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Dinoflagellate cysts, freshwater algae and fungal spores as salinity indicators in Late Quaternary cores from Marmara and Black seas

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Abstract

Seismic profiles and mollusks have been used to suggest that from ~12 500 to 7000 yr BP, the Black Sea was an isolated freshwater lake containing potable water and implying a surface salinity of <1. According to Ryan and Pitman (1999), these circumstances encouraged Neolithic settlement and farming on the shore of the Black Sea. This model conflicts with previous studies of dinoflagellate cysts and seismic profiles from the Marmara Sea. Here we investigate Ryan and Pittman's model using palynological studies of organic-walled dinoflagellate cysts, acritarchs, freshwater algae, microforaminifera, and fungal remains as tracers of changes in surface salinity for seven cores of pleniglacial to Holocene sediments from the Marmara and Black seas. Core-top data from 16 sites along a salinity gradient from 39.5 in the Aegean Sea to ~17 in the Black Sea show that the dinocyst species *Impagidinium aculeatum*, *Impagidinium patulum*, *Operculodinium israelianum*, *Polysphaeridium zoharyi* and *Nematosphaeropsis labyrinthus* are markers of Mediterranean Sea water and summer surface salinity >24, and that *Spiniferites cruciformis*, *Spiniferites inaequalis*, *Peridinium ponticum*, *Polykrikos* spp. and *Quinquecuspis concreta* characterize the lower salinity of the Marmara and/or Black seas. The core-top data and correlatable down-core assemblage changes in time-equivalent sapropelic and brown muds show that there is no evidence for differential aerobic decay of dinocysts in the study area. The main acritarchs are *Sigmopollis psilatum*, *Concentricystes* cf. *C. rubinus* and cf. Acritarch-8 of Traverse (1978), all of which are absent from the Aegean Sea and decrease in abundance with increasing salinity; the first two taxa have been reported previously as freshwater species. Fungal remains show a similar distribution pattern to the freshwater acritarchs, indicating their origin from terrestrial environments. Freshwater Chlorococcales are almost confined to the Black Sea but they have rare occurrences in the Aegean, indicating long-distance transport. Microforaminiferal linings are abundant in the Marmara Sea but are absent in deep water of the Black Sea. In the Marmara Sea, mid–late Holocene assemblages (<7 ka) are dominated by *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and halophilic Mediterranean *Spiniferites* spp. (*S. mirabilis, S. hyperacanthus, S. bentorii*), and a diversity of heterotrophic protoperidinioid and *Polykrikos* species are present in both sapropels and brown lutites. In contrast, the early Holocene interval (including sapropels) has fewer halophilic *Spiniferites* spp. and other Mediterranean taxa (*O. israelianum, Polysphaeridium zoharyi)* and more low salinity indicators (*P. ponticum*,

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Pyxidinopsis psilata and *S. cruciformis*), suggesting that the overflow of Black Sea water was greater than now. The time-equivalent early Holocene unit in the Black Sea has a higher percentage of taxa found in freshwater environments (including *S. cruciformis* forms 1–3; *Gonyaulax apiculata*, fungal remains and freshwater acritarchs) but the continued presence of *Spiniferites* morphotypes and other taxa associated with brackish (~7–18) to saline surface water indicates that there was some Mediterranean water present at this time. The late glacial and Pleniglacial sediments in the Marmara Sea contain a lower diversity of dinoflagellates, dominated by *S. cruciformis* and *P. psilata*, as in early Holocene sediments of the Black Sea but including the short-spine morphotypes of *S. cruciformis* which are not found in freshwater lakes. We conclude that although the glacial stages were marked by much lower sea-surface temperatures, there was either some periodic marine influence or the marine dinocysts were living in a brackish water environment (~7–18) with the freshwater species being transported from glacial lakes. Overall, there is no palynological evidence that the surface salinity of the Black or Marmara seas was ever as low as a freshwater lake. This finding is consistent with models that estimate the time required to desalinate the Black Sea after closing of the Marmara–Bosphorus gateway.

Keywords: dinoflagellate cysts; acritarchs; fungi; freshwater algae; Marmara Sea; Black Sea; paleosalinity; Quaternary palynology; aerobic decay

1. Introduction

Previous studies of Late Quaternary sediments from the Aegean, Black and Marmara seas have shown that dinoflagellate cyst (dinocyst) assemblages are important tracers of changes in surface water salinity in these epicontinental seas (Wall and Dale, 1973; Aksu et al., 1995a; Dale, 1996; Mudie et al., 2001). In the Mediterranean and Black seas, both calcareous and organic-walled dinocysts are found in the Holocene sediments. Of these groups, the organic-walled dinocysts are especially useful for paleoceanographic studies because they are highly resistant to dissolution which can alter the taphonomic representation of calcareous and siliceous microplankton. Early studies of Plio–Pleistocene sediments in the Black Sea by Traverse (1974) also used organic-walled dinoflagellate cysts, together with acritarchs (algal spores of unknown or uncertain biological affinity), as an index of marine versus freshwater conditions. Other freshwater colonial algae, such as *Pediastrum*, were noted as potential markers of increased runoff to the Black Sea (e.g. Roman, 1974; Traverse, 1974).

The Marmara Sea is a critical gateway for exchange of water between the Black Sea, a permanently anoxic basin, and the Aegean Sea, which is a branch of the eastern Mediterranean Sea (Fig. 1). The Marmara Sea is presently linked to the Black Sea through the ~40-m-deep Strait of Bosphorus (Strait of Istanbul) and with the Aegean Sea through the ~70-m-deep Strait of Dardanelles (Strait of Çanakkale). The importance of this gateway in the Quaternary paleoceanographic evolution of the eastern Mediterranean has long been recognized, particularly with regard to the role of freshwater runoff in promoting the development of sapropel layers (e.g. Vergnaud-Grazzini et al., 1977; Thunell and Williams, 1989; Aksu et al., 1995a,b). Previous studies have suggested that during glacial periods, the levels of the Aegean and Black seas were below the Bosphorus and Dardanelles sills so that the inland Marmara and Black seas became isolated basins, cut off from the Mediterranean Sea. Following the rise in glacio-eustatic sea level from a lowstand of −110 m at ~11 000 yr BP (Aksu et al., 1999b, 2002a), the Bosphorus sill was breached and Black Sea water was exported through the Marmara gateway to the Aegean Sea. However, the timing of this event is controversial. Aksu et al. (1995a,b) correlated this flooding event with deposition of Aegean sapropel S1 from 9600 to 6400 yr BP, while Ryan et al. (1997) and Ryan and Pitman (1999) believe that the Bosphorus was not breached until 7000 yr BP when the Marmara Sea cascaded into the Black Sea catastrophically re-filling the basin and contributing to the Noah's Flood myth.

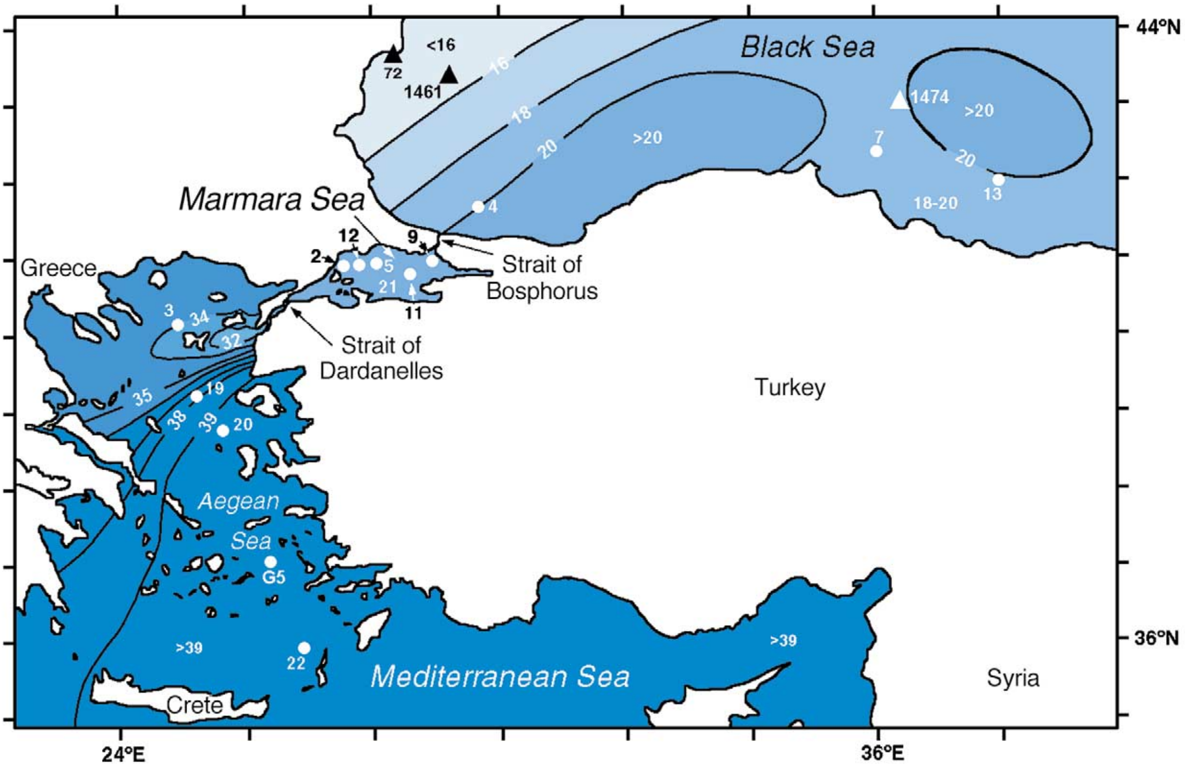


Fig. 1. Location map of the Black Sea and Marmara Sea showing the Strait of Bosphorus (= Strait of Istanbul) and Strait of Dardanelles (= Strait of Çanakkale). Triangles and filled circles are coretop sites and gravity cores discussed in the text: 2 = MAR97-02, 5 = MAR94-05, 7 = B-7, 9 = MAR98-09, 11 = MAR97-11 and 12 = MAR98-12. Isohalines are in practical salinity units (psu).

The primary objective of the present study is to investigate the history of surface salinity and water exchange between the Aegean, Marmara and Black Seas during the past ~34 000 yr, using organic-walled dinocyst assemblages, freshwater algae and acritarchs as markers of near-surface (0–50 m) water salinity and freshwater input. We also document the use of fungal remains (mostly spores and hyphal strands) as an index of terrigenous sediment influx and transport by large rivers. We examine the evidence for changes in primary paleoproductivity associated with the major oceanographic events: in particular, the possibility that apparent increases in dinoflagellate production and pollen–spore deposition are just the result of better preservation during intervals of sapropel formation (e.g. Cheddadi and Rossignol-Strick, 1995; Zonneveld et al., 2001). Finally, we present two possible scenarios for the history of desalination of the Black Sea and we draw some conclusions regarding the early Holocene salinity conditions.

2. Present oceanography

2.1. Physical properties and circulation

Water exchange between the Black Sea and the eastern Mediterranean Sea presently occurs as a two-layer flow with the cooler (5–15°C), lower salinity (17–20) Black Sea water forming a westward-flowing surface layer, 25–100 m thick. Warmer (15–20°C), saline (38–39) Mediterranean water enters the Strait of Dardanelles beneath the low salinity surface layer in the northeastern Aegean Sea and flows northeast (Özsoy et al., 1995; Polat and Tuğrul, 1996) to occupy the entire Marmara basin below the low salinity surface layer. After crossing the Strait of Bosphorus, the saline water penetrates the Black Sea and forms the bottom water mass below the 100–200-m-thick surface layer.

At present, there is a net export of ~300 km^3 yr^{-1} of water from the Black Sea into the Aegean Sea across the Straits of Bosphorus and Dardanelles (Özsoy et al., 1995). This outflow results from the excess of precipitation and river discharge to the Black Sea (~650 km^3 yr^{-1}) relative to the evaporation (~350 km^3 yr^{-1}). The Danube, Dniester, Dnieper, Southern Bug and Don rivers are the major sources of freshwater into the Black Sea, from a drainage area of ~2 million km^2.

Surface water circulation in the Black Sea is dominated by two large central cyclonic gyres and several smaller, anticyclonic coastal eddies (Oğuz et al., 1993). A narrow (< 75-km-wide) cyclonic peripheral 'rim current' separates the central basinal gyres from the coastal eddies (Aksu et al., 2002b). Weak anticyclonic eddies are also situated east and west of the Strait of Bosphorus. Surface circulation in the Marmara Sea is dominated by the outflow of low salinity Black Sea water (Beşiktepe et al., 1994), which flows as a narrow current for nearly the entire width of the basin, but broadens westward, forming large meander loops with three weak anticyclonic gyres as it approaches the Strait of Dardanelles (Aksu et al., 2002a). The bottom water circulation in the Black Sea is controlled by the rate of influx of denser Mediterranean water through the straits of Bosphorus and Dardanelles. This dense water flows eastward and cools over the shelves, then forms turbulent plumes that sink beneath the halocline and slowly travels eastward into the deep basins between 100 and 500 m water depth (Özsoy et al., 1995). Mixing of the surface water by winds and winter convection occurs down to ~200 m. Mixing of the bottom water layer (~400 m thick), however, is driven only by geothermal heat flux, with a very slow turnover rate on the order of ~2500 years.

