

Alessandro Incarbona*, Enrico Di Stefano, Rodolfo Sprovieri, and Serena Ferraro

The Uniqueness of Planktonic Ecosystems in the Mediterranean Sea: The Response to Orbital- and Suborbital-Climatic Forcing over the Last 130,000 Years

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Abstract: The Mediterranean Sea is an ideal location to test the response of organisms to hydrological transformations driven by climate change. Here we review studies carried out on planktonic foraminifera and coccolithophores during the late Quaternary and attempt the comparison of data scattered in time and space. We highlight the prompt response of surface water ecosystems to both orbital- and suborbital-climatic variations.

A markedly different spatial response was observed in calcareous plankton assemblages, possibly due to the influence of the North Atlantic climatic system in the western, central and northern areas and of the monsoon system in the easternmost and southern sites. Orbital-induced climatic dynamics led to productive surface waters in the northern, western and central Mediterranean Sea during the last glacial and to distinct deep chlorophyll maximum layers in the eastern Mediterranean Sea coinciding with bottom anoxia episodes. High-frequency planktonic modifications are well documented in the Sicily Channel and Alboran Sea and highlight the occurrence of different steps within a single stadial (cold phase)/interstadial (warm phase) oscillation.

The review of planktonic organisms in the marine

sedimentary archive casts light on the uniqueness of the Mediterranean Sea, especially in terms of climatic/oceanographic/biological interaction and influence of different climatic systems on distinct areas. Further research is needed in the eastern Mediterranean Sea where results are obscured by low-resolution sedimentary records and by a strong focus on sapropel deposition dynamics.

Keywords: Planktonic Foraminifera; Coccolithophores; Mediterranean Sea; Late Quaternary


1 Introduction

The Mediterranean region is located in a transitional zone, between subtropical and midlatitude regimes [1]; the northern area is linked to the midlatitude variability, the North Atlantic Oscillations and other teleconnection patterns, such as the Scandinavian, the East Atlantic and the East Atlantic/northern Russia patterns [2], and the southern and the easternmost parts of the region are under the influence of the descending branch of the Hadley cell and of the East African monsoon in summer [1, 3]. The monsoon system may have significantly modified the Mediterranean thermohaline circulation in the past through enhanced Nile river runoff, leading to deep water formation failure in the Adriatic and Aegean Sea and the deposition of anoxic sediments on the eastern Mediterranean sea floor [3–5].

The Mediterranean Sea is also a key laboratory to test the response of organisms to hydrological transformations driven by climate change. The reduced volume of the basin makes the Mediterranean susceptible to amplified hydrological variations that impact marine ecosystems. Significant sea surface temperature (SST), salinity, thermohaline circulation strength and nutrient availability variations have been identified in the western/central Mediterranean Sea during the late Quaternary [6–18].

***Corresponding Author: Alessandro Incarbona:** Università di Palermo, Dipartimento di Scienze della Terra e del Mare, Via Archirafi 22, 90134 Palermo, Italy; Email: alessandro.incarbona@unipa.it; Tel. +39 09123864650; Fax: 09123860834
Enrico Di Stefano, Rodolfo Sprovieri: Università di Palermo, Dipartimento di Scienze della Terra e del Mare, Via Archirafi 22, 90134 Palermo, Italy

Serena Ferraro: Università degli Studi di Urbino “Carlo Bo”, Dipartimento di Scienze della Terra, della Vita e dell’Ambiente, Campus Scientifico Località Crocicchia, 61029 Urbino, Italy; Consiglio Nazionale delle Ricerche, Istituto per l’Ambiente Marino Costiero, Sezione Capo Granitola, Via del Mare 3, 91021 Torretta Granitola (Campobello di Mazara, Trapani), Italy

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Foraminifera and coccolithophores are among the most important planktonic organisms, together with diatoms which are only rarely preserved in the Mediterranean sedimentary archive [19]. Standard ocean biozonation is not always usable, necessitating the adoption of regional planktonic foraminifera and coccolithophore schemes for the Oligocene to the present [20–22], highlighting that the Mediterranean Sea behaved as a distinct bioprovince due to its gradual isolation from oceans.

