Temporary repopulation by low-oxygen tolerant benthic foraminifera within an Upper Pliocene sapropel: Evidence for the role of oxygen depletion in the formation of sapropels

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ABSTRACT

Foraminiferal study of a continuous set of samples across the Upper Pliocene C2 sapropel (Singa section, southern Italy) revealed an interval containing substantial numbers of benthic foraminifera, bound by sediments in which benthic foraminifera are absent. The absence of benthic foraminifera is indicative of anoxic conditions. The interval with benthic foraminifera contains an association that is strongly dominated by the species *Bulimina marginata*, which is tolerant to low oxygen concentrations. The bottom water oxygenation did not improve sufficiently to allow development of a more diverse benthic foraminiferal fauna, or the return of intensively burrowing organisms. Variations in the planktic foraminiferal fauna and in the stable isotope records suggest that a surface water cooling preceded the benthic repopulation. A warming seems to have coincided with the return to bottom anoxia. The planktic productivity markers *Globigerina bulloides* and *Neogloboquadrina* show minor variations across the repopulated interval. The benthic repopulation, which reflects improved bottom water oxygenation, was probably favored by enhanced dense water formation in response to general cooling of the surface waters.

Introduction

Miocene to Recent eastern Mediterranean sequences of marine sediments contain numerous sapropels (e.g. Cita and Grignani, 1982; Thunell et al., 1984; Thunell, 1986; Hilgen, 1987, 1990; Rohling and Gieskes, 1989). Often, these sapropels display a distinctly laminated structure (a.o. Van Straaten, 1970, 1972; Mullineaux and Lohmann, 1981; Cita and Grignani, 1982; Shaw and Evans, 1984; Mangini and Schlosser, 1986; Thunell, 1986; Gudjonsson, 1987; Howell et al., 1988). Preservation of laminae is indicative of an anoxic bottom environment, hostile to burrowing benthic organisms which otherwise tend to homogenize the sediment.

Benthic foraminifera appear more tolerant

to low-oxygen conditions than most other metazoan meio- and macrofauna (Josefson and Widbom, 1988). Populations of benthic foraminifera may be extremely numerous in dysoxic environments (Sen Gupta and Machain-Castillo, 1993), and several species have been observed to survive even under completely anoxic conditions (Bernhard and Reimers, 1991; Moodley and Hess, 1992). Prolonged anoxia, however, appears lethal to benthic foraminifera (Bernhard and Reimers, 1991). Absence of benthic foraminifera, therefore, is indicative of persistently anoxic conditions.

Intervals devoid of benthic foraminifera are common within Upper Pliocene to Holocene eastern Mediterranean sapropels (Van Straaten, 1972; Nolet and Corliss, 1990; Verhallen, 1991). Additional evidence for anoxic bottom 208

water conditions at times of sapropel formation comes from the relatively high contents of organic matter, and the common abundance of pyritized foraminiferal tests and burrows (Van Straaten, 1972; Stanley, 1983; Thunell et al., 1984). These findings resulted in models of sapropel formation in basins with stagnant and consequently anoxic waters below the upper depth limit of sapropel distribution (a.o. Van Straaten, 1972; Mullineaux and Lohmann, 1981; Cita and Grignani, 1982; Ross and Kennett, 1984). Nolet and Corliss (1990) recently presented data from six eastern Mediterranean cores containing Quaternary sediments. Focusing on variations in the benthic foraminiferal records across sapropel S_5 (deposited about 120,000 yrs B.P.) they persuasively argued that reduced deep water ventilation and consequent deep water anoxia was the critical factor in the deposition of S₅. However, Nolet and Corliss (1990) also showed increased benthic foraminiferal numbers several centimeters below the sapropel, preceding the increase in organic carbon content. This could be interpreted as an increase in the organic carbon flux, which started before the actual sapropel developed.

Alternatively, Pedersen and Calvert (1990) proposed that high primary production, rather than water-column anoxia, provides the firstorder control on sapropel formation. That conclusion was also reached by Calvert (1983), who argued that stagnation alone could never have sufficed to account for sometimes very high (>15%) C_{org} contents, and by De Lange and Ten Haven (1983) and Boyle and Lea (1989), who reported increased C_{org} fluxes and Cd/Ca based evidence for increased productivity during the deposition of Quaternary sapropels, respectively.

