



Marine productivity leads organic matter preservation in sapropel S1: palynological evidence from a core east of the Nile River outflow



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ABSTRACT

The formation of Eastern Mediterranean organic matter rich deposits known as sapropels is the results of two mechanisms: (enhanced) marine productivity and preservation of organic material at depth. However, their relative contribution and their leads and lags with respect to each other remain elusive. Here, we address these questions by studying sediments deposited prior to, during, and after the most recent sapropel (S1, ~10–6 calibrated ka before present, BP) with an integrated marine and terrestrial palynological approach, combined with existing and newly generated geochemical data. The studied core was retrieved from an area under strong influence of the Nile outflow and has high average sediment accumulation rates allowing a high temporal resolution (of several decades to centuries).

Marine productivity, as reconstructed with total dinocyst accumulation rates (ARs) and biogenic CaCO₃ content, starts to increase ~1 ka prior to sapropel formation. A shift in the dinocyst taxa contributing to the productivity signal at sapropel onset indicates the rapid development of (seasonal) water column stratification. Pollen and spore ARs also increase prior to sapropel onset, but a few centuries after the increase in marine productivity. Hence, the first shift to a high marine productivity system before sapropel deposition may have been mostly favoured by the injection of nutrients via shoaling of the nutricline with a minor contribution of nutrients from land via river input and flooding of the shelves. Pollen assemblages indicate a gradual change across the sapropel onset from a savanna-like, through coastal marsh expansion, toward an open woodland assemblage, which is consistent with enhanced Nile influence and delta development. At sapropel onset a marked shift in pollen ARs could suggest increased preservation under anoxia. However, major shifts in pollen assemblages and signs of selective- or partial decomposition of terrestrial palynomorphs are absent. We therefore suggest that the high pollen ARs largely result from an increased influx of pollen by enhanced Nile discharge and extension of the freshwater plume. Three centuries after the sapropel onset, dinocyst ARs and CaCO₃ content indicate that marine productivity starts to decrease, while sapropel deposition continued. Organic carbon content decreased only later and less dramatically. This may be explained by a shift in the dominance of the organisms contributing to marine productivity, to an enhanced preservation of organic matter, or a combination of both.

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1. Introduction

At present, the Mediterranean Basin is generally oligotrophic and well-ventilated (Krom et al., 1991; Pinardi and Masetti, 2000; D'Ortenzio and Ribera D'Alcala, 2009), and its surface sediments are typically poor in organic carbon (e.g., Calvert, 1983). However, the Eastern Mediterranean late Neogene sedimentary record is

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characterized by the widespread and distinctly periodical occurrence of organic carbon-rich layers, called sapropels (e.g., Kullenberg, 1952; Rohling, 1994; Robertson et al., 1998).

The currently accepted model for the formation of most Eastern Mediterranean sapropels proposes that maxima in insolation during precession minima caused an intensification of the monsoon system on the North African continent (e.g., Rossignol-Strick et al., 1985; Hilgen, 1991; Gasse et al., 2000; Weldeab et al., 2014). Subsequently, enhanced river discharge largely impacted the Mediterranean water circulation, resulting in stratification of the water column. Ultimately, slowdown or total shutdown of deep-water formation resulted in enhanced preservation of organic matter at the sea floor (e.g., Rohling, 1994, and references therein). The primary cause triggering the formation of Eastern Mediterranean sapropels has been debated ever since their discovery (Kullenberg, 1952; Aksu et al., 1999), and productivity and preservation have been indicated as the two major contributing factors operating either separately (Williams et al., 1978; Calvert, 1990) or combined (De Lange and Ten Haven, 1983; Rohling and Gieskes, 1989; Kemp et al., 1999).

Present-day biological primary productivity is thought to be insufficient to account alone for the elevated organic carbon content observed in sapropels (Dugdale and Wilkerson, 1988; Bethoux, 1989). Elevated past primary productivity is likely to have been contributing to sapropel formation and several studies support this hypothesis (e.g., De Lange and Ten Haven, 1983; Calvert and Pedersen, 1992; Rohling, 1994; Gallego-Torres et al., 2011). Marine productivity can be boosted by freshwater input (1) directly, via nutrient input by enhanced river discharge from the Nile (e.g., Krom et al., 2002); (2) indirectly, via upward advection of the nutricline following stratification. The latter mechanism, which creates a productive deep chlorophyll maximum (DCM) in the photic zone underneath a nutrient-poor surface layer, has been used to explain high productivity rates preceding and at the onset of sapropel S5 (previous interglacial, ~125 ka BP) (e.g., Giunta et al., 2006; Grelaud et al., 2012) and during the most recent sapropel S1 (Rohling and Gieskes, 1989; Castradori, 1993; Crudeli et al., 2006).

For sapropel S1, deposited during the Holocene between ~10 and 6 cal. ka before present (BP, before 1950 AD), debate continues

on the importance of marine productivity relative to organic matter preservation. Moreover, the leads and lags between productivity and preservation remain elusive. At present nanoplankton contributes ~40% to the primary productivity of the Mediterranean Sea, and diatoms and dinoflagellates account for another ~40% (Uitz et al., 2010). Despite their large contribution to the organic carbon flux (Kemp et al., 1999) sapropel S1 is usually devoid of diatoms. Calcareous nanoplankton and coccolithophores can be abundant in sapropel S1 but may suffer from selective preservation and carbonate diagenesis (e.g., Negri et al., 1999; Negri and Giunta, 2001; Crudeli et al., 2004; Thomson et al., 2004; Crudeli et al., 2006). Remains of dinoflagellates (organic-walled dinoflagellate cysts, dinocysts) are generally abundant and well preserved in the sediments, together with pollen and spores from land plants (Aksu et al., 1995, 1999; Cheddadi and Rossignol-Strick, 1995; Rossignol-Strick, 1999; Zonneveld et al., 2001; Sangiorgi et al., 2003; Kholeif and Mudie, 2009). So far, no palynological (dinocysts, pollen and spores) study has achieved a temporal resolution sufficient to resolve fine-scale (multi-decadal to centennial scale) productivity-preservation trends and cause–effect relationships, however.

Here we present an integrated marine and terrestrial palynological study on a piston core (PS009PC) taken along the path of freshwater routing from the Nile (Fig. 1). Based on present day flow patterns and sediment provenance studies (Krom et al., 1999) the sediment composition at the coring site, including terrestrial components such as pollen, is dominated by Nile-derived particles. The core contains a ~42 cm-thick sapropel S1, which allows analyses at unprecedented high resolution. Our data, together with a suite of newly generated and available geochemical proxies (Hennekam et al., 2014) provide insights into regional climate, the source of nutrients, the contribution of marine productivity to sapropel S1 deposition, and the importance of preservation.