The trophic levels of the Mediterranean Sea are among the poorest in the world's oceans, as mirrored by the analysis of living planktonic foraminifera and coccolithophore assemblages from water samples and sediment traps. A strong seasonality, characterized by very low biomass (oligotrophic regime) during late spring-summer and higher biomass in late fall-winter (mesotrophic regime), has been noted from oceanographic cruises [23, 24], as well as from 12-year-long sediment trap samples [25]. A marked west-east trend towards oligotrophy can be seen in both calcareous plankton assemblages [23, 24] and follows the same increasing nutrient depletion trend, especially due to phosphorous shortage [26]. However, many local investigations [27–39] point out the great fragmentation of the Mediterranean marine environment that reflects the occurrence of temporary uplift of waters (local upwelling), small-scale cyclonic and anticyclonic gyres and frontal zones [40, 41].

Here we present a review of recent studies dealing with the analysis of planktonic foraminifera and coccolithophores in Mediterranean sediments of the last 130,000 years, since the last interglacial. We examine whether calcareous planktonic assemblages were modified between glacial/interglacial switches and during abrupt climatic changes, i.e. at orbital- and suborbital-scales, respectively. Finally, we compare results from different Mediterranean areas, such as from the western and eastern basins, and discuss the most likely climatic forcings that may have driven marine ecosystem variations.

2 The Calcareous Plankton Response to Glacial/Interglacial Switches

In the following we focus on modifications in calcareous plankton assemblages during the last 130,000 years (since the last interglacial period). The main reason for such a choice deals with the availability of data, given that most of the sedimentary material recovered in the Mediter-

ranean sea floor is from gravity cores (that is limited in length), and the reliability of age models that can benefit from radiocarbon datings and peak-to-peak correlations with Greenland ice cores. Specifically, the age models of Ocean Drilling Program (ODP) Site 963 and Hole 977A were assessed by calibrated accelerator mass spectrometry radiocarbon datings, oxygen isotopic and event stratigraphy [10, 11, 14, 15, 42, 43].

2.1 Planktonic Foraminifera

Late Quaternary planktonic foraminifera assemblages are dominated by *Globigerina bulloides* (which indicate high fertility surface water), *Globigerinoides ruber* (warm and oligotrophic surface water), *Neogloboquadrina pachyderma* right coiling (dx) (deep chlorophyll maximum, or DCM) and *Turborotalita quinqueloba* (high fertility surface water) [24, 25, 44, 45].

Studies carried out in the Sicily Channel (ODP Site 963) and in the Alboran Sea (ODP Hole 977A) provide the highest-resolution records for the selected time domain and illustrate planktonic foraminifera modifications across glacial/interglacial cycles in the western-central Mediterranean Sea (Fig. 1) [10, 11, 15, 42, 43]. A coherent framework emerges from the comparison of the two sites, although there are minor discrepancies due to the west-east temperature and productivity gradients. For example, there is a higher abundance of *G. ruber* and almost absence of left coiling *N. pachyderma* in the Sicily Channel. Interglacials (Holocene and MIS 5e) are characterized by positive peaks in the *G. ruber* distribution pattern (Figs. 2 and 3), suggesting the presence of warm and oligotrophic surface waters. *Globigerina bulloides*, *N. pachyderma* dx and *T. quinqueloba* dominate the assemblages during the last glacial period (MIS 4-2, Figs. 2 and 3) and indicate the presence of cold and productive waters. The scheme described above seems to be suited for a large Mediterranean area that includes other Sicily Channel and Alboran Sea sites, the Gulf of Lions, the Sardinia Channel, the Balearic, the Tyrrhenian and the Adriatic Sea [e.g. 46–54]. A few exceptions deal with, for instance, very coastal sites along the Tyrrhenian Sea where *G. bulloides*, *N. pachyderma* dx and *T. quinqueloba* are very abundant even during the Holocene [47].