Table 1
List of all the plankton-stage dinoflagellates reported from the Black Sea (see text for references) and their corresponding cyst forms

Thecal stage name	Cyst stage name
Ceratium candelabrum	no cyst
Ceratium furca	no cyst
Ceratium fusus	no cyst
Ceratium longipes	no cyst
Ceratium longirostrum	no cyst
Ceratium hexacanthum	no cyst
Ceratium pentagonum	no cyst
Ceratium tripos	no cyst
Dinophysis acuminata	no cyst
Dinophysis acuta	no cyst
Dinophysis caudata	no cyst
Dinophysis hastata	no cyst
Dinophysis homunculus	no cyst
Dinophysis ovum	no cyst
Dinophysis rotundata	no cyst
Dinophysis sacculus	no cyst
Dinophysis sphaerica	no cyst
Dinophysis sp.	no cyst
Exuviaella compressa	no cyst
Exuviaella cordata	no cyst
Gonyaulax polygramma	no cyst
Goniodoma polyedricum	no cyst
Gymnodinium rotundatum	no cyst
Gyrodinium fusiforme	no cyst
Gyrodinium pellucidum	no cyst
Gyrodinium pusillum	no cyst
Lingulodinium polyedrum	*Lingulodinium machaerophorum*
Noctiluca scintillans	no cyst
Oxytoxum milneri	no cyst
Protoperidinium cinctum	no cyst
Protoperidinium crassipes	no cyst
Protoperidinium deficiens	no cyst
Protoperidinium depressum	no cyst
Protoperidinium diabolus	no cyst
Protoperidinium divergens	*Peridinium ponticum*
Protoperidinium granii	no cyst
Protoperidinium pentagonum	*Trinovantedinium applanatum*
Protoperidinium solidicorne	no cyst
Protoperidinium steinii	no cyst
Protoperidinium sp.	no cyst
Phalacroma parvulum	no cyst
Phalacroma sp.	no cyst
Polykrikos schwartzii	*Polykrikos schwartzii*
Pronoctiluca pelagica	no cyst
Pronoctiluca spinifera	no cyst
Prorocentrum micans	brown spherical cyst
Protoceratium reticulatum	*Operculodinium centrocarpum*
Prorocentrum compressum	no cyst
Scrippsiella trochoidea	*Scrippsiella trochoidea* (calcareous cyst)

2.2. Biological oceanography

Few data are available which describe the composition of plankton and benthos in the Marmara and Aegean seas (see Aubert et al., 1990). However, there are detailed reports for the surface layer (0–50 m) of the Black Sea that comprises most of the water mass in which the dinoflagellate populations would be growing. Table 1 lists all the plankton-stage dinoflagellates reported from the Black Sea and their corresponding cyst forms. It should be noted that the plankton ecology of the Black Sea has changed significantly since 1970 because of NO_3, PO_4 and organic matter enrichment and SiO_2 reduction as a consequence of dam construction (Bodeneau, 1993; Bologa et al., 1995). In the northwest Black Sea, these changes have resulted in an eight-fold increase in non-diatom algae relative to diatoms, including frequent red tide blooms of the dinoflagellates *Prorocentrum cordatum*, *Scrippsiella trochoidea* and *Heterocapsa triquetra*, as well as the coccolithophorid *Emiliania huxleyi* and the diatoms *Nitschia*, *Skeletonema* and *Chaetoceros*. Summer blooms of the dinoflagellate *Noctiluca scintillans* occur along the coasts of Ukraine, Georgia and Turkey. Benli (1987) also reports blooms of *Protoceratium reticulatum* (cyst form = *Operculodinium centrocarpum*) and *Prorocentrum micans* in the southern Black Sea. In addition to these photosynthetic dinoflagellate blooms, Bologa et al. (1995) note that there has been an increase of ~19% in heterotrophic dinoflagellates since 1990, probably mainly *Protoperidinium pentagonum* (cyst form = *Trinovantedinium applanatum*) which blooms in the southern Black Sea (Benli, 1987). Aubert et al. (1990) also report blooms of *Peridinium steinii* and *Gymnodinium simplex* in the Black Sea, and they note that there is a large decrease in dinoflagellates in the Strait of Bosphorus and the Marmara Sea where only *E. huxleyi* forms blooms. In the Aegean Sea, however, there are blooms of *Gymnodinium* in addition to *E. huxleyi* and *Coccolithus pelagicus*. It is also notable that the diversity and production of diatoms in the Aegean Sea are relatively sparse compared to the dinoflagellates (Aubert et al., 1990).

3. Methods

Cores used in this study (Fig. 1, Table 2) were collected from the RV *Koca Piri Reis* of the Institute of Marine Sciences and Technology, Dokuz Eylül University, using a 4-m-long corer, with 10 cm internal diameter and 400 kg weight. All

Table 2

Geographic co-ordinates and water depths (in meters) for core-top samples used in this study

Sample	Locality	Latitude (°N)	Longitude (°E)	Depth (m)
22	Cretan Trough	35.8	26.8	1050
G5	Central Aegean Sea	37.4	26.2	510
20	Central Aegean Sea	38.5	24.5	700
19	North Aegean Sea	39.1	24.9	570
3	NE Aegean Sea	40.2	24.9	560
2	W Marmara Sea	40.9	27.6	1080
12	W Marmara Sea	40.8	27.8	549
5	Central Marmara Sea	40.9	28.1	1008
11	SE Marmara Sea	40.7	28.4	111
9	E Marmara Sea	40.9	28.9	64
4	SW Black Sea	41.5	29.3	112
1474	W Black Sea	42.2	37.8	2117
72	W Black Sea	43.5	28.4	15
1461	W Black Sea	43.0	30.0	1990
7	SE Black Sea	42.5	37.0	2120
13	SE Black Sea	42.0	37.9	2050

Locations of core tops in Fig. 1.

Table 3
Dinocyst core-top data

Sample number	22	G5	20	19	3	2	12	5	11	9	4	72^{a}	1461^{a}	13	7	1474^{b}
Surface salinity (psu)	39.5	39.3	39.1	38.4	34.0	24.0	23.0	22.0	22.0	20.1	17.6	15.0	17.0	22.0	22.0	22.0
Dinocysts/g × 1000	0.12	0.13	0.37	0.16	0.37	2.7	2.53	6.09	7.87	2.33	2.97	0.5	0.12	2.07	12	2–62.0
Pollen–spores/g × 1000	0.11	0.06	0.21	1.23	0.37	5.8	3.2	2.73	5.78	3.89	3.11	0.15	6	55.94	42	160
Acritarchs/g	0	0	0	0	0	1000	60	426	400	500	1 124	15	20	1 094	12 000	22 000
Pediastrum coenobia/g	0	0	24	0	0	0	50	0	0	0	0	5–20	10	2 232	7 240	common
Fungal spores/g	0	0	12	0	100	20	272	500	172	278	591	present	present	2 399	8 447	common
Microforams/g	50	10	32	5	46	8	376	0	515	500	59	nd	nd	0	0	nd
Dinocysts																
Peridinioid	32	7	18	17	6	48	21	18	10	32	7	nd	nd	76	56	nd
Algidasphaeridium? *minutum*							8	10	7.5	5						
Brigantedinium spp.	12			17		20	6	1	1	24	4			58	22	56
Pentapharsodinium dalei		1	7		3			2		2				1.7		
Peridinium ponticum						2		2							16	
Quinquecuspis concreta						2	2		0.5		2					
Selenopemphix nephroides		3	10		3		2								7	
Selenopemphix quanta						9	1									
Protoperidinium stellatum						4	1		1	0.5	1			1.7	4	
Trinovantedinium applanatum	20	3	1													
Polykrikoid species (*P. schwartzii*, *P. kofoidii*, *Polykrikos* sp.)	0	0	0	0	0	1	2	2	0	1	0			8.6	7	
Marine Gonyaulacoids	66	90	82	83	95	38	74	82	90	64	93	nd	nd	24	44	nd
cf. *Alexandrium tamarense*							1	6						1.7		
Ataxiodinium choanum		3														
Bitectatodinium tepikiense	4				10	2										
Lingulodinium machaerophorum	4	2	3	30	10	9	32	18	17	40	82	domin.		10.3	20	9
Impagidinium spp.	12	13	30	1	1											
Nematosphaeropsis labyrinthus	10	3	3	17	1	0	1	4	1							

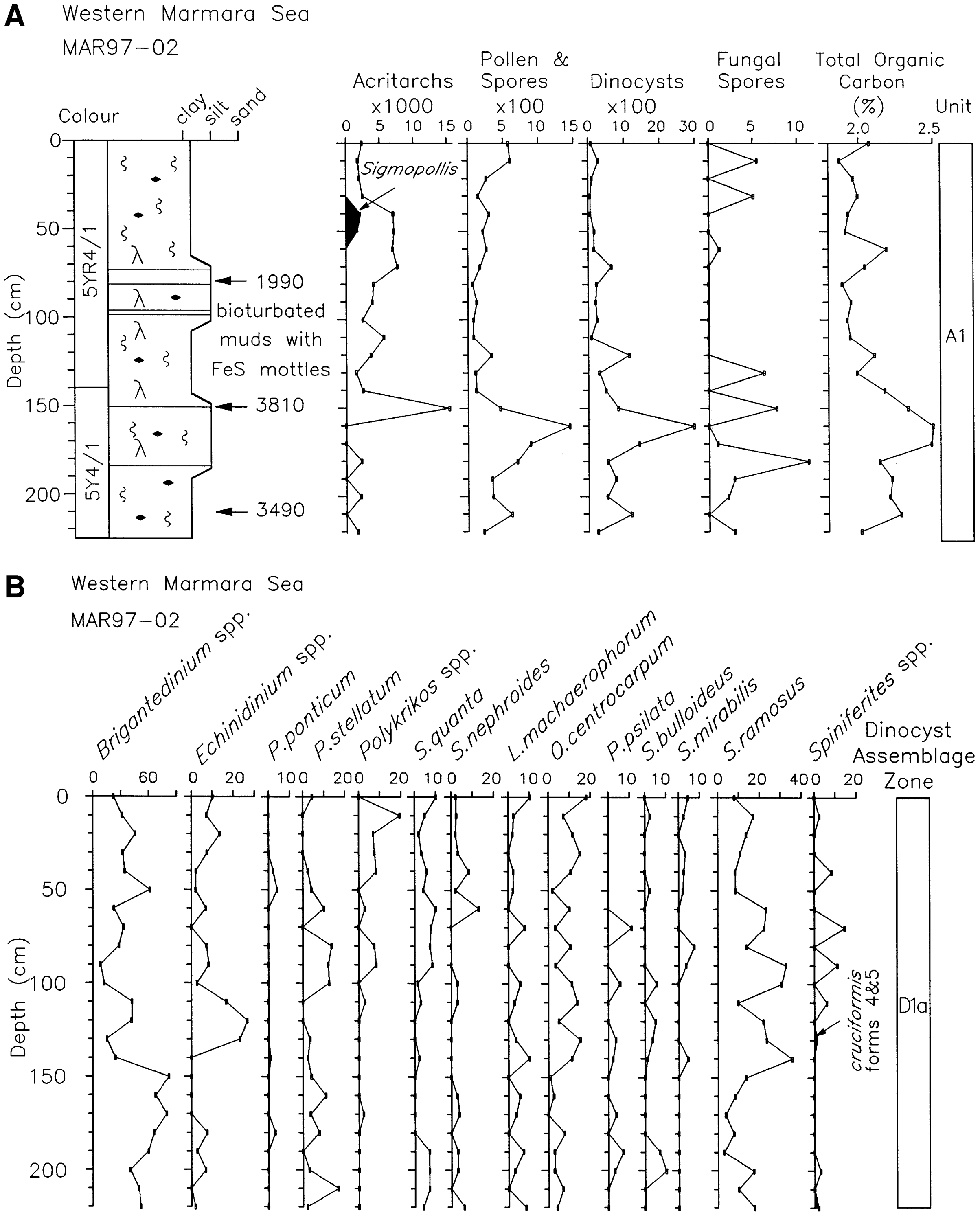
Table 3 (*Continued*).

