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Benthic foraminiferal record of ecosystem variability in the eastern Mediterranean Sea during times of sapropel S₅ and S₆ deposition

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Abstract

High-resolution benthic foraminiferal and geochemical investigations were carried out across sapropels S₅ and S₆ from two sediment cores in the Levantine Sea to evaluate the impact of climatic and environmental changes on benthic ecosystems during times of sapropel formation. The faunal successions indicate that eutrophication and/or oxygen reduction started several thousand years prior to the onset of sapropel formation, suggesting an early response of the bathyal ecosystems to climatic changes. Severest oxygen depletions appear in the early phases of sapropel formation. The initial reduction of deep-water ventilation is caused by a warming and fresh water-induced stratification of Eastern Mediterranean surface waters. During the late phase of S₅ formation improved oxygenation is restricted to middle bathyal ecosystems, indicating that at least some formation of subsurface water took place. During S₆ formation oxygen depletions and eutrophication were less severe and more variable than during S₅ formation. Estimated oxygen contents were low dysoxic at middle bathyal to anoxic at lower bathyal depths during the early phase of S₆ formation but never dropped to anoxic values in its late phase. The high benthic ecosystem variability during S₆ formation suggests that water column stratification at deep-water formation sites was in a very unstable mode and susceptible to minor temperature fluctuations at a millennial time-scale.

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1. Introduction

A major issue of paleoclimate research in the Mediterranean region addresses the processes involved in the formation of Neogene sapropels (reviews in Rohling and Hilgen, 1991; Rohling, 1994; Cramp and O'Sullivan, 1999; Emeis et al.,

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2000). Sapropel formation is closely associated with changes in humidity related to precessional forcing of the African monsoon system (Rossignol-Strick, 1983). However, the debate over the mechanisms that led to the formation of late Quaternary sapropels still remains unresolved. On the one hand, anoxia is proposed as dominant mechanism preserving organic carbon in the sediment (Rossignol-Strick et al., 1982; Thunell and Williams, 1989; Béthoux, 1993; Tang and Stott, 1993). On the other hand, an increase in productivity and corresponding organic matter fluxes is discussed as dominant mechanism (Castradori, 1993; Sancetta, 1994). To address this problem, it is essential to reconstruct the long- and short-term climatic, oceanographic, and ecological processes involved. This is necessary in order to characterize glacial and interglacial boundary conditions prevailing during the formation of the different sapropels (Schmiedl et al., 1998; Weldeab et al., *in press*) and to determine the sequence of environmental changes prior, during and after sapropel formation in great detail (Jorissen, 1999).

Recent studies indicate that in addition to orbital forcing, abrupt climatic shifts had a strong impact on the late Quaternary eastern Mediterranean circulation and freshwater run-off (Schilman et al., 2001; Rohling et al., 2002; Casford et al., 2003). In the Aegean Sea, the Holocene record of surface water temperatures exhibits marked fluctuations on a millennial time-scale. These fluctuations were attributed to northerly outbreaks of cold air that are also suggested to have triggered the interruption of Holocene sapropel S₁ formation (Rohling et al., 1997; Rohling et al., 2002). Short-term climate variability may also have been responsible for recently observed shifting of deep-water formation sites from the Adriatic to the Aegean Sea (Roether et al., 1996; Theocharis et al., 1999). These results demonstrate that eastern Mediterranean oceanography reacts very sensitively to abrupt climatic changes. Similar fluctuations may have occurred throughout the Pleistocene, controlling the characteristics of the different sapropels.

Benthic foraminifera are particularly suitable to characterize the processes linking deep-sea ecosys-

tems to the surface ocean (via productivity and deep-water formation) and, consequently, to the atmospheric circulation (e.g. via wind stress, temperature). In the recent well-ventilated Mediterranean Sea the distribution pattern of benthic foraminifera accurately reflects the trend of decreasing food availability with increasing water depth and from the western to the eastern basins (De Rijk et al., 1999). The lower bathyal and abyssal ecosystems can be presently regarded as food-limited environments exhibiting oligotrophic and well-oxygenated conditions (Pickard and Emery, 1990; Antoine et al., 1995). These ecosystems are inhabited by unusually low-diversity faunas mainly consisting of several miliolid and primitive arenaceous species (Cita and Zocchi, 1978; Mullineaux and Lohmann, 1981). In contrast, the high-diversity upper bathyal and shelf faunas include a number of shallow to deep infaunal species indicating mesotrophic to eutrophic conditions (e.g., Jorissen et al., 1992, 1995; Schmiedl et al., 2000). A number of studies showed that deep-sea benthic foraminifera from late Quaternary sediment cores of the eastern Mediterranean Sea record drastic changes in the ventilation of deep water masses associated with the formation of sapropel layers (e.g., Mullineaux and Lohmann, 1981; Nolet and Corliss, 1990). During times of sapropel formation, benthic foraminiferal numbers and diversities are always very low, with a dominance of deep infaunal taxa, or even the total fauna disappears, reflecting a strong oxygen deficiency at the bottom. Until now, only few high-resolution faunal data sets exist that allow a more detailed study of temporal and spatial patterns of benthic ecosystem variability during sapropel formation (Rohling et al., 1997; Jorissen, 1999).

In this study we present the distribution pattern of benthic foraminifera across sapropels S₅ and S₆ from two cores of the eastern Mediterranean Sea. Our main target is to describe the impact of short-term climatic and environmental changes on different deep-sea ecosystems. The core intervals have been selected in order to characterize benthic ecosystem variability during sapropel formation under different climatic boundary conditions (interglacial versus glacial). The two sites were se-

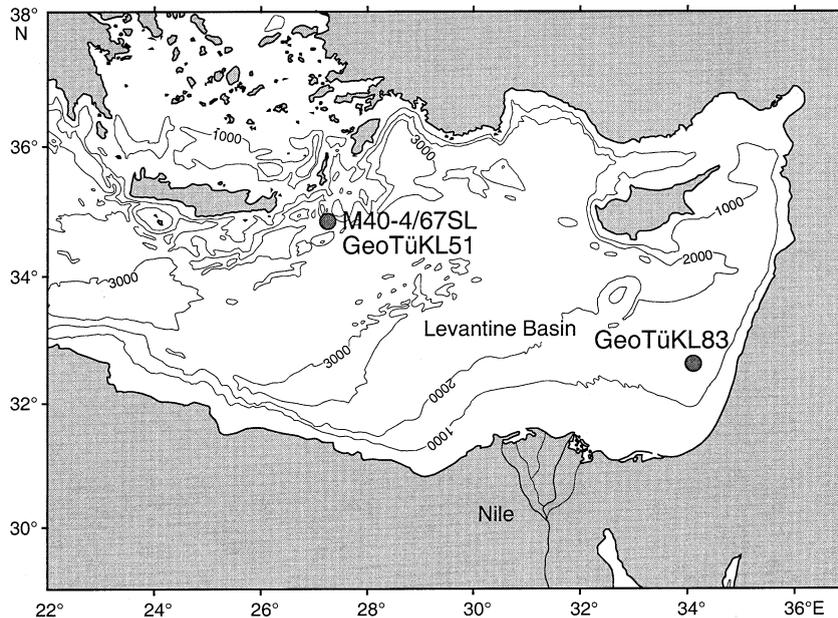


Fig. 1. Bathymetric map of the easternmost Mediterranean Sea with locations of investigated core sites M40-4/67SL and GeoTüKL51 in the western and GeoTüKL83 in the eastern Levantine Basin.

lected such as to record spatial and bathymetric differences in the response of benthic faunas to the sequence of environmental changes during sapropel formation.

2. Material and methods

Gravity core M40-4/67SL and piston core GeoTüKL51 were collected in February 1998 during *Meteor* cruise M40/4 from the lower bathyal northwestern Levantine Basin, southeast of Crete at 34°48.8'N, 27°17.8'E, 2158 m water depth. Piston core GeoTüKL83 was collected in April 1999 during *Meteor* cruise M44/3 from the middle bathyal southeastern Levantine Basin, off Israel, 32°36.9'N, 34°08.9'E, 1433 m water depth (Fig. 1). Both core sites are presently bathed by highly oxygenated eastern Mediterranean deep water.

Immediately after opening of the cores, sediment lightness and color was determined with a Minolta color spectrophotometer. The identification of sapropel intervals S₅ and S₆ was based on the graphic correlation of the $\delta^{18}\text{O}$ curves with the standard record of Martinson et al. (1987) and

lithology (Weldeab et al., 2002). Since the S₆ interval was not recovered in core M40-4/67SL it was investigated from longer core GeoTüKL51 that was taken at the same site extending down into marine stable oxygen isotope stage (MIS) 7. For faunal investigations the targeted sapropels were sampled at 2 cm spacing on average, sediment intervals below and above at 2–10 cm spacing. Samples are 1 cm in diameter and sample depths refer to midpoints of samples. Sediment samples were dried, weighed and washed through a 63- μm screen. Subsequently, the coarse fraction was dry sieved at 125 and 250 μm . The analysis of the benthic foraminiferal fauna was carried out on the size fraction > 125 μm and, for selected samples, also on the size fraction 63–125 μm . On average 250 and 150 individuals (ind.) have been counted in the coarse and fine fractions, respectively. All counts were corrected for splits and foraminiferal numbers were referred to the dry weight of the sediment. Diversities $H(S)$ were determined following the Shannon–Wiener information equation (Buzas and Gibson, 1969). Tables with census data are available at the PANGAEA data base (www.pangaea.de).

The stable isotope data were taken from [Weldeab et al. \(2002\)](#) except those from sapropel S₅ of GeoTüKL83 that have been investigated within this study. For stable isotope measurements between 15 and 20 tests of the planktic foraminifer *Globigerinoides ruber* were picked from the size fraction >250 µm. All tests were cleaned ultrasonically prior to analysis. The isotope measurements were performed at the Leibniz-Laboratory for Radiometric Dating and Isotope Research, Kiel, Germany (H. Erlenkeuser). External reproducibility for stable oxygen isotopes was <0.03‰. Primary productivity estimates are based on the distribution of 'biogenic' barium and are taken from [Weldeab et al. \(in press\)](#).

According to the age models of [Weldeab et al. \(2002\)](#) and the sapropel boundary ages compiled by [Emeis et al. \(in press\)](#) the investigated sediments cover the following time intervals. From core M40-4/67SL the section between 341 and 473 cm was sampled representing a time interval of approximately 130–115 kyr (average sedimentation rate is 8.8 cm kyr⁻¹; estimated sedimentation rate for sapropel S₅ is 18.6 cm kyr⁻¹). From core GeoTüKL51 the section between 460 and 589 cm was investigated representing a time interval of approximately 188–138 kyr (average sedimentation rate is 2.6 cm kyr⁻¹; estimated sedimentation rate for sapropel S₆ is 6.7 cm kyr⁻¹). From core GeoTüKL83 the sections of 350–500 cm and 540–640 cm were investigated representing time intervals of approximately 115–136 kyr (average sedimentation rate of 7.1 cm kyr⁻¹) and 141–180 kyr (average sedimentation rate of 2.6 cm kyr⁻¹), respectively. In core GeoTüKL83 the estimated sedimentation rate for sapropel S₅ is 5.4 cm kyr⁻¹ and for sapropel S₆ is 8.8 cm kyr⁻¹.

3. Results

3.1. Benthic foraminiferal fauna across sapropel S₅ of core M40-4/67SL, northwestern Levantine Sea

In core M40-4/67SL the boundary between MIS 6 and 5 is located at approximately 465 cm core depth, according to the stable isotope signal.

The 94-cm-thick laminated sapropel S₅ exhibits sharp lower and upper boundaries as indicated by the lightness curve. The sapropelic sediment is rich in siliceous microfossils, mainly diatoms. The benthic foraminiferal faunal pattern across the sapropel is shown in [Figs. 2 and 3](#).

3.1.1. Pre-sapropel fauna

In the >125-µm fraction (coarse fraction) benthic foraminiferal numbers (BFN) are 21 ind. g⁻¹ on average. Approximately 10 cm below S₅, values start to decrease but show a maximum in the sample just below the lower sapropel boundary. Pre-sapropel diversities are rather high in the coarse fraction with *H(S)* values around 3.1. The pre-sapropel fauna is dominated by different miliolid taxa (*Miliolinella subrotunda*, *Pyrgo murrhina*, *Pyrgo elongata*, *Quinqueloculina padana*, *Quinqueloculina patagonica*). Associated species include *Cassidulina laevigata*, *Gavelinopsis translucens*, and *Oridorsalis umbonatus*. The BFN decrease is accompanied by a stepwise drop of these species and by a rise of *Globobulimina affinis*. In the sample just below the sapropel a high abundance of *Fursenkoina mexicana*, *Globobulimina affinis* and *Chilostomella oolina* is observed. In the 63–125-µm fraction (fine fraction) pre-sapropel BFN values increase from 130 to 270 ind. g⁻¹ while diversities show a slight decrease. The fauna of the fine fraction is dominated by *Eponides pusillus* and *Anomalinoides minimus*. Their abundance is paralleling the BFN trend ([Figs. 2, 3](#)).

3.1.2. Sapropel fauna

Within sapropel S₅ few benthic foraminifera are present. The only significant occurrence is observed between 422 and 425 cm depth dominated by *Articulina tubulosa* in the coarse fraction and by *Anomalinoides minimus*, *Articulina tubulosa* and *Eponides pusillus* in the fine fraction.