A clear turnover in planktonic foraminifera assemblages is not readily observed across glacial/interglacial switches in the eastern Mediterranean Sea, where *G. ruber* is common and abundant down to levels dated to the last glacial period [48, 55–57]. The dataset (compiled from 37 sedimentary cores) used to reconstruct sea sur-

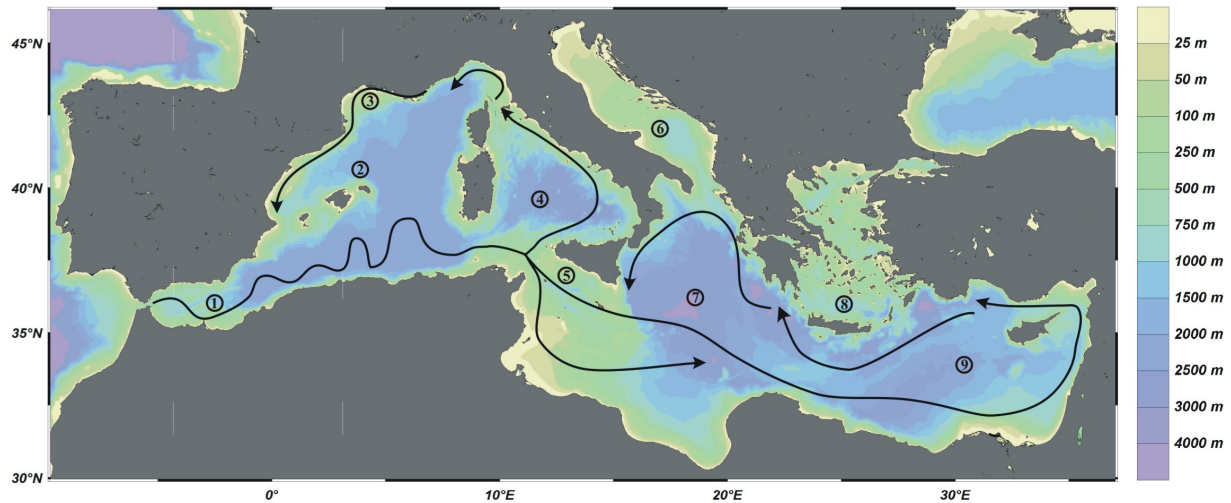


Figure 1: Bathymetric map of the Mediterranean Sea and location of ODP 963 and 977 cores. Black arrows show the path of surface water circulation [modified from (author?) 116, 117]. Black circles represent the location of basins and the main cores discussed in the text: 1) Alboran Sea, ODP Hole 977A; 2) Balearic Sea; 3) Gulf of Lions; 4) Tyrrhenian Sea; 5) Sicily Channel, ODP Site 963; 6) Adriatic Sea 7) Ionian Sea; 8) Aegean Sea; 9) Levantine Sea.

face temperature in the Mediterranean Sea during the last glacial maximum (LGM, around 20 ka) [58, data available at: <http://doi.pangaea.de/10.1594/PANGAEA.227307>] offers a suitable snapshot to assess the spatial distribution of planktonic foraminifera. In Figure 4, the ratio between *G. ruber* and (*G. bulloides* + *N. pachyderma* dx + *T. quinqueloba*) is plotted against latitude (Fig. 4a) and longitude (Fig. 4b). It is worth noting the significant correlation between the ratio and degrees longitude ($R^2 = 0.66$) that illustrates the different behaviour of planktonic foraminifera assemblages during the LGM in the western and eastern Mediterranean subbasins (Fig. 4b), characterized by cold/productive and warm/oligotrophic surface waters, respectively. The Mediterranean area between 10° and 20°E shows the highest scattering, which can readily be explained by the unevenness of geographic features, including the Sicily Channel, Tyrrhenian, Ionian and Adriatic Sea, and the wide latitudinal length (30°–45°N). The latitude is also a strong spatial factor and is significantly ($R^2 = 0.59$) correlated to the ratio (Fig. 4a). The northernmost regions where Mediterranean deep water forms (Gulf of Lions, Adriatic and Aegean Sea) experience the blow of strong northern winds that induce cooling and increased productivity. In many reports from the Adriatic and Aegean Sea, the distribution pattern of the principal planktonic foraminifera species seems to be comparable to western-central Mediterranean sites [e.g. 47, 59–62].