Summarizing, it appears that the formation of sapropels resulted from some combination of decreased oxygen advection to deep waters and increased organic production in the euphotic layer, although the relative importance of either process remains debated. In the present paper, we contribute to that discussion with the results from a detailed investigation of a Pliocene sapropel from southern Italy.

The environmental changes that have initiated and maintained the formation of sapropels may best be studied in detailed sets of samples across sapropels characterized by a high sedimentation rate. Such a set was taken across the Upper Pliocene C2 sapropel in the Singa section (Calabria, southern Italy; see Verhallen, 1987). Within that sapropel, we noticed an interval containing benthic foraminifera, bound by barren intervals. In the present paper, we evaluate the possible environmental changes that could have induced this temporary repopulation. In addition, changes in the planktic foraminiferal and stable isotope records across the repopulated interval are used to discuss the relative importance of primary productivity and deep water formation rates with respect to the process of sapropel formation.

Material and methods

Sapropel C2 has an approximate age of 1.92 Ma (Hilgen, 1991). In the Singa IV section (cf. Verhallen, 1987, 1991), the Upper Pliocene C2 sapropel has a thickness of 51 cm, and it contains a well developed internal lamination. This lamination is most prominent in the top 26.5 cm, and less so in the lower 24.5 cm. The top of C2 passes abruptly into homogeneous clay. Directly below the C2 sapropel, we found homogeneous sediments with grain size in the fine silt fraction. As can be seen in Fig. 1, these fine silts are extremely rich in foraminifera; they may be classified as foraminiferal packstones (sensu Dunham, 1962) and may be of turbiditic origin. The occurrence of foraminiferal packstones below sapropels is a rather common feature in the C-group sapropels of the Singa Section (Verhallen, 1991).

It is hard to exactly determine the amount of time involved in the formation of Pliocene sapropels, such as C2, but some constraints can



Fig. 1. Abundance distribution of planktic foraminiferal species in the Upper Pliocene sapropel C2 (Singa section, southern Italy). Upper diagram shows percentages, lower diagram shows numbers per gram dryweight. $100^*P/(P+B)$ indicates the percentage plankton per total foraminifera. The representation of lithology is schematic, and the indicated laminae are not to scale. A prominent change in the thickness of the laminae occurs at 26.5 cm below the top of the sapropel (arrow). The dotted interval consists of silty clay to sandy silt sized material. This level may be classified as a foraminiferal packstone (sensu Dunham, 1962).

TABLE 1

Percentages of the planktic foraminifera in the continuous set of samples from 21 cm above to 23.5 cm below the sapropel C2. The column "depth" gives the sample-midpoints, p/(p+b) the plankton percentage, which actually is calculated according to $[100 \times P/(P+B)]$. Ruber=G. ruber, univ=O. universa; sacc=G. sacculifer, rubesc=G. rubescens/apertura; sipho=G. siphonifera; bull=G. bulloides; infl=G. inflata; glut=G. glutinata; neogl=Neogloboquadrina; quinq=T. quinqueloba; indet=indeterminable

