

LATE QUATERNARY CHANGES IN MEDITERRANEAN INTERMEDIATE WATER DENSITY AND FORMATION RATE

Eelco J. Rohling

Institute of Earth Sciences,
University of Utrecht,
The Netherlands

Winfried W. C. Gieskes

Department of Marine Biology
University of Groningen
The Netherlands

Abstract. Three recently acquired eastern Mediterranean cores containing Late Quaternary sediments display a marked faunal contrast between the Holocene and older sapropels. It is suggested that the absence of neogloboquadrinids in the Holocene sapropel and their abundance in older sapropels reflect differences in food availability related to the extent of development of a deep chlorophyll maximum layer (DCM) and the intensity of "new" primary production associated with this layer. The depth of such a layer, which consists of phytoplankton with a characteristic taxonomic composition, is determined by the vertical hydrodynamical structure. During deposition of the older sapropels, the pycnocline was apparently positioned well above the base of the euphotic layer, a situation that favors a pronounced DCM and an associated relatively high rate of new production. Shallowing of the pycnocline implies a relatively low density of the Mediterranean Intermediate Water (MIW). On the other hand, during deposition of the Holocene sapropel the pycnocline had apparently vanished due to termination of MIW formation.

1. INTRODUCTION

In the eastern Mediterranean, sapropels were first found in cores collected during the 1947-1948 Swedish Deep Sea Expedition [Kullenberg, 1952].

Their chronostratigraphic position was established with the aid of oxygen isotope stratigraphy. In spite of the fact that Mediterranean sediments display a larger variability in oxygen isotopic values than open ocean sediments, it appeared possible to correlate Quaternary oxygen isotopic records of the Mediterranean with those of the open ocean [amongst others Emiliani, 1955; Thunell and Williams, 1983; Vergnaud-Grazzini et al., 1977]. In general, sapropels were found to have developed during Quaternary warming phases, but also (less frequently) during cool isotopic stages [e.g., Cita et al., 1977; Muerdter and Kennett, 1984; Thunell et al., 1983a; Thunell et al., 1984; Vergnaud-Grazzini, 1985].

Olausson [1961] was the first to link sapropel formation to episodes of lowered surface water salinities and subsequent stagnation of the deeper waters. This hypothesis is supported by the excess lowering of the oxygen isotopic signal at times of sapropel development [Cita et al., 1977; Cita and Grignani, 1982; Calvert, 1983; Mangini and Schlosser, 1986; Thunell et al., 1984; Vergnaud-Grazzini et al., 1977; Williams et al., 1978].

Major potential source areas for a low-salinity surface layer are the Black Sea [amongst others Buckley et al., 1982; Cita et al., 1977; Ryan, 1972; Stanley and Blanpied, 1980; Williams et al., 1978] and the Nile river [amongst others Adamson et al., 1980; Rossignol-Strick, 1985; Rossignol-Strick et al., 1982; Street and Grove, 1979]. However, the Holocene sapropel appears to be younger than the main phase of postglacial melting [Rossignol-Strick et al., 1982; Rossignol-Strick, 1985; Shaw and Evans, 1984; Williams et al., 1978] but coincides with extensive flooding of the Nile [Adamson et al., 1980; Rossignol-Strick et al., 1982; Rossignol-

Copyright 1989
by the American Geophysical Union.

Paper number 89PA00908.
0883-8305/89/89PA-00908\$10.00

Strick, 1985] and a warm humid "pluvial" in tropical Africa [Street and Grove, 1979; Rognon, 1987].

A low-salinity surface layer in the eastern Mediterranean may have caused a reversal of the vertical circulation pattern from antiestuarine to estuarine [Buckley and Johnson, 1988; Calvert, 1983; Muerdter and Kennett, 1984; Stanley et al., 1975; Ten Haven, 1986; Thunell and Williams, 1989; Thunell et al., 1983a, 1984]. An estuarine circulation acts as a nutrient trap, ensuring high nutrient levels that may be conducive to increased organic production. Enhanced organic production subsequently increases oxygen consumption in deeper waters.

This model of circulation reversal implies that stagnation is not a prerequisite for the formation of anoxic sediments [cf. Thunell and Williams, 1989]. In fact, De Lange and Ten Haven [1983] suggested that enhanced productivity exerted a major influence on the formation of eastern Mediterranean sapropels. They based their conclusions on variations of the organic carbon content in anoxic sediments underlying the brine-filled "Tyro Basin" south of Crete. Higher carbon concentrations, indicating an increased flux of organic matter, appeared to coincide with periods of sapropel formation in other parts of the eastern Mediterranean.

According to Ross and Kennett [1984], a circulation reversal cannot explain the changes in benthic foraminiferal associations in cores from the Strait of Sicily. They concluded that the present antiestuarine regime was not reversed, but merely weakened. Vergnaud-Grazzini et al. [1988] suggested that major influxes of low-salinity Atlantic water into the eastern Mediterranean surface layer occurred during both terminations Ia and Ib, causing a decrease in the aeration of the water column. They stated that this aeration further deteriorated during termination Ib, due to an additional amount of low-salinity riverine or Black Sea overflow waters that invaded the eastern Mediterranean, leading to stagnation of the deep eastern Mediterranean waters.

Furthermore, the circulation reversal hypothesis is not in accordance with the conclusions of Zahn and Sarnthein [1987]. These authors stated that, at Gibraltar, deep Mediterranean outflow occurred continuously during the last 140,000 years, although it was severely reduced at times of sapropel formation in the eastern basin. Zahn and Sarnthein's [1987] conclusions agree with the findings of Abrantes [1988], who recorded a decreasing upwelling intensity in the Alboran Sea between 14,000 and 10,000 years B.P., which she explained by the decrease in outflow of deeper Mediterranean waters over the Gibraltar sill at that time.

The circulation reversal hypothesis would imply increasing nutrient concentrations and primary

production. An alternative mechanism is proposed by enhanced runoff which, itself, may provide sufficiently large nutrient influxes [Calvert, 1983; De Lange and Ten Haven, 1983; Rossignol-Strick et al., 1982; Ten Haven, 1986]. At the same time, increased runoff would dilute surface waters, leading to a more sluggish (but not necessarily ceased) circulation of the intermediate (Mediterranean Intermediate Water (MIW); see the next sections) and deeper waters. In this scenario, enhanced productivity, in combination with lowered oxygen supply to the deeper parts of the basin, enables the formation of sapropels. It is this combination that we regard as most likely to have caused the shifts in productivity and in oxygenation of deeper waters as discussed in this paper.

In this paper, a new contribution to the discussion on the causes of sapropel formation is presented. We introduce an aspect that has not been investigated before: fluctuations of the rate of "new" primary production in a deep chlorophyll maximum (DCM) as related to variations in the depth of the boundary between surface water and Mediterranean Intermediate Water (MIW). These fluctuations are inferred from striking and consistent frequency variations in the planktonic foraminiferal group of neogloboquadrinids found in the sediment.

2. MATERIALS AND METHODS

Three gravity cores were taken south of Crete in May 1987 with the Dutch research vessel *Tyros*. These cores (T87/2/13G, 306 m water depth; T87/2/20G, 707 m; and T87/2/27G, 607 m) were sampled at close intervals (Figure 2). The geographic positions of the cores are shown in Figure 1, and the lithology and sample positions are shown in Figure 2. The samples have been investigated for their planktonic foraminiferal contents, which resulted in respectively 71, 71, and 59 elaborated samples per core, respectively.

The samples were sieved with mesh widths of 595, 150, and 63 microns. The fractions between 150 and 595 microns were split into aliquots containing about 200 planktonic foraminifera. These foraminifera have been sorted and quantified as a percentage of the total in the aliquot.