A strong orbital control is exerted on planktonic foraminifera assemblages in the eastern Mediterranean Sea. Deposition of sapropel layers coincides with max-

ima in the Northern Hemisphere summer insolation and the monsoon index [4, 63–65], which would have produced an abnormal input of freshwater runoff from the Nile [3, 5, 66]. The lack of deep water formation in the eastern Mediterranean Sea and the slowdown of the Mediterranean thermohaline circulation may have led to pycnocline/nutricline shallowing into the lower part of the photic zone [67, 68]. Peaks of *N. pachyderma* dx that coincide with late Quaternary sapropels demonstrate the occurrence of a DCM [55, 69] and represent the best evidence for the orbital-controlled switch to high-productivity conditions in the eastern Mediterranean Sea marine environment.

2.2 Coccolithophores

Although much fewer coccolithophore results are available by web data bank, the visual inspection of investigations from different Mediterranean sites strongly points to dynamics that are readily comparable to those of planktonic foraminifera. In Figure 5, coccolithophore taxa are grouped following ecological preferences [15, 70, 71] for the last 130 ka in the Sicily Channel as follows: ‘Placoliths’ are r-strategist taxa and indicate high surface productivity [72–74]; *Florisphaera profunda*, the most abundant species of ‘Lower Photic Zone’ taxa, is a proxy for a deep nutricline and low productivity conditions [14, 74–77]; ‘Upper Photic Zone’ (UPZ) taxa are K-strategist taxa and indicate surface oligotrophy [72, 78, 79]; and the ‘Mis-