depth	p/p+b	ruber	univ	sacc	rubesc	siphon	bull	infl	glut	neogl	quinq	indet	δ^{18} O	$\delta^{13}C$
2.50	81.50	16.31	0.71	0.00	2.13	0.00	12.06	35.46	2.84	29.08	0.71	0.71	0.06	-0.60
7.50	90.83	37.16	1.38	0.00	6.88	0.92	20.64	16.06	2.29	13.76	0.92	0.00	1.06	-0.59
13.00	79.17	23.68	0.00	0.00	9.87	0.00	23.68	16.45	2.63	21.05	1.97	0.66	0.92	-0.52
18.50	74.89	33.53	0.60	0.00	4.19	0.60	22.75	4.79	1.20	31.74	0.60	0.00	0.03	-0.56
22.00	70.88	34.16	1.98	0.00	2.9 7	0.50	18.81	0.50	3.47	37.13	0.50	0.00	-1.28	1.09
24.00	95.78	38.77	0.88	0.00	3.52	2.20	5.73	0.44	2.64	45.37	0.00	0.44	-1.10	1.00
26.00	95.38	36.56	1.08	0.00	9.68	1.08	11.29	0.00	1.61	38.17	0.54	0.00	- 1.00	1.22
28.00	97.34	34.43	2.73	0.00	9.84	2.19	11.48	0.00	2.73	33.88	0.55	2.19	-1.18	1.03
30.00	98.65	33.18	2.27	0.00	10.00	0.45	16.36	0.00	2.27	32.73	0.91	1.82	- 1.49	0.94
32.00	99.65	34.52	3.20	0.00	5.34	0.00	19.57	0.00	3.91	32.38	0.36	0.71	-1.81	0.80
34.00	97.99	38.36	2.74	0.00	4.79	2.05	19.18	0.68	0.68	30.14	0.00	1.37	-1.64	0.96
36.00	98.26	37.46	3.54	0.00	6.19	0.29	18.88	0.00	1.47	32.15	0.00	0.00	-1.82	0.69
37.75	73.91	31.09	2.52	0.00	0.00	0.00	37.82	0.00	0.00	28.57	0.00	0.00	-1.63	0.56
40.00	82.96	20.54	0.89	0.00	2.68	0.00	32.14	0.00	0.00	43.30	0.45	0.00		
42.00	73.04	28.67	2.15	0.00	1.43	0.00	30.47	0.00	0.72	36.56	0.00	0.00	-1.40	0.92
44.00	69.40	10.26	2.05	0.51	2.05	0.00	42.05	0.00	2.05	38.46	1.54	1.03	-1.03	1.40
46.50	72.38	19.08	2.63	0.00	10.53	1.97	32.89	0.00	0.00	32.24	0.00	0.66	-1.14	1.25
49.00	71.80	21.99	1.05	0.00	5.24	3.14	40.84	0.00	3.14	24.08	0.52	0.00		
51.00	86.84	15.45	2.42	0.00	9.09	0.61	46.06	0.00	0.61	25.76	0.00	0.00	-1.15	1.34
53.75	91.74	15.17	3.79	0.00	6.64	1.42	51.66	0.00	0.95	20.38	0.00	0.00	-0.81	1.35
56.00	95.65	33.12	3.25	0.00	5.84	1.95	38.31	0.00	1.30	14.94	0.65	0.65	-1.63	0.78
58.50	99.66	44.71	3.07	0.00	7.51	0.34	20.48	0.00	1.71	22.18	0.00	0.00	-1.68	1.01
61.50	96.92	41.36	4.55	0.00	8.18	1.36	26.36	0.00	3.18	15.00	0.00	0.00	-1.73	0.77
64.50	99.65	38.30	4.26	0.00	4.96	1.06	42.55	0.00	2.48	6.03	0.35	0.00	- 1.69	1.13
67.75	97.62	40.85	3.05	6.10	3.05	1.22	35.37	0.00	0.61	7.93	1.22	0.61	-1.05	1.22
70.50	99.69	36.76	4.36	8.72	2.80	0.31	19.00	0.31	1.87	25.23	0.31	0.31	-1.70	0.87
73.50	94.24	34.89	0.72	7.91	4.32	1.08	34.17	0.00	4.32	6.12	5.04	1.44	0.69	-0.24
76.50	95.31	37.30	0.82	8.61	1.64	1.23	36.48	0.00	4.51	3.69	1.64	4.10	1.06	-0.14
79.50	95.03	41.28	0.58	14.53	6.98	0.58	18.60	0.00	5.23	4.65	4.07	3.49	1.05	-0.18
83.00	92.89	44.90	1.53	5.10	11.73	0.00	16.33	0.00	6.12	7.14	6.63	0.51	1.29	-0.11
86.00	96.14	48.59	1.20	4.82	6.02	3.61	16.87	0.00	7.63	4.82	4.02	2.41	1.19	-0.15
89.00	95.28	60.33	2.07	3.72	4.96	0.83	12.81	0.00	6.20	4.13	4.55	0.41	0.95	-0.23
92.00	92.70	55.15	3.64	3.64	2.42	0.61	15.76	0.00	7.27	2.42	6.06	3.03	0.96	-0.23
94.50	92.90	57.65	4.12	4.12	3.24	1.47	11.47	0.00	6.76	4.41	6.76	0.00	1.09	-0.20

be made. Firstly, sapropel formation also occurred in the early Holocene, and ¹⁴C dating has shown that the early Holocene sapropel formed during a period of 2000 to 3000 years (a.o. Stanley and Maldonado, 1979; Vergnaud-Grazzini, 1985; Rasmussen, 1991; Jorissen et al., 1993). Secondly, Hilgen (1991) and Lourens et al. (1992) discussed the astronomically induced sedimentary cycles containing the Pliocene sapropels, and from these studies the average duration of sapropel formation may be estimated at about 3000 years. Tentatively, the lamination might be regarded as varves, with a dark-light couplet for every year (P.J.J.M. Verhallen, pers. commun., 1991).