3.1.3. Post-sapropel fauna

Post-sapropel BFN values show a short maximum directly above S₅ and then drop to average values around 7 ind. g⁻¹ in the coarse fraction and 100 ind. g⁻¹ in the fine fraction. In the coarse fraction, diversities are more variable and significantly lower when compared to pre-sapropel val-

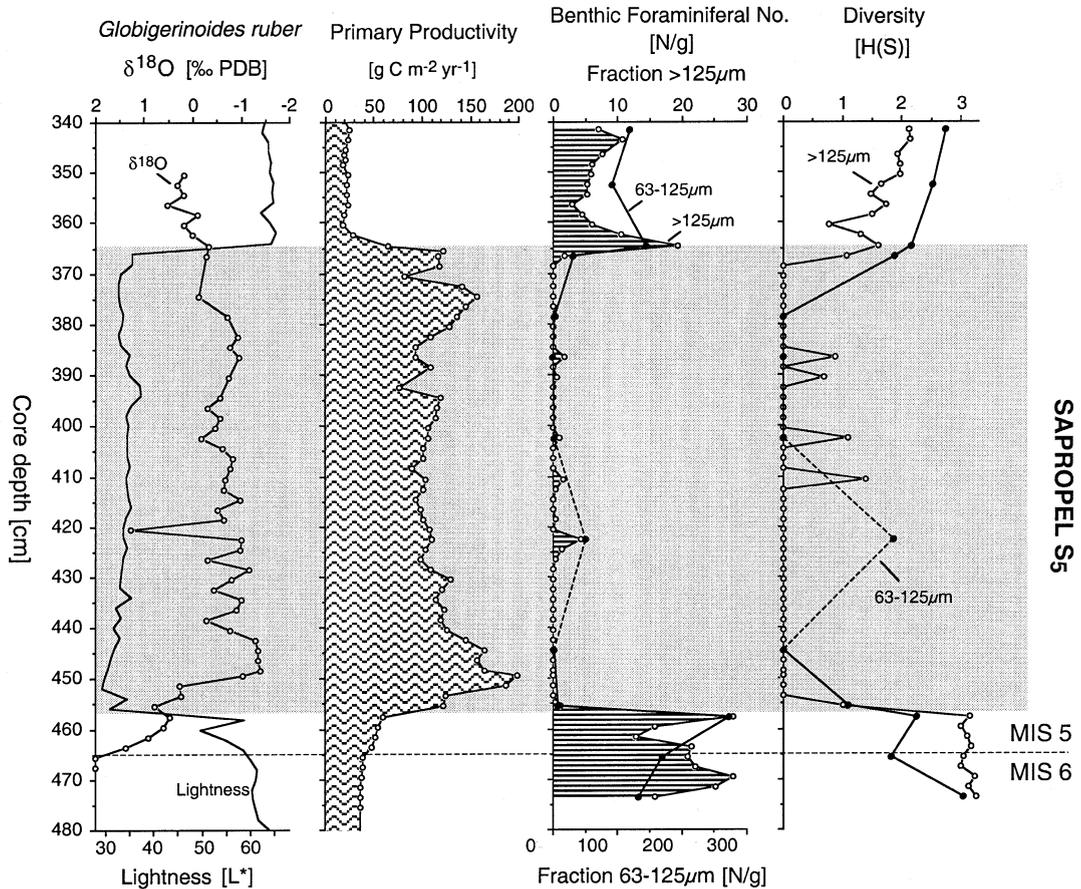
M40-4/67SL: S₅

Fig. 2. Sediment lightness, planktic stable oxygen isotope signal, primary productivity estimates based on ‘biogenic’ barium, benthic foraminiferal number, and foraminiferal diversity across sapropel S₅ in core M40-4/67SL from the lower bathyal (2158 m water depth) of the western Levantine Basin, southeast of Crete. Benthic foraminiferal results are given for size fractions 63–125 µm and >125 µm, separately. Stable isotope data and paleoproductivity estimates are from [Weldeab et al. \(in press, 2002\)](#). The stippled line indicates the boundary between MIS 6 and 5.

ues, increasing from approximately $H(S)=0.8$ to 2.1. Diversities in the fine fraction increase from $H(S)=1.9$ to 2.8. The fauna of the coarse fraction is dominated by *Fursenkoina mexicana* in the sample directly on top of S₅ and by *Gyroidinoides orbicularis* and *Articulina tubulosa* in the interval above. The general diversity increase is caused by a gradual return of different miliolid species (e.g., *Miliolinella subrotunda*). The post-sapropel abundance of *Anomalinoides minimus* and *Eponides pusillus* in the fine fraction is considerably lower when compared to pre-sapropel values (Figs. 2, 3).

3.2. Benthic foraminiferal fauna across sapropel S₅ of core GeoTüKL83, southeastern Levantine Sea

In core GeoTüKL83 the boundary between MIS 6 and 5 is located at approximately 428 cm core depth, according to the stable isotope signal. The 27-cm-thick sapropel S₅ exhibits sharp lower and upper boundaries, but with lower lightness contrasts in comparison with sapropel S₅ of M40-4/67SL. The sapropel displays a slight darkening from the base to the top. The benthic foraminiferal faunal pattern across the sapropel is shown in Figs. 4 and 5.

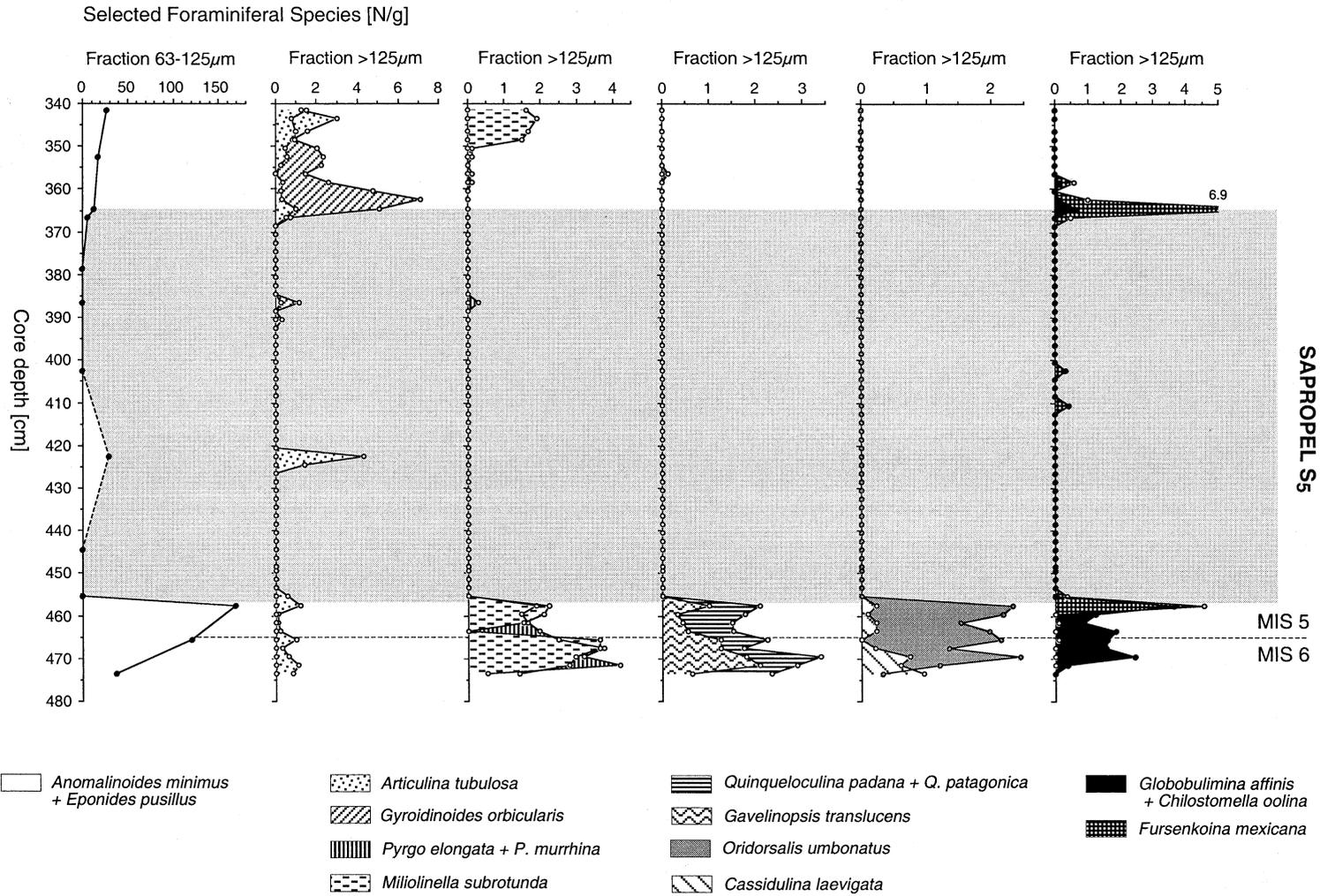


Fig. 3. Abundance of selected benthic foraminiferal species across sapropel S₅ in core M40-4/67SL from the lower bathyal (2158 m water depth) of the western Levantine Basin, southeast of Crete. The stippled line indicates the boundary between MIS 6 and 5.

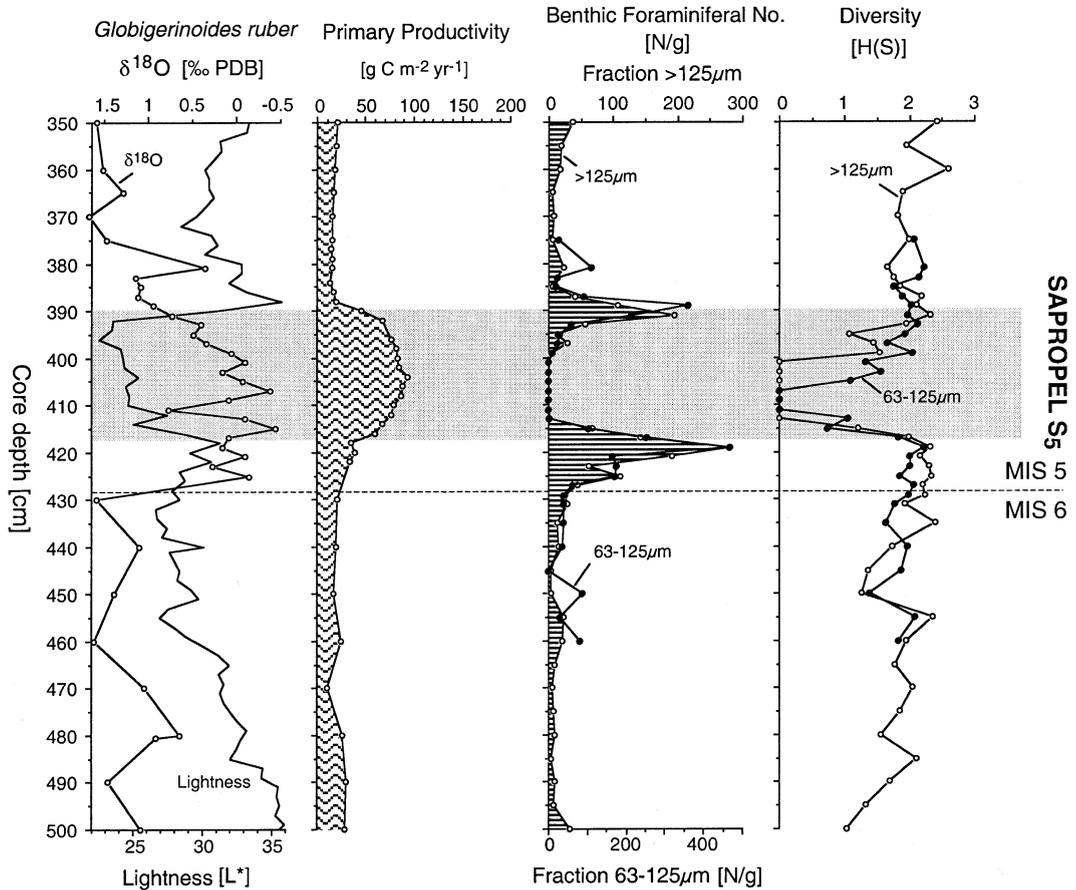
GeoTüKL83: S₅

Fig. 4. Sediment lightness, planktic stable oxygen isotope signal, primary productivity estimates based on ‘biogenic’ barium, benthic foraminiferal number, and benthic foraminiferal diversity across sapropel S₅ in core GeoTüKL83 from the middle bathyal (1433 m water depth) of the eastern Levantine Basin, off Israel. Benthic foraminiferal results are given for size fractions 63–125 µm and > 125 µm, separately. Paleoproductivity estimates are from Weldeab et al. (in press). The stippled line indicates the boundary between MIS 6 and 5.

3.2.1. Pre-sapropel fauna

In the glacial interval, between 500 and 428 cm core depth, BFN values of the coarse fraction are 14 ind. g⁻¹ on average. Approximately 10 cm below S₅, values start to rise significantly and reach a maximum of 280 ind. g⁻¹ in the sample just below the lower sapropel boundary. Pre-sapropel glacial diversities are $H(S)=1.8$ on average with significant fluctuations, diversities just below S₅ are around $H(S)=2.3$. The glacial fauna is dominated by *Hoeglundina elegans*, *Bolivina variabilis*, *Miliolinella subrotunda*, and *Gyroidinoides orbicularis*. The BFN increase below S₅ is accompanied

by a rise in the abundance of several species, including *Bolivina variabilis*, *Brizalina dilatata*, *Globulimina affinis*, *Cassidulina laevigata*, and *Hyalinea balthica*. The sample just below the sapropel boundary is dominated by *Fursenkoina mexicana* and *Chilostomella oolina*. Both BFN and diversity trends of the fine fraction are paralleling those of the coarse fraction. The maximum BFN of 466 ind. g⁻¹ in the sample just below the sapropel is mainly due to *Eponides pusillus*, with different bolivinids, *Articulina tubulosa*, *Cassidulina laevigata* and *Anomalinoidea minimus* as associated species (Figs. 4, 5).