2. Materials and methods

2.1. Core location, sediments and age model

The sediment samples used in this study were taken from piston core PS009PC, recovered from the continental slope ~50 km off the

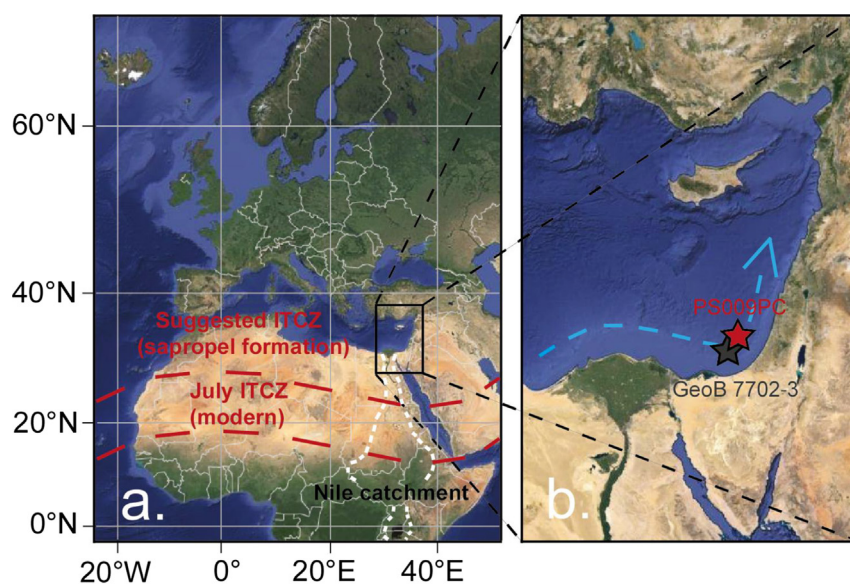


Fig. 1. (a) Satellite image of the Mediterranean region. Dashed lines indicate the Nile catchment and the assumed position of the Intertropical Convergence Zone (ITCZ) during onset of sapropel deposition and at present (Gasse, 2000). (b) Location of the studied core, PS009PC (32°07.7'N, 34°24.4'E; 552 m water depth), and the location of core GeoB 7702-3, for which sea surface temperatures were reconstructed by Castañeda et al. (2010; Fig. 4f). The blue arrow indicates the prevailing surface current in the Levantine basin. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coast of Tel Aviv, Israel (Fig. 1a, b; 32°07.7'N, 34°24.4'E; 552 m water depth), in the southeastern part of the Levantine Basin. Core PS009PC was recovered during the PASSAP cruise in May 2000 with RV *Pelagia*; its total length is 690 cm. The recovered sediments consist of >90% of clays and silts (Hennekam and De Lange, 2012). Surface waters in the Levantine Basin move in an anticlockwise direction (e.g., Pinardi and Masetti, 2000), implying that Nile-derived sediments, the main sediment source for the Eastern Mediterranean, are transported eastward from the Nile outflow to our coring site (Weldeab et al., 2002; Kholeif and Mudie, 2009; Fig. 1b). The sedimentary record of PS009PC may thus be expected to directly reflect changes in the outflow of the Nile and its hinterland, which makes it exceptionally well suited for the objectives of our study.

Our study focuses on the interval between 265 and 174 cm, which spans 12 to 5 cal. ka BP. The age model relies on four ¹⁴C accelerator mass spectrometry (AMS) measurements in the studied interval (see Table S1; supplementary information). The sedimentation rate for this interval is high, ~12.5 cm/ka (i.e., 1 cm = ~80 years), and relatively constant between 285.2 and 191.2 cm (13,460 ± 204 and 6118 ± 169 cal. ka BP, respectively; Hennekam et al., 2014). Sediment accumulation rates are in agreement with those found in the Nile Cone area (Stanley and Maldonado, 1977; Kholeif and Mudie, 2009), and other nearby sites (e.g., Hamann et al., 2008; Castañeda et al., 2010). Between 241 and 197 cm the two phases of sapropel S1 deposition (S1a and S1b) and its interruption are recorded. The identification of the sapropel layer, i.e., a distinct increase in sedimentary organic carbon content (C_{org}), for PS009PC this corresponds to C_{org} > 1 wt. %, its age model and the S1a and S1b phases follow Hennekam et al. (2014). The onset of unit S1a for PS009PC is at 10.1 cal. ka BP and its termination is at 8.2 cal. ka BP. The onset of S1b is at 7.9 cal. ka BP followed by its termination at 6.5 cal. ka BP. The sapropel interruption lasts ~300 years, as in other Mediterranean S1 records (Bar-Matthews et al., 1999; Marino et al., 2009; Pross et al., 2009), and correlates well with the 8.2 ka BP cooling event in the Northern Hemisphere (Alley et al., 1997; Rohling and Pälike, 2005).

2.2. Palynological processing

Fifty-nine sediment samples were selected with particular high sampling resolution (every 0.5 cm; 40 years) around sapropel onset. Sediment samples were freeze-dried, and crushed and homogenized using an agate pestle and mortar. Subsequently, between 0.6 and 2.5 g of sediment per sample was treated with ~10% HCl and ~38% HF to dissolve carbonates and silicates, respectively. A known amount of *Lycopodium clavatum* marker spores was added to enable quantification of the palynomorphs and their accumulation rates (ARs) to the sediment. After decantation of the solution samples were exposed to ultrasonic treatment, to remove minerals and disaggregate clouds of (amorphous) organic matter. Samples were then sieved over a 10-μm sieve, after which the remaining residues were concentrated and mounted on slides for microscope analysis. On average ~170 (min. 151; max. 202) dinocysts per sample were counted and identified to genus or species level at 400× magnification. Dinocyst taxonomy follows Rochon et al. (1999) and Fensome and Williams (2004). Total pollen and spores were also counted in all dinocyst samples.

After dinocyst analysis 19 samples were selected for detailed pollen and spore analysis. To optimize identification of pollen and spores palynological residues were acetolysed, following Erdtman (1960). After acetolysis, samples 202.45 cm and 203.45 cm were combined (composite sample 202.95 cm; 7 cal. ka BP) because of the small sample size to ensure statistically relevant counts. On average ~440 pollen and spores per sample were counted and

identified. All samples and slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands.

Dinocyst and pollen and spores ARs (palynomorphs/cm²/yr) were calculated multiplying the amount of dinocysts and pollen and spores per gram sediment dry weight (palynomorphs/g sed. dw.), by the mass accumulation rates (g/cm²/yr) derived from Hennekam et al. (2014).

2.3. CaCO₃ analysis

Calcium (Ca) was measured by X-ray fluorescence (XRF) at the Institute of Chemistry and Biology of the Marine Environment (ICBM) in Oldenburg using a Philips PW 2400 X-ray spectrometer on glass beads. CaCO₃ content (wt. %) was calculated assuming that all Ca was related to CaCO₃.

All measurements and analyses, including the geochemical data from Hennekam et al. (2014), were performed on the same samples to optimize comparability of the signals and to avoid correlation issues (e.g., age model differences).

2.4. Approach and proxy interpretation

Marine palynology mainly studies organic-walled dinoflagellate cysts, fossilizable resting stages produced by some dinoflagellates mostly during the sexual reproduction stage in the life cycle (Wall and Dale, 1966). Notably, most dinoflagellates are either photosynthetic, i.e., they need light and nutrients, or heterotrophic and feed on organic material and other phytoplankton (e.g., Jacobson and Anderson, 1986). Dinocysts are sensitive recorders of environmental conditions of the surface waters (Zonneveld et al., 2013) also in the area where our core was collected (e.g., Elshani et al., 2010). Therefore their fossil assemblages, concentrations and accumulation rates in marine sediments can be successfully employed to reconstruct palaeoenvironmental surface water conditions, providing information on nutrient availability, productivity, temperature, salinity, stratification, and oxygenation (e.g., Dale, 1996; De Vernal and Marret, 2007; Zonneveld et al., 2008, 2012). Heterotrophic cysts are usually very abundant in high productivity zones (De Vernal and Marret, 2007, and references therein) and are therefore used to indicate trends in productivity. However, they are also the most sensitive to oxygenation (Zonneveld et al., 1997, 2001; Versteegh and Zonneveld, 2002). Their occurrence may therefore be biased by differential preservation. By plotting this group separately, information on productivity trends and preservation can also be derived.