We sampled a continuous record across the C2 sapropel, from 21 cm above the top to 23.5 cm below the base. The 21 cm of homogeneous clay above C2 is covered by 4 samples, the 51

TABLE 2

Numbers of specimens per gram dry weight, except for column p/(p+b) which gives the plankton percentage $(100*P/{P+B})$. For column-titles, see caption of Table 1. Also shown are the numbers of planktic and benthic foraminifera per gram

depth	n/	ruber/	univ/	sacc/	rubesc/	sinhon/	bull/	inf/	glut/	neo/	auin/	indet/	plank./	benth./
	p+b	g	g	g	g	g	g	g	g	g	g	g	g	g
2.50	81.50	57.94	2.52	0.00	7.56	0.00	42.82	125.95	10.08	103.28	2.52	2.52	439.19	99.68
7.50	90.83	180.98	6.70	0.00	33.51	4.47	100.54	78.20	11.17	67.03	4.47	0.00	585.42	59.08
13.00	79.17	87.39	0.00	0.00	36.41	0.00	87.39	60.69	9.71	77.68	7.28	2.43	461.16	121.36
18.50	74.89	176.99	3.16	0.00	22.12	3.16	120.10	25.28	6.32	167.51	3.16	0.00	621.19	208.30
22.00	70.88	255.64	14.82	0.00	22.23	3.70	140.79	3.70	25.93	277.87	3.70	0.00	841.26	345.67
24.00	95.78	198.90	4.52	0.00	18.08	11.30	29.38	2.26	13.56	232.81	0.00	2.26	632.86	27.88
26.00	95.38	205.15	6.03	0.00	54.30	6.03	63.35	0.00	9.05	214.20	3.02	0.00	682.52	33.03
28.00	97.34	86.89	6.90	0.00	24.83	5.52	28.96	0.00	6.90	85.52	1.38	5.52	377.75	10.32
30.00	98.65	118.03	8.08	0.00	35.57	1.62	58.21	0.00	8.08	116.42	3.23	6.47	484.37	6.61
32.00	99.65	140.58	13.04	0.00	21.74	0.00	79.71	0.00	15.94	131.88	1.45	2.90	538.89	1.92
34.00	97.99	139.47	9.96	0.00	17.43	7.47	69.73	2.49	2.49	109.58	0.00	4.98	495.60	10.18
36.00	98.26	166.85	15.77	0.00	27.59	1.31	84.08	0.00	6.57	143.20	0.00	0.00	579.63	10.26
37.75	73.91	194.81	15.80	0.00	0.00	0.00	236.94	0.00	0.00	179.02	0.00	0.00	738.23	260.55
40.00	82.96	100.70	4.38	0.00	13.13	0.00	157.62	0.00	0.00	212.34	2.19	0.00	613.32	125.95
42.00	73.04	128.28	9.62	0.00	6.41	0.00	136.30	0.00	3.21	163.56	0.00	0.00	562.42	207.63
44.00	69.40	32.55	6.51	1.63	6.51	0.00	133.46	0.00	6.51	122.07	4.88	3.26	430.78	189.99
46.50	72.38	60.43	8.34	0.00	33.34	6.25	104.20	0.00	0.00	102.11	0.00	2.08	435.64	166.23
49.00	71.80	92.89	4.42	0.00	22.12	13.27	172.51	0.00	13.27	101.73	2.21	0.00	543.22	213.31
51.00	86.84	61.00	9.57	0.00	35.88	2.39	181.79	0.00	2.39	101.66	0.00	0.00	532.52	80.69
53.75	91.74	50.16	12.54	0.00	21.94	4.70	170.85	0.00	3.13	67.40	0.00	0.00	476.21	42.88
56.00	95.65	159.96	15.68	0.00	28.23	9.41	185.05	0.00	6.27	72.14	3.14	3.14	634.67	28.85
58.50	99.66	238.19	16.36	0.00	40.00	1.82	109.09	0.00	9.09	118.18	0.00	0.00	690.90	2.36
61.50	96.92	141.31	15.53	0.00	27.95	4.66	90.07	0.00	10.87	51.25	0.00	0.00	500.05	15.91
64.50	99.65	330.52	36.72	0.00	42.85	9.18	367.25	0.00	21.42	52.03	3.06	0.00	1027.18	3.64
67.75	97.62	230.73	17.22	34.44	17.22	6.89	199.74	0.00	3.44	44.77	6.89	3.44	730.15	17.81
70.50	99.69	889.36	105.52	211.03	67.83	7.54	459.75	7.54	45.22	610.49	7.54	7.54	2589.55	8.07
73.50	94.24	1335.07	27.53	302.80	165.16	41.29	1307.55	0.00	165.16	233.98	192.69	55.05	3994.03	244.24
76.50	95.31	1444.10	31.74	333.25	63.48	47.61	1412.36	0.00	174.56	142.82	63.48	158.69	4043.90	198.88
79.50	95.03	595.79	8.39	209.78	100.70	8.39	268.52	0.00	75.52	67.13	58.74	50.35	1617.84	84.65
83.00	92.89	411.42	14.03	46.75	107.53	0.00	149.61	0.00	56.10	65.45	60.78	4.68	1092.24	83.59
86.00	96.14	478.92	11.87	47.50	59.37	35.62	166.24	0.00	75.20	47.50	39.58	23.75	1167.69	46.90
89.00	95.28	635.60	21.77	39.18	52.24	8.71	134.96	0.00	65.30	43.53	47.89	4.35	1237.80	61.38
92.00	92.70	387.84	25.57	25.57	17.05	4.26	110.81	0.00	51.14	17.05	42.62	21.31	887.92	69.96
94.50	92.90	608.13	43.44	43.44	34.13	15.51	121.01	0.00	71.36	46.54	71.36	0.00	1242.32	95.00