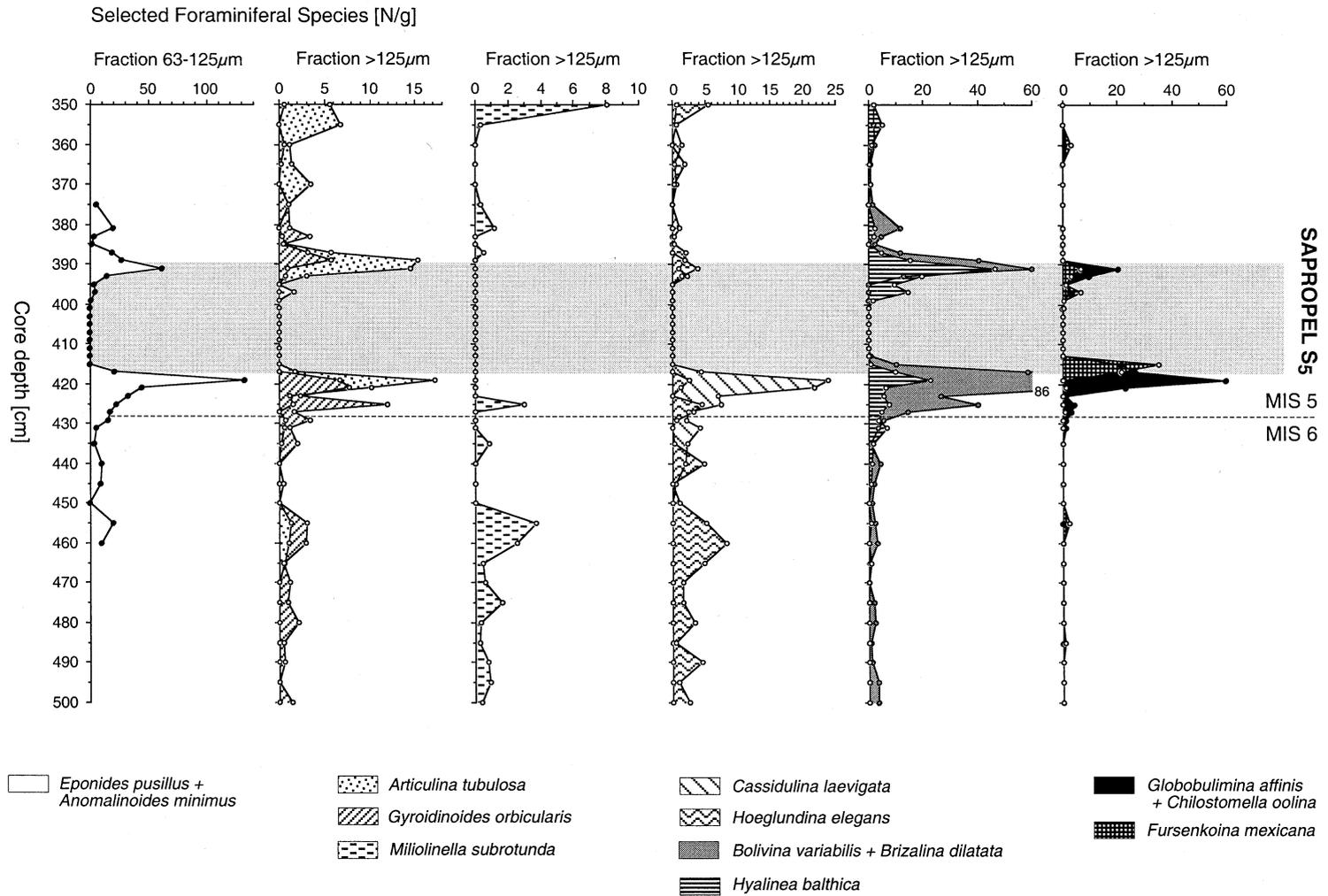


Fig. 5. Abundance of selected benthic foraminiferal species across sapropel S₅ in core GeoTüKL83 from the middle bathyal (1433 m water depth) of the eastern Levantine Basin, off Israel. The stippled line indicates the boundary between MIS 6 and 5.

3.2.2. Sapropel fauna

In the lower part of sapropel S₅ benthic foraminifera are very rare or absent in both size fractions. From the middle part of the sapropel upwards BFN values and faunal diversities show a stepwise increase. This repopulation starts in the fine fraction with the appearance of *Articulina tubulosa*, *Eponides pusillus* and *Anomalinoidea minimus*. In the coarse fraction the repopulation starts with *Hyalinea balthica*, *Globobulimina affinis*, *Chilostomella oolina*, *Fursenkoina mexicana*, and *Articulina tubulosa* in low abundance. These species become abundant in the uppermost part of the sapropel where they occur together with *Bolivina variabilis*, *Brizalina dilatata*, *Gyroidinoides orbicularis*, *Cassidulina laevigata* and *Hoeghundina elegans*.

3.2.3. Post-sapropel fauna

Post-sapropel BFN values display a rapid drop from 190 ind. g⁻¹ at the upper sapropel boundary to average values of 15 ind. g⁻¹ above. In the fine fraction a similar trend is visible, however, with a density maximum of 469 ind. g⁻¹ occurring 2 cm above that of the coarse fraction. Mean post-sapropel diversities are similar to pre-sapropel values with $H(S)$ around 2.0 in both size fractions. The numbers of *Bolivina variabilis*, *Brizalina dilatata*, *Articulina tubulosa*, and *Gyroidinoides orbicularis* (coarse fraction) and *Eponides pusillus* and *Anomalinoidea minimus* (fine fraction) exhibit a drastic decrease within the first 15 cm above the sapropel. Above this interval the fauna resembles the glacial pre-sapropel fauna, however, with higher abundance of *Articulina tubulosa* and *Miliolinella subrotunda* and lower abundance of *Bolivina variabilis* and *Hoeghundina elegans* (Figs. 4, 5).

3.3. Benthic foraminiferal fauna across sapropel S₆ of core GeoTüKL51, northwestern Levantine Sea

Sapropel S₆ of GeoTüKL51 consists of two parts (S₆ subunits 1 and 2, each 17 cm thick), separated by a 6-cm-thick dispersed ash layer. The sapropel exhibits sharp lower and upper boundaries, and significant color fluctuations throughout. Thin reoxygenation layers are obvious at 542 and 566 cm core depth. In the sedi-

ment section above S₆ another ash layer is present between 507 and 510 cm. The benthic foraminiferal faunal pattern across the sapropel interval is shown in Figs. 6 and 7.

3.3.1. Pre-sapropel fauna

Within approximately 10 cm below the sapropel, BFN values of the coarse fraction rise significantly from 13 to 153 ind. g⁻¹. In the fine fraction 1730 ind. g⁻¹ are present in the sample directly below the sapropel boundary. Pre-sapropel diversities are around $H(S)=2.5$ in the coarse fraction and 1.7 in the fine fraction. The pre-sapropel fauna is dominated by *Eggerella bradyi*, *Cassidulina laevigata* and *Gyroidinoides neosoldanii*. Important associated species include *Melonis barleeannum*, *Cibicoides pachydermus*, *Miliolinella subrotunda* and *Globobulimina affinis*. The fine fraction is dominated by *Anomalinoidea minimus* and *Eponides pusillus*.

3.3.2. Sapropel fauna

In the lower part of S₆ subunit 1 benthic foraminifera are almost absent in both size fractions. From the upper part of S₆ subunit 1 upwards benthic foraminifera are present throughout the rest of the sapropel. BFN values significantly fluctuate in both size fractions with elevated values below and above the ash layer and a maximum of 418 ind. g⁻¹ just below the reoxygenation layer of S₆ subunit 2. In the fine fraction diversities are $H(S)=1.8$ on average. In the lower part of the sapropel these moderately high diversities are caused by the occurrence of different shallow water species (e.g., *Nonion depressulum*, *Rosalina bradyi*, *Rosalina floridensis*). Diversities of the coarse fraction are between $H(S)=0$ and 1 in the lowermost part of the sapropel, rising significantly to $H(S)=2.7$ in the upper part of S₆ subunit 1, and fluctuate around $H(S)=1.6$ in subunit 2 of the sapropel. The first step of repopulation starts in the upper part of S₆ subunit 1 and extends into the lower part of subunit 2. It is characterized by a dominance of *Eponides pusillus* and *Anomalinoidea minimus* in the fine fraction and *Cassidulina laevigata*, *Bolivina variabilis* and *Brizalina dilatata* in the coarse fraction. The BFN maximum at 544 cm core depth mainly consists

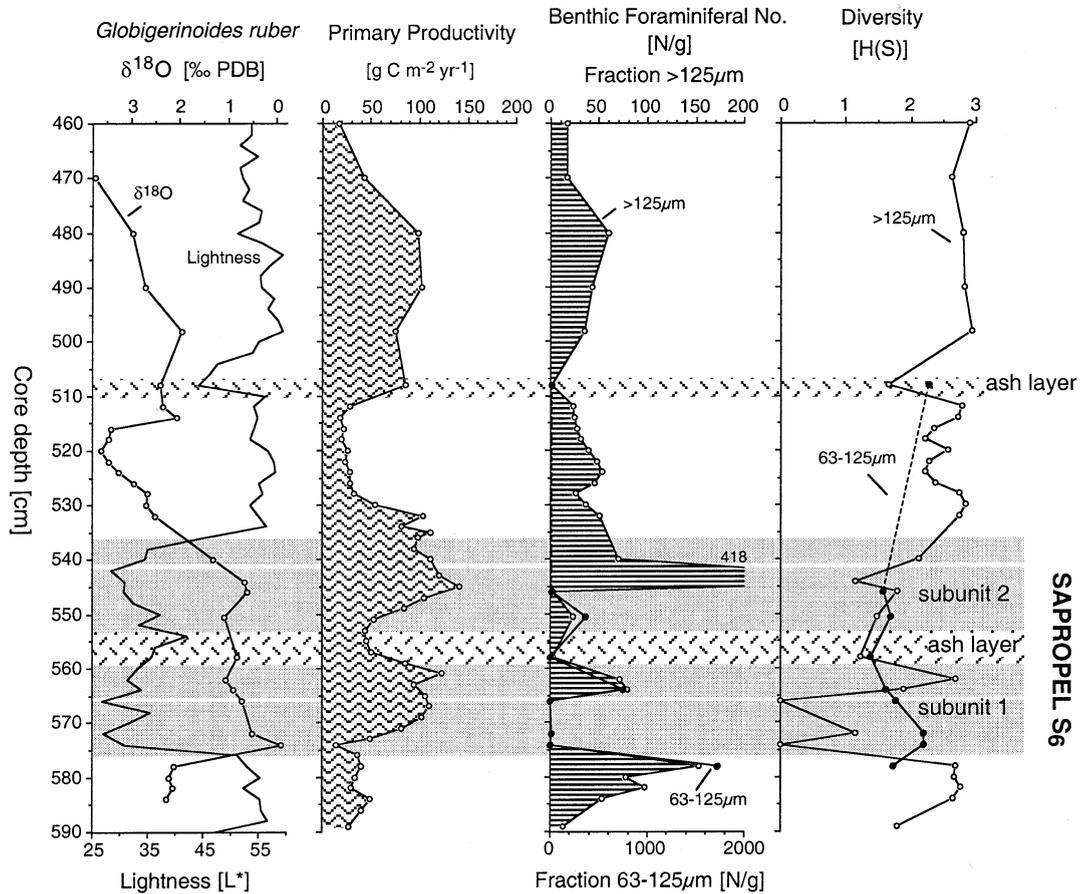
GeoTüKL51: S₆

Fig. 6. Sediment lightness, planktic stable oxygen isotope signal, primary productivity estimates based on ‘biogenic’ barium, benthic foraminiferal number, and benthic foraminiferal diversity across sapropel S₆ in core GeoTüKL51 from the lower bathyal (2158 m water depth) of the western Levantine Basin, southeast of Crete. Benthic foraminiferal results are given for size fractions 63–125 µm and > 125 µm, separately. Stable isotope data and paleoproductivity estimates are from [Weldeab et al. \(2002, in press\)](#).

of *Gyroidinoides neosoldanii*, *Bulimina exilis*, and *Globobulimina affinis*. The uppermost part of S₆ subunit 2 is dominated by *Eggerella bradyi* and *Bulimina striata mexicana*.

3.3.3. Post-sapropel fauna

Post-sapropel BFN values of the coarse fraction vary between 16 and 59 ind. g⁻¹. Decreasing values in the first 25 cm above the sapropel are followed by a broad high between 500 and 470 cm core depth. Post-sapropel diversities of the coarse fraction are similar to pre-sapropel values with an

average of $H(S)=2.6$, excluding the low value of the upper ash layer. The coarse fraction of the post-sapropel fauna is dominated by *Bulimina striata mexicana*. Associated species include *Miliolinella subrotunda*, *Pyrgoella sphaera* and *Quinqueloculina padana* (mainly in the lower post-sapropel interval), and *Triloculina tricarinata* and *Cassidulina laevigata* (mainly in the upper post-sapropel interval). For the fine fraction only one data point is present from the upper ash layer at 508 cm with a dominance of *Eponides pusillus* and *Cassidulina laevigata* (Figs. 6, 7).