Sample number	22	G5	20	19	3	2	12	5	11	9	4	72[a]	1461[a]	13	7	1474[b]
Surface salinity (psu)	39.5	39.3	39.1	38.4	34.0	24.0	23.0	22.0	22.0	20.1	17.6	15.0	17.0	22.0	22.0	22.0
Operculodinium centrocarpum	8	6	13	1	13	16	10	24	32	7	4	comm.			1	
Operculodinium israelianum	12	15	7													
Operculodinium psilatum			3													
Polysphaeridium zoharyi		9	10	14	17											
Pyxidinopsis psilata										5				1.7	2	
Spiniferites bentorii							1	2	1			present			2	
Spiniferites bulloideus							1	3	8							35
Spiniferites delicatus	12	18		25												
Spiniferites membranaceus		3			7		2		0.4	0.5	1	present		3.4		
Spiniferites mirabilis	4	3			7	4		4	8	5	5.2					
Spiniferites ramosus	4	15	13	1	3	7	2	18		0.5	5			6.9	16	
Tectatodinium pellitum							2									
Tuberculodinium vancampoae					3											
Freshwater Gonyaulacoids																
Spiniferites cruciformis							0.5	6							2	
Spiniferites inaequalis															2	
Spiniferites spp.					30		11		6		1					
Acritarchs																
Acritarch-8 of Traverse, 1978											160	present		558	4425	present
Concentricystes spp.						8			57	5	148	present		148	1 199	present
Cymatiosphaera spp.							30					present		50	200	900
Sigmopollis psilatum								40	57	24	148			2 232	7 240	
cf. *Echinidinium*						500										

[a] Roman (1974).

[b] Wall and Dale (1974).

List of core-top reference samples, corresponding summer surface water salinities (in psu), concentrations of main groups of sporomorphs and percentage abundances of the dinoflagellate cyst species.


A
Western Marmara Sea
MAR97-02
Colour
clay
silt
sand
Depth (cm)
0
50
100
150
200
5YR4/1
5Y4/1
1990
bioturbated
muds with
FeS mottles
3810
3490
Acritarchs x1000
0 5 10 15
Sigmopollis
Pollen & Spores x100
0 5 10 15
Dinocysts x100
0 10 20 30
Fungal Spores
0 5 10
Total Organic Carbon (%)
2.0 2.5
Unit
A1
B
Western Marmara Sea
MAR97-02
Brigantedinium spp.
Echinidinium spp.
P.ponticum
P.stellatum
Polykrikos spp.
S.quanta
S.nephroides
L.machaerophorum
O.centrocarpum
P.psilata
S.bulloideus
S.mirabilis
S.ramosus
Spiniferites spp.
0 60
0 20
10
0 20
0 20
10
0 20
10
0 20
10
10
10
0 20 40
0 20
Dinocyst Assemblage Zone
cruciformis forms 4&5
D1a
Depth (cm)
0
50
100
150
200

cores were stored upright on board ship and were shipped to Memorial University of Newfoundland (MUN), where they were split, described and photographed, except Core BLA90-07 (= Core B-7), which was split, described and sampled in Turkey. Stratigraphic studies were made on six cores from the Marmara Sea and Black Sea, the sedimentology of which is described in detail by Hiscott and Aksu (2002). One box core was studied from the southeastern Black Sea, the sedimentology of which is described by Duman (1992), and for which initial dinoflagellate cyst studies were made by Mudie et al. (2001). Additional core-top data for interpretation of the dinocyst ecostratigraphies and associated sporomorph assemblages were obtained from six Aegean Sea sites (see Aksu et al., 1995a) and from five Black Sea sites, including published data of Roman (1974), Wall and Dale (1974) and Traverse (1974).

Palynomorphs were extracted from samples of 2–5 cm^3 volume, using standard methods for Quaternary marine sediments (Rochon et al., 1999): sieving at 20- and 125-μm mesh sizes, digestion in HCl and HF, and adding exotic spores to obtain estimates of palynomorph concentration per cm^3. Palynomorph preservation is good in most sections of the cores, but sandy intervals often contain many oxidized and abraded grains, while some levels also contain common reworked pre-Quaternary (mainly Pliocene) pollen or spores and more rarely, dinoflagellate cysts. These reworked palynomorphs were primarily recognized by their distinctive morphology, but flattened and/or yellowish grains of extant pollen types were also scored as reworked.

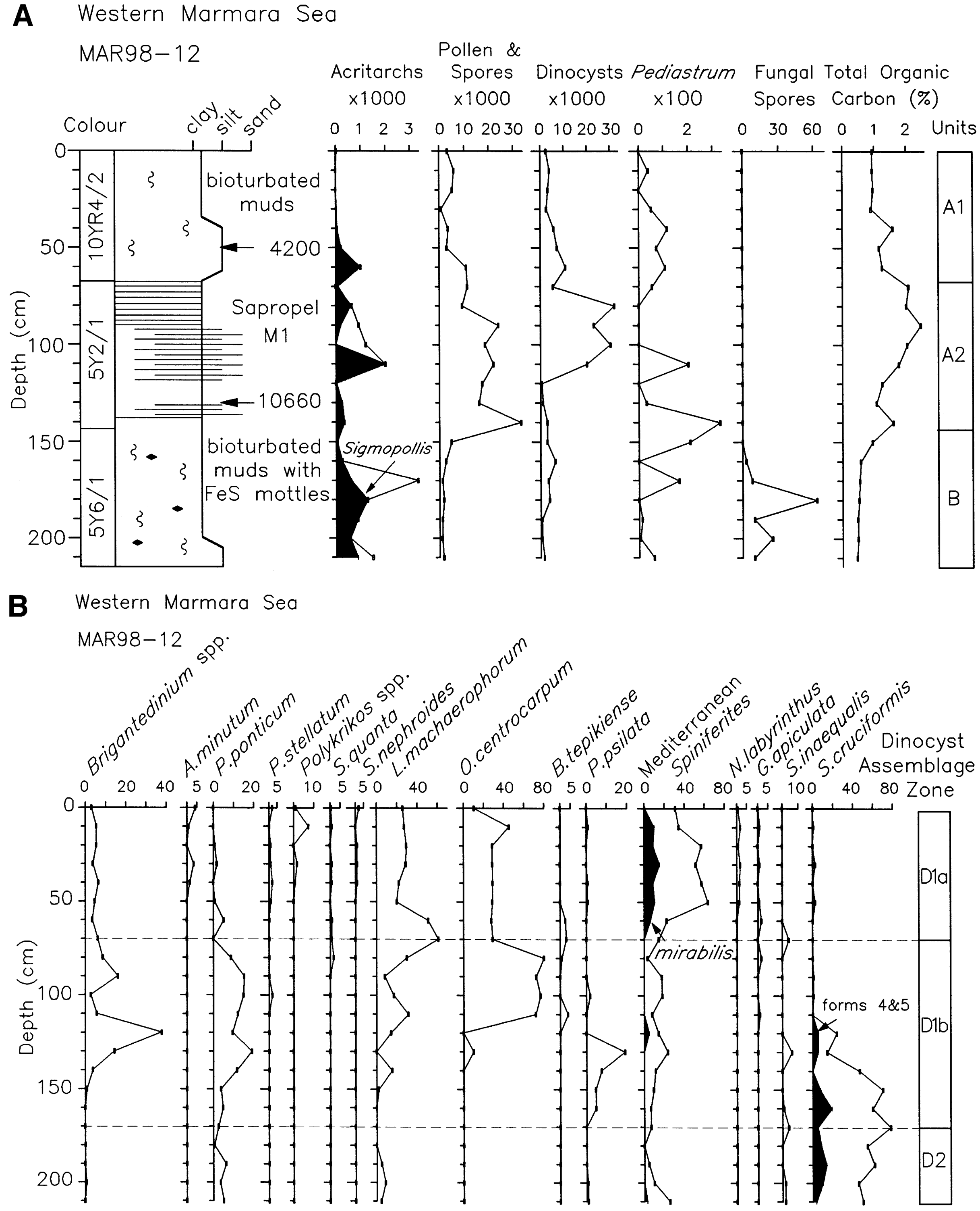
One or two slides of each processed sample were counted at ×25 magnification, until a minimum of 300 exotic spores was reached. This yielded counts of 100–200 for total dinocysts in the middle to upper Holocene samples; however, in the late glacial to early Holocene oxidized deltaic intervals, counts were as low as 25–50 for two slides and >1000 exotic spores. Nomenclature of the dinocysts follows that used by Williams et al. (1998) and Rochon et al. (1999) except where noted. Pollen and spore concentrations reported here are from Mudie et al. (2002). During the counting of dinocysts, pollen and fern+moss spores, records were kept of the number of microforaminiferal linings, acritarchs, fungal remains and freshwater algae, including coenobia of *Pediastrum* and *Botryococcus*. Identification of freshwater algal coenobia and fungal remains follows the treatments of Matthiessen and Brenner (1996), Kohlmeyer and Kohlmeyer (1979) and Jarzen and Elsik (1986), respectively. Counts were also made of the 'baggy cysts' (saccocysts) of Traverse (1974, 1988) because of their abundance in the Black Sea sediments and their apparent association with low salinity.

4. Results

4.1. Core-top distributions of dinocysts and other palynomorphs

Table 3 shows the abundances of dinocysts and other sporomorphs in the core-top samples (Fig. 1) from a south–north transect of the Aegean Sea (GC22-KC3), from a transect of the Marmara Sea (MAR97-2 to MAR98-9) and from the western (MAR98-4 to 72) and southeastern Black Sea (BS-13 to 1474). There is a general decrease in the concentration of most sporomorphs with distance away from the relatively low salinity (<23), nutrient-rich surface water of the Marmara and Black Seas, although low values of dinocysts are also found off the Danube River (sites 72, 1461). The main exception is in the microforaminiferal linings of foraminifera, the shapes of which mostly resemble benthic species, but large trocho-

Fig. 2. Distribution of dinoflagellate cysts and other sporomorphs in MAR97-02. (A) Summary diagram showing lithofacies, variations in organic-walled palynomorphs and total organic carbon (OC). Arrows show levels with uncorrected ^{14}C ages in yr BP. Units and OC data are from Hiscott and Aksu (2002) and Abrajano et al. (2002), respectively. (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.


A
Western Marmara Sea
MAR98-12
Colour
clay silt sand
10YR4/2
5Y2/1
5Y6/1
bioturbated muds
4200
Sapropel M1
10660
bioturbated muds with FeS mottles
Depth (cm)
0
50
100
150
200
Acritarchs x1000
0 1 2 3
Sigmopollis
Pollen & Spores x1000
0 10 20 30
Dinocysts x1000
0 10 20 30
Pediastrum x100
0 2
Fungal Spores
0 30 60
Total Organic Carbon (%)
0 1 2
Units
A1
A2
B
B
Western Marmara Sea
MAR98-12
Brigantedinium spp.
0 20 40
A.minutum
5
P.ponticum
0 20
P.stellatum
5
Polykrikos spp.
10
S.quanta
5
S.nephroides
5
L.machaerophorum
0 40
O.centrocarpum
0 40 80
B.tepikiense
5
P.psilata
0 20
Mediterranean Spiniferites
0 40 80
mirabilis
N.labyrinthus
5
G.apiculata
5
S.inaequalis
10
S.cruciformis
0 40 80
forms 4&5
Dinocyst Assemblage Zone
D1a
D1b
D2
Depth (cm)
0
50
100
150
200

spiroidal forms with the shapes of planktonic species are also sometimes present (see Aksu et al., 2002a and references therein). These marine palynomorphs show maximum abundances in the Marmara Sea and are well represented in the Aegean Sea but are absent in the anoxic Black Sea basins. Dinocyst abundances reach their maximum abundance in the southeastern Black Sea and parts of the Marmara Sea. Unfortunately, our palynological data do not include the calcareous cysts of *Scrippsiella trochoidea* that produces red tide blooms in this area (Bodeneau, 1993), and are also common to abundant in the eastern Mediterranean Sea (Zonneveld et al., 2001). However, scanning electron micrographs of Ross and Degens (1974) show abundant cysts of *S. trochoidea* in the sapropelic unit of the southeastern Black Sea, in the path of the saline Mediterranean water inflow. In contrast, a search for calcareous cysts in Marmara Sea cores did not reveal any specimens although coccoliths and diatoms are present (H. Gillespie, unpublished data).

The core-top distributions of chlorococcalean algae, acritarch and fungal spore concentrations show an order of magnitude decrease from the Black Sea to Marmara Sea, and are absent at most sites in the Aegean Sea. The chlorococcaleans are mostly (90%) coenobia of the freshwater alga *Pediastrum boryanum*, with minor amounts of *Botryococcus*, which lives in both fresh (<1) and brackish ($\sim$1–10) waters (Matthiessen and Brenner, 1996; Kunz-Pirrung, 1998). According to Batten (1996b), most fungal sporomorphs in palynological preparations are usually derived from soils in the watersheds and fringing marshlands because there are no known aquatic or marine fungi that produce fossilizable spores or other remains. In the core-top samples, most of the fungal remains are dark brown unicellular (*Lycoperdon*- and *Tilletia*-type) or dicellular (*Puccinellia*-type) spores, but in the Black Sea, short, unbranched hyphal strands are common, along with occasional pluricellular spores.