cm thick sapropel itself by 22 samples, and the 23.5 cm below C2 by 8 samples. The samples were dried and subsequently weighed. Thereafter, the samples were washed over a set of sieves with meshwidths of 63, 150, and 595 μ m.

Planktic foraminiferal counts were made in the 150 to 595 μ m fraction of all 34 samples. An Otto microsplitter was used to reduce residues into suitable aliquots of at least 200 specimens. The results are presented both as percentages per total planktic foraminiferal count, and as numbers per gram dry weight (Tables 1 and 2; Fig. 1). Also shown is the percentage plankton with respect to the total of foraminifera in each aliquot $[100 \times P/(P+B)]$. In addition, Table 2 and Fig. 2 show the numbers of benthic and planktic foraminifera per gram.

Furthermore, stable isotope ratios of the planktic foraminiferal species *Globigerinoides ruber* have been determined. Standard laboratory procedures, as described by Shackleton and Opdyke (1973), were followed, and analyses were performed on a Sira-9 mass-spectrometer. The results are reported as ppm-de-



Fig. 2. The absolute numbers of planktic and benthic foraminifera per gram dry weight. Solid line (marked B) indicates the benthic number. Dashed line (marked P) indicates the planktic number.

viations from the PDB-1 standard. In the Mediterranean, G. ruber is far more abundant in summer than in winter, inhabiting the warm mixed layer above the seasonal thermocline (Vergnaud-Grazzini et al., 1986). Besides salinity, the δ^{18} O values of G. ruber reflects sea surface temperatures in the mixed layer (Ganssen, 1983; Deuser, 1987; Hemleben et al., 1989), while its δ^{13} C values are close to those of surface Σ CO₂ (Pujol and Vergnaud-Grazzini, 1989).

Results and discussion

Sapropel C2 is generally devoid of benthic foraminifera, except for an approximately 15 cm thick interval in which benthics are abundant. In Figs. 1 and 3, and Tables 1 and 2, this interval within C2 shows up by reduced values of the plankton percentage $[100 \times P/(P+B)]$, and in Table 2 and Fig. 2 it is very obvious in the number of benthics per gram. The amount of time captured in this repopulated interval may be roughly estimated at about 900 years, assuming that the entire sapropel took about 3000 years to develop (see Introduction).

Preservation of all foraminifera is good troughout sapropel C2, indicating that dissolution effects may not explain the observed faunal patterns. In view of the study of Hutson (1977), dissolution-if relevant-should result in substantial relative enrichment of Neogloboquadrina and Globorotalia inflata, at the expense of Globigerinoides ruber, Globigerinita glutinata, and Globigerina bulloides. In the repopulated interval, however, G. ruber and G. bulloides display opposite abundance variations, instead of being both reduced, whereas Neogloboquadrina does not seem to display anything but a gradual increase throughout sapropel C2. Moreover, the preservation of pteropod remains throughout C2 also excludes an important role of dissolution.