GeoTüKL51: S₆

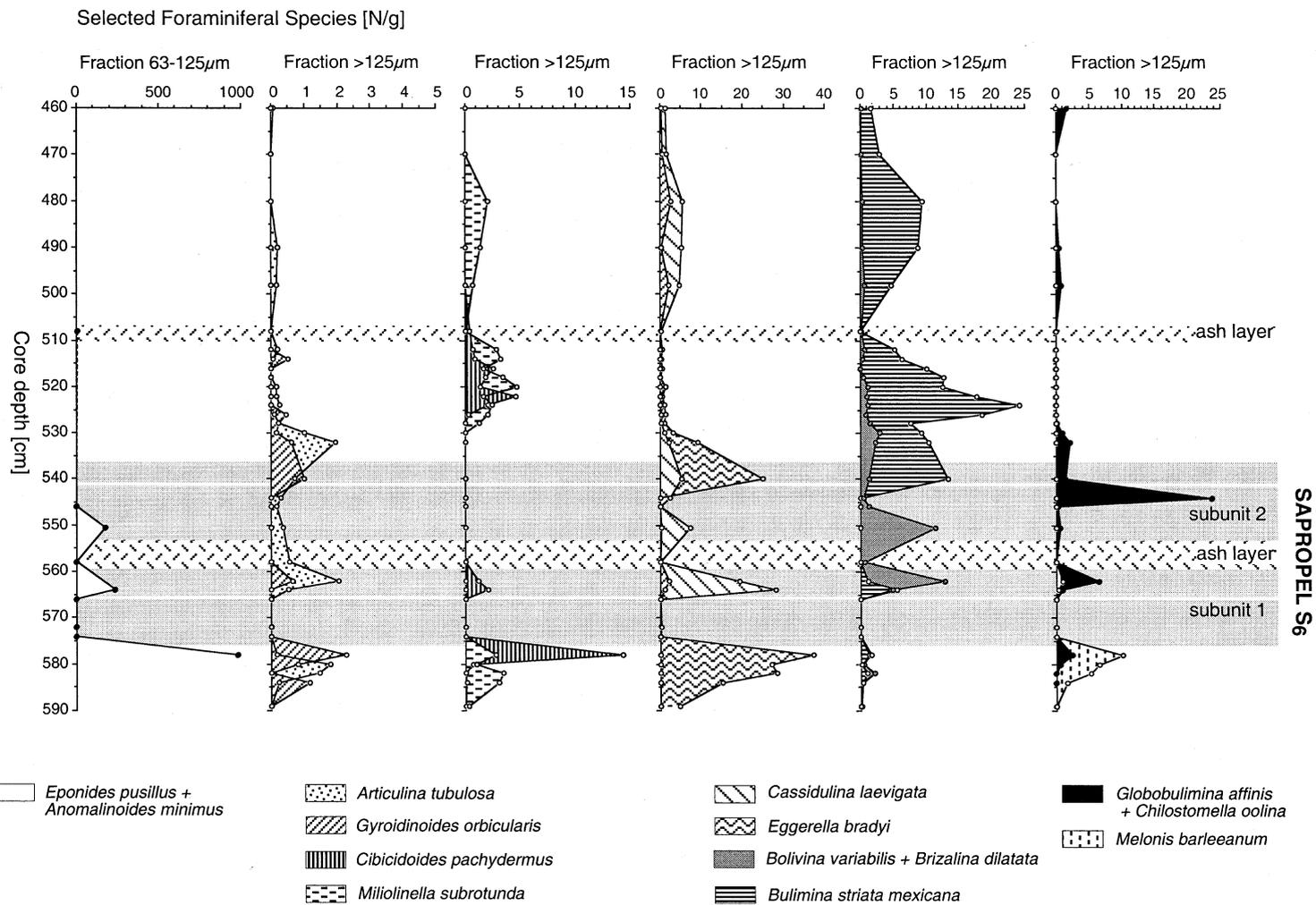


Fig. 7. Abundance of selected benthic foraminiferal species across sapropel S₆ in core GeoTüKL51 from the lower bathyal (2158 m water depth) of the western Levantine Basin, southeast of Crete.

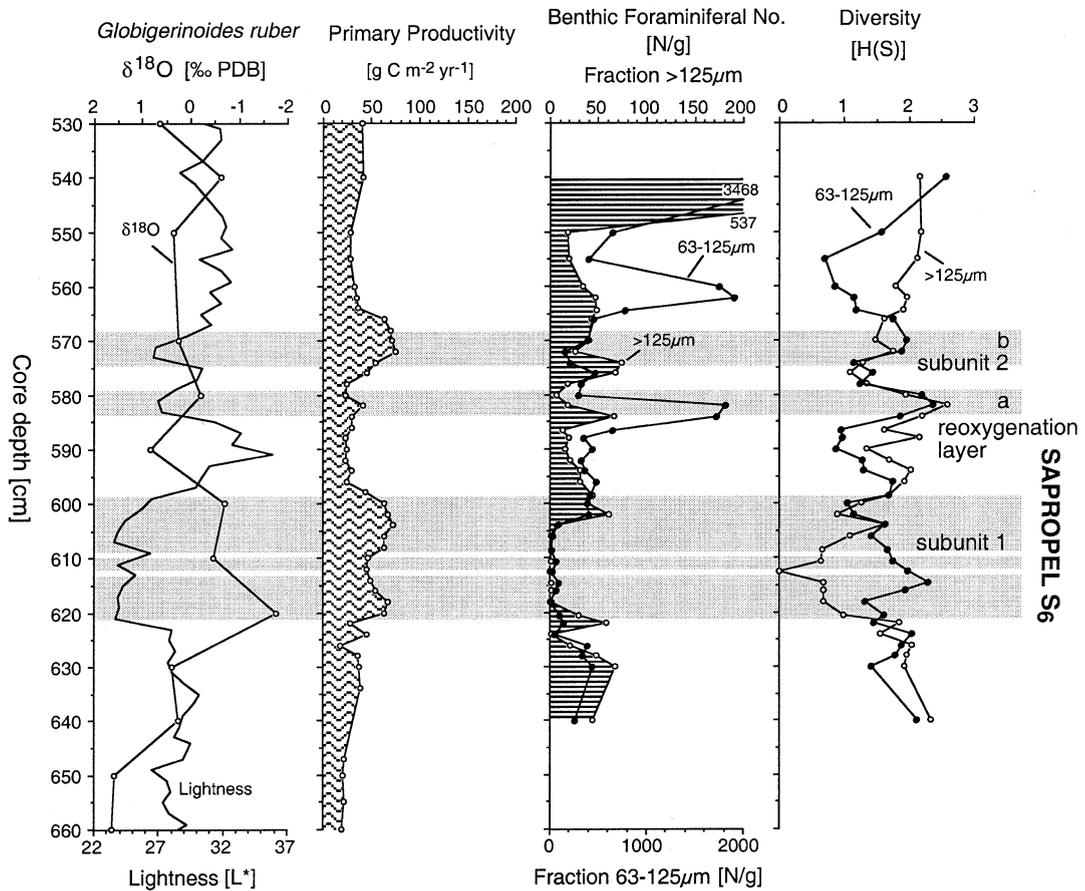
GeoTüKL83: S₆

Fig. 8. Sediment lightness, planktic stable oxygen isotope signal, primary productivity estimates based on ‘biogenic’ barium, benthic foraminiferal number, and benthic foraminiferal diversity across sapropel S₆ in core GeoTüKL83 from the middle bathyal (1433 m water depth) of the eastern Levantine Basin off Israel. Benthic foraminiferal results are given for size fractions 63–125 µm and > 125 µm, separately. Stable isotope data and paleoproductivity estimates are from [Weldeab et al. \(2002, in press\)](#).

3.4. Benthic foraminiferal fauna across sapropel S₆ of core GeoTüKL83, southeastern Levantine Sea

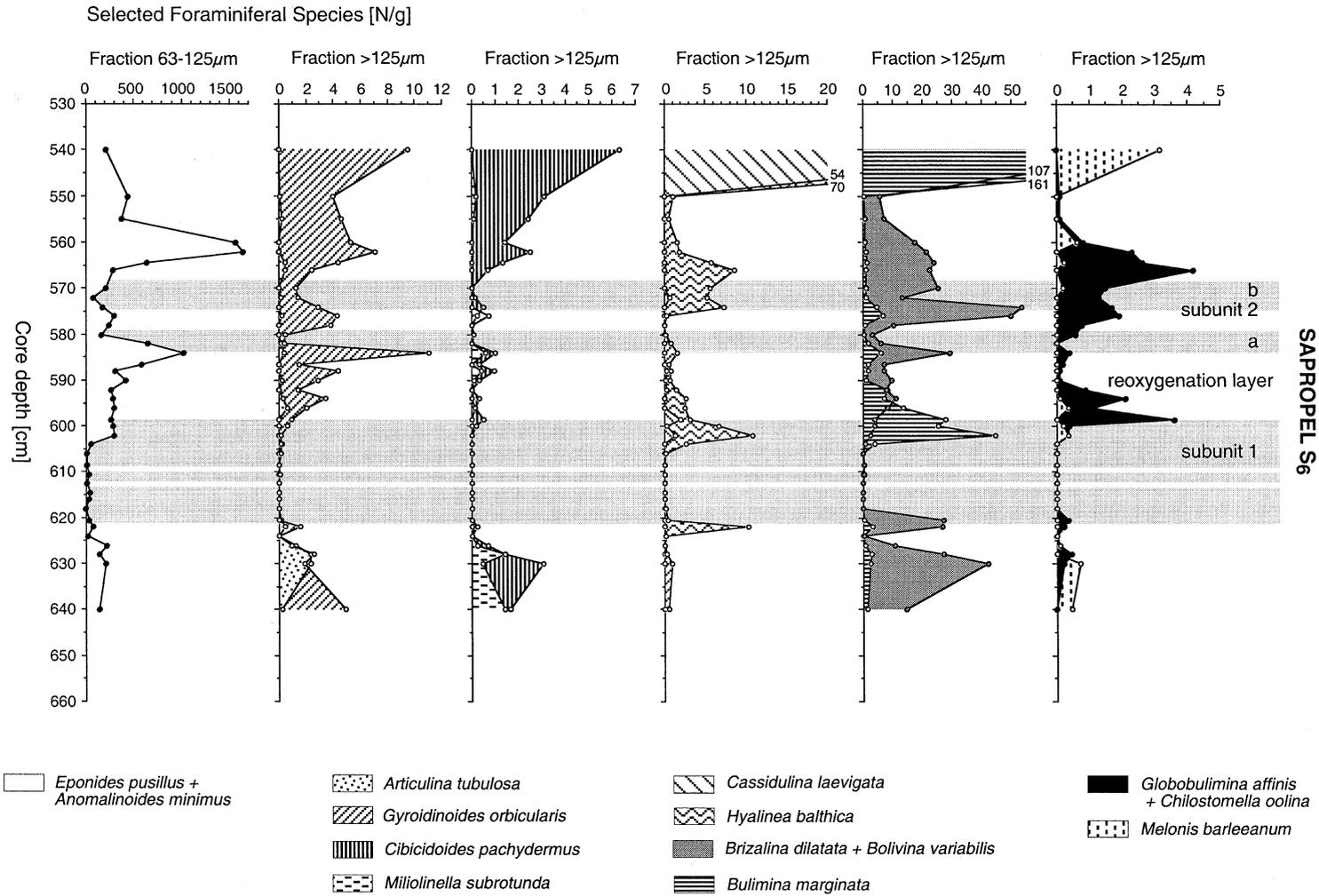
Sapropel S₆ of GeoTüKL83 consists of a 23-cm-thick lower (S₆ subunit 1) and 16-cm-thick upper part (S₆ subunit 2) separated by a 14-cm-thick reoxygenation layer. Within subunit 1 two light layers are observed, each 1 cm thick. Subunit 2 is subdivided into two parts by a slightly lighter 4-cm-thick interval. The lower part of subunit 2 contains several very thin sandy layers. The sapropel intervals exhibit sharp lower and upper boundaries, with weak lightness contrasts between sapropel and pre- and post-sapropel sediments.

The benthic foraminiferal faunal pattern across the sapropel interval is shown in [Figs. 8 and 9](#).

3.4.1. Pre-sapropel fauna

BFN values are 40 and 270 individuals g⁻¹ on average in the coarse and fine fractions, respectively. Approximately 10 cm below S₆, values start to decrease but show a maximum in the sample just below the lower sapropel boundary. Pre-sapropel diversities are around $H(S) = 2.0$ in the coarse fraction and $H(S) = 1.8$ in the fine fraction with a general trend to lower values when approaching the sapropel. The pre-sapropel fauna of the coarse fraction is dominated by *Brizalina*

GeoTüKL83: S₆



SAPROPEL S₆

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Fig. 9. Abundance of selected benthic foraminiferal species across sapropel S₆ in core GeoTüKL83 from the middle bathyal (1433 m water depth) of the eastern Levantine Basin off Israel.

dilatata, with significant amounts of *Bulimina marginata*, *Cibicidoides pachydermus*, and *Articulina tubulosa*. The fine fraction mainly comprises *Eponides pusillus* and *Anomalinoidea minimus*.

