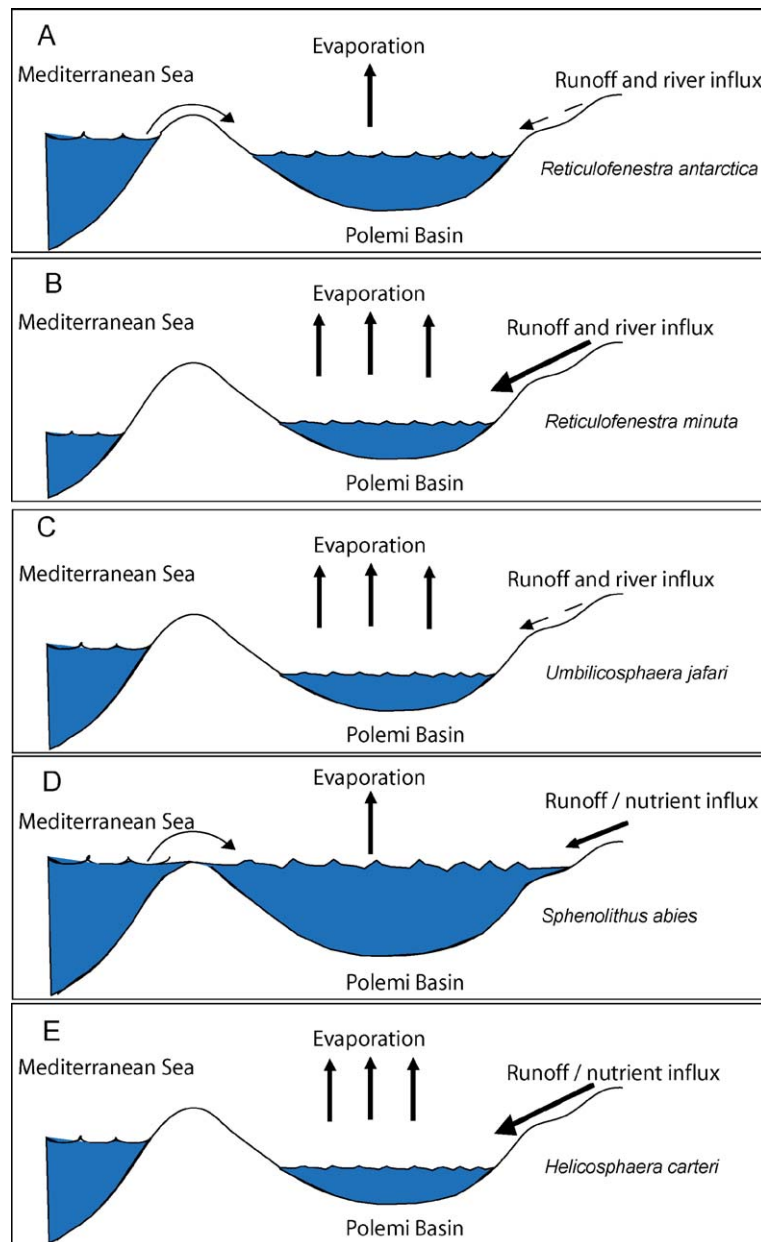
Fig. 5. Palaeoenvironmental model of the Polemi Basin during the early stages of the Messinian Salinity Crisis. Bathymetry fluctuations resulted from shifts in the Mediterranean sea-level and the tectonically active sill. The variations in surface water fertility, salinity and bathymetry are inferred to have resulted in the almost monospecific assemblages of certain species. (A)–(E) refer to assemblages in Fig. 3. Multiple evaporation arrows indicate periods of enhanced salinity. (A) *R. antarctica* environment. Influxes of marine water into the basin from the Mediterranean Sea provide a normal marine salinity within a shallow (~50 m) basin. (B) A shallow, hypersaline environment with periodic influxes of fresh, nutrient rich water results in an extreme environment with highly fluctuating salinity levels and elevated abundances of *R. minuta*. (C) Sea-level fall in The Mediterranean Sea and/or uplift prevents marine influxes. The Polemi Basin therefore desiccates resulting in a hypersaline environment with common *U. jafari*. (D) *S. abies* environment with repeated influxes of marine water into the basin from the Mediterranean Sea. Runoff/river influx provides nutrients. Water depth approximately 100 m. (E) *H. carteri* became dominant in eutrophic conditions where increased runoff resulted in elevated surface water productivity.