3. TIME-STRATIGRAPHIC FRAMEWORK

The rough time-stratigraphic framework is provided by plotting cumulative frequencies of the species *Globigerinoides ruber*, *Globigerinella siphonifera*, *Globigerinoides tenellus*, *Globobulborotalia rubescens*, *Orbulina universa*, *Globigerina digitata*, *Globigerinoides trilobus* and *Hastigerina pelagica* (Figure 3.). This plot is considered to approximate the surface water temperature pattern



Fig. 1. Location map of cores T87/2/13G, T87/2/20G, and T87/2/27G.

through time. It has been correlated to a Mediterranean oxygen isotopic profile [Vergnaud-Grazzini et al., 1977; Vergnaud-Grazzini, 1985] for assessing the chronology of the sapropel sequence (Figure 3.).

The non-Holocene sapropels from the three cores presented in this study are correlated with the S_3 , S_4 , and S_5 succession (Figure 3), which is generally accepted to have developed in the interglacial oxygen isotopic stage 5 [Cita et al., 1977; Muerdter and Kennett, 1984; Rossignol-Strick, 1985; Thunell et al., 1984; Vergnaud-Grazzini et al., 1977; Vergnaud-Grazzini, 1985]. Therefore, these sapropels will in the following discussion be referred to as the isotope-5 (I-5) sapropels. The cold interval between the Holocene (I-1) and I-5 parts of the cores will be referred to as I-2, I-3, and I-4 glacial. The cold interval below the I-5 parts is called the I-6 glacial (Figure 3).

4. RESULTS AND DISCUSSION

4.1. Downcore Distribution of *Neogloboquadrinids*

Neogloboquadrinids have been counted as one category including two morphotypes: *Neogloboquadrina dutertrei* and dextrally coiled *Neogloboquadrina pachyderma*. Both types are considered to represent ecophenotypes within a cline, with *N. dutertrei* being the warm-water end-member and sinistrally coiled *N. pachyderma* the cold-water end-member [amongst others Srinivasan and Kennett, 1976; Van Leeuwen, 1989]. Dextrally coiled *N. pachyderma* (cf. P-D-intergrade morphotypes) [Kipp, 1976] is considered to occupy an intermediate position. Although *N. dutertrei* and *N. pachyderma* are not considered different species, we refrain from a strict approach and label them in italics as if they were.

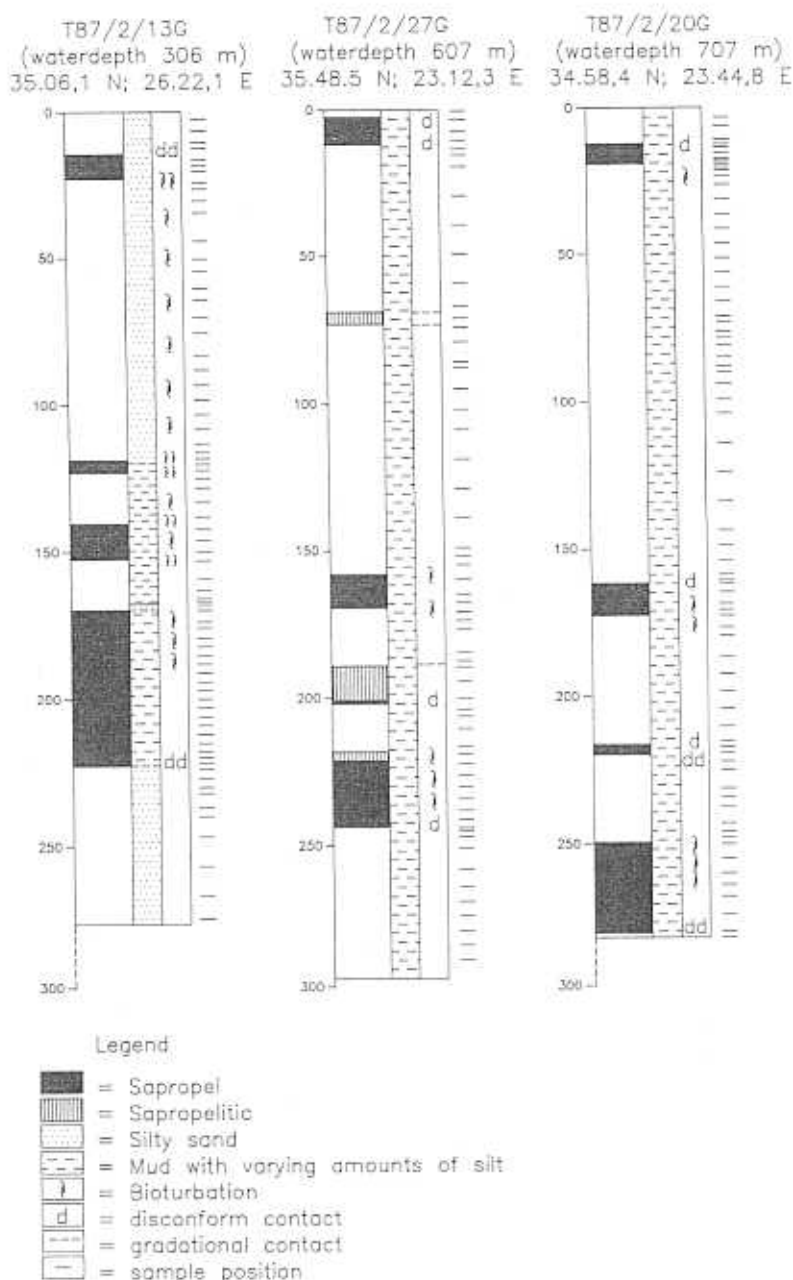


Fig. 2. Lithology and sample positions of cores T87/2/13G, T87/2/27G, and T87/2/20G. The distinction between sapropel and sapropelitic is made purely visually.

The frequency distributions of neogloboquadrinids show a marked difference between the S_1 and the other sapropels in the three investigated cores. The S_1 is nearly devoid of neogloboquadrinids, whereas the other sapropels contain peak abundances of this group (Figure 4). A similar difference has been reported by Thunell et al. [1977].

Sinistrally coiled *N. pachyderma* appeared to be nearly absent in all three cores. The neogloboquadrinids in the I-5 parts of the cores were predominantly *N. dutertrei* types (especially in S_8), whereas dextrally coiled *N. pachyderma*-types dominate the glacial associations.