The marine sediments also yield pollen and spores, produced by terrestrial vegetation, which are transported into the marine environment mainly via river discharge and wind (e.g., Mudie and McCarthy, 1994). Transport mode influences the type and richness of the assemblage (Hooghiemstra, 1988; Traverse, 1990), which allows determination of the relative changes in river input. Pollen transport through air and water is selective, and typically, larger, heavier types are transported less far (Holmes, 1990), affecting total diversity in the assemblage. Exception to the rule is bisaccate conifer pollen that is predominantly wind-transported and floats on the water so that their relative abundance instead increases with distance to the shore (Mudie, 1982).

Combined marine and terrestrial palynology thus provide an integrated signal of synchronous changes occurring in the marine and continental environments. Our palynological data were integrated with available geochemical data (Hennekam et al., 2014), i.e., C_{org} and stable oxygen isotopic composition of the surface dwelling planktonic foraminifer *Globigerinoides ruber* (white) (δ¹⁸O_{ruber}) and new CaCO₃ data. Therefore this set of samples is optimally suited to

reconstruct the palaeoenvironmental conditions during sapropel formation in high-resolution.

3. Results

3.1. Dinocysts

Core PS009PC contains abundant and well-preserved dinocysts. Their concentration ranges from 600 to 10,000 cysts per gram of dry sediment. Assemblages are overall dominated by cysts produced by autotrophic/phototrophic dinoflagellates (Fig. 2b), mostly gonyaulacoids (percentage data are shown in Fig. S1; supplementary information). Cysts of heterotrophic dinoflagellates, i.e., most of the proteroperidinioids (Fig. 2b), form less than 10% of the total assemblage prior to and after sapropel deposition and during its interruption. Within the sapropel proteroperidinioids are relatively more abundant and represent up to 35% of the assemblage.

The total dinocyst AR (Fig. 2c) rapidly increases to ~75 cysts $\text{cm}^{-2} \text{yr}^{-1}$, between 10.8 and 10.3 cal. ka BP. A sudden decrease to 40 cysts $\text{cm}^{-2} \text{yr}^{-1}$ is observed from 10.3 cal. ka BP to just before S1 onset. *Spiniferites* spp. is chiefly responsible for this pattern in the total dinocyst AR, with minor contributions of cysts of *Pentapharsodinium dalei*, *Lingulodinium machaerophorum* and proteroperidinioids (*Brigantidinium* spp., *Echinidinium* spp. and *Stelladinium stellatum*, Fig. 2c).

At the onset of S1 the total dinocyst AR increases again and reaches the maximum value for the entire record of 80 cysts $\text{cm}^{-2} \text{yr}^{-1}$ at 10.1 cal. ka BP and remains high until 9.7 cal. ka BP. The maximum in the total dinocyst AR at the onset of S1a is mainly the result of a major increase in the AR of *L. machaerophorum*, but the ARs of *Spiniferites* spp., cysts of *P. dalei* and proteroperidinioids are also high. Afterwards, the total AR rapidly drops to approximately 40 cysts $\text{cm}^{-2} \text{yr}^{-1}$ and gradually decreases throughout the sapropel to around ~20 cysts $\text{cm}^{-2} \text{yr}^{-1}$ at sapropel termination.

After sapropel termination the total dinocyst AR remains generally below sapropel values. Only the AR of *Operculodinium israelianum* shows a peak at 5.5 cal. ka BP.

3.2. Pollen and spores

Prior to sapropel S1 deposition, the total pollen and spores AR (Fig. 3b) increases from ~5 to ~20 grains $\text{cm}^{-2} \text{yr}^{-1}$, between ~10.5 and 10.1 cal. ka BP (Fig. 3b inset). On average, about 25% of the pollen assemblages are tree pollen, dominated by *Quercus* (Fig. 3c, d), while herbs dominate the pollen assemblages, with percentages up to ~70% (Fig. 3f). Asteraceae subf. Liguliflorae and Chenopodiaceae (Fig. 3f, g) are the dominant herb pollen types. Prior to the onset of the sapropel, at 10.1 ka BP, Chenopodiaceae increases from ~25% to almost 40% of the total pollen assemblage. The less abundant (<10%) *Ephedra fragilis*, typical of arid conditions, decreases simultaneously (Fig. 3h).

At the onset of S1a the total pollen and spores AR increases exponentially, reaching up to ~180 grains $\text{cm}^{-2} \text{yr}^{-1}$ at 9.8 cal. ka BP. From this maximum onwards the AR gradually decreases to 50 grains $\text{cm}^{-2} \text{yr}^{-1}$ at the termination of S1a. Total herb pollen types gradually decrease over S1a to a rather stable value around 50% for the remainder of the record. Tree pollen, still dominated by *Quercus*, increase up to ~40% of the total pollen sum. At the onset of S1a Asteraceae subf. Liguliflorae drop from 20% to below 5%, subsequently Chenopodiaceae rapidly decrease from ~40% to around 20%. Poaceae and *Rumex acetosella* type (Fig. 3i, j) become relatively more abundant during S1a. *R. acetosella* presence is mainly restricted to S1a, while Poaceae remain a relatively constant contributor to the total pollen assemblage (~10%) for the remainder of the record. Within the sapropel interruption the total pollen AR decreases to 13 grains $\text{cm}^{-2} \text{yr}^{-1}$, subsequently the AR rises again to above 100 grains $\text{cm}^{-2} \text{yr}^{-1}$ in S1b. Followed by a gradual decrease, towards values below 20 grains $\text{cm}^{-2} \text{yr}^{-1}$ after the sapropel. From the sapropel interruption onwards, *Pinus* pollen become relatively

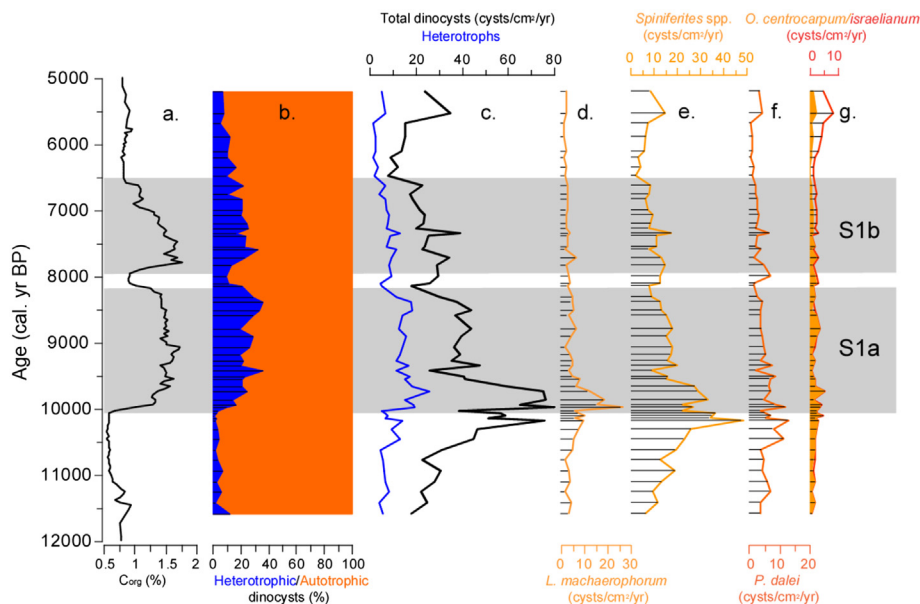


Fig. 2. Overview of selected geochemical and dinocyst data of core PS009PC. ARs are shown for dinocyst species/genera with a flux that exceeds 5 cysts/ cm^2 /yr. (a) Organic carbon content (C_{org}) (Hennekam et al., 2014). (b) Relative abundances of heterotrophic (blue) and autotrophic dinocysts (orange). (c) The total dinocyst accumulation rate (AR; black) and the AR of heterotrophic cysts (blue). ARs of *Lingulodinium machaerophorum* (d), *Spiniferites* spp. (e), cysts of *Pentapharsodinium dalei* (f), *Operculodinium centrocarpum* (orange) and *Operculodinium israelianum* (red) (g). Grey zones indicate the two sapropel phases S1a and S1b, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