3.4.2. Sapropel fauna

In the lower and middle parts of S₆ subunit 1, BFN values are extremely low both in the coarse and fine fractions. At 613 cm sediment depth no benthic foraminifera are present in the coarse fraction, while in the fine fraction foraminifera are present throughout. Above this interval BFN values are significantly higher and vary between 6 and 74 ind. g⁻¹ (mean of 33) in the coarse fraction and, with a similar trend, between 80 and 1725 (mean of 516) ind. g⁻¹ in the fine fraction. In the lower part of S₆ subunit 1 diversities of the coarse fraction are below $H(S)=1$. Above this interval values exhibit a general increase throughout the reoxygenation layer, reaching a maximum of $H(S)=2.4$ in the lowermost part of S₆ subunit 2, followed again by lower values. In the fine fraction diversities fluctuate between $H(S)=0.9$ and 2.4. While benthic foraminifera of the coarse fraction are generally rare in the lower and middle parts of S₆ subunit 1, the fauna above is dominated by *Brizalina dilatata* and *Bulimina marginata*, with significant proportions of *Globobulimina affinis* and *Hyalinea balthica*. In the fine fraction, *Eponides pusillus* and *Anomalinoidea minimus* are present throughout the sapropel with high abundance in the reoxygenation interval and S₆ subunit 2 (Figs. 8, 9).

3.4.3. Post-sapropel fauna

BFN values of the coarse fraction are around 35 ind. g⁻¹ in the first 20 cm above the sapropel, followed by a rapid increase with a maximum of 537 ind. g⁻¹ in the topmost sample at 540 cm core depth. A similar BFN trend is mirrored by the fine fraction, reaching a maximum of 2930 ind. g⁻¹ in the topmost sample. Post-sapropel diversities of the coarse fraction show a steadily increase from $H(S)=1.6$ to 2.2. In the fine fraction post-sapropel diversities decrease from $H(S)=1.8$ to 0.7 in the first 15 cm above the sapropel followed again by an increase with a maximum of $H(S)=2.6$ in the topmost sample. The coarse

fraction of the post-sapropel fauna is dominated by *Brizalina dilatata*, *Bulimina marginata*, with increasing abundance of *Cassidulina laevigata*, *Melonis barleeanum*, and *Cibicidoides pachydermus*, and decreasing abundance of *Globobulimina affinis*. In the fine fraction *Eponides pusillus* and *Anomalinoidea minimus* exhibit a maximum between 5 and 10 cm above the sapropel.

4. Discussion

4.1. Ecological significance of the benthic foraminiferal fauna across sapropels

4.1.1. Benthic foraminiferal number and diversity

In open ocean areas, the benthic foraminiferal accumulation rate has been used as proxy for the assessment of past organic matter flux rates (e.g., Herguera and Berger, 1991). However, further studies revealed that the applicability of this proxy for quantitative interpretations is limited in dysoxic areas (Naidu and Malmgren, 1995). Across sapropel intervals of the eastern Mediterranean Sea the BFN exhibits drastic fluctuations attributed to severe changes in oxygen concentrations and organic matter fluxes (Oggioni and Zandini, 1987; Diester-Haass et al., 1998; Schmiedl et al., 1998). Therefore, at times of sapropel deposition, elevated organic matter fluxes may not be reflected correctly by the BFN because of a suppression of the benthic fauna by low dysoxic or anoxic conditions.

Several studies have demonstrated that meio-benthic species diversity is strongly dependent on the stability of an ecosystem (e.g. Cronin and Raymo, 1997; Gooday et al., 1998). Stable ecosystems favor the development of complex and highly diverse faunas, whereas in ecosystems that exhibit severe environmental fluctuations diversities are generally low. Accordingly, pre-sapropel faunas are highly diverse because they developed under oxic and oligo- to mesotrophic conditions (Schmiedl et al., 1998). In contrast, diversity at times of sapropel deposition is very low or even the whole fauna disappears. The increase of benthic foraminiferal diversity after re-ventilation can be used to assess the severity of

the preceding anoxia and the repopulation potential of distinct species at different sites and after different sapropels. In the deep Ionian and Levantine basins post-sapropel benthic foraminiferal diversities are often considerably lower when compared to pre-sapropel values (Vismara Schilling, 1986; Nolet and Corliss, 1990; Schmiedl et al., 1998). This observation suggests a low recovery potential of faunas inhabiting the oligotrophic deep-sea ecosystems (Schmiedl et al., 1998; De Rijk et al., 1999).

4.1.2. Benthic foraminiferal species

The life strategies of most benthic foraminiferal species related to sapropels are well known from different studies on the distribution pattern and microhabitat of recent benthic foraminifera from the Mediterranean (e.g., Mullineaux and Lohmann, 1981; Jorissen et al., 1992, 1995; De Stigter et al., 1998; De Rijk et al., 1999; Schmiedl et al., 2000) and other areas (e.g., Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Sen Gupta and Machain-Castillo, 1993; Gooday, 1994; Loubere, 1996). According to this information and the summary of Jorissen (Jorissen, 1999, and references therein) the dominant taxa of this study can be classified into the following groups.

(A) Taxa with a deep infaunal microhabitat, especially resistant to very low oxygen conditions: *Globobulimina affinis* (and *Globobulimina* spp.), *Chilostomella oolina*, *Fursenkoina mexicana*, and *Bulimina exilis*. These taxa are common in low-oxygen habitats or eutrophic continental margins where they feed from degraded organic matter at the dysoxic/anoxic boundary (e.g., Corliss, 1985; Mackensen and Douglas, 1989; Schmiedl et al., 2000). Within oxygen minimum zones they occur together with different shallow infaunal taxa according to the intensity of oxygen depletion (Sen Gupta and Machain-Castillo, 1993). In the eastern Mediterranean Sea, *Globobulimina affinis*, *Chilostomella oolina*, and *F. mexicana* commonly occur in restricted intervals prior to and after sapropel formation lacking any other species in significant numbers. Although generally rare in the eastern Mediterranean, a mass occurrence of *Bulimina exilis* has been described from sapropel

S₆ where this species appears together with the other low-oxygen indicators (Vismara Schilling, 1986; Oggioni and Zandini, 1987; Schmiedl et al., 1998; Jorissen, 1999).

(B) Taxa with a shallow to intermediate infaunal microhabitat, more opportunistic, but less resistant for low oxygen conditions: *Bolivina variabilis*, *Bolivina pseudopunctata*, *Brizalina dilatata*, *Bulimina marginata*, *Bulimina striata mexicana*, *Cassidulina laevigata*, *Eggerella bradyi*, *Gavelinopsis translucens*, *Gyroidinoides neosoldanii*, *Hoeglundina elegans*, *Hyalinea balthica*, *Melonis barleeanum*, *Oridorsalis umbonatus*. These taxa are common in mesotrophic to eutrophic environments with moderate oxygen depletions in the bottom and pore water (e.g., Lutze and Coulbourn, 1984; Sen Gupta and Machain-Castillo, 1993; Gooday, 1994; Rathburn and Corliss, 1994). In the Mediterranean Sea significant occurrences of these species are restricted to the deeper shelf and upper bathyal areas (Jorissen et al., 1992; Rohling et al., 1997; De Stigter et al., 1998; De Rijk et al., 1999; Schmiedl et al., 2000).

(C) Taxa with an epifaunal to shallow infaunal microhabitat, more or less opportunistic, adapted to high oxygen conditions and oligo- to mesotrophic conditions: *Cibicidoides pachydermus* and *Gyroidinoides orbicularis*. In the western Mediterranean Sea, the distribution of *Cibicidoides pachydermus* is associated with oligotrophic and well-ventilated conditions. Elevated numbers are observed at the oligo- to mesotrophic open slope while at higher trophic levels its number decreased in favor of infaunal taxa (Schmiedl et al., 2000). The species *Gyroidinoides orbicularis* is one of the few rotaliid species inhabiting the recent deep basin areas (De Rijk et al., 1999). It is obviously adapted to very oligotrophic conditions although it also occurs in significant numbers at higher trophic levels of the bathyal continental slope (Schmiedl et al., 2000). Our results show that *Gyroidinoides orbicularis* co-occurs with *Articulina tubulosa* across several pre- and postsapropel intervals (e.g., Figs. 5, 7). This observation may suggest an opportunistic life style of *Gyroidinoides orbicularis*.

(D) Small, epifaunal, opportunistic taxa, suspected to be phytodetritus feeders, indicative of

a high trophic level in combination with sufficiently high oxygen concentrations: *Eponides pusillus* and *Anomalinoidea minimus*. The species *Eponides pusillus* (= *Alabaminella weddellensis* of Gooday and Lamshead, 1989, p. 57, figs. 1D–F, 3A–D; = *Eponides tumidulus* of Vismara Schilling, 1986, figs. 6, 7, and Oggioni and Zandini, 1987, fig. 6.9) has been described together with *Epistominella exigua* from the deep Atlantic Ocean where it is adapted to the seasonal formation of freshly produced phytodetritus in a highly oxic environment (Gooday, 1993). In the bathyal and abyssal eastern Mediterranean *Eponides pusillus* co-occurs with *Anomalinoidea minimus* and *Epistominella exigua*. Their association with sapropels suggests a high recolonization potential of deep-sea areas following anoxic periods (Oggioni and Zandini, 1987; Jorissen, 1999). Living specimens of small benthic foraminifera, including *Anomalinoidea minimus* and *Bolivina* spp. have been repeatedly found in net hauls in the Mediterranean Sea during different *Meteor* expeditions (own observations). These observations suggest that their dispersal may be controlled by release and transport of embryonic juveniles or passive suspension and transport of various growth stages (Banner et al., 1985; Alve, 1999).

(E) Assorted miliolid taxa, epifaunal to deep infaunal, indicative of oligotrophic to mesotrophic Mediterranean deep-sea environments: *Articulina tubulosa*, *Miliolinella subrotunda*, *Pyrgo murrhina*, *Pyrgo elongata*, *Pyrgoella sphaera* and *Quinqueloculina padana*, *Quinqueloculina patagonica*, *Triloculina tricarinata*. These taxa inhabit the recent well-ventilated lower bathyal and abyssal areas of the eastern Mediterranean Sea (Mullineaux and Lohmann, 1981; De Rijk et al., 1999). The close association of *Articulina tubulosa* with sapropels suggests a highly opportunistic life style (Jorissen, 1999). This species is probably able to colonize the basin areas very quickly during short oxygenation pulses under unstable environmental conditions. Its low abundance in non-sapropelic sediments suggests that it is repressed by other species in a stable and highly diverse ecosystem (Schmiedl et al., 1998).

Our knowledge on the environmental significance of the benthic foraminiferal fauna as dis-

cussed above was used to assess the changes in oxygenation during formation of sapropels S_6 and S_5 in the Levantine Basin. High proportions of miliolid taxa (except those of the highly opportunistic *Articulina tubulosa*) and the preferentially epifaunal species *Cibicidoides pachydermus* and *Gyroidinoides orbicularis* together with high diversities were interpreted to indicate well-ventilated conditions. In contrast, high proportions of the deep infaunal taxa *Fursenkoina* spp., *Chilostomella oolina*, and *Globobulimina* spp. together with low diversities were interpreted to indicate low oxygen contents. To illustrate the changes in oxygen contents we have developed the following formula: $(HO/(HO+LO)+Div) \times 0.5$, with HO = relative abundance of high oxygen indicators (Miliolids – *Articulina tubulosa* + *Cibicidoides pachydermus* + *Gyroidinoides orbicularis*), LO = relative abundance of low oxygen indicators (*Fursenkoina* spp., *Chilostomella oolina*, *Globobulimina* spp.), and Div = normalized benthic foraminiferal diversity. Diversities were normalized relative to the maximum $H(S)$ value of each sapropel interval. The term was multiplied by 0.5 to distinguish between anoxic (minimum value = 0) and oxic (maximum value = 1) conditions. Although this approach seems to yield rather reasonable results, oxygenation may be overestimated in sapropel intervals with extremely low benthic foraminiferal numbers and underestimated in ash layers and post-sapropel intervals where the fauna may be in disequilibrium with environmental conditions. The results are shown in Fig. 10.

4.2. Benthic ecosystem variability during S_5 and S_6 deposition: evolution of bottom water oxygenation and organic matter fluxes in the Levantine Basin

4.2.1. Oxygenation and productivity changes during S_5 deposition

Our estimates indicate that most sustained oxygen depletions occurred during deposition of sapropel S_5 at the lower bathyal site of M40/4-67SL southeast of Crete, followed by S_5 at middle bathyal depth off Israel. Sapropel S_5 was formed between approximately 127 and 122 kyr BP (Emeis et al., in press) within MIS 5.e under fully developed interglacial conditions. At that time the sea