The abundance of *N. dutertrei* types in most

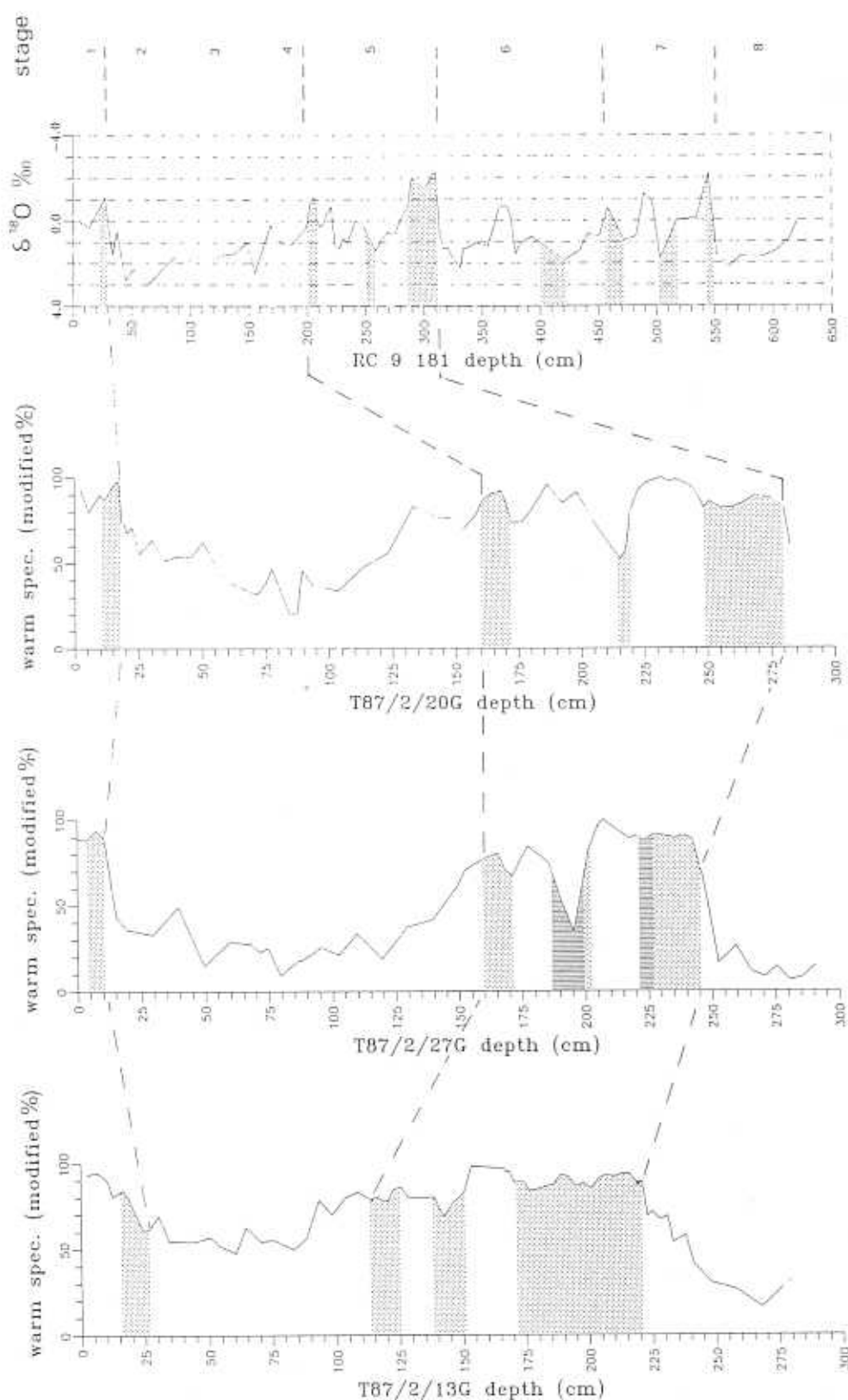


Fig. 3. (Opposite) Plots of the cumulative frequencies of *G. ruber*, *G. siphonifera*, *G. tenellus*, *G. rubescens*, *O. universa*, *G. digitata*, *G. trilobus*, and *H. pelagica* versus *G. quinqueloba*, *G. scitula*, *G. inflata*, *G. truncatulinoides*, *G. glutinata*, and *G. anfracta* for cores T87/2/13G, T87/2/27G, and T87/2/20G. These plots are considered to approximate the surface water temperature through time. They are compared with the oxygen isotope profile of *G. ruber* in core RC 9-181 (modified after Vergnaud-Grazzini [1985]) for assessing the chronology of the sapropel sequence. Sapropel (stippled) and sapropelitic (hatched) results are shown.

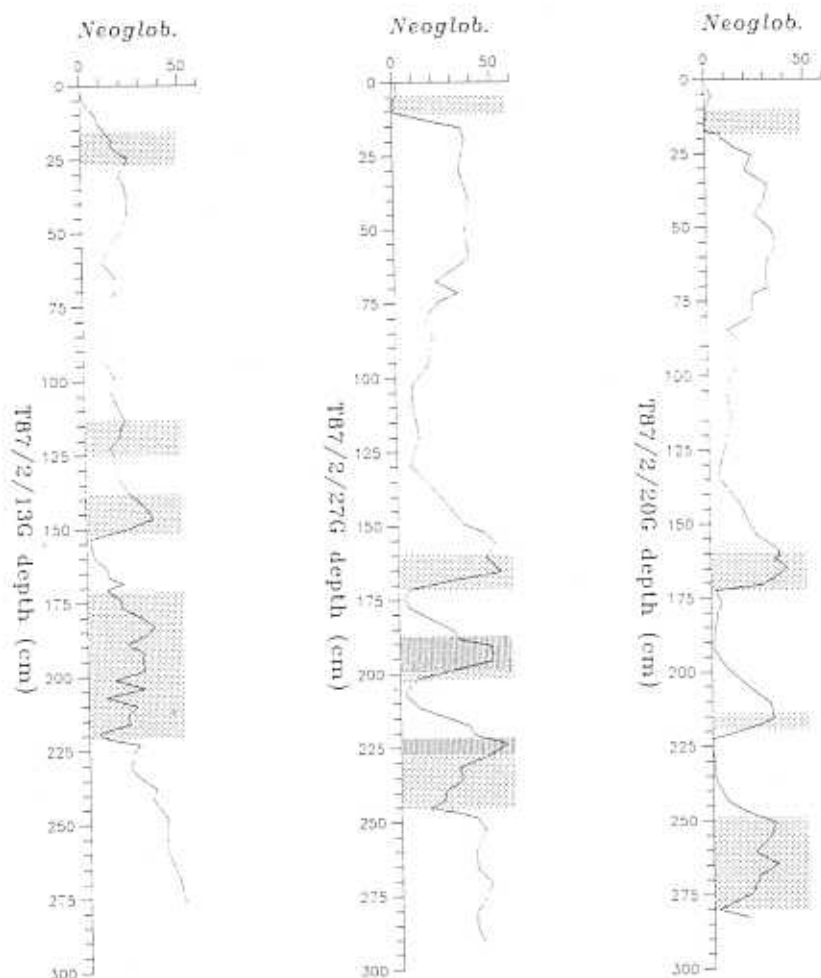


Fig. 4. Downcore frequency distribution of neogloboquadrinids in cores T87/2/13G, T87/2/27G and T87/2/20G. Sapropel (stippled) and sapropelitic (hatched) distributions are shown.

late Quaternary sapropels was first noted by Kullenberg [1952] and later confirmed by others (Figure 5).

4.2. Recent Distribution of *Neogloboquadrinids* and Possible Relation to the Deep Chlorophyll Maximum

Neogloboquadrinids are rare to absent in oligotrophic waters such as the open ocean's central water masses [amongst others Bé and Hamlin, 1967; Kipp, 1976; Tolderlund and Bé, 1971; Schott, 1966], the eastern Mediterranean [Cifelli, 1974; Thunell, 1978], and the Gulf of Aqaba [Almogi-Labin, 1984]. On the other hand, they are well represented in eutrophic waters [amongst others Bé et al., 1985; Kipp, 1976; Tolderlund and Bé, 1971; Schott, 1966].

N. dutertrei appears most prolific in low-latitude oceanic divergences, particularly in the

equatorial divergence [Cullen and Prell, 1984; Jones, 1967; Kipp, 1976; Parker and Berger, 1971]. Therefore, a high abundance of *N. dutertrei* has often been attributed to upwelling [Coulbourn et al., 1980; Duplessy et al., 1981; Kipp, 1976; Thunell et al., 1983b; Thunell and Reynolds, 1984; Thiede, 1975; Zhang, 1985]. Coastal upwelling zones, however, are usually dominated by *G. bulloides* rather than by neogloboquadrinids [cf. Coulbourn et al., 1980; Cullen and Prell, 1984; Duplessy et al., 1981; Schott 1966; Van Leeuwen, 1989; Zhang, 1985].