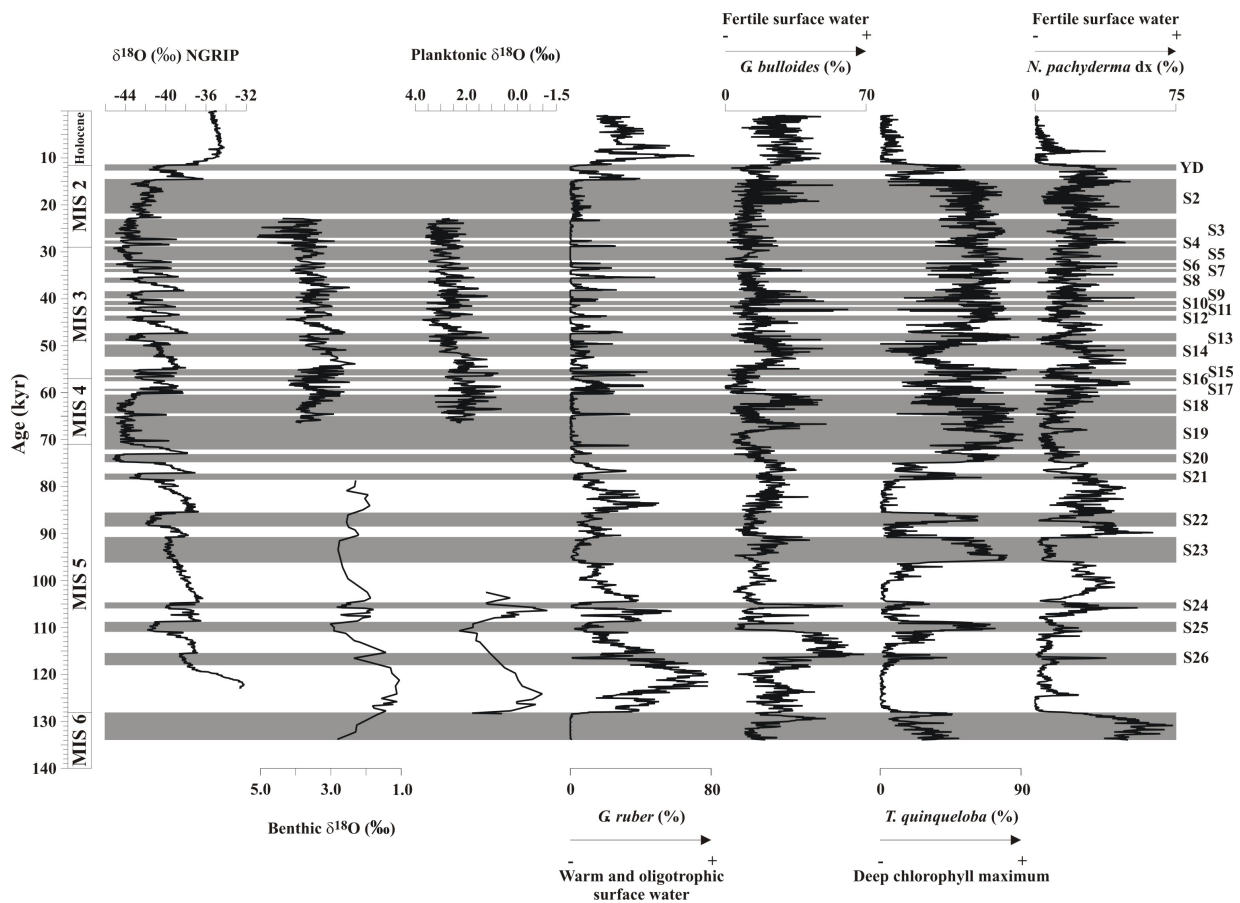


Figure 2: Downcore variations of geochemical data and planktonic foraminifera species at ODP Site 963, plotted versus calibrated age (kyr). From the left, oxygen isotopic record of Greenland ice cores (NGRIP members, 2004); benthic and planktonic oxygen isotopic records at ODP Site 963 [11, 17]; distribution patterns of *G. ruber*, *G. bulloides*, *T. quinqueloba* and *N. pachyderma* dx at ODP Site 963, expressed as percentage values [11, 15, 17, 80] and their ecological preference. Light grey bands mark stadials, white bands mark interstadials. S26 to S2 show the sequence of stadials. YD: Younger Dryas.

cellaneous' group includes species with diverse ecological preferences that on the whole may be assimilated to a weak K-strategist tendency [15, 72, 80]. Coccolithophore distribution patterns show very high abundance of placoliths during the last glacial period, as well as abundance peaks of *Florisphaera profunda* and UPZ taxa during the Holocene and MIS 5 (especially MIS 5e). The switch between high productivity (*Gephyrocapsa* spp. and *Emiliana huxleyi* blooming) during glacials and a deep nutricline and surface oligotrophy during interglacials is further highlighted by the N ratio [74, 81]. At the base of the Holocene, the *F. profunda* increase (and the N ratio decrease) may also be detected in the Balearic and Tyrrhenian Sea [49, 82].

The analysis of the number of coccoliths per gram of sediment in the Alboran Sea displays an opposite behaviour (the highest productivity during Holocene sediments) and interpretation. This may be due to the fact that

the lower global sea level during the last glacial period led to a marked decrease in the Atlantic/Mediterranean exchange and a significant density gradient between surface and subsurface water [83, 84], which may have impacted surface ecosystems, limiting the nutrient uplift. However, we argue that, first, a correction for the dry bulk density and for sedimentation rates would be needed to address a real coccolithophore flux signal [e.g. 77, 85]. In other words, the number of coccoliths per gram of sediment is dependent on many factors different than production, for instance dilution by terrigenous material, which is expected to be much higher during glacials. Second, we argue that the impact of a significant density gradient on marine ecosystems would be largely dependent on the horizon location within the water column. To our knowledge, a numerical estimate of the density gradient depth between surface and subsurface water does not exist, and it is reasonable that during the 110-15 ka interval (or 70-15 ka, tak-