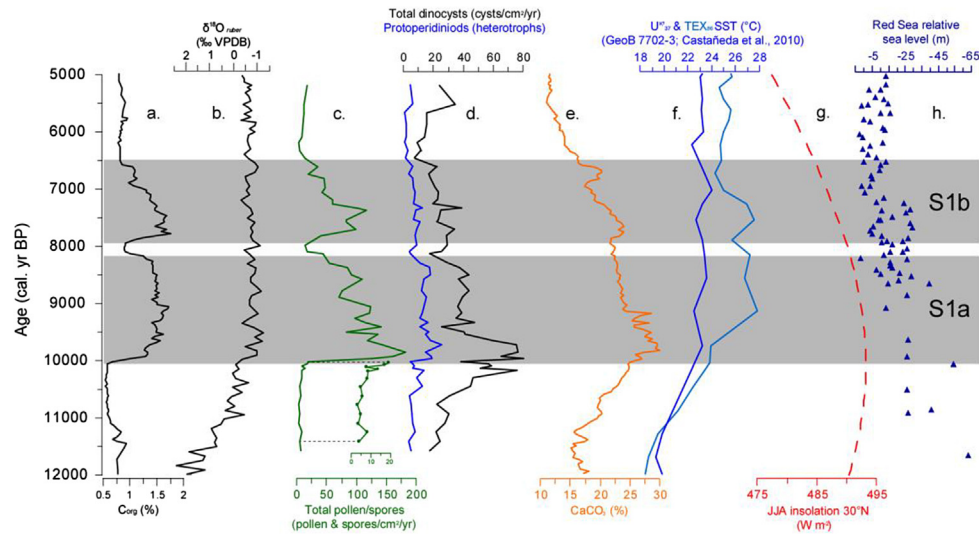


Fig. 4. Overview of different paleoenvironmental parameters, CaCO_3 content, total pollen and spores AR and dinocyst and dinocyst accumulation rates (ARs) of core PS009PC (a) Organic carbon content (C_{org}), (b) $\delta^{18}\text{O}_{\text{ruber}}$ (Hennekam et al., 2014). (c) The total pollen and spores AR. (d) The total dinocyst AR (black) and the AR of protopteridinioid cysts (blue) (e.g., Zonneveld et al., 2001). (e) CaCO_3 (%). (f) Sea surface temperature reconstructions based on $U^{K_{37}}$ and TEX_{86} for Geob 7702-3 (Castañeda et al., 2010). (g) June–July–August insolation at 30°N (Laskar et al., 2004). (h) Red Sea relative sea level record (Grant et al., 2012). Grey zones indicate the two sapropel phases S1a and S1b, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

marine productivity by introducing additional land-derived nutrients from flooded shelves. Compared to the present-day productivity estimates as derived from dinocyst AR in proximity of the studied core location (Elshanawany et al., 2010), productivity was at least double compared to nowadays, prior to sapropel deposition.

The brief, but noteworthy decrease in the total dinocyst AR between 10.3 and 10 cal. ka BP coincides with a 0.7‰ increase in $\delta^{18}\text{O}_{\text{ruber}}$ (Hennekam et al., 2014; Fig. 4b), which may indicate temporary decreased Nile discharge and, by inference, increased SSS.

The pre-S1 pollen assemblages are typical for a savanna-like ecosystem dominated by herbs, e.g., Asteraceae subf. Liguliflorae, Poaceae, and significant amounts of *Ephedra* characteristic for warm and arid regions (Van Campo, 1984; Boessenkool et al., 2001; Langgut et al., 2011). The increase in the total pollen and spores AR at 10.5 cal. ka BP lags the increase in marine productivity by a few centuries, suggesting that increased sediment input (carrying pollen) was initially accommodated in the Nile delta (Fig. 1b). This would have led to expansion of coastal habitat and brackish marsh environments. A relative increase in Chenopodiaceae pollen, typical for dry levees or salt flats (Kholeif and Mudie, 2009; Scott et al., 2014), supports such expansion of tidally influenced brackish habitat in the Nile delta. The brief decrease observed in the total dinocyst AR, between 10.3 and 10 cal. ka BP, is not observed in the total pollen and spores AR. This may have been caused by a relatively brief period of delta progradation and vegetation expansion due to increased Nile sediment discharge in a phase that is generally dominated by marine transgression (Stanley and Warne, 1993; Kholeif and Mudie, 2009).

4.2. Sapropel: ~10.1–6.5 cal. ka BP

A maximum in the total dinocyst and biogenic CaCO_3 content, indicative of maximum marine productivity, is reached at the onset of sapropel formation, i.e., at 10 cal. ka BP. This productivity maximum lasts for about three centuries and coincides with maximum summer insolation at 30°N (Laskar et al., 2004; Fig. 4h) and a depleted $\delta^{18}\text{O}_{\text{ruber}}$ of approximately -1.3‰ , related to the

highest Nile activity and inferred lowest SSS values for the entire Holocene (Fontugne et al., 1994; Almogi-Labin et al., 2009). This scenario is further supported by synchronous maximum values in the Ba/ Ca_{ruber} (Weldeab et al., 2014), and independent indicator of maximum Nile discharge, obtained from a core in a nearby location. The maximum in the dinocyst AR mainly results from peaks of *L. machaerophorum*, cysts of *P. dalei* and heterotrophic protopteridinioids. High occurrences of *L. machaerophorum* have been found in eutrophic areas under the influence of river plumes (Sangiorgi and Donders, 2004; Sangiorgi et al., 2005; Zonneveld et al., 2009), in areas where (seasonal) stratification occurs. *P. dalei* is a cosmopolitan euryhaline species (Zonneveld et al., 2013). A recent study on eutrophication trends in the Mediterranean Sea reveals that production of cysts of *P. dalei* increases when upper water column phosphate concentrations increase (Zonneveld et al., 2012). The large peak in the AR of both species, recorded at the onset of sapropel deposition, therefore suggests a rapid shift, within a century, towards nutrient-rich, (seasonally) highly stratified surface waters. In this view, the sudden rapid increase in C_{org} could be explained in terms of enhanced preservation of organic matter, as bottom water ventilation most probably reduced due to freshwater stratification. However, given the different trends in the ARs of dinocysts, all with different sensitivity to oxygenation (Zonneveld et al., 1997, 2001; Versteegh and Zonneveld, 2002), we conclude that stratification-induced preservation alone was not sufficient to account for the early stages of sapropel S1 deposition. Moreover, sluggish circulation and water stratification also promotes the accumulation and availability of regenerated nutrients (e.g., Slomp et al., 2002), which in turn positively feedback on productivity.