The acritarch *Concentricystes* sp. appears to be the same as *C. rubinus* Rossignol (1961) which was reported as being of freshwater origin; Roman (1974) also notes that it is also found in soils of Romania. The acritarchs *Cymatiosphaera* and *Sigmopollis psilatum* are commonly found in estuarine environments (Wall and Dale, 1974; Mudie, 1992; Solomon et al., 2000). The 'baggy spores' (cf. Acritarch-8) of Traverse (1978) are thin-walled, pale brown leiospheres like his 'baggy cysts' (Traverse, 1978) and saccocysts (Traverse, 1988), but with no discernible archeopyle. Both these taxa are common to abundant in the modern sediments of the Black Sea and are presumably from fresh or low salinity environments because they are not present in the core tops where summer surface salinity is greater than 18.

The modern dinocyst assemblages are mostly dominated by gonyaulacoid species, particularly *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and *Spiniferites ramosus*. There is a large increase in the abundance of protoperidinioid species (mostly *Brigantedinium* spp.) in the Black Sea. This is in accord with the higher primary production of this sea, but may partly reflect better preservation of these oxygen-sensitive cysts (Zonneveld et al., 1997, 2001) in the highly anaerobic/anoxic sediments of the deep basins. On the other hand, the maximum abundances of the moderately oxygen-sensitive species *Spiniferites delicatus*, *S. ramosus*, *S. membranaceus* and *S. mirabilis* are highest in the Aegean Sea where the surface sediments are slightly oxidized (Aksu et al., 1995b). However, relatively high percentages of protoperidinioids may be found in parts of the Marmara and Aegean where surface sediments are oxidized (e.g. sites 97-2, GC22), and the sensitive protoperidinioid cyst *Trinovantedinium applanatum* is also confined to the Aegean Sea,

Fig. 3. Distribution of dinoflagellate cysts and other sporomorphs in MAR98-12. (A) Summary diagram showing lithofacies, variations in organic-walled palynomorphs and total organic carbon (OC). Arrows show levels with uncorrected ^{14}C ages in yr BP. Units and OC data are from Hiscott and Aksu (2002) and Abrajano et al. (2002), respectively. (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.

although its thecate form, *Protoperidinium pentagonum*, is abundant in the southern Black Sea.

In order to distinguish between assemblage differences resulting from potential aerobic decay versus salinity preferences, we can consider the salinity ranges of only the most oxidation-resistant cyst species of the Mediterranean Sea region, viz. *Impagidinium aculeatum*, *Operculodinium israelianum*, *Polysphaeridium zoharyi* and *Nematosphaeropsis labyrinthus* (Zonneveld et al., 2001). The first three of these oxidation-resistant species are common in the Mediterranean, Adriatic and Alboran seas (see Mudie et al., 2001 and references therein) and they are absent from the surface sediments of the Marmara or Black seas. Therefore, it appears that these taxa are reliable indicators of Mediterranean Sea water and summer salinities >24. It is also notable that two other species of *Spiniferites* (*S. cruciformis* and *S. inaequalis*) are found only in the low salinity Black and Marmara seas, while *Peridinium ponticum* and *Polykrikos* (mostly *P. kofoidii*) have a similar distribution in the inland seas. *Quinquecuspis concreta* is present in the intermediate salinities of the Marmara Sea, in keeping with its maximum abundance in the stratified relatively low salinity waters at the head of the Persian Gulf (Bradford and Wall, 1984).

4.2. Marmara Sea ecostratigraphy

In the western Marmara Sea, two cores were studied from basinal sediments (MAR97-02 and MAR94-05) and one (MAR98-12) from the saddle between the basins. In the eastern Marmara Sea, one core (MAR97-11) was studied from the southern shelf edge and one (MAR98-09) from near the entrance to the Bosphorus Strait (Fig. 1). Multiple radiocarbon ages for mollusk shells (see Aksu et al., 2002a,b) in the western cores show that the sediments cover an age range from 1990 to 29 540 yr BP (Figs. 2–4), while the eastern cores have ages from 4500 to 15 590 yr BP (Figs. 5 and 6).

The Holocene sediments, Unit A, in all the cores except the condensed sequence of MAR94-05, show a two- to three-fold increase in dinocysts down-core, followed by a return to modern concentrations or lower numbers in the early Holocene. Dinocyst assemblages throughout Unit A are dominated by the euryhaline species *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and *Spiniferites ramosus*, with variable amounts of *Brigantedinium* and other protoperidinioid cysts. Two Holocene dinocyst sub-zones are recognized. The youngest sub-zone, D1a (0–∼7000 yr BP) is dominated by *L. machaerophorum* or, near the Aegean Sea, by *O. centrocarpum*, together with a relatively high percentage of *Spiniferites mirabilis* (here grouped with *Spiniferites hyperacanthus*), rare occurrences of *Operculodinium israelianum* and/or *Bitectatodinium tepikiense* (MAR98-12, MAR97-11 and MAR98-09), and a diversity of heterotrophic taxa, including *Algidasphaeridium*? *minutum*, *Polykrikos kofoidii*, *Selenopemphix quanta*, *Selenopemphix nephroides* and *Protoperidinium* (*Stelladinium*) *stellatum*. The early Holocene (∼7000–10 000 yr BP) sub-zone D1b is dominated by *O. centrocarpum*, with variable amounts of the low salinity indicators *Peridinium ponticum*, *Pyxidinopsis psilata* and *Spiniferites cruciformis*, absence of *Polykrikos* and a lower diversity of euryhaline *Spiniferites* and protoperidinioid species.

Concentrations of pollen and spores in Unit A show approximately the same trend as the dinocyst concentrations, but there are clear differences in the duration of the early–mid Holocene maxima, with the pollen–spore peak beginning several thousand years earlier than the dinocyst peak in Cores MAR97-11 and MAR98-09. All other sporomorphs in Unit A are marked by two or three large peaks and troughs that roughly correspond to intervals of about 2000 years. The only clear pattern is the co-occurrence of peaks of freshwater indicators, including *Pediastrum*, acritarchs and multicellular fungal spores at about 9000–10 000 yr BP. These peaks are concurrent with the maxima found in the early Holocene Unit 3 of Black Sea Core B-7 (see 4.3. Black Sea ecostratigraphy).

The late glacial maximum (LGM) to early postglacial Unit B (∼25 000–11 000 yr BP) in Cores MAR98-12, MAR94-05 and MAR97-11 is distinguished throughout by low concentrations of dinocysts dominated (40–80%) by *Spiniferites cruci-*

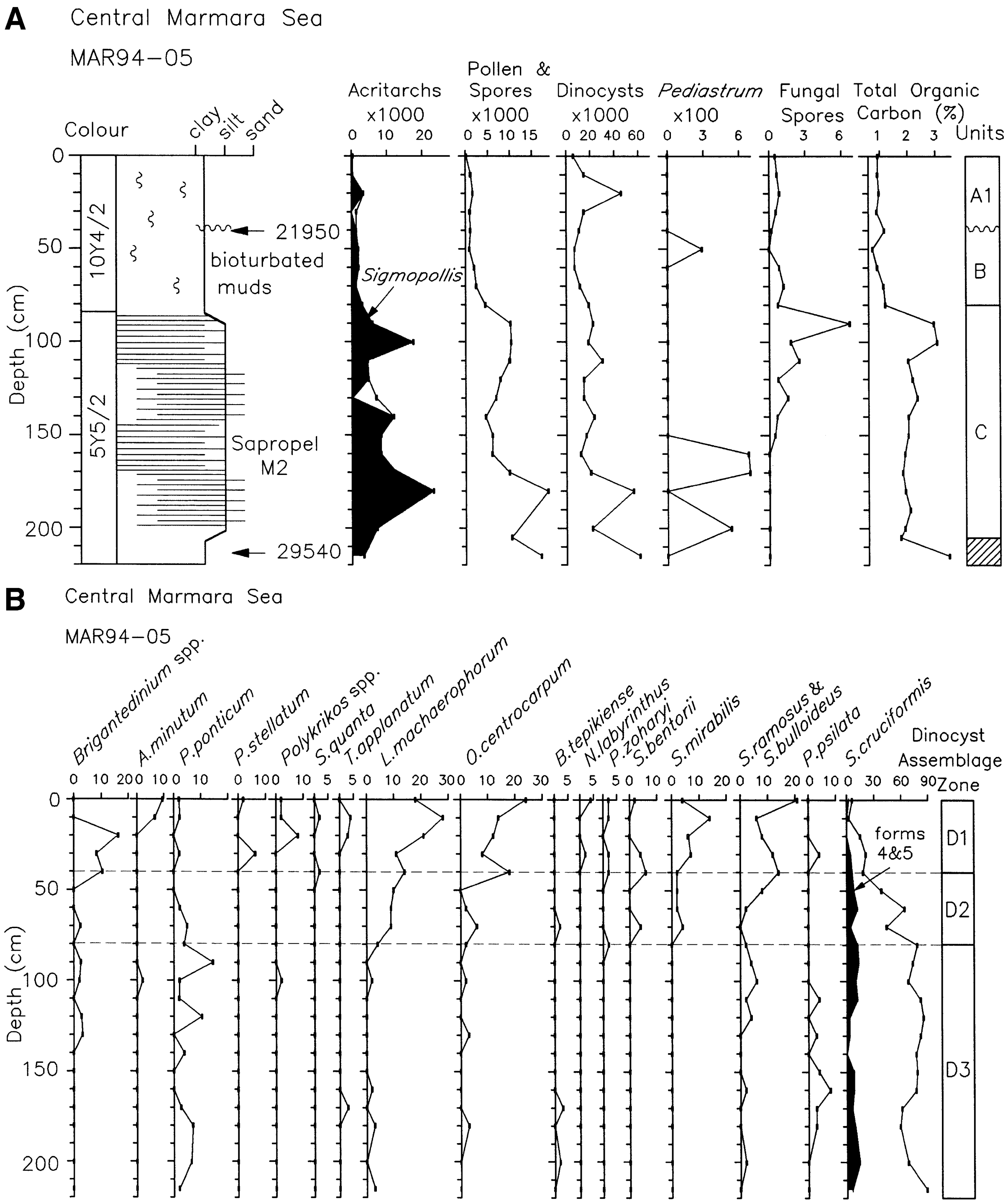


Fig. 4. Distribution of dinoflagellate cysts and other sporomorphs in MAR94-05. (A) Summary diagram showing lithofacies, variations in organic-walled palynomorphs and total organic carbon (OC). Arrows show levels with uncorrected ^{14}C ages in yr BP. Units and OC data are from Hiscott and Aksu (2002) and Abrajano et al. (2002), respectively. (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.