This faunal contrast between oceanic divergences and coastal upwelling zones is thought to be caused by differences in hydrodynamical conditions. In zones of large-scale divergence, the pycnocline (usually the thermocline) lies shallower than in nondivergent and convergent regions due to Ekman pumping [Bryan and Sarmiento, 1985; Pond and Pickard, 1983; Tolmazin, 1985; Wells,

characteristic of the DCM layer. The mixed-layer phytoplankton assemblage of the open Atlantic is dominated by prokaryota (mainly cyanobacteria) and coccolithophorids. Primary production is coupled to rapid nutrient recycling within this layer [Gieskes and Kraay, 1986; Goering et al., 1970; Jenkins and Goldman, 1985]. On the other hand, the deep assemblage, near the base of the euphotic zone, consists mainly of eukaryota (green algae, coccolithophorids and chrysophyceae); it thrives at depth due to the influx of new nutrients into the lower euphotic zone (described above). Entrapment of new nutrients by the cells in the DCM was suggested by Anderson [1969] and Goering et al. [1970]. New (or net) primary production, derived from pulses of new nutrients from deeper water, is mainly restricted to the lower part of the euphotic zone [Jenkins and Goldman, 1985]. Up to 20% of the total primary production in the open tropical Atlantic was found to be new production [Gieskes and Kraay, 1986].

Such a vertical structure of two distinct phytoplankton assemblages in the euphotic layer does not only occur in the Atlantic Ocean but has also been reported from eastern Indonesian waters [Gieskes et al., 1988] and other parts of both the open Pacific and Atlantic oceans [Furuya and Marumo, 1983; Glover et al., 1985; Murphy and Haugen, 1985; Venrick, 1982]. In addition, differences in size class structure between the deep (mainly nanoplankton and picoplankton) and the shallow (mainly picoplankton) assemblages have been noted [Gieskes and Kraay, 1986; Herbrand et al., 1985]. Similar differences have been found in the Adriatic Sea (M. Gilmartin, personal communication, 1988).

Shoaling of the pycnocline within the euphotic zone enables extension of the DCM into shallower waters with higher light intensities. This should enhance primary production in the DCM, and thus the chlorophyll concentrations, since most production at depth is new production (see the previous section). This relation between shoaling of the pycnocline and increasing chlorophyll concentrations in the DCM is illustrated by Gieskes and Kraay [1986, Figure 1]: a shallower DCM contains higher chlorophyll concentrations. In the "typical tropical system" [Herbrand et al., 1983; Herbrand and Voituriez, 1979], the subsurface primary production and chlorophyll maxima coincide in depth with the top of the nutricline, and integrated primary production correlates with nutricline depth [Hayward, 1987]. The DCM in the Gulf of Mexico varies significantly with changes in pycnocline depth [Hobson and Lorenzen, 1972]. Herbrand et al. [1985] stated that the chlorophyll *a* maximum followed doming of the nutriclines in the Guinea Dome with higher values.

In the Panama Basin, Fairbanks and Wiebe [1980] and Fairbanks et al. [1982] demonstrated that

peak abundances of several nonspinoso planktonic foraminiferal species, especially *N. dutertrei*, are associated with the DCM. A similar relationship between peak abundances of dextrally coiled *N. pachyderma* and the DCM has been observed in the Gulf of Alaska, where cyclonal circulation induces a shallow pycnocline position in winter [Reynolds and Thunell, 1986].

The occurrence of high abundances of *N. dutertrei* in areas with a distinct DCM supposedly is similar for the low-temperature variant *N. pachyderma*. This is actually confirmed by the fact that *N. pachyderma* blooms at North Atlantic high latitudes in summer [e.g. Tolderlund and B , 1971]. In summer only, a shallow pycnocline (within the euphotic layer) develops in these waters due to heating and decreased storm activity, and this creates favorable conditions for the development of a distinct DCM.

The relation between high abundances of neogloboquadrinids and a shallow pycnocline/nutricline (and therewith a high rate of new production in a DCM) may be indicative of their preferential grazing upon the deep phytoplankton assemblage, either because of a preference for the species typically found at depth, or due to a size preference (larger cells at depth; see above). Although their preferred food may also be present in the shallow phytoplankton assemblage, its higher density in the DCM will enable the existence of significant amounts of neogloboquadrinids. In fact, neogloboquadrinids are virtually absent in areas where the pycnocline/nutricline lies well below the euphotic zone. In such areas, for example the ocean's central water masses, there hardly is a distinct DCM; in other words there is no deep phytoplankton assemblage to support neogloboquadrinids.

Considering its present distribution pattern, we find no reasons to believe in any direct relation between a high abundance of *N. dutertrei* and lowered surface water salinities, as has been suggested by Ryan [1972], Thunell [1978], Thunell and Williams [1982, 1983], Vergnaud-Grazzini et al. [1977], and Williams et al. [1978].

4.3. The DCM in the Eastern Mediterranean

Since a DCM was also reported in the Levantine Basin of the eastern Mediterranean [Berman et al., 1984a, b], we assume that in that oligotrophic region, as well, two superimposed assemblages are present (conform section 4.2).

The pycnocline in the eastern Mediterranean is maintained by the salinity contrast between the nutrient-depleted surface waters and the somewhat more nutrient-rich Mediterranean Intermediate Water (MIW), as illustrated by property distribution profiles of McGill [1961] and Miller et al. [1970]. Therefore, the pycnocline and nutri-

cline depths are closely related and are affected in roughly the same way by changes in the MIW depth. The pycnocline lies at about 150 m depth in the area south of Crete and even deeper in non-divergent regions further west from the area where MIW formation takes place [Wüst, 1961; Miller et al., 1970]. Due to this deep pycnocline position, compared to the depth of the euphotic zone (about 120 m) in the eastern Mediterranean, there is no distinct DCM. This situation is similar to that in oceanic central gyres where the pycnocline also lies deep with respect to light penetration.

The water below the pycnocline in the eastern Mediterranean Levantine Basin (the MIW) is much more depleted in nutrients than subpycnocline waters in the Atlantic Ocean. Although both regions do have a DCM, this nutrient limitation causes primary production in the DCM to be much lower in the Levantine Basin than in the Atlantic Ocean. Average chlorophyll concentrations in the Levantine Basin as reported by Berman et al. [1984b] are 1 order of magnitude lower than those in the tropical Atlantic [Gieskes and Kraay, 1986].

4.4. Interpretation of the Downcore Distribution of *Neoglobobulimina*

A marked difference exists between the sapropel S_1 , which is nearly devoid of *neoglobobulimina*, and the older sapropels, which generally contain high abundances of this group (Figures 4 and 5). At times of deposition of the S_3 , S_4 , and S_5 sapropels, *neoglobobulimina* were highly abundant, indicating favorable growth conditions, presumably (see section 4.2) due to high rates of primary production in a distinct DCM.

As we have argued above, enhanced production in a DCM can be realized by shallowing of the pycnocline to a depth that falls well within the euphotic layer. Therefore, the MIW to surface water density contrast should be decreased. This density contrast depends on climatic parameters such as evaporation rate and winter cooling. Since MIW spreads laterally from its source area, the MIW to surface water density contrast would decrease if prevailing dilution effects were relatively higher near the area of MIW formation than further away from it. Also, a relative decrease of surface temperature with increasing distance from the MIW source area (i.e., an increased east to west temperature gradient over the Mediterranean) would result in a decrease of the aforementioned density contrast. As argued in the introduction, we think that enhanced runoff triggered sapropel formation by both diluting surface waters and increasing nutrient concentrations. Since (1) the effects of dilution decrease with increasing distance from the diluting freshwater source(s) and

(2) modern MIW originates in the eastern Levantine Basin, one could reason that the major diluting source should have been the Nile river. It remains, however, to be proven that MIW always originated at its present location, since it may as well have been formed in other areas (e.g., parts of the Aegean). We will further restrict ourselves to interpreting the evolution of the vertical hydrodynamical structure through time, since the causative mechanisms still require much study.