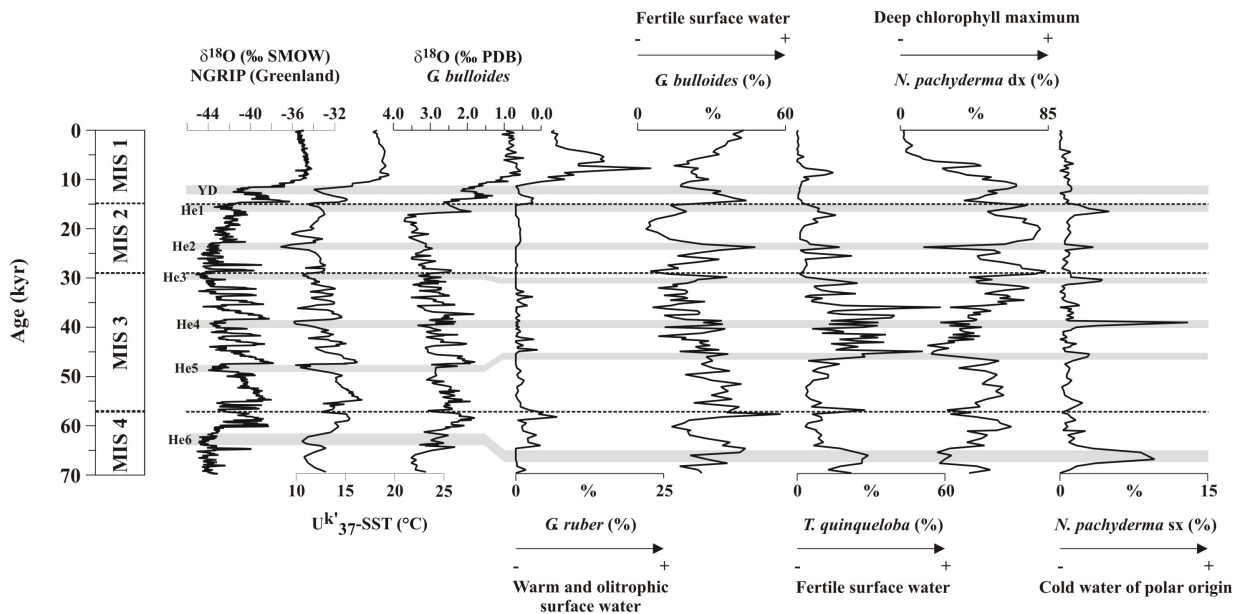


Figure 3: Downcore variations of geochemical data and planktonic foraminifera species at ODP Hole 977A, plotted versus calibrated age (kyr). From the left, oxygen isotopic record of Greenland ice cores [106]; alkenone-derived sea surface temperature and the *G. bulloides* oxygen isotopic record at ODP Hole 977A [12]; distribution patterns of *G. ruber*, *G. bulloides*, *T. quinqueloba*, *N. pachyderma* dx and *N. pachyderma* sx at ODP Hole 977A, expressed as percentage values [42] and their ecological preference. Light grey bands mark Heinrich events (He6-He1). Note that Heinrich events between geochemical and micropaleontological data are slightly misaligned, because they are plotted following the age model provided by [12, 42], respectively. YD: Younger Dryas.

ing into account the whole MIS 5 as an interglacial) there was a wide set of vertical fluctuations. In any case, less volume exchanged at Gibraltar implies a thinner Atlantic surface water inflow, which today is about 200 metres-thick and covers the whole photic zone (e.g. [86, 87]). Thus, paradoxically, the reduced water exchange at Gibraltar may even favour surface fertility through the shallowing of intermediate water masses that are nutrient-enriched [26].