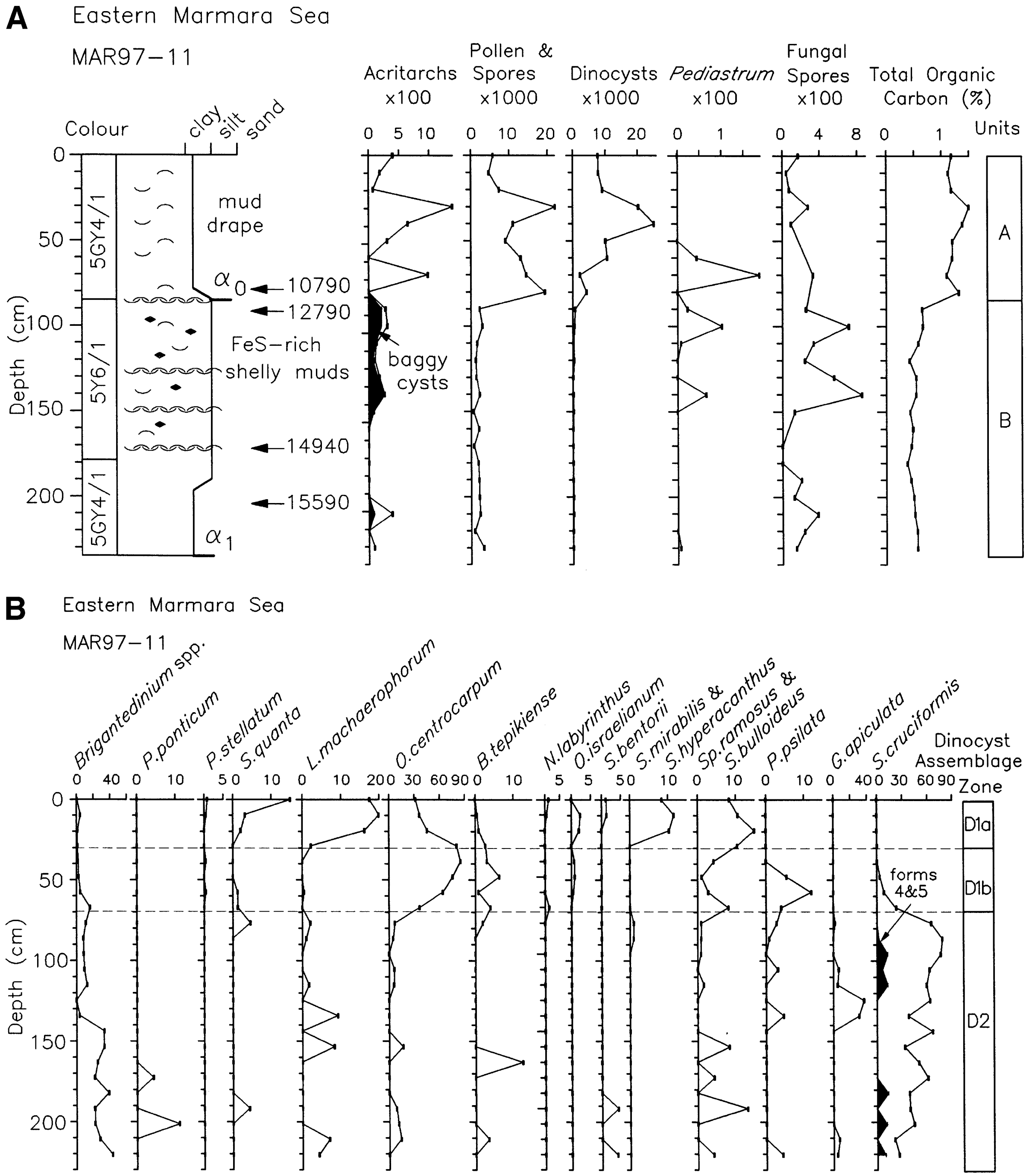


Fig. 5. Distribution of dinoflagellate cysts and other sporomorphs in MAR97-11. (A) Summary diagram showing lithofacies, variations in organic-walled palynomorphs and total organic carbon (OC). Arrows show levels with uncorrected ^{14}C ages in yr BP. Units and OC data are from Hiscott and Aksu (2002) and Abrajano et al. (2002), respectively. (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.

formis (predominantly forms 1 and 2 of Mudie et al., 2001), together with minor amounts of *Peridinium ponticum*, *Pyxidinopsis psilata* and the freshwater dinoflagellate, *Gonyaulax apiculata*. In Cores MAR98-12, small amounts of *Spiniferites inaequalis* are also present: this species has previously only been reported from the low salinity Unit 3 of Core B7 and other Late Quaternary cores from the Black Sea (Wall et al., 1973). The halophilic Mediterranean species *Spiniferites mirabilis, Spiniferites hyperacanthus, Spiniferites bentorii* and the hypersaline species *Operculodinium israelianum* and *Polysphaeridium zoharyi* are absent, but there are minor amounts of euryhaline species including *Spiniferites ramosus, Spiniferites bulloideus*, *Lingulodinium machaerophorum* and *Operculodinium centrocarpum*. *Brigantedinium* is also common in the lower interval (LGM > 15 000 yr BP) of the deltaic sequence in Core MAR97-11, despite the relatively low total organic carbon (TOC) content. There are also rare occurrences of cf. *Lophocysta cruciformis* that marks the cold, low salinity Pleniglacial-YD unit in Core MAR98-04 (see Fig. 1) of the southwestern Black Sea (Rochon, unpublished data; Abrajano et al., 2002).

Pollen and spore concentrations are also low in the late glacial, but concentrations of acritarchs and fungal spores are high, and there are sporadic peaks of *Pediastrum*. In MAR98-12, *Sigmopollis psilatum* is the only acritarch present, while fungal spores are dominated by an unknown cf. *Tetraploa* sp. with branched processes. Elsewhere, this unusual palynomorph is only known from the Canadian Arctic channels (Mudie and Rochon, 2002).

The dinoflagellate cysts in the Late Glacial–Pleniglacial Units C and D (~25 000–33 000 yr BP) of Core MAR94-05 (Fig. 4B) are marked by high concentrations of a low diversity *Spiniferites cruciformis–Pyxidinopsis psilata* assemblage, as described in detail by Mudie et al. (2001). Presence of the euryhaline species, *Lingulodinium machaerophorum*, *Operculodinium centrocarpum*, and brackish water morphotypes of *S. cruciformis* (forms 4 and 5) suggests that although salinity was very low, the surface water was not entirely fresh (< 1). The freshwater dinocyst *Gonyaulax apiculata* (Kouli et al., 2001) is also not present in this Pleniglacial unit. Pollen–spore concentrations are high in these units, particularly in Unit C that is a sapropel (M2 of Aksu et al., 2002a).

4.3. *Black Sea ecostratigraphy*

Core B-7 is from 2120 m water depth in the deep basin of the southeastern Black Sea, about 100 km from the location of Core 1474 studied by Wall and Dale (1973). Core B-7 contains three lithofacies (Fig. 7A) which correspond to facies 1–3 at Site 1474 (see Ross and Degens, 1974; Mudie et al., 2001). Facies I is a highly organic (2.5–5% TOC) coccolith-rich mud containing varved intervals; Facies II is a sapropel with 5–18% TOC; and Facies III is a silty mud (0.5% TOC) with occasional carbonate beds containing up to 2.5% TOC (Ross and Degens, 1974; Degens, 1974). Correlation with dinocyst assemblage zones in the ^{14}C-dated cores studied by Wall and Dale (1974) and with regional lake pollen zones (Mudie et al., 2002) show that the zone 1/2 and 2/3 boundaries have ages of about 2900 and 7140 yr BP, respectively. The bottom of the core has a probable age of ca. 9 ka based on land–sea pollen correlation (Mudie et al., 2001) and supported by an age of 8600 yr BP for a depth of 120 cm in other cores from this basin (Ross and Degens, 1974).

In contrast to the Marmara Sea cores, the dinocyst concentrations in the Holocene sediments of the Black Sea (Fig. 7A) show major increases in the middle Holocene unit II and in sections of the early Holocene Unit III. Assemblages in Units I and II are dominated by *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and *Spiniferites* spp. (mostly *S. mirabilis, S. ramosus* and *S. bentorii*), with variable amounts of *Brigantedinium* and other protoperidinioid cysts (Fig. 7B). Unit I (0–20 cm) has assemblages (A in Fig. 7B) almost identical to those of sub-zone D1a in the Marmara Sea, being dominated by *L. machaerophorum* and *Spiniferites* species that are common in the Mediterranean–Aegean seas (*S. mirabilis*, *S. hyperacanthus*, *S. bulloideus*, *S. delicatus* and *S. bentorii*) and a diversity of heterotrophic taxa, including *Brigantedinium* spp., *Algidasphaeridium*?

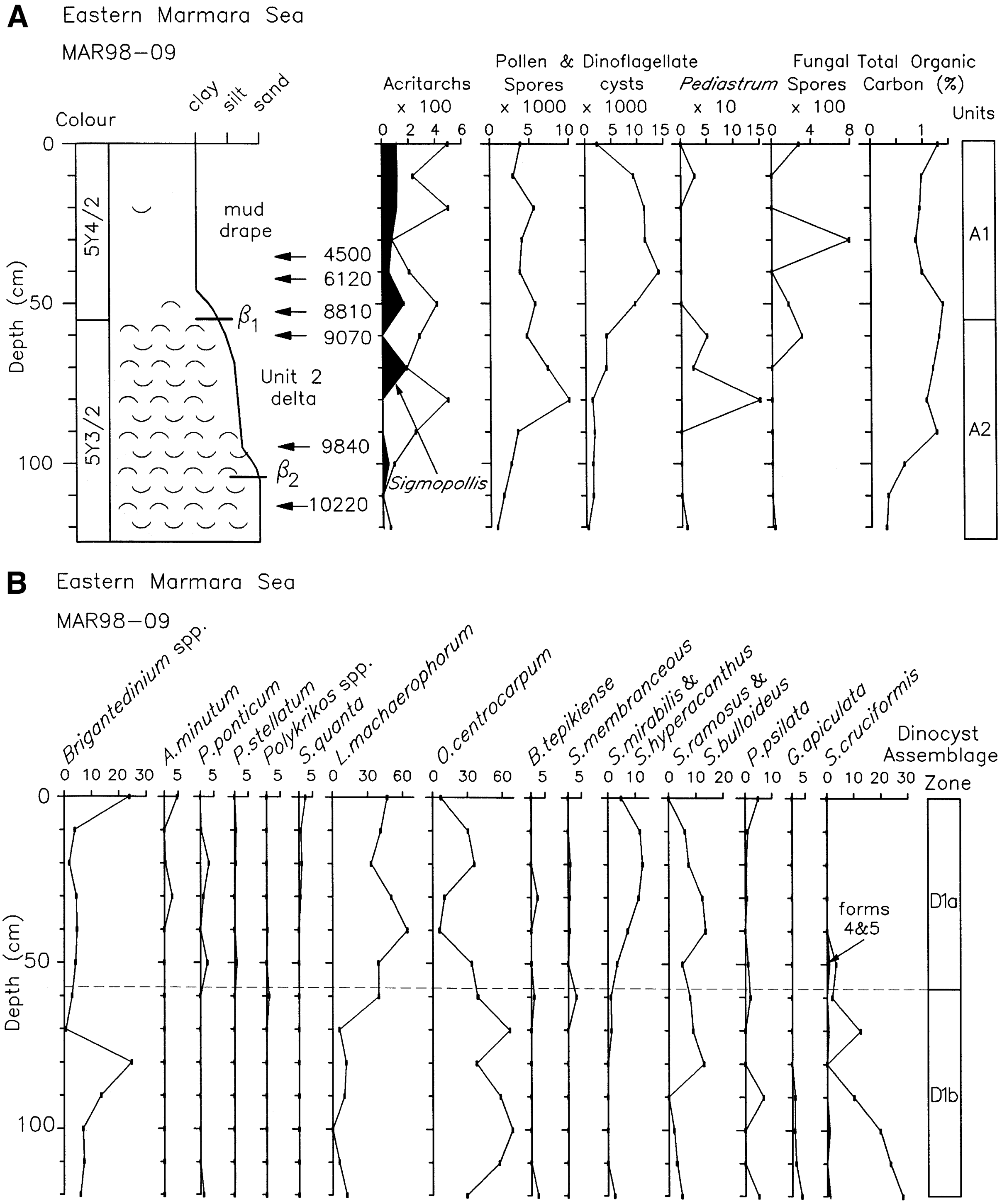


Fig. 6. Distribution of dinoflagellate cysts and other sporomorphs in MAR98-09. (A) Summary diagram showing lithofacies, variations in organic-walled palynomorphs and total organic carbon (OC). Arrows show levels with uncorrected ^{14}C ages in yr BP. Units and OC data are from Hiscott and Aksu (2002) and Abrajano et al. (2002), respectively. (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.