The comparable increase in the relative abundance of heterotrophic protopteridinioids (Fig. 2c) during S1a and S1b suggests a mixed signal of both enhanced marine productivity and improved preservation (Zonneveld et al., 1997, 2001; Versteegh and Zonneveld, 2002). S1a has a much higher total dinocyst AR and CaCO_3 content, together with rather elevated protopteridinioid ARs, than S1b. We infer that at least for the first half of unit S1a, marine productivity worked in tandem with preservation. During sapropel

interruption and deposition of unit S1b the dinocyst ARs, including that of protoperidinioids, and CaCO₃ content are much lower, potentially implying lower productivity than during S1a. C_{org} and the relative abundance of the redox sensitive element vanadium (Hennekam et al., 2014), which gets enriched during anoxia, remain initially high in S1b. We infer that, during deposition of S1b, either other organisms became more important than dinoflagellates and calcareous plankton for primary productivity, that preservation of organic matter dominated over the productivity signal, or a combination of both.

Total pollen and spores ARs seem to be closely associated with C_{org}, which may lead to the conclusion that their occurrence is purely the result of preservation as previously suggested by terrestrial palynological studies in the same region (e.g., Cheddadi and Rossignol-Strick, 1995; Langgut et al., 2011). However, a mild oxidation (acetolysis; Erdtman, 1960) is occasionally used in pollen preparation. Experiments on processing (with and without acetolysis), and pollen grazing by marine microorganisms show some but no significant alteration of pollen preservation (Mudie and McCarthy, 2006). The gradual change in pollen assemblages and absence of signs of selective or partial decomposition of terrestrial palynomorphs, which may be the result of the high sedimentation rates in this region, suggest that, besides enhanced preservation of pollen and spores, other processes, i.e., enhanced vegetation cover (pollen production), increased transport (eolian, but predominantly riverine pollen transport), and geomorphological changes in the Nile delta, have played a significant role. The geomorphology of the Nile delta during the studied period was mainly influenced by long-term marine transgression up to ~8 cal. ka BP (Stanley and Warne, 1993; Butzer, 2002). Hence, no abrupt changes that might explain the abrupt shift in the pollen AR occurred. An increase in pollen production is expected to have occurred as vegetation cover gradually increased during the “Green Sahara” period (e.g., Claussen and Gayler, 1997), but this again cannot explain the recorded rapid changes. The final option would then be increased transport. We suggest that due to the rapid development of stratification and coinciding sluggish circulation, the freshwater plume of the Nile expanded across the Eastern Mediterranean surface waters. The extension of the freshwater plume would then have transported pollen and spores much further away from the Nile outflow. Based on the previously discussed depleted $\delta^{18}\text{O}_{\text{ruber}}$ and related inflow of Nile freshwater, this likely explains part of the rapid and large increase in the pollen AR at sapropel S1 onset.

The pollen assemblages show that during sapropel deposition the terrestrial hinterland, i.e., river plain of the Nile, developed from semi-arid savanna to open woodlands, exhibited by decreasing herb pollen and increasing tree pollen, which is consistent with a more direct Nile-derived signal. Further supported by somewhat higher taxa richness during S1a, indicating a higher proportion of river transported pollen. Our observations are in agreement with Langgut et al. (2011), who show that this trend started well before sapropel formation. The relatively high abundance, during S1a, of *Rumex acetosella* type is often attributed to human influence (e.g., Tinner et al., 2009), but predates large-scale ancient Egyptian and Middle Eastern agricultural practice. However, in this region it is consistent with natural semi-open woodland with patches of grassland and herbs where *R. acetosella* type typically occupies floodplains and moist soils, supporting increased Nile influence. The gradually increased *Pinus* pollen and decreased rarefaction diversity during S1b are indicative for increased distance of the core site to the coast due to sea level rise and a relatively gradual drying of the continent, in line with decreasing summer insolation (Fig. 4h), promoting a southward shift of the Intertropical Convergence Zone (ITCZ).

4.3. Post-sapropel: 6.5–5 ka BP

After sapropel termination marine primary productivity generally reaches minimum values for the studied record, as reflected by low dinocyst and biogenic CaCO₃ content. Beside low marine productivity, this interval is characterized by a reduced extension of the freshwater plume as suggested by low ARs of *L. machaerophorum* and cysts of *P. dalei* and by low transport of pollen and spores to the studied site. Low productivity and low preservation are expressed in the low C_{org} content. The ITCZ shifts back to a more southern position, which leads to the termination of the African Humid Period and its relatively rich vegetation (Gasse et al., 2000; Renssen et al., 2003), gradually causing decreased pollen production and drier conditions.

Notably, this interval is characterized by an increase in the AR of *Operculodinium israelianum*, which, at present, dominates (sub) tropical regions, with well-ventilated bottom waters and relatively high SSS (Bradford and Wall, 1984; Zonneveld et al., 2013). Conditions similar to present-day Eastern Mediterranean were established. The relatively high abundances of spores and aquatic pollen types, based on three samples for the studied interval after the sapropel termination (6.5–5 cal. ka BP; Fig. 3k, l) typically point to a disturbed, erosional signal, potentially linked to human activity, e.g., deforestation.

5. Conclusions

A marine and terrestrial palynological approach was employed within a multi-proxy study on a core collected in a region of the eastern Mediterranean under strong influence of Nile discharge, in order to understand the roles of productivity and preservation in sapropel S1 formation and their leads and lags. We found that marine productivity, as derived from dinocyst ARs and CaCO₃ content, started to increase ~1 ka prior to the onset of sapropel S1 at 10.8 cal. ka BP. Such increase in productivity is due to enhanced nutrient input. Nutrients were partly derived from increased Nile River discharge, as inferred from a coinciding decrease in $\delta^{18}\text{O}_{\text{ruber}}$, and from flooded shelves during marine transgression and subsequent expansion of the coastal marsh habitat as indicated by an increase in Chenopodiaceae pollen. Additionally, shoaling of the nutricline may have played a role.

At sapropel onset, high ARs of *L. machaerophorum* and cysts of *P. dalei*, suggest maximum Nile discharge, which resulted in (seasonal) stratification of surface waters, occurring at a maximum in the Northern Hemisphere summer insolation. Persistent stratification led to reduce or shutdown bottom water ventilation, promoting enhanced carbon sequestration at the sediment–water interface, within one century. We suggest that the abrupt increase in the total pollen and spores AR at sapropel onset, partly favoured by better preservation, is mostly the result of increased surface transport, which is most consistent with a slowdown in the water circulation and greater extension of the freshwater plume of the Nile. Pollen assemblages exhibit a gradual shift from a savanna-like ecosystem to moist open woodland during sapropel deposition, fitting the long-term trend.

In conclusion, a combination of high marine productivity and stratification-induced preservation were critical for triggering sapropel formation with marine productivity playing a leading role for at least the first three centuries after sapropel deposition. Marine productivity seems to have played a secondary role during the remainder of sapropel formation. Pollen assemblages in S1b and after the sapropel (up to ~5 cal. ka BP) are indicative of aridification and disturbance of the natural landscape, while dinocyst assemblages after sapropel termination point to environmental conditions comparable with the present-day situation.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2014.11.014>.