A decreased MIW density would undoubtedly affect the rate of formation of eastern Mediterranean Deep Water (EMDW) [cf. Mangini and Schlosser, 1986]. EMDW is formed in the Adriatic Sea and possibly also in the Aegean Sea [Dietrich et al., 1980; King, 1975; Wüst, 1961]. Its formation occurs due to winter cooling and large-scale convection in areas where the MIW is brought close to the surface by persistent divergence in cyclonal circulations. High salinity (characteristic of the MIW), in combination with lowered surface water temperatures, generates water with densities higher than those of the MIW. This water then sinks to the deeper parts of the eastern Mediterranean Basin [Dietrich et al., 1980; King, 1975; Wüst, 1961].

We may therefore safely assume that a decrease in the MIW density caused a decline in the rate of EMDW production, thereby contributing to the preservation of organic material and thus to the formation of sapropels. Although Mangini and Schlosser [1986] showed that EMDW production in the Adriatic Sea would cease following even very small density decreases, we stress that even a diminution of EMDW production, combined with enhanced production during deposition of the 1-5 sapropels, could be conducive to the development of anoxic conditions (Figure 6).

The newly collected cores south of Crete indicate that the upper depth limit of S_3 , S_4 , and S_5 is at least as shallow as 300 m (core T87/2/13G). Even in this shallow core, the sapropelic sediments and near absence of benthic foraminifera (especially in S_5) seem to indicate that anoxic conditions prevailed at depths as shallow as 300 m and that the anoxic and dysoxic influence probably reached still shallower waters.

According to our reconstruction, the upper "limit" of the MIW was probably situated within the euphotic layer (<120 m) during the formation of S_3 , S_4 , and S_5 . In that case, the upper limit of the anoxic conditions (<300 m) may have coincided with the top of the transitional water layer between EMDW and MIW (Figure 6), which at present lies at about 600 m depth (Figure 6) [King, 1975; Wüst, 1961]. If this is true, the MIW resided in a layer that was much thinner than at present; it probably was produced in smaller volumes, which may have caused reduction of the EMDW production as well as the lowered MIW densities did.

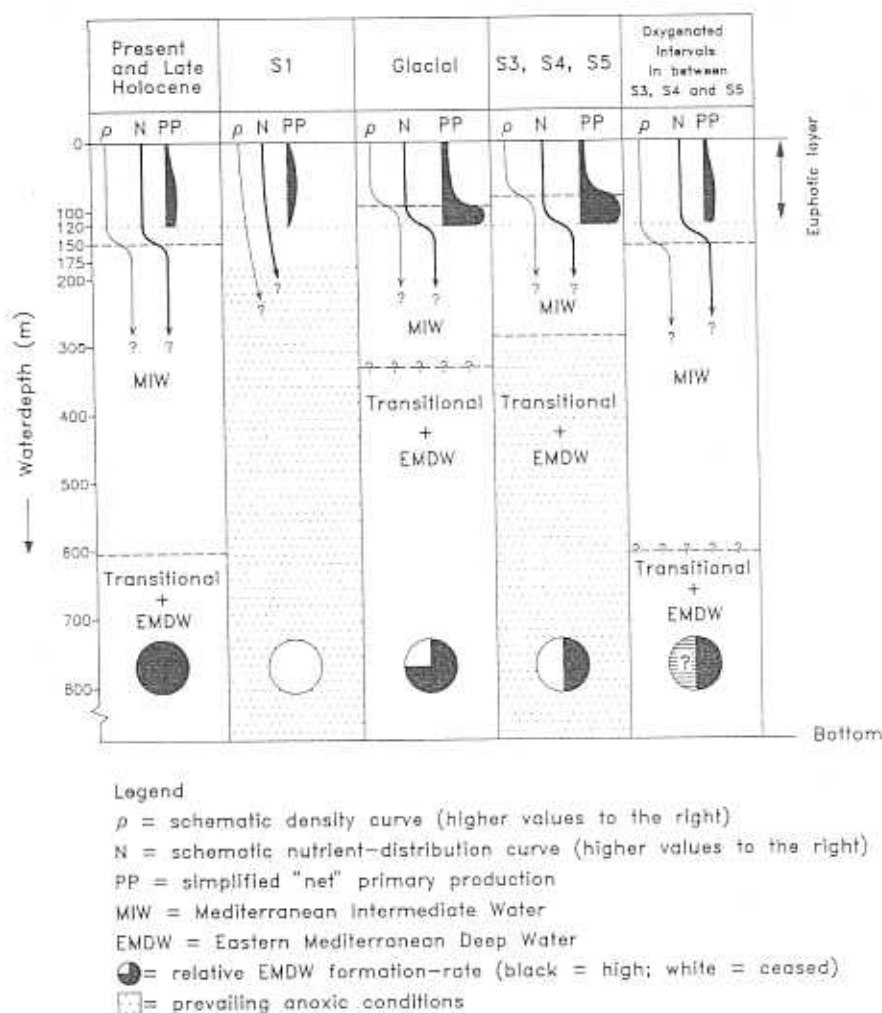


Fig. 6. Schematic presentation of depth changes of the pycnocline between MIW and surface waters and its influences on net primary production. Relative MIW densities and formation rates are reflected in the depth of the pycnocline and "thickness" of the MIW layer, which influence the EMDW formation rates.

During the deposition of S_1 , conditions seem to have been very unfavorable for the neogloboquadrinids, indicating absence of a deep chlorophyll maximum layer. This may, as we explained above, have been caused by a deepening of the pycnocline far below the euphotic zone, or even by complete degradation of the pycnocline (Figure 6). The upper depth limit of S_1 lies at about 180 m, according to organic carbon measurements in several Aegean cores [Anastasakis, 1986]. Anoxic conditions thus prevailed below 180 m. This probably implies a (nearly) complete shutdown of MIW formation, causing a diminished oxygen supply at intermediate depths up to about 180 m, and at the same time a disintegration of the pycnocline

and associated DCM. The shutdown of the MIW production during deposition of S_1 curtailed EMDW production, thus allowing anoxic conditions to expand to even the deepest parts of the basin.

Recently, and in the late Holocene, neogloboquadrinids are rare in the region of the Cretan cores (Figure 4), as they generally are in the eastern Mediterranean [Cifelli, 1974; Thunell, 1978]. Since neogloboquadrinids are also rare in the I-5 non sapropelic intervals (Figure 4), we assume that the hydrodynamic structure during deposition of these intervals was much like that of the present day (Figure 6).

The glacial parts of the cores generally contain intermediate to very high frequencies of neoglobo-

quadrinids. Because of this abundance, glacial conditions can best be compared to conditions during formation of the I-5 sapropels. An important difference is the fact that glacial sedimentation appears to have occurred in oxygenated waters. The similarity between the glacial conditions and those during I-5 sapropel formation can be related to the fact that the MIW to surface water density contrast was of the same order of magnitude during these periods. The absolute densities may have differed considerably between the glacials and the I-5 sapropelic periods. According to Thunell et al. [1987], using a model developed by Bryden and Stommel [1984], salinities of glacial Mediterranean water masses far exceeded those in interglacials (see also Thunell and Williams [1989]).