Oxygenation

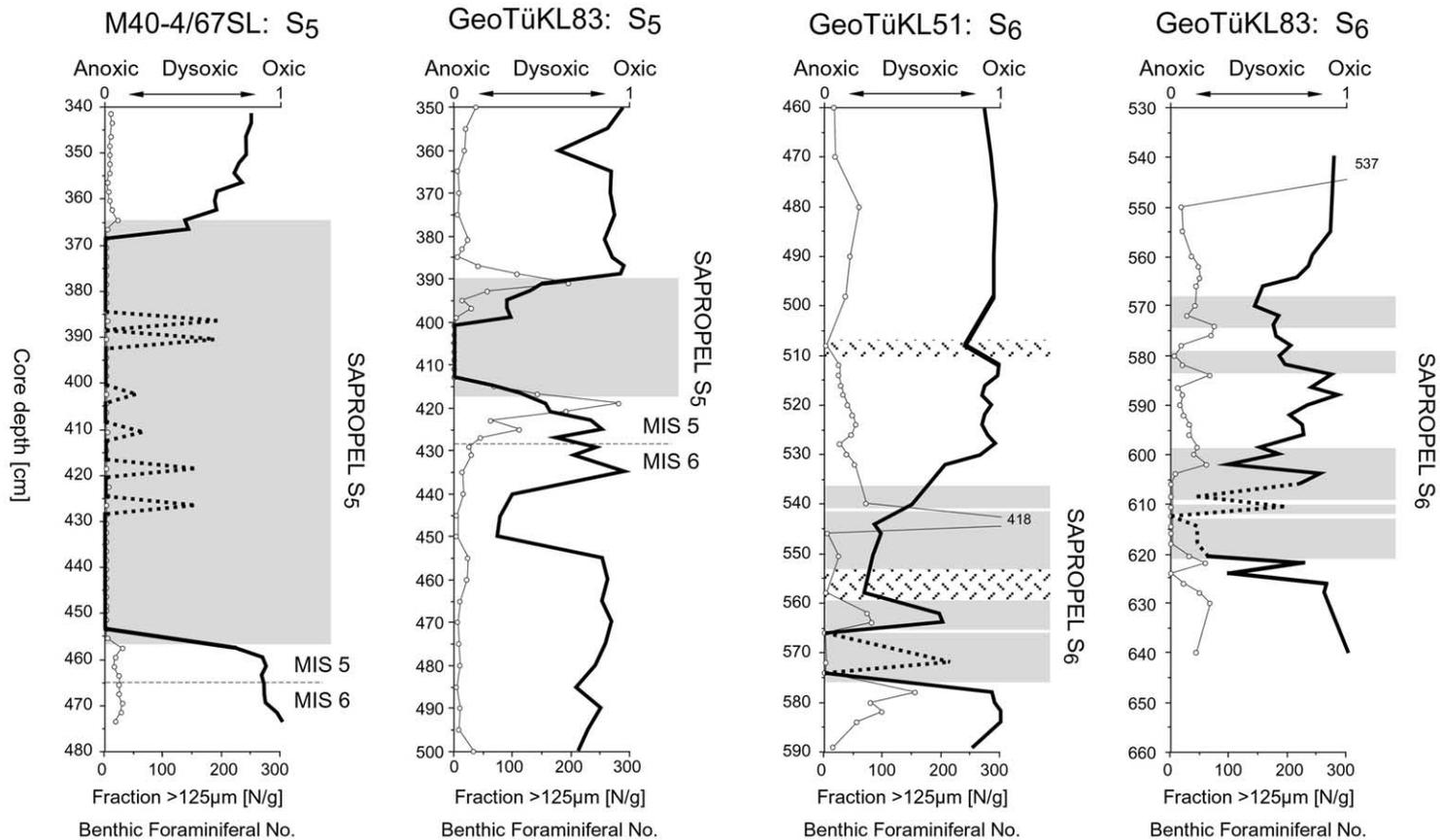


Fig. 10. Relative changes of benthic ecosystem oxygenation (thick line) across sapropels S₅ and S₆ from cores M40-4/67SL and GeoTüKL51 of the lower bathyal western Levantine Basin and GeoTüKL83 of the middle bathyal eastern Levantine Basin. Oxygen estimates are based on the ratio $(HO/(HO+LO)+Div) \times 0.5$, with HO = relative abundance of high oxygen indicators (*Miliolids*—*Articulina tubulosa*+*Cibicidoides pachydermus*+*Gyroidinoides orbicularis*), LO = relative abundance of low oxygen indicators (*Fursenkoina* spp., *Chilostomella oolina*, *Globobulimina* spp.), and Div = normalized benthic foraminiferal diversity ($H(S)$ normalized). Intervals where oxygen contents are likely to be overestimated due to very low benthic foraminiferal numbers are indicated by stippled line. The benthic foraminiferal number of the size fraction > 125 µm is given for comparison (thin line with dots).

level was several meters higher than at present, reflecting reduced polar ice volume and higher global temperatures (Chappell and Shackleton, 1986; Waelbroeck et al., 2002). Late Quaternary benthic foraminiferal successions suggest that wind-induced mixing was reduced during interglacials resulting in lower surface water productivity and organic matter fluxes compared to glacial intervals (Schmiedl et al., 1998). Based on U_{37}^k estimates, Emeis et al. (1998, in press) showed that in the eastern Mediterranean, sea surface temperatures rise from below 15°C in MIS 6 to more than 20°C at the top of S₅. Pollen data indicate a reduction of steppe plants and a rise of woody taxa across the boundary of MIS 6 and MIS 5, suggesting a drastic increase of humidity in the eastern Mediterranean borderlands with onset of interglacial conditions (Mommersteeg et al., 1995). Based on geochemical investigations (alkenones, stable oxygen isotopes, Sr and Nd isotopes) the southern catchment (e.g., Nile river) is proposed as major freshwater source (Emeis et al., in press; Weldeab et al., 2002).

In the record of M40-4/67SL the decrease of BFN, drops in the abundance of different miliolid taxa and the rise of low-oxygen indicators (*Globobulimina affinis*) suggest a stepwise reduction of oxygen concentrations starting approximately 3000 years before the onset of sapropel formation (Figs. 2, 3). This time lead was estimated based on a MIS 6 to 5 stage boundary age of 129.8 kyr (Martinson et al., 1987) and a lower boundary age of sapropel S₅ of 127 kyr (Emeis et al., in press). A similar stepwise disappearance pattern of benthic foraminifera preceding S₅ formation has been observed in the abyssal Ionian Sea (Wagner, 2000). The oxygen reduction was obviously not accompanied by a significant eutrophication at that time since the abundance of infaunal species remained low. The BFN rise in both of the investigated size fractions just a few centimeters below the lower sapropel boundary shows that significant eutrophication started rather late, with only low profit for non-opportunistic benthic foraminiferal species that were already suppressed by an early oxygen depletion. However, the inferred stepwise decrease of oxygen content is not mirrored by our oxygen index, suggesting a more

sudden drop at the beginning of sapropel deposition (Fig. 10). This discrepancy is due to the pre-sapropel diversity pattern of the fauna. Diversities of the coarse fraction remain unusually high until the onset of sapropel formation, indicating that oxygen supply and thus deep-water formation was still present to some extent. At site Geo-TüKL83 off Israel the sequence of environmental changes preceding S₅ deposition shows striking differences when compared to that of the western Levantine Basin. Here, the initial increase of organic matter fluxes started together with the first drops of oxygen already at the boundary between MIS 6 and 5 and is reflected by a rise of BFN and the abundance of different shallow and deep infaunal taxa (*Brizalina dilatata*, *Bolivina variabilis*, *Cassidulina laevigata*, *Hyalinea balthica*, *Globobulimina affinis*). A more drastic oxygen decrease is marked by a drop in diversity and BFN and rise of the low-oxygen indicator *Fursenkoina mexicana* and appears with onset of sapropel deposition (Figs. 4, 5). The comparison of stable isotope signals between the two investigated sites suggests that at middle bathyal water depth sapropel deposition and, thus, anoxia started considerably later than at lower bathyal water depth (Figs. 2, 4).

At both sites the faunal results are generally in accordance with barium records of Weldeab et al. (in press), although it is not possible to test the quantitative reliability of the geochemically derived productivity estimates. The barium record indicates a slight productivity increase already a few centimeters below the onset of sapropel deposition but extremely high values within the sapropel (Figs. 2, 4). Emeis et al. (in press) reported that a decrease of $\delta^{18}O_{\text{surface water}}$ is already observed several centimeters below the base of the sapropel S₅, which is interpreted as evidence for an early freshwater runoff from the southern catchment. This early input of fresh water together with rising temperatures likely enhanced stratification at deep-water formation sites well before the onset of sapropel deposition.

With the onset of S₅ deposition the fauna at both investigated sites disappeared since oxygen contents have obviously been too low to support benthic life. The lack of oxygen explains why eu-

trophication, suggested from the ‘biogenic’ barium record (Figs. 2, 4; Weldeab et al., in press), is not mirrored by the fauna within the sapropel. Between 422 and 425 cm core depth of M40-4/67SL the presence of highly opportunistic taxa (*Articulina tubulosa*, *Eponides pusillus*, and *Anomalinoidea minimus*) indicates a short reoxygenation event accompanied by rapid repopulation and followed by a sudden drop in the planktic $\delta^{18}\text{O}$ signal (Figs. 2, 3). The rapidity of this reoxygenation event is supported by observations of Jorissen (1999). He concluded that the main factor controlling the pre- and post-sapropel foraminiferal successions is the time involved in the onset of anoxic conditions or reoxygenation of the benthic ecosystem. A gradual change of oxygenation is reflected by the presence of less opportunistic low-oxygen indicators (e.g., *Globobulimina*, *Chilostomella*, *Fursenkoina*) while rapid reoxygenation favors the repopulation by highly opportunistic species (e.g., *Anomalinoidea*, *Eponides*, *Epistominella*). In the upper part of S₅ of M40-4/67SL, repeatedly, few poorly preserved foraminiferal tests were observed in the fraction > 125 μm , however, without contribution of opportunistic species in the fine fraction (Figs. 2, 3, 10). Therefore, we assume an allochthonous origin for these tests. Within S₅ of GeoTüKL83 no reoxygenation event was recorded. This event was probably missed due to discontinuous sampling (2 cm spacing) and lower temporal resolution at this site.

Repopulation events indicating temporary reoxygenation in association with an interruption of sapropel deposition were reported from sapropels S₁ (Rohling et al., 1997; Sperling et al., 2003), S₆ (Oggioni and Zandini, 1987; Schmiedl et al., 1998; Casford et al., 2003) and a Pliocene sapropel (Rohling et al., 1993). The S₁ reoxygenation event has been attributed to rapid drops in temperature leading to an onset of deep-water formation and ventilation of the deep basins (Rohling et al., 1997; De Rijk et al., 1999; Myers and Rohling, 2000). Recent results indicate that this cold spell is part of the millennial-scale climate variability of the northern hemisphere (Alley et al., 1997; Bond et al., 1997; Rohling et al., 2002). Similarly, the reoxygenation event ob-

served within S₅ and the stepwise pre-sapropel disappearance and post-sapropel repopulation patterns may be explained as an expression of abrupt climate fluctuations superimposed on the orbital insolation signal. Short-term cooling fostered the formation of dense oxygen-rich subsurface water, thus, passing on the atmospheric signal to the deep-sea ecosystems.

At the lower bathyal site of M40-4/67SL the sea floor remained anoxic until post-S₅ reventilation is indicated by the return of the low-oxygen indicator *Fursenkoina mexicana* and opportunistic taxa (*Gyroidinoidea orbicularis*, *Anomalinoidea minimus*, *Eponides pusillus*) (Fig. 3). In contrast, at site GeoTüKL83 the gradual return of deep and shallow infaunal taxa demonstrates that in the middle bathyal eastern Levantine Sea environmental conditions considerably improved already in the late phase of S₅ formation (Figs. 4, 5). This environmental pattern is consistent with climate reconstruction based on southern European pollen data that indicate an early temperature maximum with a transition to colder climate halfway through the sequence of the last interglacial maximum (Frogley et al., 1999; Rioual et al., 2001). The gradual cooling may have favored the formation of dense water at intermediate- and deep-water formation sites. Our faunal results suggest that the density of newly formed subsurface water masses was not high enough to reach the deep basin areas but ventilated at least the middle bathyal benthic ecosystems.

According to the discussion above, one of the reasons that may explain the observed faunal differences between M40-4/67SL and GeoTüKL83 is the different water depth at the investigated sites (2158 m at M40-4/67SL versus 1433 m at GeoTüKL83). The effect of water depth on sapropel formation and benthic foraminiferal distribution has been described in a number of papers (e.g., Maldonado and Stanley, 1976; Ross and Kennett, 1983; Cramp and O’Sullivan, 1999). According to the model of Maldonado and Stanley (1976) the depth interval between 1000 and 2000 m was partly ventilated while the water mass below was stagnant and anoxic. Consequently, some oxygen may have been present during S₅ formation at site GeoTüKL83. Our findings are corroborated by

data sets on benthic foraminiferal successions across lower bathyal and abyssal sapropels (summary in [Jorissen, 1999](#)). Unfortunately, no comparable information is available from the depth interval between 1000 and 2000 m.

In addition to deep water ventilation, oxygen concentrations at the sea floor may have been influenced by spatial differences of organic matter fluxes and resulting oxygen consumption rates ([Casford et al., 2003](#)). This idea is supported by geochemical investigations along a core transect of the eastern Mediterranean Sea ([Weldeab et al., in press](#)). This study revealed an east to west productivity increase during S₅ formation. Highest paleoproductivity was estimated for the region south of Crete. This finding was attributed to pycnocline shoaling probably associated with the presence of a submesoscale cyclonic gyre system south of Crete, similar to that of recent oceanographic conditions ([Pinardi and Masetti, 2000](#)). High availability of nutrients fostered opportunistic silicious plankton, resulting in high opal accumulation rates and elevated oxygen consumption at the sea floor south and southeast of Crete ([Thunell and Williams, 1982](#)).

[Jorissen \(1999\)](#) argued that the end of S₅ deposition was accompanied by a rapid turnover of the water column and quick reoxygenation of the benthic environment. His conclusions were based on abyssal faunal records and are supported by findings of [Wagner \(2000\)](#) from the abyssal Ionian Basin. In contrast, our observations show that post-S₅ reoxygenation at shallower water depths occurred more gradually, following the general temperature development of the last interglacial maximum (MIS 5.e) (see above). The post-sapropel decrease of BFN at both sites mirrors the drop of organic matter fluxes and the transition to oligotrophic conditions. In core M40-4/67SL, post-sapropel diversities are considerably lower than pre-sapropel values. The contrast between pre- and post-sapropel diversities has been previously described ([Vismara Schilling, 1986](#); [Nolet and Corliss, 1990](#); [Schmiedl et al., 1998](#)) and may be attributed to a low recovery potential of the basin fauna under oligotrophic conditions following severe and sustained anoxia. While the repopulation strategies of the opportunistic taxa

(*Articulina tubulosa*, *Gyroidinoides orbicularis*, *Eponides pusillus*, *Anomalinoidea minimus*) allow a fast return into the reoxygenated habitats, other less opportunistic species (including most of the miliolid taxa) return considerably delayed (several thousand years) after the end of sapropel formation. A slow recovery of the deep-sea fauna after severe anoxia and under the prevalence of oligotrophic conditions may also account for the recent low-diversity eastern Mediterranean deep-water faunas that likely have not yet recovered from the S₁ stagnation ([Schmiedl et al., 1998](#); [De Rijk et al., 1999](#)). At the middle bathyal Israelian continental margin pre- and post-sapropel diversities are very similar. At this site oxygen depletions were less severe and reoxygenation started considerably earlier than in the deeper western Levantine Basin. The early return of the different taxa resulted in a complete recovery of the fauna already in the late stage of sapropel formation. It was likely fostered by a close location of benthic foraminiferal refuge areas during basin anoxia.