The temporary invasion of benthic foraminifera within the C2 sapropel is strongly dominated by the species *Bulimina marginata*, which has previously been interpreted as tolerant of low-oxygen conditions with high food concentrations (Seiglie, 1968; Verhallen, 1986, 1987; Jorissen, 1987, 1988). Two other taxa, *Plectofrondicularia* spp. and *Bolivina alata*, are present in much smaller numbers. The perfect preservation of thinwalled *B. marginata* in the repopulated interval again argues against any dissolution of significance.

B. marginata is a common species in the Adriatic Sea, in an area extending south of the Po river delta marked by coastal eutrophication (Jorissen, 1988). A study of living benthic foraminifera in the Adriatic Sea characterized B. marginata as a potentially infaunal species (Barmawidjaja et al., 1992). During periods of dysoxic bottom waters in summer and autumn, following algal blooms in the surface waters, this species was found concentrated near the sediment surface. In winter, however,



Fig. 3. The records of plankton percentage $[100 \times P/(P+B)]$, G. ruber, $\delta^{18}O$ and ^{13}C , and the ratio of Neogloboquadrina over G. bulloides, across the Upper Pliocene sapropel C2. Also indicated is the level of transition from less distinct coarse lamination in the lower half of C2, to very distinct fine lamination in the upper half. Note the close correspondence between the level marking the onset of (temporary) enrichment in the stable isotope records, and that marking the onset of (temporary) G. ruber abundance decrease; both lie well below the onset of temporary benthic repopulation (shown by the record of plankton percentage). The change in dominance between G. bulloides and Neogloboquadrina approximately matches the change in lamination characteristics.

when oxygen concentrations in the bottom water returned to normal values, *B. marginata* invaded deeper levels of the sediment, whereas most other species remained at the sediment surface. The apparent preference of *B. marginata* for an infaunal microhabitat indicates its relative tolerance to low-oxygen conditions. Its characteristic tapered-cylindrical test morphology and numerous pores evenly distributed over the entire test surface, may constitute adaptations for survival in an oxygen-poor environment (Corliss, 1985).

We think that throughout the repopulated interval within C2 dysoxic conditions prevailed, possibly alternating with anoxia on a seasonal time scale. Such conditions would permit a specialized low-oxygen resistant fauna to maintain a sizable population in this interval. Oxygen concentrations, however, remained sufficiently low to prevent the development of a diverse benthic foraminiferal fauna. Lamination is not disturbed in the repopulated interval, suggesting that sediment pore-waters remained completely anoxic, preventing benthic foraminifera to live below the sediment surface. A modern analogue of such conditions may be found in the dysoxic Santa Barbara Basin in the Californian Pacific margin, from which living foraminiferal faunas have been described by Phleger and Soutar (1973) and Bernhard and Reimers (1991). These faunas are extremely rich in individuals, but little diverse and dominated by presumably infaunal taxa.

The association of persistently low diversity in the repopulated interval within C2 contrasts with the rapidly diversifying benthic association which occurs above that sapropel. The initial benthic foraminiferal assemblage in the uppermost sample of C2 is again dominated by *B. marginata*, but is rapidly replaced by very diverse faunas in the homogeneous clay on top of C2.

The temporary repopulation of benthic foraminifera within C2 coincides with a relevant decrease in the percentages of the planktic species Globigerinoides ruber (Fig. 1). This decrease is genuine, and not the result of a closedsum effect, since the number of G. ruber per gram dry weight also shows a decrease (by about a factor 3). In general, G. ruber seem to live at the very surface during its entire life cycle (upper 30 m; Hemleben and Spindler, 1983), in the relatively warm mixed layer waters (e.g. Tolderlund and Bé, 1971; Fairbanks et al., 1982; Bé et al., 1985). It is an omnivorous species that bears dinoflagellate symbionts (Bé, 1982; Hemleben et al., 1989 and references therein). Bé (1982) argued that, since secondary producers such as copepods predominate oligotrophic waters, this might explain the predominance of (partly) spinose carnivorous foraminifera (such as G. ruber) in those settings.