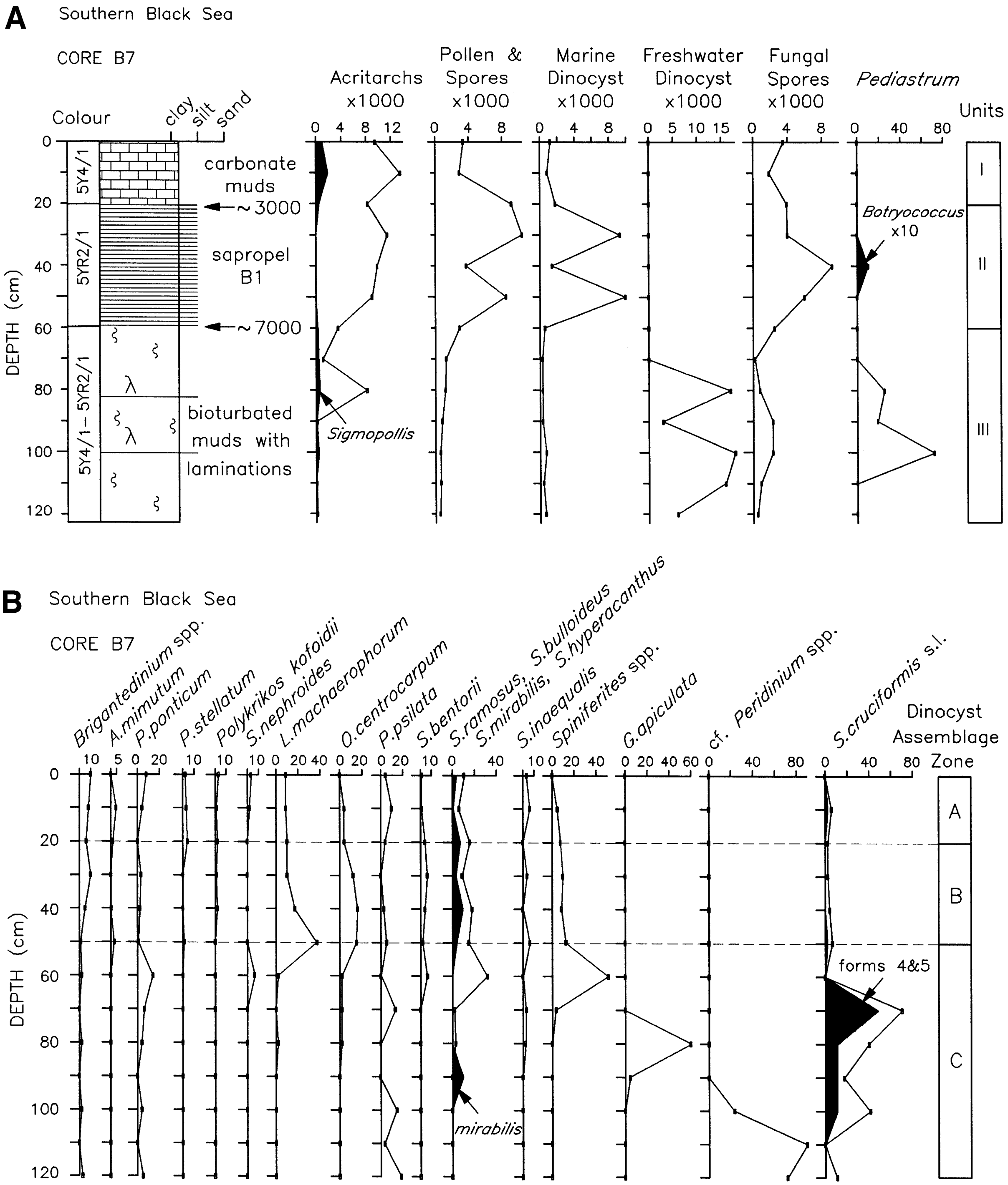


Fig. 7. Distribution of dinoflagellate cysts and other sporomorphs in Core B-7. (A) Summary diagram showing lithofacies and variations in organic-walled palynomorphs. Arrows show levels with uncorrected ^{14}C ages in yr BP. Units are from Ross and Degens (1974). (B) Dinocyst diagram showing down-core variations in abundance and in relative abundances of major species.

minutum, *Polykrikos kofoidii*, *Selenopemphix quanta*, *Selenopemphix nephroides* and *Protoperidinium* (*Stelladinium*) *stellatum*. The main difference between the Black and Marmara sea late Holocene dinocyst assemblages is the presence in the lower salinity Black Sea of *Peridinium ponticum*, *Pyxidinopsis psilata*, *Spiniferites inaequalis* and *Spiniferites cruciformis*. Furthermore, there is an absence of common Mediterranean Sea species (see Aksu et al., 1995a; Mudie et al., 2001 and references therein) such as *Operculodinium israelianum*, *Bitectatodinium tepikiense* and *Nematosphaeropsis labyrinthus*.

Dinocyst assemblages (B in Fig. 7B) in the mid-Holocene sapropelic unit 2 (20–60 cm) of Core B-7 differ from the late Holocene assemblages in having higher percentages of *Operculodinium centrocarpum*, a lower diversity of organic-walled protoperidinioid species although abundant calcareous cysts of *Scrippsiella trochoidea* are present (e.g. Ross and Degens, 1974). There is also an increase in *Spiniferites* spp. with very short processes. The latter may be morphotypes of *Spiniferites ramosus* as found in seen in low salinity waters of the Baltic Sea (Ellegaard, 2000) but their specific identity is presently uncertain.

Dinocyst assemblages (C in Fig. 7B) in the early Holocene Unit III (60–120 cm) of the Black Sea are almost identical to those of dinocyst zone B in the Marmara Sea, being distinguished by low concentrations dominated (40–80%) by *Spiniferites cruciformis* (including all five forms of Mudie et al., 2001), together with minor amounts of *Peridinium ponticum*, *Pyxidinopsis psilata*, *Spiniferites inaequalis*, *Spiniferites ramosus* and *Spiniferites mirabilis*, and with sporadic occurrences of *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and *Brigantedinium* spp. The main difference in the Black Sea dinocyst assemblages are: (1) higher percentages of *S. cruciformis* forms 4 and 5; and (2) greater abundance of the freshwater dinoflagellate, *Gonyaulax apiculata* (see Kouli et al., 2001), and the 'baggy dinoflagellate cysts' of Traverse (1974, 1988) which we tentatively ascribe to the genus *Peridinium* on the basis of the similarity of some specimens to the freshwater taxon Type D cysts described by Norris and McAndrews (1970).

As in the Marmara Sea cores, pollen–spore concentrations in Core B-7 (Fig. 7A) show almost the same trend as the marine dinocyst concentrations, but with the mid-Holocene rise beginning less abruptly and prior to the sapropel deposition. In the Black Sea, the upper pollen concentration peak also occurs higher in the late Holocene Unit 1. In contrast to the Marmara cores, however, most of the other sporomorph groups in the Holocene sediments of the Black Sea show sustained mid–upper Holocene high abundances. The only exception is the restricted occurrence of chlorococcalean coenobia in the earlier Holocene, with a notable peak in *Pediastrum* corresponding to peaks in concentrations of fungal spores and freshwater dinocysts around ∼9 ka. Fungal remains in Units 2 and 3 are also much more abundant than in the Marmara cores, being dominated by various pluricellular taxa, including *Tetraploa*. Acritarchs in Units 1 and 2 are dominated by *Cymatiosphaera* spp., with occasional occurrences of cf. Acritarch-8 of Traverse (1978).

5. Interpretation and discussion

5.1. Variations in palynomorph concentrations and assemblage composition as a function of post-depositional oxidation

Before valid interpretations can be made of the down-core and inter-basin variations in palynomorph assemblages, it is necessary to examine possible effects of aerobic decay (oxidative diagenesis) on the assemblages in the Marmara and Black sea cores.

The earliest interpretations of changes in Black Sea palynomorph concentrations and assemblage composition (e.g. Traverse, 1974; Wall and Dale, 1974) did not investigate possible effects of oxidative diagenetic overprinting, thereby leaving unanswered the question of how much assemblages can change as a function of preservation in sapropelic vs. non-sapropelic units. In contrast, recent work on the palynology of sapropel S1 from the Bannock Basin area of the southeastern Mediterranean Sea (Cheddadi et al., 1991; Cheddadi and Rossignol-Strick, 1995; Zonneveld et al., 2001) has shown that pollen–spore concentrations and dinocyst assemblage composition are differentially affected by changes in the redox potential of the sediments, with all palynomorph groups being well represented in anaerobic sapropel layers but with subsequent differential loss of oxidation-sensitive species during post-depositional oxidative diagenesis of the sapropel. Of particular importance is the evidence for aerobic decay of protoperidinioid dinoflagellates in the upper sapropelic unit (Zonneveld et al., 2001) which led to the conclusion that changes in protoperidinioid concentrations and percentages are not always reliable indicators of changes in paleoproduction or paleoceanographic conditions.

In contrast to these southeast Mediterranean studies, however, Aksu et al. (1995a) studied the dinocysts, pollen and other acid-resistant particulate organic matter in cores on a north–south transect of the Aegean Sea in order to test various hypotheses about the origin of the early Holocene sapropel S1, particularly the debate regarding its origin from increased marine primary production vs. increased input of TOC during conditions of high freshwater runoff and strong stratification. The Aegean Sea cores show maximum dinocyst abundances in the late glacial non-sapropelic mud unit (> 9600 yr BP), when low diversity assemblages were dominated by euryhaline, moderately oxidation resistant species of *Operculodinium centrocarpum* and *Nematosphaeropsis labyrinthus*. S1 deposition (9600–6400 yr BP) is marked by a large increases in terrigenous sporomorphs and refractive humic compounds, but only small increases in dinocysts, mainly from larger amounts of *Brigantedinium simplex* and *Bitectatodinium tepikiense* which are species associated with cold, relatively low salinity (~ 30–34) or strongly stratified waters in the North Atlantic (Rochon et al., 1999).

In these Aegean cores, the sapropel boundaries are marked by peaks in Ba and silt-size pyrite and they do not show a 'floating' Mn marker above the visible sapropel which indicates post-depositional oxidation of the sapropelic layer in the SE Mediterranean core studied by Zonneveld et al. (2001). Furthermore, organic geochemistry studies of low molecular weight *n*-alkanes in one Aegean Sea core showed that the onset of sapropel formation was marked by a decline in marine productivity (Aksu et al., 1999a), while an increase of high molecular weight *n*-alkanes indicated higher terrigenous carbon input. In the Aegean Sea sapropel S1, therefore, it is clear that the low abundance of organic-walled dinocysts and high pollen–spore concentrations are a primary function of increased runoff and terrigenous organic carbon deposition and not the result of oxidation-related diagenesis of organic matter.

The new data on palynomorph concentrations and dinocyst composition in sapropels M1, M2 and B1 of the Marmara and Black sea cores (see Figs. 3A, 4A and 7A) provide further opportunity to examine the question of how to distinguish between changes in paleoproductivity and changes arising from diagenesis of oxidation-sensitive palynomorphs. Our results show that in all the cores, there are increases in pollen–spore concentrations associated with the organic-rich sapropels, but the increases begin prior to and end after the termination of sapropel deposition. The sapropel boundaries are sharply delimited, therefore mixing is not likely to be the cause of the extended pollen–spore maxima. Furthermore, there are large changes in abundance of oxidation-sensitive pollen species, e.g. *Quercus*, within the non-sapropelic units (see Mudie et al., 2002). Therefore, it is clear that that amelioration of climate conditions is the primary reason for the pollen–spore increases, while the concomitant increases in river discharge merely enhance the influx of terrigenous organic matter (including pollen, spores and humic compounds), during the time of sapropel deposition (see Aksu et al., 1999a).

Likewise, it is evident that the same patterns of down-core changes in total dinocyst concentrations occur in the Holocene sediments of the Marmara Sea cores regardless of the presence or absence of a mid-Holocene sapropel. As in the Aegean Sea Core 20 (Aksu et al., 1999a), the base of the Holocene sapropel M1 is marked by an increase in oxidation-sensitive *Brigantedinium* species although %TOC is not much higher than in the underlying mud unit (Fig. 3A). In contrast, the mid-Holocene B1 sapropel, with up to 18%

TOC (Ross and Degens, 1974), and the glacial-stage M2 sapropel, with up to 3% TOC, show no increases in *Brigantedinium* or other sensitive protoperidinioid species. In all the cores there is a down-core decrease in diversity of oxidation sensitive protoperidinioids and *Polykrikos* spp. regardless of the presence or absence of sapropelic units. Overall, then, for our study area we do not see any clear evidence of major changes in dinocyst concentrations or assemblage composition changes that can be attributed to oxidative diagenesis.

5.2. Concentrations of acritarchs, fungal spores and freshwater sporomorphs

5.2.1. Acritarchs

All previous palynological studies of Holocene sediments in the low salinity Black Sea have drawn attention to the abundance of small, simple sphaeromorphic acritarchs, primarily *Cymatiosphaera* spp. (Wall and Dale, 1974), cf. *Micrhystridium* spp. (echinate spheres of Acritarch-7 Traverse, 1978) and leiosphaerids (wrinkled bag-like Acritarch-8 of Traverse, 1978). Variable numbers of these taxa are also present in the Marmara Sea cores and in Core B-7. In addition, we found large amounts of *Sigmopollis* spp., primarily *S. psilatum*, in glacial-stage sections of the Marmara Sea cores, as well as variable lesser amounts in the Holocene sediments.

The biological origin of the acritarchs in our cores is not known with certainty but some sphaeroidal acritarchs, including *Leiosphaeridia* spp., are believed to be prasinophycean green algae (Batten, 1996a). Although some modern prasinophytes like *Halosphaera* are restricted to marine environments, very low $\delta^{13}C$ values of fossil deposits indicate that other taxa are associated with low salinities and temperatures (Guy-Ohlson, 1996).

Traverse (1978) assumed that all the acritarchs and dinocysts were indicators of marine water inflow to the Black Sea. He therefore added the total acritarch and dinocyst concentrations to obtain a 'marine influence index' in which high and low values apparently corresponded to sea level highstands and intervals of periodic isolation from the Aegean Sea, respectively. Our new core-top data, however, show that the acritarchs are most abundant in modern sediments beneath the low salinity waters (~ 22) of the Black Sea and they are absent from the Aegean Sea. Furthermore, as reported in 4.1. Core-top distributions of dinocysts and other palynomorphs, the acritarch *Concentricystes rubinus* is believed to be of freshwater or soil origin. Therefore, it is probably not appropriate to group these fresh/brackish water indicators with well-known marine dinoflagellate species in compiling an index of marine influence.