4.2.2. Oxygenation and productivity changes during S₆ deposition

At both investigated sites BFN and diversity fluctuations, and the disappearance and repopulation patterns of the different epifaunal, shallow and deep infaunal species suggest that environmental variability during S₆ formation was much higher than during S₅ formation (Figs. 6–10). Sapropel S₆ was deposited between approximately 176 and 170 kyr BP ([Emeis et al., in press](#)) during interstadial 6.e of the penultimate glaciation. Sapropel S₆ deposition followed an insolation maximum of 537 W m⁻² that almost matches the maximum preceding S₅ (548 W m⁻²) ([Berger, 1978](#); [Rossignol-Strick, 1985](#)). Sapropel S₆ is accompanied by a depletion of the planktic δ¹⁸O signal of approximately 2.6–3‰ ([Thunell et al., 1983](#); [Emeis et al., in press](#)). At the same time surface temperatures varied between 12 and 18°C and were significantly lower than MIS 5.e temperatures ([Emeis et al., in press](#)). The freshwater sources for the strong depletion at times of glacial S₆ formation are still under debate but likely involve enhanced monsoonal rainfall in the southern catchment ([Rossignol-Strick, 1985](#);

Masson et al., 2000; Emeis et al., in press; Weldeab et al., 2002) rather than massive melt water discharge from the northern catchment (Thunell et al., 1983).

In both investigated cores, the non-sapropelic benthic foraminiferal fauna is dominated by shallow infaunal and epifaunal taxa, suggesting that trophic levels during glacials were higher than during interglacials. The glacial increase of productivity and corresponding organic matter fluxes in the Mediterranean Sea is corroborated by several micropaleontological and geochemical studies (Abrantes, 1988; Caralp, 1988; Rohling and Gieskes, 1989; Schmiedl et al., 1998; Weldeab et al., 2003, in press). Rohling and Gieskes (1989) attributed this productivity increase to a shoaling of the pycnocline and nutricline into the euphotic zone because of a relatively low density contrast between surface and intermediate water. In addition, atmospheric circulation models indicate a glacial intensification and southward shift of the westerlies (e.g., Kutzbach and Guetter, 1986; Lautenschlager and Herterich, 1990; Joussaume, 1993). High wind stress together with low winter temperatures and increased salinity (Thunell et al., 1987; Thunell and Williams, 1989; Rohling and Gieskes, 1989; Emeis et al., in press) may have favored vertical instability of the water column in the eastern Mediterranean Sea, even during times of sapropel formation. As a consequence of enhanced vertical mixing, more nutrients from subsurface waters should have reached the photic zone, resulting in higher productivity rates (Schmiedl et al., 1998).

At the lower bathyal western Levantine Basin (GeoTüKL51) the pre-sapropel BFN increase and rise of the abundance of several epi- and infaunal species indicate a strong increase of organic matter fluxes preceding the onset of sapropel formation. However, high diversity and abundance of epifaunal taxa (*Cibicoides pachydermus*), and low abundance of low-oxygen indicators just below the sapropel boundary prove that bottom waters were still oxic at that time. With onset of sapropel deposition the sudden BFN drop and vanishing of the fauna indicates a rapid reduction of deep-water ventilation (Figs. 6, 10). At the middle bathyal Israelian continental margin (Geo-

TüKL83) the benthic foraminiferal fauna indicates only minor eutrophication prior to sapropel deposition, which is in agreement with the productivity estimates of Weldeab et al. (in press) (Figs. 8, 9). At the same time oxygen depletion seems to have occurred in two steps (Fig. 10).

Within both investigated S_6 sapropels BFN and diversity lows indicate two phases of significant oxygen reduction comprising an anoxic or low dysoxic interval in the initial phase (S_6 subunit 1) and a dysoxic interval in the late phase (S_6 subunit 2) of sapropel formation. The two sapropel subunits are separated by a sustained reoxygenation interval which is mirrored by the presence of a diverse fauna containing epifaunal and shallow infaunal taxa (Figs. 6–10). This asymmetric pattern of deep-water oxygenation during S_6 deposition may be explained by the temperature development at that time. Emeis et al. (in press) showed that the onset of S_6 deposition is associated with a rapid warming phase followed by an immediate surface water cooling of approximately 2°C. As a consequence, surface water stratification was more stable during the initial warm phase and became more unstable with decreasing temperatures in the later phase. In this unstable state, the water column stratification at deep-water formation sites was probably very susceptible to minor climate fluctuations at a millennial time-scale, similar to those observed during the Holocene (Schilman et al., 2001; Rohling et al., 2002; Casford et al., this volume; Sperling et al., this volume) and during phases of oceanographic instability before and after the period of S_5 stratification (see above). This oceanographic sensitivity may explain the high variability of benthic foraminiferal diversity and abundance, particularly observed in the fine fraction at site GeoTüKL83 (Figs. 8, 9).

The occurrence of *Eponides pusillus* and *Anomalinoides minimus* in low numbers across S_6 subunit 1, lacking any other species in significant numbers, suggests that middle bathyal deep-water ventilation was not totally shut down at that time but rather persisted at least on a decadal scale. During the early phase of S_6 deposition the small opportunistic species may have been able to repeatedly colonize the middle bathyal deep-sea

floor even during short events of ventilation. An allochthonous origin may also account for the occurrence of foraminifera in the fine fraction of this sapropel interval. The potential influence of downslope transport is also suggested by several thin sandy layers in the lower part of S₆ subunit 2. However, since shallow water species do not contribute to the fine fraction at site GeoTüKL83 in significant numbers (on average less than 2% of the total fauna), we assume an autochthonous origin of *Eponides pusillus* and *Anomalinoidea minimus*. In contrast, individuals of these opportunistic species are almost absent in the fine fraction of the lower part of S₆ subunit 1 at site GeoTüKL51 and the few present benthic foraminifera comprise different small allochthonous shallow-water species (on average 15% of the total fauna). An allochthonous origin of small epiphytic species in sapropelic sediments was previously reported by Vismara Schilling (1986) and Oggioni and Zandini (1987), assuming transport by means of vegetal phytoclasts. Our results suggest more sustained anoxic conditions at lower bathyal depth southeast of Crete during the early period of S₆ deposition and the importance of reworking and downslope transport in this region.

At site GeoTüKL51 drops in foraminiferal number and diversity are associated with two ash layers, the V-1 ash layer separating S₆ subunits 1 and 2, and the post-S₆ W-3 ash layer (according to Keller et al., 1978). Although an immediate impact on the fauna is observed along with both ash layers, no long-term influence is suggested since the post-ash fauna resembles the fauna prior to ash deposition (Figs. 6, 7). This interpretation is supported by results of Hess et al. (2001), who studied the repopulation pattern after the Pinatuba ash fall of 1991. Their results suggest a fast recovery of the fauna within several years to decades after the deposition of the ash layer.

5. Conclusions

(1) Sapropel S₅ was deposited between approximately 127 and 122 kyr BP during the warm and humid period of MIS 5.e representing fully devel-

oped interglacial conditions. At lower bathyal water depth of the western Levantine Basin, the disappearance patterns of different miliolid and deep infaunal taxa suggest a stepwise reduction of deep-water ventilation starting approximately 3000 years before the onset of S₅ deposition. At this site, anoxic conditions prevailed throughout S₅ deposition except for a short reoxygenation event that is accompanied by repopulation of a few highly opportunistic species. Post-sapropel diversities are low and return only very gradually to pre-sapropel values. This trend indicates that under oligotrophic conditions the basin fauna recovers only very slowly following sustained anoxia.

(2) At middle bathyal water depth of the eastern Levantine Basin, oxygen depletion during S₅ deposition was less severe and improved earlier when compared to the deeper site. As a result, pre- and post-sapropel diversities are very similar, indicating a full recovery of the fauna shortly after the end of sapropel deposition. Significant eutrophication during sapropel S₅ formation is reflected by pre- and late-sapropel maxima of shallow and deep infaunal taxa. Middle bathyal and shallower ecosystems were subject to a stepwise reoxygenation preceding the more sudden reoxygenation of the deeper basin ecosystems.

(3) Sapropel S₆ was formed between approximately 176 and 170 kyr BP during MIS 6.e of the penultimate glaciation. The general dominance of shallow infaunal species in non-sapropelic sediments indicates mesotrophic glacial levels relative to oligotrophic interglacial levels. Strong fluctuations in benthic foraminiferal number, diversity, and species composition suggests that organic matter fluxes and oxygen depletion during S₆ formation have been less severe and more variable when compared to S₅ formation. Estimated oxygen contents range from anoxic to suboxic at lower bathyal depths of the western Levantine Basin, and from low dysoxic to oxic at middle bathyal depth of the eastern Levantine Basin. At both sites an asymmetric oxygen development is reconstructed with strongest oxygen depletion in the early phase of sapropel S₆ deposition. This asymmetric pattern of deep-water ventilation is caused by an initial warming and subsequent cooling of

surface waters during S₆ formation as reconstructed from alkenone data (Emeis et al., in press).

(4) The high benthic ecosystem variability during S₆ formation and during the initial and late phases of S₅ formation suggests that deep-water formation and organic matter fluxes were subject to high-frequency changes superimposed on the general pattern of solar insolation. We suppose that deep-water formation and eutrophication during these time intervals were very susceptible to minor climate fluctuations at a millennial time-scale. Similarly, the reoxygenation event observed within S₅ may be explained as an expression of abrupt cooling comparable to that described from the Holocene sapropel S₁ (Rohling et al., 1997).

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References

- Abrantes, F., 1988. Diatom productivity peak and increased circulation during the latest Quaternary: Alboran Basin (western Mediterranean). *Mar. Micropaleontol.* 13, 79–96.
- Alley, R.B., Mayewski, P.A., Sowers, T., Stuiver, M., Taylor, K.C., Clark, P.U., 1997. Holocene climatic instability: a prominent, widespread event 8200 yr ago. *Geology* 25, 483–486.
- Alve, E., 1999. Colonization of new habitats by benthic foraminifera: a review. *Earth Sci. Rev.* 46, 167–185.
- Antoine, D., Morel, A., André, J.-M., 1995. Algal pigment distribution and primary production in the eastern Mediterranean as derived from coastal zone color scanner observations. *J. Geophys. Res.* 100, 16193–16209.
- Banner, F.T., Pereira, C.P.G., Desai, D., 1985. ‘Tretomphaloid’ float chambers in the Discorbidae and Cymbaloporidae. *J. Foraminifer. Res.* 15, 159–174.
- Berger, A., 1978. Long-term variations of caloric insolation resulting from the Earth’s orbital elements. *Quat. Res.* 9, 139–167.
- Béthoux, J.-P., 1993. Mediterranean sapropel formation, dynamic and climatic viewpoints. *Oceanol. Acta* 16, 127–133.
- Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., Priore, P., Cullen, H., Hajdas, I., Bonani, G., 1997. A pervasive millennial-scale cycle and glacial climates. *Science* 278, 1257–1266.
- Buzas, M.A., Gibson, T.G., 1969. Species diversity: benthonic foraminifera in Western North Atlantic. *Science* 163, 72–75.
- Caralp, M.-H., 1988. Late glacial to recent deep-sea benthic foraminifera from the Northeastern Atlantic (Cadiz Gulf) and Western Mediterranean (Alboran Sea): paleoceanographic results. *Mar. Micropaleontol.* 13, 265–289.
- Casford, J.S.L., Rohling, E.J., Abu-Zied, R.H., Jorissen, F.J., Leng, M., Thomson, J., 2003. A dynamic concept for eastern Mediterranean circulation and oxygenation during sapropel formation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* this volume S0031-0182(02)00601-6
- Castradori, D., 1993. Calcareous nannofossils and the origin of eastern Mediterranean sapropels. *Paleoceanography* 8, 459–471.
- Chappell, J., Shackleton, N.J., 1986. Oxygen isotopes and sea level. *Nature* 324, 137–140.
- Cita, M.B., Zocchi, M., 1978. Distribution patterns of benthic foraminifera on the floor of the Mediterranean Sea. *Oceanol. Acta* 1, 445–462.
- Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. *Nature* 314, 435–438.
- Corliss, B.H., Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. *Deep-Sea Res.* 37, 381–400.
- Cramp, A., O’Sullivan, G., 1999. Neogene sapropels in the Mediterranean: a review. *Mar. Geol.* 153, 11–28.
- Cronin, T.M., Raymo, M.E., 1997. Orbital forcing of deep-sea benthic species diversity. *Nature* 385, 624–627.
- De Rijk, S., Troelstra, S.R., Rohling, E.J., 1999. Benthic foraminiferal distribution in the Mediterranean Sea. *J. Foraminifer. Res.* 29, 93–103.
- De Stigter, H.C., Jorissen, F.J., Van der Zwaan, G.J., 1998. Bathymetric distribution and microhabitat partitioning of live (Rose Bengal stained) benthic foraminifera along a shelf to deep sea transect in the southern Adriatic Sea. *J. Foraminifer. Res.* 28, 40–65.
- Diester-Haass, L., Robert, C., Chamley, H., 1998. Paleoproductivity and climate variations during sapropel deposition in the eastern Mediterranean Sea. In: Robertson, A.H.F., Emeis, K.-C., Richter, C., Camerlenghi, A. (Eds.), *Proc. Ocean Drilling Program, Sci. Res.* 160. ODP, College Station, TX, pp. 227–248.