Glacial primary production rates appear to have ranged from moderate to as high as during the I-5 sapropel formation. This, and the fact that anoxia did not develop during the entire glacial time span, leads to the hypothesis that EMDW production could take place more effectively during glacials than in I-5, causing a higher oxygen supply to deeper parts of the basin (Figure 6). Possibly, the lower glacial temperatures and higher salinity of the surface waters [Thunell et al., 1987] were the cause of this more effective glacial EMDW formation.

Sapropels have been found in some glacial intervals in the eastern Mediterranean (S_2 , S_6 , S_8 ; amongst others Cita et al. [1977], Muerdter and Kennett [1984], Thunell et al. [1983a, 1984] and Vergnaud-Grazzini et al. [1977]). According to our model, the occurrence of these sapropels can be attributed to (glacial) periods of less efficient EMDW production. The possibility of excess primary production, however, cannot be ruled out, especially for the S_6 sapropel which is known to contain excessive amounts of neogloboquadrinids (Figure 5).

5. CONCLUSIONS

A deep chlorophyll maximum layer is restricted to the base of the euphotic zone of oligotrophic water and develops when the vertical density structure is in support of the establishment of a deep phytoplankton population. We suggest that the faunal contrast between the S_1 and older sapropels reflects differences in primary production and food availability during their deposition. The new (i.e. net) primary production near the base of the euphotic zone in the deep chlorophyll maximum layer [Gieskes and Kraay, 1986; Jenkins and Goldman, 1985] supports neogloboquadrinids that feed on the DCM-related phytoplankton assemblage. Neogloboquadrinids should be (almost)

absent where a DCM is less pronounced or absent. Sapropel formation requires net production and, indeed, nearly all sapropels are associated with neogloboquadrinid blooms which are related to the high net primary production of the deep phytoplankton assemblage.

We have formulated the hypothesis that relates variations in the abundance of neogloboquadrinids to relative differences in the density and formation intensity of the MIW. This mechanism has previously been mentioned as a possible nutrient regulator [Muerdter and Kennett, 1984]. The model we present accounts for the relative depth of the pycnocline between the MIW and the surface waters.

We propose that shoaling of the pycnocline is induced by relatively low surface water salinity in the MIW source area due to increased river runoff (during sapropel formation) and by possibly increased east to west surface temperature gradients (during glacials).

MIW production probably ceased when the S_1 developed. Relative MIW densities and formation rates were "intermediate" during the I-5 sapropel formation and during glacial periods. They were highest in I-5 nonsapropelic intervals, as they are in the present-day situation (Figure 6).

The Holocene sapropel S_1 developed under special conditions of absence of a deep chlorophyll maximum layer; there was no deep (DCM-related) phytoplankton assemblage. Since the remaining shallow phytoplankton assemblage, being recycled rapidly [cf. Gieskes and Kraay, 1986; Jenkins and Goldman, 1985], normally contributes only minutely to net production, oxygen advection due to MIW and EMDW flow must have been severely reduced in order to allow formation of the S_1 sapropel. This implies (nearly) total stagnation down from the upper depth limit of S_1 at 180 m.

Acknowledgements. We thank W. J. Zachariasse for initiating this research and W. J. Zachariasse, L. Kesters, F. Jorissen, and M. Gilmartin for their valuable suggestions and critical reviewing. Thanks are also due to G. J. Weltje and R. Van Rijckevorsel for their assistance in the gathering of data, G. van't Veld and G. Ittman for preparing the samples, T. Van Hinte for drafting services, and A. Pouw for editing the manuscript.

REFERENCES

- Abrantes, F., Diatom productivity peak and increased circulation during latest Quaternary: Alboran Basin (western Mediterranean), *Mar. Micropaleontol.*, 13, 79-96, 1988.
- Adamson, D. A., F. Gasse, F. A. Street, and M. A.

- J. Williams, Late Quaternary history of the Nile, *Nature*, 288, 50-55, 1980.
- Almogi-Labin, A., Population dynamics of planktic Foraminifera and Pteropoda -- Gulf of Aqaba, Red Sea, *Proc. K. Ned. Akad. Wet., Ser. B. Phys. Sci.* 87(4), 481-511, 1984.
- Anastasakis, G. C., A new uppermost limit of sapropelic sequence deposition in the Aegean Sea, *Rapp. P. V. Reun. Comm. int. Explor. Sci. Mer Mediterr., Fasc. 2*, 30, 72, 1986.
- Anderson, G. C., Subsurface chlorophyll maximum in the Northeast Pacific ocean, *Limnol. Oceanogr.*, 14, 386-391, 1969.
- Bé, A. W. H., and W. H. Hamlin, Ecology of Recent planktonic foraminifera, 3, Distribution in the North Atlantic during the summer of 1962, *Micropaleontology*, 13, 87-106, 1967.
- Bé, A. W. H., J. K. B. Bishop, M. S. Sverdløve, and W. D. Gardner, Standing stock, vertical distribution and flux of planktonic foraminifera in the Panama Basin, *Mar. Micropaleontol.*, 9, 307-333, 1985.
- Berman, T., Y. Azov, and D. Townsend, Understanding oligotrophic oceans: Can the eastern Mediterranean be a useful model?, in *Marine Phytoplankton and Productivity*, edited by O. Holm-Hansen, L. Bolis, and R. Gills, pp. 101-111, Springer-Verlag, New York, 1984a.
- Berman, T., D. W. Townsend, S. Z. El Sayed, C. C. Trees, and Y. Azov, Optical transparency, chlorophyll and primary productivity in the eastern Mediterranean near the Israeli coast, *Oceanol. Acta*, 7, 367-372, 1984b.
- Bryan, K., and J. L. Sarmiento, Modeling ocean circulation, in *Advances in Geophysics*, vol. 28, *Issues in Atmospheric and Oceanic Modeling: Part A*, edited by S. Manabe, pp. 433-459, Academic, San Diego, Calif., 1985.
- Bryden, H. L., and H. M. Stommel, Limiting processes that determine basic features of the circulation in the Mediterranean Sea, *Oceanol. Acta*, 7, 289-296, 1984.
- Buckley, H. A., and L. R. Johnson, Late Pleistocene to Recent sediment deposition in the central and western Mediterranean, *Deep Sea Res.*, 35, 749-766, 1988.
- Buckley, H. A., L. R. Johnson, N. J. Shackleton, and R. A. Blow, Late glacial to recent cores from the eastern Mediterranean, *Deep Sea Res.*, 29, 739-766, 1982.
- Calvert, S. E., Geochemistry of Pleistocene sapropels and associated sediments from the eastern Mediterranean, *Oceanol. Acta*, 6, 255-267, 1983.
- Cifelli, R., Planktonic foraminifera from the Mediterranean and adjacent Atlantic waters (cruise 49 of the *Atlantis II*, 1969), *J. Foraminiferal Res.*, 4, 171-183, 1974.
- Cita, M. B., and D. Grignani, Nature and origin of late Neogene Mediterranean sapropels, in *Nature and Origin of Cretaceous Carbon-Rich Facies*, edited by S. O. Schlanger and M. B. Cita, pp. 165-196, Academic, San Diego, Calif., 1982.
- Cita, M. B., C. Vergnaud-Grazzini, C. Robert, H. Chamley, N. Ciaranfi, and S. d'Onofrio, Paleoclimatic record of a long deep sea core from the eastern Mediterranean, *Quat. Res.*, 8, 205-235, 1977.
- Coulbourn, W. T., F. L. Parker, and W. H. Berger, Faunal and solution patterns of planktonic foraminifera in surface sediments of the North Pacific, *Mar. Micropaleontol.*, 5, 329-399, 1980.
- Cullen, J. L., and W. L. Prell, Planktonic foraminifera of the Northern Indian Ocean: Distribution and preservation in surface sediments, *Mar. Micropaleontol.*, 9, 1-52, 1984.
- De Lange, G. J., and H. L. Ten Haven, Recent sapropel formation in the eastern Mediterranean, *Nature*, 305, 797-798, 1983.
- Dietrich, G., K. Kalle, W. Krauss, and G. Siedler, *General Oceanography*, 2nd ed., 626 pp., John Wiley, New York, 1980.
- Dortch, Q., J. R. Clayton, S. S. Thoresen, J. S. Cleveland, S. L. Bressler, and S. I. Ahmed, Nitrogen storage and use of biochemical indices to assess nitrogen deficiency and growth rate in natural plankton populations, *J. Mar. Res.*, 43, 437-464, 1985.
- Duplessy, J.-C., A. W. H. Bé, and P. L. Blanc, Oxygen and carbon isotope composition and biogeographic distribution of planktonic foraminifera in the Indian Ocean, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33, 9-46, 1981.
- Emiliani, C., Pleistocene temperature variations in the Mediterranean, *Quaternaria*, 2, 87-98, 1955.
- Fairbanks, R. G., and P. H. Wiebe, Foraminifera and chlorophyll maximum: Vertical distribution, seasonal succession, and paleoceanographic significance, *Science*, 209, 1524-1525, 1980.
- Fairbanks, R. G., M. Sverdløve, R. Free, P. H. Wiebe, and A. W. H. Bé, Vertical distribution of living planktonic foraminifera from the Panama Basin, *Nature*, 298, 841-844, 1982.
- Furuya, K., and R. Marumo, The structure of the phytoplankton community in the subsurface chlorophyll maxima in the western North Pacific Ocean, *J. Plankton Res.*, 5, 393-406, 1983.
- Gieskes, W. W., and G. W. Kraay, Floristic and physiological differences between the shallow and the deep nannophytoplankton community in the euphotic zone of the open tropical Atlantic revealed by HPLC analysis of pigments, *Mar. Biol.*, 91, 567-576, 1986.
- Gieskes, W. W. C., G. W. Kraay, A. Nontji, D. Setiapermana, and Sutomo, Monsoonal alternation of a mixed and a layered structure in the phytoplankton of the euphotic zone of the Banda Sea (Indonesia): A mathematical analysis of algal pigment fingerprints, *Neth. J. Sea Res.*, 22(2), 123-137, 1988.
- Glover, H. E., A. E. Smith, and L. Shapiro, Diurnal