It has previously been noted that sphaeromorphic acritarchs are most abundant and diverse in fresh to brackish water estuarine environments of the circum-arctic shelves (Solomon et al., 2000; Kunz-Pirrung, 1998), and that high numbers of *Sigmopollis psilatum* are usually associated with river discharge (e.g. Mudie, 1992; Head, 1993). In general, then, the down-core increases in acritarchs and *S. psilatum* seen in most of the Marmara cores suggest periodic intervals of increased runoff, and the pleniglacial interval in Core MAR94-05 shows a sustained increase in these low salinity indicators.

5.2.2. Freshwater algae

The Marmara Sea and Black Sea cores contain fossilizable remains of two groups of freshwater algae: coenobia of the colonial Chlorococcales genera, *Pediastrum* and (rarely) *Botryococcus*, and cysts of the freshwater dinoflagellates *Gonyaulax apiculata* and *Spiniferites cruciformis* forms 1–3 of Mudie et al., 2001). It is also likely that the 'baggy dinoflagellate cysts' of Traverse (1978) are fresh or brackish water taxa because they have not been recorded for marine sediments.

The best known freshwater markers are the colonial chlorococcalean algae, *Pediastrum boryanum* var. *boryanum* and *Botryococcus* cf. *B. braunii*. *Pediastrum boryanum* is a stenohaline species associated with a wide range of temperature and trophic conditions, while *Botryococcus* is a more salt-tolerant taxon, sometimes living in brackish water (Batten, 1996a; Matthiessen and Brenner, 1996). Most modern species of *Pediastrum* live in freshwater ponds, lakes and slow-moving rivers and their occurrence in marine environments indicates fluvial transport (Batten, 1996a; Matthiessen et al., 2000). In modern sediments of the southern Baltic Sea where salinity averages 5.95–7.71, *Pediastrum* and *Botryococcus* comprise more than 75% of the aquatic palynomorphs, with the remainder being the euryhaline dinocyst species *Operculodinium centrocarpum*, a short-spined form of *Spiniferites bulloideus* and the brackish water species *Pyxidinopsis psilata* (Matthiessen and Brenner, 1996).

At present, *Pediastrum boryanum* is absent or very rare (< 50/g) in core-top samples outside the Black Sea where concentrations range from 5 to 72/g. This concentration is much lower than in recent lake sediments where influxes of *Pediastrum* coenobia are about 1000–2000 cm^2 yr^{-1} (e.g. Burden et al., 1986). The present Black Sea concentrations are also much lower than in Arctic estuaries where concentrations of coenobia range from < 500 to 3500/g, suggesting influx rates of the order of 50–350 cm^2 yr^{-1} (Matthiessen et al., 2000). In our cores, there is a general increase in *Pediastrum* concentrations in the late glacial–early Holocene intervals of both the Marmara and Black sea cores (Figs. 3A, 5A and 7A), with peak abundances of ~400–700 coenobia/g occurring in during late Pleniglacial to LGM time in Core MAR94-05. However, these chlorococcalean freshwater indicators are not consistently abundant in any of our cores and their relative abundance never exceeds that of the dinocysts.

Gonyaulax apiculata is a fairly common dinoflagellate in European lakes (Kouli et al., 2001). However, cysts of *G. apiculata* are known only from modern sediments in Lake Zurich in Switzerland and from late glacial–early Holocene sediments of Lake Kastoria in northern Greece (Kouli et al., 2001). It is therefore believed that high concentrations of *G. apiculata* cysts (e.g. 500 000 cysts/ml in Lake Kastoria) indicate alpine lacustrine environments. Cysts of *G. apiculata* are absent from our core-top samples, the late Holocene sediments of MAR97-2 and the Pleniglacial–LGM sediments of MAR94-5. Very low concentrations occur sporadically in the late glacial and Holocene sediments of most other Marmara Sea cores (Figs. 3B, 5B and 6B), suggesting long-distance transport during periods of increased freshwater runoff from rivers draining alpine lakes. The largest concentration (1000–2000 cysts/g) occurs as a single peak during the early Holocene and corresponds to a peak in *Pediastrum* coenobia. This spiky distribution also suggests periodic catastrophic flooding from alpine or periglacial lakes rather than the existence of a freshwater lake in the Black Sea basin.

In Lake Kastoria, abundant morphotypes of *Spiniferites cruciformis* with expanded periphragms and well-developed spines (forms 1–3 of Mudie et al., 2001) co-occur with cysts of *Gonyaulax apiculata*. It has therefore been suggested that the occurrence of *S. cruciformis* in the Black Sea may indicate freshwater lake conditions (Kouli et al., 2001). In the Greek lake, there is a late glacial succession from dominance of *Botryococcus* followed by *Pediastrum*, then abundant *S. cruciformis* and *G. apiculata*, together with an increase in fungal remains. In contrast, no such succession is observed in the early Holocene of Core B-7 during the time that it is purported to have been a freshwater lake (cf. Ryan and Pitman, 1999). Furthermore, it is notable that in the Black and Marmara seas, *S. cruciformis* morphotypes with reduced or no processes (forms 4 and 5 of Mudie et al., 2001) are always present. These morphotypes are not found in Lake Kastoria and it is likely that the reduced process length reflects the stress of variable brackish surface water conditions in the Black Sea (Mudie et al., 2001).

It is also likely that the 'baggy dinoflagellate cysts' of Traverse (1978) are fresh or brackish water taxa because they have not been recorded for marine sediments. The most common morphotypes in our samples have a thin, pale brown two-layered wall, discontinuous paracingulum and a five-sided archeopyle, resembling some of the cysts ascribed to *Tectatodinium psilatum* by Wall et al. (1973), and listed as a brackish–freshwater taxon (< 7). Other morphotypes closely resemble *Peridinium cinctum* cysts and Cyst type D of Norris and McAndrews (1970) that were first described from sediments of inland lakes. These cysts are not present in our core-top samples and they are only common in the early Holocene sediments of the Black Sea where they co-occur with *Gonyaulax apiculata*.

5.2.3. *Fungal remains*

In general, relatively little is known about fungi in marine environments and there is some question regarding the production of fossilizable remains by aquatic marine fungi (e.g. Kohlmeyer and Kohlmeyer, 1979). However, Cross et al. (1966) and Traverse (1974) have argued that the correlation between dinocyst and fungal spore concentrations in some nearshore environments indicates a common origin in nutrient-rich marine waters. Yet there are no records of extant marine fungi apart from a few taxa that grow on saltmarsh and mangrove plants (Kohlmeyer and Kohlmeyer, 1979; Batten, 1996b) and it is generally believed that most fungal spores in marine environments are of freshwater or terrigenous origin.

In our core-top samples, from the Aegean and Marmara seas, most of the fungal remains are dark brown unicellular (*Lycoperdon*- and *Tilletia*-type) or dicellular (*Puccinellia*-type) spores. These are also the only types of fungal spores found in the Holocene Unit A of the Marmara cores. In Units I and II of the Black Sea Core B-7, however, there is a greater diversity of fungal remains, including common short, unbranched hyphal strands and occasional pluricellular spores (e.g. *Geoglossum sphagnophilum* Type 77A of Van Geel, 1986), in addition to simple sordariaceous spores.

According to Kohlmeyer and Kohlmeyer (1979), only two kinds of smooth-walled aseptate brown spores are produced by marine fungi and there are no marine taxa that produce complex brown spores or septate hyphae. The aseptate brown spores originate from fungi growing on saltmarsh grasses or mangrove leaves. Therefore, it is likely that the brown aseptate spores present in the late Holocene units of all our cores come from saltmarshes in the estuaries and deltas of rivers entering the Marmara and Black seas. In the Black Sea, the presence of pluricellular spores and hyphae in the late Holocene Units I and II of the Black Sea suggests greater transport from freshwater peat deposits where various fungal spore types and fruiting bodies are common (e.g. Van Geel, 1978 and references therein; Head, 1993).

Simple brown ascospores are rare or absent in the late glacial and Pleniglacial Units B and C of the Marmara cores. The most common fungal remains (~50%) in these units are annulate circular spores with psilate or granulate outer surfaces which split in half to form saucer-shaped discs with psilate inner walls. These fungal remains closely resemble spores of the *Exesisporites* sp. of Jarzen and Elsik (1986) which characterize the high water zone of rivers in Zambia. Other common fungal remains in these older units include *Tetraploa*, *Dyadosporites*, *Polyadosporites* and *Pluricellaesporites* species, most of which are also common in the high water river zone (Jarzen and Elsik, 1986). Head (1993) notes that *Tetraploa* is saprophytic on grasses, while other species are found in soils and coastal ponds.

More work is required to determine the precise relationship between the fossil fungal remains in our cores and their fungal sources. However, it is highly likely that all of the fungal remains in the late Holocene sections of our cores indicate terrigenous particulate organic carbon input, including leafy debris from saltmarshes. The change in fungal assemblage composition down-core indicates reduction or die-out of saltmarshes and increased inflow of organic material during flooding of riverbanks and peatmarshes. It is notable that similar assemblages of fungal remains are markers of river flooding in the modern Mackenzie Delta (Solomon et al., 2000).

5.2.4. *Microforaminiferal linings*

Microforaminiferal linings of planktonic and benthic foraminifera are abundant in the Marmara Sea and are well represented in the Aegean Sea but are absent in the anoxic Black Sea basins. These findings are consistent with the distributions of foraminiferal tests (see Aksu et al., 2002a and references therein) for the low oxygen bottom sediments of the Aegean and Marmara seas and the high benthic productivity of the Marmara gateway. However, these workers did not examine cores from the lower salinity waters of the Black Sea so it remains to be shown whether the absence of microforaminiferal linings denotes absence of foraminifera or a lack of preservation of these calcareous and arenaceous microfossils in deep water of the Black Sea.

5.3. Dinocyst assemblages and surface water salinity and implications for glacial–interglacial paleoceanography

In the Marmara Sea cores, two Holocene sub-assemblages are recognized. The youngest sub-assemblage, D1a (0–∼7000 yr BP) is dominated by *Lingulodinium machaerophorum* or, near the Aegean Sea, by *Operculodinium centrocarpum*, together with a relatively high percentage of *Spiniferites mirabilis* (here grouped with *Spiniferites hyperacanthus*), rare occurrences of *Operculodinium israelianum* and/or *Bitectatodinium tepikiense* (MAR98-12, MAR97-11 and MAR98-9), and a diversity of heterotrophic taxa, including *Algidasphaeridium*? *minutum*, *Polykrikos kofoidii*, *Selenopemphix quanta*, *Selenopemphix nephroides* and *Protoperidinium* (*Stelladinium*) *stellatum*. The early Holocene (∼7000–10 000 yr BP) sub-assemblage D1b is dominated by *O. centrocarpum*, with variable amounts of the low salinity indicators *Peridinium ponticum*, *Pyxidinopsis psilata* and *Spiniferites cruciformis*, absence of *Polykrikos* and a lower diversity of salt-tolerant euryhaline *Spiniferites* and protoperidinioid species.

The dominant species in these assemblages, *Operculodinium centrocarpum* and *Lingulodinium machaerophorum*, are well-known euryhaline species with a wide range of temperature tolerance (Dale, 1996; Rochon et al., 1999). However, *O. centrocarpum* appears to be more tolerant of low surface temperatures (Mudie, 1992; Dale, 1996; Rochon et al., 1999), possibly accounting for its greater dominance in the early Holocene sub-assemblage D1b. Disappearance of the halophilic Mediterranean species, *Spiniferites mirabilis* and *Operculodinium israelianum*, in D1b and replacement by species associated with low salinities (∼3–17 psu) also clearly indicate that more fresh water was flowing into Marmara Sea at this time.

In the Black Sea, the late Holocene assemblages of Unit I are almost identical to those of sub-zone D1a in the Marmara Sea. The main difference is the presence of the low salinity indicator *Peridinium ponticum*, *Pyxidinopsis psilata*, *Spiniferites inaequalis*, *Spiniferites cruciformis* and the absence of the halophilic Mediterranean/Atlantic species *Operculodinium israelianum*, *Bitectatodinium tepikiense* and *Nematosphaeropsis labyrinthus*. The assemblages in Unit 2 (∼3000–6000 yr BP) are virtually the same as those in sub-zone D1b of the Marmara Sea cores. Assemblages in the early Holocene Unit III of the Black Sea differ in being dominated by *S. cruciformis*, including both freshwater forms 1–3 and the brackish water forms 4 and 5. The predominance of *S. cruciformis* clearly indicates that the surface salinity in the Black Sea was lower than present during the early Holocene. However, the presence of the brackish water forms of *S. cruciformis* and other species not known from modern freshwater environments (*P. ponticum*, *S. inaequalis*, *Spiniferites ramosus*, *Spiniferites mirabilis*, *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and *Brigantedinium* spp.) makes it unlikely that the Black Sea was a freshwater lake.