- Emeis, K.-C., Schulz, H., Struck, U., Sakamoto, T., Doose, H., Erlenkeuser, H., Howell, M., Kroon, D., Paternò, M., 1998. Stable isotope and temperature records of sapropels from ODP Sites 964 and 967: constraining the physical environment of sapropel formation in the Eastern Mediterranean Sea. In: Robertson, A.H.F., Emeis, K.-C., Camerlenghi, A. (Eds.), *Proc. Ocean Drilling Program, Sci. Res. 160*. ODP, College Station, TX, pp. 309–331.
- Emeis, K.-C., Sakamoto, T., Wehausen, R., Brumsack, H.-J., 2000. The sapropel record of the eastern Mediterranean Sea – results of Ocean Drilling Program Leg 160. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 158, 371–395.
- Emeis, K.-C., Schulz, H., Struck, U., Rossignol-Strick, M., Erlenkeuser, H., Howell, M.W., Kroon, D., Mackensen, A., Ishizuka, S., Oba, T., Sakamoto, T., Koizumi, I., in press. Eastern Mediterranean surface water temperatures and $\delta^{18}\text{O}$ composition during deposition of sapropels in the late Quaternary. *Paleoceanography*.
- Frogley, M.R., Tzedakis, P.C., Heaton, T.H.E., 1999. Climate variability in Northwest Greece during the last interglacial. *Science* 285, 1886–1889.
- Gooday, A.J., 1993. Deep-sea benthic foraminiferal species which exploit phytodetritus: characteristic features and controls on distribution. *Mar. Micropaleontol.* 22, 187–205.
- Gooday, A.J., 1994. The biology of deep-sea foraminifera: a review of some advances and their applications in paleoceanography. *Palaios* 9, 14–31.
- Gooday, A.J., Lamshead, P.J.D., 1989. Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Mar. Ecol. Prog. Ser.* 58, 53–67.
- Gooday, A.J., Bett, B.J., Shires, R., Lamshead, P.J.D., 1998. Deep-sea benthic foraminiferal species diversity in the NE Atlantic and NW Arabian Sea: a synthesis. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 45, 165–201.
- Herguera, J.C., Berger, W.H., 1991. Paleoproductivity from benthic foraminifera abundance: glacial to postglacial change in the west-equatorial Pacific. *Geology* 19, 1173–1176.
- Hess, S., Kuhnt, W., Hill, S., Kaminski, M.A., Holbourn, A., de Leon, M., 2001. Monitoring the recolonization of the Mt Pinatubo 1991 ash layer by benthic foraminifera. *Mar. Micropaleontol.* 43, 119–142.
- Jorissen, F.J., 1999. Benthic foraminiferal successions across Late Quaternary Mediterranean sapropels. *Mar. Geol.* 153, 91–101.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S., Van der Zwaan, G.J., 1992. Vertical distribution of benthic foraminifera in the northern Adriatic Sea: the relation with the organic flux. *Mar. Micropaleontol.* 19, 131–146.
- Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Mar. Micropaleontol.* 26, 3–15.
- Joussaume, S., 1993. Paleoclimatic tracers: an investigation using an atmospheric general circulation model under ice age conditions 1. Desert dust. *J. Geophys. Res.* 98, 2767–2805.
- Keller, J., Ryan, W.B.F., Ninkovich, D., Altherr, R., 1978. Explosive volcanic activity in the Mediterranean over the past 200,000 yr as recorded in deep-sea sediment. *Geol. Soc. Am. Bull.* 89, 591–604.
- Kutzbach, J.E., Guetter, P.J., 1986. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18 000 years. *J. Atmos. Sci.* 43, 1726–1759.
- Lautenschlager, M., Herterich, K., 1990. Atmospheric response to ice age conditions: climatology near the Earth's surface. *J. Geophys. Res.* 95, 22547–22557.
- Loubere, P., 1996. The surface ocean productivity and bottom water oxygen signals in deep water benthic foraminiferal assemblages. *Mar. Micropaleontol.* 28, 247–261.
- Lutze, G.F., Coulbourn, W.T., 1984. Recent benthic foraminifera from the continental margin of northwest Africa: community structure and distribution. *Mar. Micropaleontol.* 8, 361–401.
- Mackensen, A., Douglas, R.G., 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland. *Deep-Sea Res.* 36, 879–900.
- Maldonado, A., Stanley, D.J., 1976. Late Quaternary sedimentation and stratigraphy in the Strait of Sicily. *Smithson. Contrib. Earth Sci.* 16, 1–73.
- Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C., Jr., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: development of a high-resolution 0 to 300,000 year chronostratigraphy. *Quat. Res.* 27, 1–29.
- Masson, V., Braconnot, P., Jouzel, N., de Noblet, R., Cheddadi, R., Marchal, O., 2000. Simulation of intense monsoons under glacial conditions. *Geophys. Res. Lett.* 27, 1747–1750.
- Mommersteeg, H.J.P.M., Loutre, M.F., Young, R., Wijmstra, T.A., Hooghiemstra, H., 1995. Orbital forced frequencies in the 975000 year pollen record from Tenagi Philippon (Greece). *Clim. Dyn.* 11, 4–24.
- Mullineaux, L.S., Lohmann, G.P., 1981. Late Quaternary stagnations and recirculation of the Eastern Mediterranean: changes in the deep water recorded by fossil benthic foraminifera. *J. Foraminifer. Res.* 11, 20–39.
- Myers, P.G., Rohling, E.J., 2000. Modelling a 200-yr interruption of the Holocene sapropel S1. *Quat. Res.* 53, 98–104.
- Naidu, P.D., Malmgren, B.A., 1995. Do benthic foraminifer records represent a productivity index in oxygen minimum zone areas? An evaluation from the Oman Margin, Arabian Sea. *Mar. Micropaleontol.* 26, 49–55.
- Nolet, G.J., Corliss, B.H., 1990. Benthic foraminiferal evidence for reduced deep-water circulation during sapropel deposition in the eastern Mediterranean. *Mar. Geol.* 94, 109–130.
- Oggioni, E., Zandini, L., 1987. Response of benthic foraminifera to stagnant episodes – a quantitative study of core Ban 81-23, eastern Mediterranean. *Mar. Geol.* 75, 241–261.
- Pickard, G.L., Emery, W.J., 1990. *Descriptive Physical Oceanography, an Introduction*. Pergamon Press, Oxford.
- Pinardi, N., Masetti, E., 2000. Variability of the large scale general circulation of the Mediterranean Sea from observa-

- tions and modelling: a review. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 158, 153–174.
- Rathburn, A.E., Corliss, B.H., 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. *Paleoceanography* 9, 87–150.
- Rioual, P., Andrieu-Ponel, V., Rietti-Shati, M., Battarbee, R.W., de Beaulieu, J.-L., Cheddadi, R., Reille, M., Svoboda, H., Shemesh, A., 2001. High-resolution record of climate stability in France during the last interglacial period. *Nature* 413, 293–296.
- Roether, W., Manca, B.B., Klein, B., Bregant, D., Georgopoulos, D., Beitzel, V., Kovacevic, V., Luchetta, A., 1996. Recent changes in Eastern Mediterranean deep waters. *Science* 271, 333–335.
- Rohling, E.J., 1994. Review and new aspects concerning the formation of eastern Mediterranean sapropels. *Mar. Geol.* 122, 1–28.
- Rohling, E.J., Gieskes, W.C., 1989. Late Quaternary changes in Mediterranean intermediate water density and formation rate. *Paleoceanography* 4, 531–545.
- Rohling, E.J., Hilgen, F.J., 1991. The eastern Mediterranean climate at times of sapropel formation: a review. *Geol. Mijnb.* 70, 253–264.
- Rohling, E.J., De Stigter, H.C., Vergnaud-Grazzini, C., Zaalberg, R., 1993. Temporary repopulation by low-oxygen tolerant benthic foraminifera within an upper Pliocene sapropel: evidence for the role of oxygen depletion in the formation of sapropels. *Mar. Micropaleontol.* 22, 207–219.
- Rohling, E.J., Jorissen, F.J., De Stigter, H.C., 1997. 200 year interruption of Holocene sapropel formation in the Adriatic Sea. *J. Micropalaeontol.* 16, 97–108.
- Rohling, E.J., Mayewski, P.A., Abu-Zied, R.H., Casford, J.S.L., Hayes, A., 2002. Holocene atmosphere-ocean interactions: records from Greenland and the Aegean. *Clim. Dyn.* 18, 587–593.
- Ross, C.R., Kennett, J.P., 1983. Late Quaternary paleoceanography as recorded by benthic foraminifera in Strait of Sicily sediment sequences. *Mar. Micropaleontol.* 8, 315–336.
- Rosignol-Strick, M., 1983. African monsoons, an immediate climate response to orbital insolation. *Nature* 304, 46–49.
- Rosignol-Strick, M., 1985. Mediterranean Quaternary sapropels, an immediate response of the African monsoon to variation of insolation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 49, 237–263.
- Rosignol-Strick, M., Nesteroff, W., Olive, P., Vergnaud-Grazzini, C., 1982. Mediterranean stagnation and sapropel formation. *Nature* 295, 105–110.
- Sancetta, C., 1994. Mediterranean sapropels: seasonal stratification yields high production and carbon flux. *Paleoceanography* 9, 195–196.
- Schilman, B., Almogi-Labin, A., Bar-Matthews, M., Labeyrie, L., Paterne, M., Luz, B., 2001. Long- and short-term carbon fluctuations in the eastern Mediterranean during the Holocene. *Geology* 29, 1099–1102.
- Schmiedl, G., Hemleben, C., Keller, J., Segl, M., 1998. Impact of climatic changes on the benthic foraminiferal fauna in the Ionian Sea during the last 330,000 years. *Paleoceanography* 13, 447–458.
- Schmiedl, G., de Bovée, F., Buscail, R., Charrière, B., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. *Mar. Micropaleontol.* 40, 167–188.
- Sen Gupta, B.K., Machain-Castillo, M.L., 1993. Benthic foraminifera in oxygen-poor habitats. *Mar. Micropaleontol.* 20, 183–201.
- Sperling, M., Schmiedl, G., Hemleben, C., Emeis, K.-C., Erlenukeuser, H., Grootes, P.M., 2003. Black Sea impact on formation of eastern Mediterranean sapropel S1? evidence from the Marmara Sea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* this volume S0031-0182(02)00596-5
- Tang, C.M., Stott, L.D., 1993. Seasonal salinity changes during Mediterranean sapropel deposition 9000 years B.P.: evidence from isotopic analyses of individual planktonic foraminifera. *Paleoceanography* 8, 473–493.
- Theocharis, A., Nittis, K., Kontoyiannis, H., Papageorgiou, E., Balapoulos, E., 1999. Climatic changes in the Aegean Sea influence the Eastern Mediterranean thermohaline circulation (1986–1997). *Geophys. Res. Lett.* 26, 1617–1620.
- Thunell, R.C., Williams, D.F., 1982. Paleoclimatographic events associated with termination II in the eastern Mediterranean. *Oceanol. Acta* 5, 229–233.
- Thunell, R.C., Williams, D.F., Cita, M.B., 1983. Glacial anoxia in the eastern Mediterranean. *J. Foraminifer. Res.* 13, 283–290.
- Thunell, R.C., Williams, D.F., Howell, M., 1987. Atlantic-Mediterranean water exchange during the late Neogene. *Paleoceanography* 2, 661–678.
- Thunell, R.C., Williams, D.F., 1989. Glacial-Holocene salinity changes in the Mediterranean Sea: hydrographic and depositional effects. *Nature* 338, 493–496.
- Vismara Schilling, A., 1986. Foraminiferi bentonici profondi associati a eventi anossici del Pleistocene medio e superiore nel Mediterraneo Orientale. *Riv. It. Paleont. Trat.* 92, 103–148.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E., Labracherie, M., 2002. Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quat. Sci. Rev.* 21, 295–305.
- Wagner, R., 2000. Benthische Foraminiferen als Anzeiger für kurzfristige Umweltveränderungen im Ionischen Meer im Bereich des Sapropel S5 (Eem). Diplom Thesis, University of Tübingen, Tübingen.
- Weldeab, S., Emeis, K.-C., Hemleben, C., Schulz, H., Venneemann, T.W., 2002. Sr, Nd isotope and geochemical composition of Late Pleistocene sapropels and non-sapropel sediments from the Eastern Mediterranean Sea: implications for detrital influx and climatic conditions in the source areas. *Geochim. Cosmochim. Acta.* 66, 3585–3598.
- Weldeab, S., Emeis, K.-C., Hemleben, C., Schmiedl, G.,

- Schulz, H., in press. Spatial productivity variations during formation of sapropels S5 and S6 in the Mediterranean Sea: evidence from Ba concentrations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*
- Weldeab, S., Siebel, W., Wehausen, R., Emeis, K.-C., Schmiedl, G., Hemleben, Ch., 2003. Late Pleistocene sedimentation in the western Mediterranean Sea: implications for productivity changes and climatic conditions in the catchment areas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* S0031-0182(02)00602-8