ditions, depending on the extent of evaporation versus freshwater input. Fluctuations in bathymetry and salinity are indicated by benthic foraminifera, such as *Tri-*

loculina spp. (rare to common in sample 9) which is indicative of hypersaline conditions (Dix et al., 1999). Sample 15 contained *Bulimina* and *Elphidium* spp.

which are stress tolerant taxa, indicative of shallow water environments with a highly variable salinity and low O_2 (Cann and De Dekker, 1981; Miller and Lohmann, 1982; Murray, 1991). Large and rapid fluctuations in the water budget and shifts from hypo to hypersaline conditions are also detected in stable isotope analysis of coeval basins (e.g. Bellanca et al., 2001 and references therein).

Palaeoecological data provided by the calcareous nannofossil and siliceous microfossils suggest that the Polemi Basin was a semi-enclosed, neritic to littoral environment, experiencing desiccation and repeated reinstallation of marine waters and influxes of freshwater (Fig. 5). This is shown by the absence of open marine restricted nannoplankton (e.g. *Discoaster*), and the presence of freshwater and brackish diatoms (e.g. *T. eccentrica*, *Melosira* spp.). Environmental conditions at the onset of the Messinian Salinity Crisis in the Polemi Basin were thus analogous to a hypersaline lagoon with repeated marine incursions and influxes of freshwater.

5. Conclusions

Calcareous nannofossil assemblages from the southern part of the Polemi Basin, western Cyprus, are low diversity, in some cases almost monospecific assemblages and lacking open ocean taxa. One of five species, *R. antarctica*, *R. minuta*, *H. carteri*, *S. abies* and *U. jafari*, consistently dominated the assemblages. These species are considered to be r-selected opportunists, able to flourish in stressed, highly fluctuating environments. The rapid variability seen in the calcareous nannoplankton assemblages is thought to have been stimulated by the extreme fluctuations of surface water salinity, bathymetry and nutrient levels.

Acknowledgements

Appendix A. Calcareous nannofossil taxonomic appendix

Amaurolithus primus (Bukry and Percival, 1971) Gartner and Bukry, 1975

Calcidiscus leptoporus (Murray and Blackman, 1898) Loeblich and Tappan, 1978

Calcidiscus macintyrei (Bukry and Bramlette, 1969) Loeblich and Tappan, 1978

Coccolithus pelagicus (Wallich, 1877) Schiller, 1930

Discoaster variabilis Martini and Bramlette, 1963

Emiliania huxleyi (Lohmann, 1902) Hay and Mohler, 1967

Helicosphaera carteri (Wallich, 1877) Kamptner, 1954

Pontosphaera discopora Schiller, 1925

Pontosphaera japonica (Takayama, 1967) Nishida, 1971

Pontosphaera multipora (Kamptner, 1948) Roth, 1970

Reticulofenestra antarctica (Haq, 1976) Driever, 1988

Reticulofenestra haqii Backman, 1978

Reticulofenestra minuta Roth, 1970

Reticulofenestra pseudoumbilicus (Gartner, 1967) Gartner, 1969

Rhabdosphaera clavigera Murray and Blackman, 1898

Scyphosphaera pulcherrima Deflandre, 1942

Sphenolithus abies Deflandre, 1954

Triquetrorhabdulus striatus Müller, 1974b

Umbilicosphaera jafari Müller, 1974a

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