In the Marmara Sea, the LGM–late glacial dinocyst assemblages B and C are also dominated by *Spiniferites cruciformis* and other ‘Black Sea’ species and they are similar in composition to the low salinity early Holocene assemblages in Unit III. It is therefore clear that although the glacial stages were marked by much lower sea-surface temperatures, there was either some periodic marine influence or the marine dinocysts were living in a brackish water environment with the freshwater species being transported from glacial lakes. The latter scenario may explain the relative sparsity of chlorococcaleans and the relatively low concentrations of the freshwater dinocysts compared to fungal remains.

5.4. Implications of Aegean Sea–Marmara Sea–Black Sea linkages

The framework for the history of salinity changes in the Marmara gateway begins in the late Miocene–early Pliocene when the Mediterranean, Black and Caspian seas were linked to form a large marine basin, known as the Paratethys

(Ross, 1978; Schrader, 1978). During the Pliocene, the Black Sea became semi-isolated, having a restricted connection with the Mediterranean Sea through a network of straits and inland seas. Microfossils from DSDP Leg 42 (Schrader, 1978; Gheorghian, 1978) suggest that the Plio–Pleistocene Black Sea was a low salinity (<5) to brackish (5–15) lake, with intervals of stronger marine influence (15–20) during sea level highstands in the youngest marine isotopic stages (MIS) 9, 7, 5 and 1.

Recently, however, some studies have postulated that after the last glacial maximum ~20 000 yr BP, the Black Sea became a freshwater lake and that from ~12 500 to 7000 yr BP, it was isolated from the Marmara Sea (Ryan and Pitman, 1999). During this time of lowered water level, it has been suggested that the Black Sea contained potable water which encouraged the settlement of humans and their livestock, and which led to farming and crop irrigation on the emergent deltas (e.g. Ryan and Pitman, 1999, pp. 230–233). However, for drinking water and sustained agricultural usage, water salinity must be <1 (see Mudie, 1974). We have also shown that marine or brackish water-tolerant dinoflagellates persist in most sections of our cores and that there is no palynological evidence for early forest clearance or agriculture in the southern Black Sea (Mudie et al., 2002). We therefore consider it necessary to examine the processes controlling salination and desalination of the Black Sea in order to evaluate the likelihood of reaching truly freshwater (i.e. <1) lake conditions in the time-frame of the Late Quaternary glacial lowstands. If desalination during these lowstands is impossible, then the postulated early agriculture must have depended on ‘the constant, if sluggish flow of water’ in the valleys and deltas of the reduced rivers which Ryan and Pitman (1999, pp. 230–231) described for the dry YD and 8-ka European cold intervals.

At present, the Straits of Dardanelles and Bosphorus, and the intervening land-locked Marmara Sea constitute the gateway linking the Mediterranean and Black seas and controlling the flux of saline water to and from the Black Sea. However, the Strait of Bosphorus may have formed only during the last ~100 000 years (Oktay et al., 2002) and before this, the Black and Marmara seas were connected via the Sakarya Bosphorus strait (Pfannenstiel, 1944) in the lower reach of the present Sakarya River and the Bolayır Channel linked the Marmara and Aegean seas. During the Quaternary, there were periods of complete isolation of the Black Sea from the Mediterranean Sea during glacial maxima when the straits were subaerially exposed because of glacio-eustatic variations in global sea level and local tectonic factors. These glacial-stage intervals of isolation alternated with interglacial periods of connection and water exchange between the two seas.

The first major post-Pliocene incursion of saline Mediterranean waters into the Black Sea occurred at ca. 300 000 yr BP (Schrader, 1978; Ross, 1978) when three indigenous coccolith species appeared (Percival, 1978), concurrently with influxes of marine diatoms and silicoflagellates (Schrader, 1978). This event marks the start of water exchange between the Black and Marmara seas (initially through the Sakarya Bosphorus channel) and commencement of the Quaternary salination–desalination cycles. During this early flooding interval, surface salinity values exceeded 12 (Schrader, 1978). By the mid–late Quaternary, benthic foraminifera were dominated by brackish water taxa, with sporadic occurrences of euryhaline and stenohaline species (Gheorghian, 1978). The long time-frame of these micropaleontological changes suggests that replacement of the brackish waters in deep Black Sea basins with saline Mediterranean waters took many thousands of years, similar to the processes modelled for the last glacial–Holocene transition (e.g. Boudreau and Leblond, 1989).

The salinity history of Black Sea for the last 300 000 years is controlled primarily by the depths of the connecting channels and global sea level, but it is also further modulated by climate, the volume of water exchange and the rate of upward mixing of saltwater within the Black Sea. The climate controls the amount of freshwater fluvial input to the Black Sea basin as well as the balance between precipitation and evaporation (P–E), whereas the water exchange via the Marmara gateway controls the amount of salt water input.

Of critical importance is the fact that a saline layer of Mediterranean water only penetrates into the Black Sea (here called a salination phase) when thick enough to fill the bottom of the entrance strait. Any thinner developing salt wedge will be entrained by the outflowing surface current, with salt returning to the Marmara Sea, as part of the desalination phase. Further desalination of the Black Sea requires overturn of the relict Mediterranean bottom water and its removal by outflow through the Marmara Sea. At present, this process is poorly understood (Özsoy et al., 1996) but in the deep basins, it is partly driven by the geothermal gradient which is assumed to have been constant during the past 300 000 years. Two scenarios will examine the extremes of a range of possible Black Sea salinity cycle models, as outlined below.

5.4.1. Scenario 1: Black Sea LGM surface water salinity was higher than today

Seismic reflection and sediment core data from the Black Sea shelves show that during the transition from the LGM to the Holocene, the Black Sea water level was ~110 m below present (Aksu et al., 2002a,b). The sea level started to fall between MIS 3 and 2, at which time the Black Sea was isolated from the Marmara Sea. When the level of the Black Sea fell below the breach depth of Bosphorus Strait (~−40 m), desalination of the Black Sea ceased because there was no outflow across the Bosphorus; therefore the Black Sea salinity must have progressively increased as the water level dropped to its minimum, ~20 000 yr BP. Once isolated from global sea level, the continued water level lowering from −40 to −110 m must have been caused by a reduction in freshwater inflow into the basin during a period of $P \ll E$. The climate in central Europe remained very cold and dry from the peak of the LGM at ~18 ka until approximately 9500 yr BP (e.g. Harrison et al., 1993, 1996) and the discharges of the largest rivers with headwaters in central-eastern Europe must have been substantially reduced. Hence, although pollen evidence (Prentice et al., 1992; Mudie et al., 2002) indicates that P:E remained relatively high in northern Anatolia and around the Marmara Sea, the total water balance for the Black Sea must have been tilted toward $P < E$ in order to maintain a lowered sea level in the Black Sea basin. This scenario requires that salinity would increase in the isolated inland sea, and is in total disagreement with the freshwater conditions suggested by Ryan and Pitman (1999, pp. 230–231) for this time interval. The closest approximation to the 'freshwater lake' scenario would be a lake with low salinity surface water and saline bottom water, surrounded by extensive salt flats. These circumstances would provide neither potable lake water for humans nor favorable pastoral conditions (see Mudie, 1974) and they are not compatible with the algal and fungal evidence for high fluvial runoff presented in this paper.

5.4.2. Scenario 2: Black Sea LGM surface water salinity was lower than today

Desalination of the Black Sea can take place only if the level of the Black Sea is above that of the Strait of Bosphorus but the water is not deep enough to allow full penetration of the Mediterranean salt wedge along the length of the Bosphorus Strait (e.g. Scholten, 1974). Under these conditions the Black Sea would spill over into the Marmara Sea, and through time would progressively deplete the salt reservoir in the Black Sea basin. The time required to achieve such freshening can be estimated if the freshwater input to the Black Sea basin and the mixing of the water masses are known. The present volume of the Black Sea is ~534 000 km^3 of which 650 km^3 is from freshwater runoff. The average salinities of the surface and bottom water masses are 18 and 22, respectively (Özsoy et al., 1991), and the radiocarbon age of the bottom water mass is ~2000 yr BP. For our minimum salinity scenario, we shall set the level of the Black Sea at the end of MIS 3 (~34 000 yr BP), at the breach depth of Bosphorus Strait, and maintain the freshwater outflow during the European cold dry period at ~10% of its present value (i.e. 65 km^3). With no penetration of saline Mediterranean water, it would require ~13 000, ~25 000 and ~53 000 years for the surface salinity values to reach 10, 5 and 1, respectively. Thus the lowest salinity expected at ~9000 yr BP would be closer to 5 than to the <1 required for potable water and sustained agriculture. If there was a large throughflow of glacial meltwater from ~20 to 15 ka, as postulated by Ryan and Pitman (1999), there may have been a 5000-yr interval of somewhat more rapid desalination. However, with a colder, thicker layer of surface water, mixing of the fresh surface and saline bottom water layers is more likely to have been slower, not faster than the present day because of the reduced salt gradient within the isolated basin.

It is clear from these models that the desalination of the Black Sea, although not impossible, requires a considerably longer period of time than assumed by Ryan and Pitman (1999), in order to reach the level of potable surface water that could be used for irrigation. Because the level of the Black Sea dropped during the last glacial, reaching its lowstand of −110 m during the LGM, the salinity of the Black Sea basin actually probably increased slightly during this period. This leaves the only source of potable and irrigation water as the rivers discharging into the slightly brackish lake. It seems that it would also have been necessary to desalinate the emergent delta and terrace soils, which is a daunting task even in modern times. Therefore, it is questionable that the early farmers would have settled on the shores of the Black Sea. Furthermore, if there was an early settlement, then attempts at growing crops and fruit trees would have been limited to the most salt-tolerant species, e.g. barley, beets and pomegranates. This scenario of a low salinity/brackish water lake with very little or no early agriculture is the one most compatible with the Black Sea pollen data of Mudie et al. (2002) and with the microfloral evidence presented in this report.

6. Conclusions

In the epicontinental seas adjoining the eastern Mediterranean, pollen and dinocyst assemblages do not show any clear evidence of major changes in concentration or assemblage composition that can be attributed to aerobic decay. Pollen–spore assemblages also show no evidence of aerobic decay in the Marmara gateway cores. This finding allows us to interpret down-core assemblage changes in terms of fluctuations in paleoproduction and surface water conditions, primarily as related to changes in freshwater runoff and climate (P–E).

Modern sediment samples from transects in the Aegean and Marmara seas and parts of the Black Sea show that the concentrations of dinocysts, acritarchs, chlorococcalean algae, pollen and fungi generally decrease with distance from the low salinity surface water of the Black Sea. Microforaminiferal linings of planktonic and benthic foraminifera show the opposite trend and they are absent in the southeastern Black Sea basin. The dinocyst species *Impagidinium aculeatum*, *Operculodinium israelianum*, *Polysphaeridium zoharyi* are presently restricted to the Mediterranean and Aegean seas and indicate summer salinities >24. In contrast, *Spiniferites cruciformis*, *Spiniferites inaequalis*, *Peridinium ponticum* and *Polykrikos* spp. (mostly *P. kofoidii*) are found only in the low salinity Black and Marmara seas. *Quinquecuspis concreta* is only present in the intermediate salinities of the Marmara Sea.

Late Quaternary dinocyst assemblages in the Marmara Sea show a succession from relatively low diversity Pleniglacial and late glacial assemblages dominated by *Spiniferites cruciformis* and other 'Black Sea' species associated with salinities of ~3–18 to late Holocene assemblages similar to those presently found in the Black Sea. Early Holocene assemblages in the Black Sea indicate lower surface salinity than present but there is no clear evidence that the surface salinity was ever as low as a freshwater lake.

Fungal remains (mostly spores and hyphal strands) are useful markers of terrigenous sediment influx and transport by large rivers. These sporomorphs, together with freshwater dinocysts and *Pediastrum* coenobia, clearly show that in contrast to the Ryan and Pitman model, the early Holocene Black Sea received a large volume of river runoff and was undoubtedly overflowing into the Marmara Sea during the early Holocene.

Of two possible desalination models examined for the late glacial–early Holocene interval in the Black Sea, only Scenario 2 provides surface water conditions compatible with our data and trending towards the freshwater conditions postulated by Ryan and Pitman (1999). This model requires a sustained (~25 000 year) outflow of fresh water from the Black Sea during the late glacial and early postglacial in order to achieve surface salinity as low as 5. The model also indicates that the isolated Black Sea would not have totally fresh surface water suitable for agricultural settlement.

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