Since G. ruber is especially abundant in the Mediterranean in the summer season (Vergnaud-Grazzini et al., 1986), characterized by a distinct (seasonal) thermocline below a warm and relatively oligotrophic mixed layer, its temporary decrease in abundance within C2 presumably reflects shortening of the "stratified" summer season. Roughly, this would imply that surface waters were cooler as averaged over a year, compared to times when G. ruber accumulated in larger numbers in the sediments. The onset of this "cooling" appears to have preceded the beginning of benthic repopulation, while the subsequent increase of *G. ruber* ("warming") corresponds to the end of the temporary repopulation. This interpretation in terms of sea surface temperature (SST) fluctuations seems to be supported by the record of δ^{18} O, which shows depleted values for the whole of C2, except for the interval with reduced abundances of *G. ruber* where heavier δ^{18} O values are recorded.

Alternatively, the temporary enrichment in δ^{18} O values within C2 may be explained in terms of a temporary return to rather normal surface water salinities within a period characterized by relatively low salinities. Variations in freshwater input, mainly in the form of runoff, would also explain the observed variations in the δ^{13} C record across C2. The middle part of C2 would then be deposited under conditions of relatively reduced freshwater input, resulting in a return to higher surface water salinities (δ^{18} O enriched) as well as decreased input of continental organic matter (δ^{13} C enriched).

However, as mentioned before, a marked change in thickness of the laminae was observed at 26.5 cm from the top of C2. Above that level, C2 consists of very prominent and thin laminae, whereas less prominent and thicker laminae prevail in the lower half. This suggests that terrigenous input was higher during the formation of the lower half of C2, and relatively reduced during the formation of the upper half. The transition between the coarsely laminated lower half and the finely laminated upper half occurs near the center of the interval characterized by enriched stable isotope values (Fig. 3). The variations in freshwater input (runoff) that could be inferred from the stable isotope records, therefore, do not correspond to the variations in terrigeneous input (runoff) inferred from the observed change in lamination.

The planktic foraminiferal indicators for en-

hanced productivity, *Globigerina bulloides* and Neogloboquadrina, display only moderate abundance variations across the repopulated interval. In the vicinity of river mouths, high abundances of G. bulloides may result from riverine discharge of particulate organic matter (e.g. Barmawidiaia et al., 1989; Van Leeuwen, 1989). High abundances of Neogloboquadrina seem to be related to enhanced levels of primary production in the Deep Chlorophyll Maximum layer in the thermocline, fueled by upward mixing of nutrients from deeper water (e.g. Fairbanks and Wiebe, 1982; Bé et al., 1985; Vergnaud-Grazzini et al., 1986; Rohling and Gieskes, 1989). G. bulloides seems to be more abundant in the lower half of C2, whereas Neogloboquadrina reaches higher abundances in the upper half. The change in dominance between the two taxa (Fig. 3) coincides roughly with the change from the coarsely laminated lower half of C2 to the finely laminated upper half. We think that this change in dominance between G. bulloides and Neogloboquadrina reflects a change in the main process of eutrophication, namely from higher riverine input of organic matter during the deposition of the lower half of C2, to upward mixing of nutrients from deeper waters into the euphotic layer during deposition of the upper half of the sapropel. This scenario would support the changes in freshwater input we inferred from the change from coarse to fine lamination, rather than that which might be inferred from the combined stable isotope records. Note, in addition, that the abundance fluctuations of G. ruber are considerably larger than those of Neogloboquadrina and G. bulloides, suggesting that total productivity variations were of minor importance relative to the average surface water cooling. Moreover, the isotopic anomalies match the anomaly in G. ruber abundance, rather than the transition in dominance between G. bulloides and Neogloboquadrina. Combined, these arguments suggest that a main reduction in freshwater input occurred at about halfway the time of deposition of C2, accounting for the onset of fine lamination, and a change from a mainly riverinduced process of eutrophication to a more "oceanic" process of eutrophication. This change would have occurred at about the middle of a slightly cooler interval, depicted by markedly decreased abundances of G. ruber and enriched δ^{18} O values.