References

- Aksu, A.E., Yaşar, D., Mudie, P.J., 1995. Paleoclimatic and paleoceanographic conditions leading to development of sapropel layer S1 in the Aegean Sea basins. *Palaeoclimatol. Palaeogeogr. Palaeoecol.* 116, 71–101.
- Aksu, A.E., Abrajano, J., Mudie, P.J., Yaşar, D., 1999. Organic geochemical and palynological evidence for terrigenous origin of the organic matter in Aegean Sea sapropel S1. *Mar. Geol.* 153, 303–318.
- 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.
- Almogi-Labin, A., Bar-Matthews, M., Shriki, D., Kolosovsky, E., Paterne, M., Schilman, B., Ayalon, A., Aizenshtat, Z., Matthews, A., 2009. Climatic variability during the last ~90ka of the southern and Northern Levantine Basin as evident from marine records and speleothems. *Quat. Sci. Rev.* 28, 2882–2896.
- Bar-Matthews, M., Ayalon, A., Kaufman, A., Wasserburg, G.J., 1999. The Eastern Mediterranean paleoclimate as a reflection of regional events: Soreq Cave, Israel. *Earth Planet. Sci. Lett.* 166, 85–95.
- Bethoux, J.P., 1989. Oxygen consumption, new production, vertical advection and environmental evolution of the Mediterranean Sea. *Deep-Sea Res.* 36 (5), 769–781.
- Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *Holocene* 2, 1–10.
- Boessenkool, K.P., Brinkhuis, H., Schönfeld, J., Targarona, J., 2001. North Atlantic sea-surface temperature changes and the climate of western Iberia during the last deglaciation; a marine palynological approach. *Glob. Planet. Change* 30, 33–39.
- Bradford, M.R., Wall, D.A., 1984. The distribution of recent organic-walled dinoflagellate cysts in the Persian Gulf, Gulf of Oman, and northwestern Arabian Sea. *Palaeontographica B* 192, 16–84.
- Butzer, K., 2002. Geoarchaeological implications of recent research in the Nile Delta. In: van den Brink, E.C.M., Levy, T.E. (Eds.), *Egypt and the Levant*. Leicester University Press, London, pp. 83–97.
- Calvert, S.E., 1983. Geochemistry of Pleistocene sapropels and associated sediments from the Eastern Mediterranean. *Oceanol. Acta* 6, 255–267.
- Calvert, S.E., 1990. Geochemistry and origin of the Holocene sapropel in the Black Sea. In: Ittekkot, V., Kempe, S., Michealis, W., Spitzky, A. (Eds.), *Facets of Modern Biogeochemistry*. Springer-Verlag, Berlin, pp. 328–353.
- Calvert, S.E., Pedersen, T.F., 1992. Organic carbon accumulation and preservation in marine sediments: how important is anoxia? In: Whelan, J.K., Farrington, J.W. (Eds.), *Productivity, Accumulation and Preservation of Organic Matter in Recent and Ancient Sediments*. Columbia University Press, pp. 231–263.
- Casford, J.S.L., Rohling, E.J., Abu-Zied, R., Cooke, S., Fontanier, C., Leng, M., Lykousis, V., 2002. Circulation changes and nutrient concentrations in the late Quaternary Aegean Sea: a nonsteady state concept for sapropel formation. *Paleoceanography* 17, 1024–1034.
- Castaneda, I.S., Schefuss, E., Patzold, J., Sinninghe Damsté, J.S., Weldeab, S., Schouten, S., 2010. Millennial-scale sea surface temperature changes in the eastern Mediterranean (Nile River Delta region) over the last 27,000 years. *Paleoceanography* 25, 1208. <http://dx.doi.org/10.1029/2009PA001740>.
- Castradori, D., 1993. Calcareous nannofossils and the origin of eastern Mediterranean sapropels. *Paleoceanography* 8, 459–471.
- Cheddadi, R., Rossignol-Strick, M., 1995. Improved preservation of organic matter and pollen in eastern Mediterranean sapropels. *Paleoceanography* 10, 301–309.
- Claussen, V., Gayler, V., 1997. The greening of the Sahara during the mid-Holocene: results of an interactive atmosphere-biome model. *Glob. Ecol. Biogeogr. Lett.* 6, 369–377. <http://dx.doi.org/10.2307/2997337>.
- Crudeli, D., Young, J.R., Erba, E., De Lange, G.J., Henriksen, K., Kinkel, H., Slomp, C.P., Ziveri, P., 2004. Abnormal carbonate diagenesis in Holocene–Late Pleistocene sapropel-associated sediments from Eastern Mediterranean; evidence from *Emiliana huxleyi* coccolith morphology. In: Villa, G., Lees, J.A., Bown, P.R. (Eds.), *Calcareous Nannofossil Palaeoecology and Palaeoenvironmental Reconstructions*. Mar. Micropaleontol. 52 (1–4), 217–240.
- Crudeli, D., Young, J.R., Erba, E., Geisen, M., Ziveri, P., De Lange, G.J., Slomp, C.P., 2006. Fossil record of holococcoliths and selected hetero-holococcolith associations from the Mediterranean (Holocene-late Pleistocene): evaluation of carbonate diagenesis and paleoecological–paleogeographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 237, 191–212.
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansoni, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Dallas, pp. 1249–1276.
- De Lange, G.J., Ten Haven, H.L., 1983. Recent sapropel formation in the Eastern Mediterranean. *Nature* 305, 797–798.