- variations in photosynthetic rates: Comparisons of ultraphytoplankton with a larger phytoplankton size fraction, *J. Plankton Res.*, 7, 519-535, 1985.
- Goering, J. J., D. D. Wallen, and R. M. Naumann, Nitrogen uptake by phytoplankton in the discontinuity layer of the eastern subtropical Pacific Ocean, *Limnol. Oceanogr.*, 15, 789-796, 1970.
- Hayward, T. L., The nutrient distribution and primary production in the central North Pacific, *Deep Sea Res.*, 34, 1593-1627, 1987.
- Herbland, A., and B. Voituriez, Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean, *J. Mar. Res.*, 37, 87-101, 1979.
- Herbland, A., R. Le Borgne, A. Le Bouteiller, and B. Voituriez, Structure hydrologique et production primaire dans l'Atlantique tropical oriental, *Oceanogr. Trop.*, 18, 223-248, 1983.
- Herbland, A., A. Le Bouteiller, and P. Raimbault, Size structure of phytoplankton biomass in the equatorial Atlantic Ocean, *Deep Sea Res.*, 32, 819-836, 1985.
- Hobson, L. A., and C. J. Lorenzen, Relationships of chlorophyll maxima to density structure in the Atlantic Ocean and Gulf of Mexico, *Deep Sea Res.*, 19, 279-306, 1972.
- Jenkins, W. J., and J. C. Goldman, Seasonal oxygen cycling and primary production in the Sargasso Sea, *J. Mar. Res.*, 43, 465-491, 1985.
- Jones, J. I., Significance of distribution of planktonic foraminifera in the Equatorial Atlantic Undercurrent, *Micropaleontology*, 13, 489-501, 1967.
- Kiefer, D. A., R. J. Olson, and O. Holm-Hansen, Another look at the nitrate and chlorophyll maxima in the central North Pacific, *Deep Sea Res.*, 23, 1199-1208, 1976.
- King, C. A. M., *Introduction to Physical and Biological Oceanography*, Edward Arnold, London, 1975.
- Kipp, N. G., New transfer function for estimating past sea-surface conditions from sea-bed distribution of planktonic foraminiferal assemblages in the North Atlantic, Investigation of Late Quaternary Paleooceanography and Paleoclimatology, edited by R. M. Cline and J. D. Hays, *Mem. Geol. Soc. Am.*, 145, 3-41, 1976.
- Klein, P., and J. H. Steele, Some physical factors affecting ecosystems, *J. Mar. Res.*, 43, 337-350, 1985.
- Kullenberg, B., On the salinity of the water contained in marine sediments, *Medd. Oceanogr. Inst. Goteborg*, 21, 1-38, 1952.
- Lohrenz, S. E., D. A. Wiesenburg, I. P. DePalma, K. S. Johnson, and D. E. Gustafson Jr., Interrelationships among primary production, chlorophyll, and environmental conditions in frontal regions of the western Mediterranean Sea, *Deep Sea Res.*, 35, 793-810, 1988.
- Mangini, A., and P. Schlosser, The formation of Mediterranean sapropels, *Mar. Geol.*, 72, 115-124, 1986.
- McGill, D. A., A preliminary study of the oxygen and phosphate distribution in the Mediterranean Sea, *Deep Sea Res.*, 8, 259-269, 1961.
- Miller, A. R., P. Tchernia, H. Charnock, and D. A. McGill, *Mediterranean Sea Atlas of Temperature, Salinity, Oxygen: Profiles and Data From Cruises of R.V. Atlantis and R.V. Chain, With Distribution of Nutrient Chemical Properties*, edited by A. E. Maxwell et al., 190 pp., Alpine, Braintree, Mass., 1970.
- Muerdter, D. R., Low salinity surface water incursions across the Strait of Sicily during late Quaternary sapropel intervals, *Mar. Geol.*, 58, 401-414, 1984.
- Muerdter, D. R., and J. P. Kennett, Late Quaternary planktonic foraminiferal biostratigraphy, Strait of Sicily, Mediterranean Sea, *Mar. Micropaleontology*, 8, 339-359, 1984.
- Murphy, L. S., and E. Haugen, The distribution and abundance of phototrophic ultraplankton in the North Atlantic, *Limnol. Oceanogr.*, 30, 47-58, 1985.
- Olausson, E., Studies of deep-sea cores, *Rep. Swed. Deep Sea Exped. 1947-1948*, 8, 353-391, 1961.
- Parker, F. L., and W. H. Berger, Faunal and solution patterns of planktonic foraminifera in surface sediments of the South Pacific, *Deep Sea Res.*, 18, 73-107, 1971.
- Pond, S., and G. L. Pickard, *Introductory dynamical oceanography*, 329 pp., Bergamon, New York, 1983.
- Reynolds, L. A., and R. C. Thunell, Seasonal production and morphologic variation of *Neogloboquadrina pachyderma* (Ehrenberg) in the northeast Pacific, *Micropaleontology*, 32, 1-18, 1986.
- Rognon, P., Aridification and abrupt climatic events on the Saharan northern and southern margins, 20,000 Y BP to present, *Abrupt Climatic Change: Evidence and Implications*, edited by W. H. Berger and L. D. Labeyrie, *NATO Adv. Study Inst., Ser. C, Math. Phys. Sci.*, 216, 209-220, 1987.
- Ross, C. R., and J. P. Kennett, Late Quaternary paleoceanography as recorded by benthonic foraminifera in Strait of Sicily sediment sequences, *Mar. Micropaleontology*, 8, 315-337, 1984.
- Rosignol-Strick, M., Mediterranean Quaternary sapropels, and immediate response of the African monsoon to variations of insolation, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 49, 237-263, 1985.
- Rosignol-Strick, M., V. Nesteroff, P. Olive, and C. Vergnaud-Grazzini, After the deluge; Mediterranean stagnation and sapropel formation, *Nature*, 295, 105-110, 1982.
- Ryan, W. B. F., Stratigraphy of late Quaternary sediments in the eastern Mediterranean, in *The*