In this scenario, the variations in the δ^{13} C record are not easy to understand, but may be attributed to the degree of oligotrophy (and related efficiency of carbon cycling), which is linked to the effectiveness of stratification resulting from the presence of a strong seasonal thermocline. High abundances of G. ruber in the lower and upper parts of C2 would reflect strong prevalence of the seasonal thermocline, with consequently low nutrient advection into the mixed layer. In such a configuration, efficient recycling of CO₂ in the mixed layer would effectuate depletions in the δ^{13} C values. During the interval containing reduced abundances of G. ruber, which we interpreted as the result of shortening of the thermally stratified season (average "cooling"), enhanced $\delta^{13}C$ values would have resulted from more proseasonal ventilation of the nounced thermocline.

We now have five keys to understand the environmental changes that induced the benthic repopulation within the C2 sapropel. (1) The repopulation itself indicates that the bottom waters were no longer persistently anoxic. (2) The bottom water did, however, remain poorly oxygenated during the benthic repopulation. (3) A surface water cooling seems to have preceded the benthic repopulation. (4) A surface water warming coincided with the return to persistently anoxic bottom conditions. (5) Primary productivity seems to have remained fairly constant throughout the formation of the C2 sapropel, although the character of nutrient supply may have changed from predominantly riverborne to more "oceanic".

These arguments strongly suggest a causal link between surface water cooling and benthic

repopulation. Cooling may have triggered more efficient dense water formation, which would have augmented oxygenation of waters near the sea floor. This, in turn, enabled the repopulation by low-oxygen tolerant benthic foraminifera. However, throughout the roughly estimated 900 years of deposition of the repopulated interval, oxygenation of the waters near the sea floor remained very poor, inhibiting the replacement of the stress tolerant fauna by a more diverse, balanced, fauna. This suggests that the hydrographic changes were not of a very drastic nature.

The onset of cooling seems to have preceded benthic repopulation. The interval between these two events has a thickness of about 5 cm, and with an estimated 3000 years for the total formation period of C2, this offset equals some 300 years. Apparently, such a period of cooler conditions was necessary to restore oxygen concentrations near the sea floor to a sufficiently high level to support the low-oxygen tolerant benthic fauna. The return to warmer surface water conditions acted inversely, and the re-installment of persistently anoxic conditions at the sea floor again resulted in total disappearance of the benthic fauna.

In addition to the above discussion, we speculate that the anoxic conditions that prevailed at the sea floor, at times of sapropel formation, may have been restricted to a 'blanket' at the sea floor, while most of the water-column still contained some oxygen. Such a configuration with a distinct oxygen minimum near the sediment-water interface would result from mineralisation of organic matter that rapidly sinks to the sea floor (pellets). In that case, anoxic conditions could be found at the sea floor, despite of some ongoing dense water formation (cf. Rohling and Gieskes, 1989). The 'blanket' must have been sufficiently thick to prevent colonisation of the sea floor by epibenthic macrofauna extending above the sea floor, or endobenthic macrofauna (e.g. molluscs) capable of extending breathing tubes into the overlying bottom waters. Cramp et al. (1988) suggested

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that such a restriction of anoxia to a level at or near the sediment-water interface prevailed during the formation of the Holocene sapropel S_1 , in the northwestern Aegean Sea. This 'blanket' hypothesis would allow rather subtle improvements in dense water formation to interrupt persistently anoxic conditions near the sea floor. In this respect, the 'blanket' hypothesis contrasts strongly with hypotheses inferring that anoxic conditions prevailed everywhere below the upper depth limit of sapropel formation. In the latter concept, strong oxygen advection to deeper layers (resulting from drastic improvement of dense water formation) would be necessary to accomplish a change from anoxic to dysoxic conditions near the sea floor.

Concluding remarks

The faunal, isotopic, and sedimentological changes across the interval repopulated by benthic foraminifera, within the Upper Pliocene C2 sapropel, demonstrate that decreased rates of dense water formation, and subsequently decreased rates of oxygen advection to deep waters, seem to have played a very important role in the process of sapropel formation. In that respect, our findings endorse those of Nolet and Corliss (1990), who studied the Quaternary sapropel S₅.

In the repopulated interval within C2, the benthic fauna is strongly dominated by the species *B. marginata.* Together with the fact that lamination is well preserved, this suggests that conditions at the sea floor did not improve sufficiently to allow further diversification, or invasion of larger burrowing organisms. In other words, conditions at the sea floor were no longer anoxic, but definitely remained strongly dysoxic. A similar pattern shows in the topmost sample of C2, but there it is succeded immediately by homogenized sediments containing a diverse benthic foraminiferal association. At that time, oxygenation had apparently improved more drastically, thus determining the end of the formation of sapropel C2.

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