- De Vernal, A., Marret, F., 2007. Organic-walled dinoflagellates: tracers of sea-surface conditions. In: Hillaire-Marcel, de Vernal (Eds.), *Proxies in Late Cenozoic Paleoenvironment*. Elsevier, pp. 371–408.
- D’Ortenzio, F., Ribera d’Alcala, M., 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosciences* 6, 139–148.
- Dugdale, R.C., Wilkerson, F.P., 1988. Nutrient sources and primary production in the Eastern Mediterranean. *Oceanol. Acta* 9, 179–184.
- Elshani, R., Zonneveld, K.A.F., Ibrahim, M.I., Kholeif, S.E.A., 2010. Distribution patterns of recent organic-walled dinoflagellate cysts in relation to environmental parameters in the Mediterranean Sea. *Palynology* 34, 233–260.
- Erdtman, G., 1960. The acetolysis method. *Sven. Bot. Tidskr.* 54, 561–564.
- Fensome, R.A., Williams, G.L., 2004. The Lentin and Williams Index of Fossil Dinoflagellates, 2004 Edition. In: American Association of Stratigraphic Palynologists Contribution Series 42, 909 pp.
- Fontugne, M.R., Arnold, M., Labeyrie, L., Paterne, M., Calvert, S.E., Duplessy, J.C., 1994. Palaeoenvironment, sapropel chronology and River Nile discharge during the last 20,000 years as indicated by deep sea sediment records in the Eastern Mediterranean. In: Bar-Yosef, O., Kra, R.S. (Eds.), *Late Quaternary Chronology and Paleoclimates of the Eastern Mediterranean*. Radiocarbon 75–88.
- Gallego-Torres, D., Martinez-Ruiz, F., Meyers, P.A., Paytan, A., Jimenez-Espejo, F.J., Ortega-Huertas, M., 2011. Productivity patterns and N-fixation associated with Pliocene–Holocene sapropel: paleoceanographic and paleoecological significance. *Biogeosciences* 8, 415–431.
- Gasse, F., 2000. Hydrological changes in the African tropics since the Last Glacial Maximum. *Quat. Sci. Rev.* 19, 189–211.
- Giunta, S., Negri, A., Maffioli, P., Sangiorgi, F., Capotondi, L., Morigi, C., Principato, M.S., Corselli, C., 2006. Phytoplankton dynamics in the eastern Mediterranean Sea during marine isotopic stage 5e. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 235, 28–47.
- Grant, K.M., Rohling, E.J., Bar-Matthews, M., Ayalon, A., Medina-Elizalde, M., Bronk, R.A., Satow, C., Roberts, A.P., 2012. Rapid coupling between ice volume and polar temperature over the past 150,000 years. *Nature* 491, 744–747. <http://dx.doi.org/10.1038/nature11593>.
- Grelaud, M., Marino, G., Ziveri, P., Rohling, E.J., 2012. Abrupt shoaling of the nutricline in response to massive freshwater flooding at the onset of the last interglacial sapropel event. *Paleoceanography* 27.
- Hamann, Y., Ehrmann, W., Schmiel, G., Krüger, S., Stuut, J.B., Kuhnt, T., 2008. Sedimentation processes in the Eastern Mediterranean Sea during the Late Glacial and Holocene revealed by end-member modelling of the terrigenous fraction in marine sediments. *Mar. Geol.* 248, 97–114.
- Hennekam, R., De Lange, G.J., 2012. X-ray fluorescence core scanning of wet marine 604 sediments: methods to improve quality and reproducibility of high-resolution 605 paleoenvironmental records. *Limnol. Oceanogr. Methods* 10, 991–1003.
- Hennekam, R., Jilbert, T., Schnetger, B., De Lange, G.J., 2014. Solar forcing of Nile discharge and sapropel S1 formation in the early to middle Holocene eastern Mediterranean. *Paleoceanography* 29 (5), 343–356.
- Hilgen, F.J., 1991. Astronomical calibration of Gauss to Matuyama sapropels in the Mediterranean and implication for the geomagnetic Polarity Time Scale. *Earth Planet. Sci. Lett.* 104, 226–244.
- Holmes, P.L., 1990. Differential transport of pollen and spores: a laboratory study. *Rev. Palaeobot. Palynol.* 64, 289–296.
- Hooghiemstra, H., 1988. Palynological records from northwest African marine sediments: a general outline of the interpretation of the pollen signal. *Philos. Trans. R. Soc. Lond.* 318, 431–449.
- Jacobson, D.M., Anderson, D.M., 1986. Thecate heterotrophic dinoflagellates: feeding behavior and mechanisms. *J. Phycol.* 22, 249–258.
- Kemp, A.E.S., Pearce, R.B., Koizumi, I., Pike, J., Rance, S.J., 1999. The role of mat-forming diatoms in the formation of Mediterranean sapropels. *Nature* 398, 57–61.
- Kholeif, S.E.A., Mudie, P.J., 2009. Palynological records of climate and oceanic conditions in the late Pleistocene and Holocene of the Nile Cone, southeastern Mediterranean, Egypt. *Palynology* 33, 1–24.
- Krom, M.D., Kress, N., Brenner, S., Gordon, L.L., 1991. Phosphorus limitation of primary productivity in the Eastern Mediterranean-Sea. *Limnol. Oceanogr.* 36, 424–432.
- Krom, M.D., Cliff, R.A., Eijssink, L.M., Herut, B., Chester, R., 1999. The characterisation of Saharan dusts and Nile particulate matter in surface sediments from the Levantine basin using Sr isotopes. *Mar. Geol.* 155, 319–330.
- Krom, M.D., Stanley, J.D., Cliff, R.A., Woodward, J.C., 2002. Nile River sediment fluctuations over the past 7000 yr and their key role in sapropel development. *Geology* 30, 71–74.