- Mediterranean Sea: A Natural Sedimentation Laboratory*, edited by D. J. Stanley, pp. 149-169, Dowden, Hutchinson and Ross, Stroudsburg, Pa., 1972.
- Schott, W., Foraminiferenfauna und stratigraphie der tiefsee sedimente im Nordatlantischen Ozean, *Rep. Swed. Deep Sea Exped. 1947-1948, Fasc. 8, Sediment Cores North Atlantic Ocean*, 8, 357-469, 1966.
- Shaw, H. F., and G. Evans, The nature, distribution and origin of a sapropelic layer in sediments of the Cilicia Basin, northeastern Mediterranean, *Mar. Geol.*, 61, 1-12, 1984.
- Spencer, C. P., The micronutrient elements, in *Chemical Oceanography*, vol. 2, 2nd ed., edited by J. P. Riley and G. Skirrow, Academic, San Diego, Calif., pp. 245-300, 1975.
- Srinivasan, M. S., and J. P. Kennett, Evolution and phenotypic variation in the late Cenozoic *Neogloboquadrina dutertrei* plexus, *Prog. Micropaleontology*, 329-355, 1976.
- Stanley, D. J., and C. Blampied, Late Quaternary water exchange between the eastern Mediterranean and the Black Sea, *Nature*, 266, 537-541, 1980.
- Stanley D. J., A. Maldonado, and R. Stuckenrath, Strait of Sicily depositional rates and patterns, and possible reversal of currents in the late Quaternary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 18, 279-291, 1975.
- Street, A. F., and A. T. Grove, Global maps of lake-level fluctuations since 30,000 Y BP, *Quat. Res.*, 12, 83-118, 1979.
- Tchernia, P., *Descriptive regional oceanography*, Pergamon Mar. Ser., vol. 3, edited by J. C. Swallow, 253 pp., Pergamon, New York, 1980.
- Ten Haven, H. L., Organic and inorganic geochemical aspects of Mediterranean late Quaternary sapropels and Messinian evaporitic deposits, *Geol. Ultraetina*, 46, 1-206, 1986.
- Thiede, J., Distribution of foraminifera in surface waters of a coastal upwelling area, *Nature*, 253, 712-714, 1975.
- Thunell, R. C., Distribution of recent planktonic foraminifera in surface sediments of the Mediterranean Sea, *Mar. Micropaleontology*, 3, 147-173, 1978.
- Thunell, R. C., and L. A. Reynolds, Sedimentation of planktonic foraminifera: Seasonal changes in species flux in the Panama Basin, *Micropaleontology*, 30, 243-262, 1984.
- Thunell, R. C., and D. F. Williams, Paleooceanographic events associated with termination II in the eastern Mediterranean, *Oceanol. Acta*, 5, 229-233, 1982.
- Thunell, R. C., and D. F. Williams, Paleotemperature and paleosalinity history of the eastern Mediterranean during the late Quaternary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 44, 23-39, 1983.
- Thunell, R. C., and D. F. Williams, Glacial-Holocene salinity changes in the Mediterranean Sea: Hydrographic and depositional effects, *Nature*, 338, 493-496, 1989.
- Thunell, R. C., D. F. Williams, and J. P. Kennett, Late Quaternary paleoclimatology, stratigraphy and sapropel history in eastern Mediterranean deep-sea sediments, *Mar. Micropaleontology*, 2, 371-388, 1977.
- Thunell, R. C., D. F. Williams, and M. B. Cita, Glacial anoxia in the eastern Mediterranean, *J. Foraminiferal Res.*, 13, 283-290, 1983a.
- Thunell, R. C., W. B. Curry, and S. Honjo, Seasonal variation in the flux of planktonic foraminifera: Time series sediment trap results from the Panama Basin, *Earth Planet. Sci. Lett.*, 64, 44-45, 1983b.
- Thunell, R. C., D. F. Williams, and P. R. Belyea, Anoxic events in the Mediterranean Sea in relation to the evolution of late Neogene climates, *Mar. Geol.*, 59, 105-134, 1984.
- Thunell, R. C., D. F. Williams, and M. Howell, Atlantic-Mediterranean Water exchange during the late Neogene, *Paleoceanography*, 2(6), 661-678, 1987.
- Tolderlund, D. S., and A. W. H. Be, Seasonal distribution of planktonic foraminifera in the western North Atlantic, *Micropaleontology*, 17, 297-329, 1971.
- Tolmazin, D., *Elements of Dynamic Oceanography*, 181 pp., Allen and Unwin, Boston, 1985.
- Van Leeuwen, R. J. W., Sea-floor distribution and late Quaternary faunal patterns of planktonic and benthic foraminifera in the Angola Basin, edited by C. W. Drooger, *Utrecht Micropaleontol. Bull.*, 38, 288 pp., 1989.
- Venrick, E. L., Phytoplankton in an oligotrophic ocean: Observations and questions, *Ecol. Monogr.*, 52, 129-154, 1982.
- Vergnaud-Grazzini, C., Mediterranean late Cenozoic stable isotope record: Stratigraphic and paleoclimatic implications, in *Geological Evolution of the Mediterranean Basin*, edited by D. J. Stanley and F. C. Wezel, pp. 413-451, Springer-Verlag, New York, 1985.
- Vergnaud-Grazzini, C., W. B. F. Ryan, and M. B. Cita, Stable isotopic fractionation, climatic change and episodic stagnation in the eastern Mediterranean during the late Quaternary, *Mar. Micropaleontology*, 2, 353-370, 1977.
- Vergnaud-Grazzini, C., A. M. Borsetti, F. Cati, P. Colantoni, S. D'Onofrio, J. F. Saliege, R. Sartori, and R. Tampieri, Palaeoceanographic record of the last deglaciation in the Strait of Sicily, *Mar. Micropaleontology*, 13, 1-21, 1988.
- Wells, N., *The Atmosphere and Ocean: A Physical Introduction*, 337 pp., Taylor and Francis, London, 1986.
- Williams, D. F., R. C. Thunell, and J. P. Kennett, Periodic fresh-water flooding and stagnation of

- the eastern Mediterranean Sea during the late Quaternary, *Science*, 201, 252-254, 1978.
- Wüst, G., On the vertical circulation of the Mediterranean Sea, *J. Geophys. Res.*, 66, 3261-3271, 1961.
- Zahn, R., and M. Sarnthein, Benthic isotope evidence for changes of the Mediterranean outflow during the late Quaternary, *Paleoceanography*, 2(6), 543-559, 1987.
- Zhang, J., Living planktonic foraminifera from the Eastern Arabian Sea, *Deep Sea Res.*, 32, 789-798, 1985.
- W. W. C. Gieskes, Department of Marine Biology, University of Groningen, P. O. Box 14, 9750 AA Haren, The Netherlands.
- E. J. Rohling, Department of Stratigraphy and Micropaleontology, Institute of Earth Sciences, University of Utrecht, P. O. Box 80.021, 3508 TA Utrecht, The Netherlands.

(Received January 9, 1989;
revised April 26, 1989;
accepted May 2, 1989.)