- Kullenberg, B., 1952. On the salinity of water contained in marine sediments. Göteborgs Kungl. Vetens. Vitter. Handl. Ser. B 6, 3–37.
- Langgut, D., Almogi-Labin, A., Bar-Matthews, M., Weinstein-Evron, M., 2011. Vegetation and climate changes in the South Eastern Mediterranean during the Last Glacial-Interglacial cycle (86 ka): new marine pollen record. *Quat. Sci. Rev.* 30 (27), 3960–3972.
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A.C.M., Levrard, B., 2004. A long-term numerical solution for the insolation quantities of the Earth. *Astron. Astrophys.* 428, 261–285.
- Marino, G., Rohling, E.J., Sangiorgi, F., Hayes, A., Casford, J.L., Lotter, A.F., Kucera, M., Brinkhuis, H., 2009. Early and middle Holocene in the Aegean Sea: Interplay between high and low latitude climate variability. *Quat. Sci. Rev.* 28, 3246–3262. <http://dx.doi.org/10.1016/j.quascirev.2009.08.011>.
- Mudie, P.J., 1982. Pollen distribution in recent marine sediments, eastern Canada. *Can. J. Earth Sci.* 19, 729–747.
- Mudie, P.J., McCarthy, F.M., 1994. Late Quaternary pollen transport processes, western North Atlantic: data from box models, cross-margin and NS transects. *Mar. Geol.* 118 (1), 79–105.
- Mudie, P.J., McCarthy, F.M., 2006. Marine palynology: potentials for onshore-offshore correlation of Pleistocene-Holocene records. *Trans. R. Soc. S. Afr.* 61, 139–157.
- Negri, A., Giunta, S., 2001. Calcareous nannofossil paleoecology in the sapropel S1 of the eastern Ionian Sea: paleoceanographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 169, 101–112.
- Negri, A., Capotondi, L., Keller, J., 1999. Calcareous nannofossils, planktic foraminifers and oxygen isotope in the late Quaternary sapropels of the Ionian Sea. *Mar. Geol.* 157, 84–99.
- Pinardi, N., Masetti, E., 2000. Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 158, 153–174.
- Pross, J., Kotthoff, U., Müller, U.C., Peyron, O., Dormoy, I., Schmiedl, G., Kalaitzidis, S., Smith, A.M., 2009. Massive perturbation in terrestrial ecosystems of the Eastern Mediterranean region associated with the 8.2 kyr B.P. climatic event. *Geology* 37, 887–890.
- Renssen, H., Brovkin, V., Fichefet, T., Goosse, H., 2003. Holocene climatic instability during the termination of the African Humid Period. *Geophys. Res. Lett.* 30 (4), 1184 doi:10.2929/2002GL016636.
- Robertson, A.H.F., Emeis, K.-C., Richter, C., Camerlenghi, A. (Eds.), 1998. Proceedings of the Ocean Drilling Program, Scientific Results 160, College Station, (TX), 817 pp.
- Rochon, A., de Vernal, A., Turon, J.L., Mathiessen, J., Head, M.J., 1999. Distribution of Recent Dinoflagellate Cysts in Surface Sediments from the North Atlantic Ocean and Adjacent Seas in Relation to Sea-surface Parameters. AASP Contributions Series number 35. American Association of Stratigraphic Palynologists Foundation, Dallas, TX, 152 pp.
- 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.W., 1989. Late Quaternary changes in Mediterranean intermediate water density and formation rate. *Paleoceanography* 4, 531–545.
- Rohling, E.J., Pälike, H., 2005. Centennial-scale climate cooling with a sudden cold event around 8,200 years ago. *Nature* 434, 975–979.
- Rossignol-Strick, M., 1985. Mediterranean Quaternary sapropels, an immediate response of the African monsoon to variation of insolation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 49, 237–263.
- Rossignol-Strick, M., 1999. The Holocene climatic optimum and pollen records of sapropel 1 in the eastern Mediterranean, 9000–6000 BP. *Quat. Sci. Rev.* 18, 515–530.
- Sangiorgi, F., Donders, T.H., 2004. Reconstructing 150 years of eutrophication in the north western Adriatic Sea (Italy) using dinoflagellate cysts, pollen and spores. *Estuar. Coast. Shelf Sci.* 60, 69–79.
- Sangiorgi, F., Capotondi, L., Combourieu Nebout, N., Vigiotti, L., Brinkhuis, H., Giunta, S., Lotter, A.F., Morigi, C., Negri, A., Reichert, G.-J., 2003. Holocene seasonal sea-surface temperature variations in the southern Adriatic Sea inferred from a multiproxy approach. *J. Quat. Sci.* 18, 723–732.
- Sangiorgi, F., Fabbri, D., Comandini, M., Gabbianelli, G., Tagliavini, E., 2005. The distribution of sterols and organic-walled dinoflagellate cysts in surface sediments of the North-western Adriatic Sea (Italy). *Estuar. Coast. Shelf Sci.* 64, 395–406.
- Scott, D.B., Frail-Gauthier, J., Mudie, P.J., 2014. Coastal Wetlands of the World: Geology, Ecology, Distribution and Applications. Cambridge University Press.
- Slomp, C.P., Thomson, J., De Lange, G.J., 2002. Enhanced regeneration of phosphorus during formation of the most recent eastern Mediterranean sapropel (S1). *Geochim. Cosmochim. Acta* 66, 1171–1184. [http://dx.doi.org/10.1016/S0016-7037\(01\)00848-1](http://dx.doi.org/10.1016/S0016-7037(01)00848-1).
- Stanley, D.J., Maldonado, A., 1977. Nile Cone: late Quaternary stratigraphy and sediment dispersal. *Nature* 266, 129–135.
- Stanley, J.-D., Warne, A.G., 1993. Nile delta: recent geological evolution and human impact. *Science* 260, 628–634.
- Thomson, J., Crudeli, D., De Lange, G.J., Slomp, C.P., Erba, E., Corselli, C., Calvert, S.E., 2004. *Florisphaera profunda* and the origin and diagenesis of carbonate phases in eastern Mediterranean sapropel units. *Paleoceanography* 19, 3003. <http://dx.doi.org/10.1029/2003PA000976>.
- Tinner, W., van Leeuwen, J.F.N., Colombaroli, D., Vescovi, E., van der Knaap, W.O., Henne, P.D., Pasta, S., D'Angelo, S., La Mantia, T., 2009. Holocene environmental and climatic changes at Gorgo Basso, a coastal lake in southern Sicily, Italy. *Quat. Sci. Rev.* 28, 1498–1510.
- Traverse, A., 1990. Studies of pollen and spores in rivers and other bodies of water, in terms of source vegetation and sedimentation, with special reference to Trinity River and Bay, Texas. *Rev. Palaeobot. Palynol.* 64, 297–303.
- Uitz, J., Claustre, H., Gentili, B., Stramski, D., 2010. Phytoplankton class-specific primary production in the world's oceans: seasonal and inter-annual variability from satellite observations. *Glob. Biogeochem. Cycles* 24, 3016–3035.
- Van Campo, M.M., 1984. Relations entre la végétation de l'Europe et les températures de surface océaniques après le dernier maximum glaciaire. *Pollen Spores* 26, 497–518.
- Versteegh, G.J.M., Zonneveld, K.A.F., 2002. Use of selective degradation to separate preservation from productivity. *Geology* 30 (7), 615–618.
- Wall, D., Dale, B., 1966. "Living fossils" in Western Atlantic plankton. *Nature* 211, 1025–1026.
- Weldeab, S., Emeis, K.-C., Hemleben, C., Siebel, W., 2002. Provenance lithogenic surface sediments and path ways of riverine suspended matters in the eastern Mediterranean Sea: evidence from $^{143}\text{Nd}/^{144}\text{Nd}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. *Chem. Geol.* 186, 139–149. [http://dx.doi.org/10.1016/S0009-2541\(01\)00415-6](http://dx.doi.org/10.1016/S0009-2541(01)00415-6).
- Weldeab, S., Emeis, K.-C., Hemleben, C., Schmiedl, G., Schulz, H., 2003. Spatial productivity during formation of Sapropels S5 and S6 in the Mediterranean Sea: evidence from Ba contents. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 191, 169–190.
- Weldeab, S., Menke, V., Schmiedl, G., 2014. The Pace of East African Monsoon evolution during the Holocene. *Geophys. Res. Lett.* 41, 1724–1732. <http://dx.doi.org/10.1002/2014GL059361>.
- Williams, D.F., Thunell, R.C., Kennett, J.P., 1978. Periodic freshwater flooding and stagnation of the eastern Mediterranean Sea during the late Quaternary. *Science* 201, 252–254.
- Zonneveld, K.A.F., Versteegh, G.J.M., De Lange, G.J., 1997. Preservation of organic walled dinoflagellate cysts in different oxygen regimes: a 10,000 yr natural experiment. *Mar. Micropaleontol.* 29, 393–405.
- Zonneveld, K.A.F., Versteegh, G.J.M., De Lange, G.J., 2001. Palaeoproductivity and postdepositional aerobic organic matter decay reflected by dinoflagellate cyst assemblages of the Eastern Mediterranean S1 sapropel. *Mar. Geol.* 172, 181–195.
- Zonneveld, K.A.F., Versteegh, G., Kodrans-Nsiah, M., 2008. Preservation and organic chemistry of Late Cenozoic organic-walled dinoflagellate cysts: a review. *Mar. Micropaleontol.* 68, 179–197.
- Zonneveld, K.A.F., Chen, L., Möbius, J., Mahmoud, M.S., 2009. Environmental significance of dinoflagellate cysts from the proximal part of the Po-river discharge plume (off southern Italy, Eastern Mediterranean). *J. Sea Res.* 62, 189–213.
- Zonneveld, K.A., Chen, L., Elshaniwany, R., Fischer, H.W., Hoins, M., Ibrahim, M.I., Pittauerova, D., Versteegh, G.J., 2012. The use of dinoflagellate cysts to separate human-induced from natural variability in the trophic state of the Po-River discharge plume over the last two centuries. *Mar. Pollut. Bull.* 64, 114–132.
- Zonneveld, K.A.F., Marret, F., Versteegh, G.J.M., Bogus, K., Bonnet, S., Bouimetarhan, I., Crouch, E., de Vernal, A., Elshaniwany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K., Henry, M., Holzwarth, U., Kieft, J.F., Kim, S.Y., Ladouceur, S., Ledu, D., Chen, L., Limoges, A., Londeix, L., Lu, S.H., Mahmoud, M.S., Marino, G., Matsouka, K., Mathiessen, J., Mildenhall, D.C., Mudie, P., Neil, H.L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.L., Verleye, T., Wang, Y., Wang, Z., Young, M., 2013. Atlas of modern dinoflagellate cyst distribution based on 2405 data points. *Rev. Palaeobot. Palynol.* 191, 1–197.