In the eastern Mediterranean basin, the orbitally controlled sapropel dynamics drive coccolithophore assemblage modifications. The nutricline shallowing produces distinct DCM levels, as evidenced by *F. profunda* abundance peaks [57, 77, 85, 88–92]. The establishment of a DCM does not necessarily imply that the coccolithophore productivity increased. Recent studies demonstrate that *F. profunda* peaks during sapropel S5 and S1 are accompanied by a concomitant decrease in the total flux of coccoliths [77, 85, 91]. Specifically, the number of coccoliths $\times \text{cm}^{-2} \times \text{kyr}^{-1}$ is markedly higher below and above sapropel layers. This is in agreement with the significant anticorrelation between *F. profunda* percentage values in surface sediments of both the Sicily Channel and eastern Mediterranean Sea and primary productivity derived by satellite imagery (Fig. 6) [77, 85].

Decreased coccolithophore fluxes within sapropels would apparently contradict the well-established geo-

chemical evidence of increased productivity, such as high values in the Ba/Al ratio and light values in the $\delta^{15}\text{N}$ [e.g. 93–98]. One possible explanation deals with increased primary productivity in a different phytoplankton compartment. Diatoms may successfully compete with coccolithophores in eutrophic environments [99]. A study of rarely preserved siliceous remains in the sapropels S5 layer recovered south of Crete points to the crucial role of mat-forming diatoms to explain enhanced primary productivity in the lower photic zone [19].

3 The Calcareous Plankton Response to Suborbital-Climatic Fluctuations

High-frequency climatic variations in the Northern Hemisphere over the last 130 kyr, which are not due to the Earth's orbital motion, were initially traced in both Greenland ice and North Atlantic cores [100, 101]. They are characterized by marked fluctuations called Dansgaard-Oeschger (D-O) oscillations during the last glacial period, with stadials (cold phases) and interstadials (warm phases) that alternate about every 1,500 years and are rec-

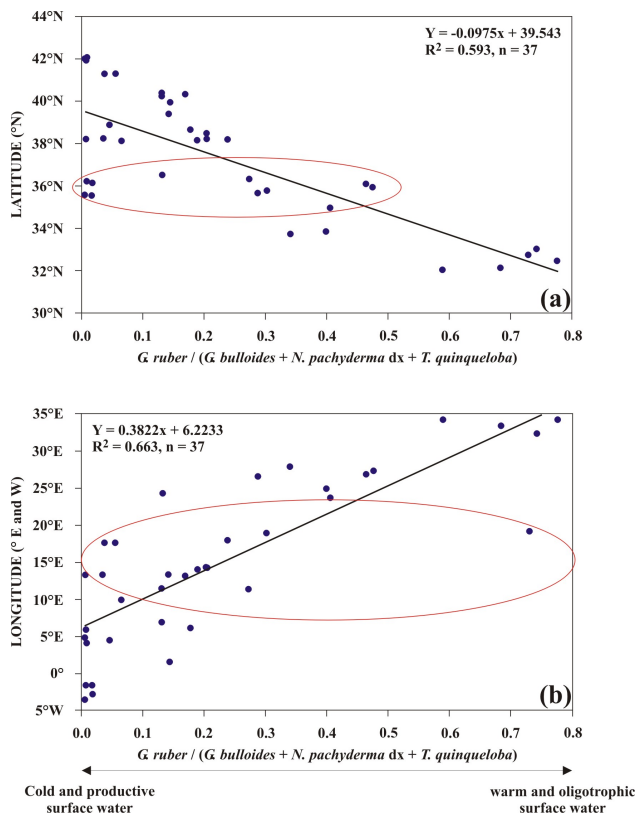


Figure 4: Plots of the planktonic foraminifera ratio between *G. ruber* and (*G. bulloides* + *N. pachyderma* dx + *T. quinqueloba*) versus the location (Fig. 4a latitude; Fig. 4b longitude) of Mediterranean cores selected by [58] for sea surface temperature reconstructions during the last glacial maximum (around 20 ka; the data set is available at <http://doi.pangaea.de/10.1594/PANGAEA.227306>). Correlation indices are shown. Red ellipses in both Figure 4a and 4b shows scattered points whose meaning is discussed in the text.

ognized across the whole Northern Hemisphere [102, 103]. Climatic instability is also documented within the last interglacial and Holocene [104–106].

The stadial/interstadial alternation drove the Mediterranean thermohaline circulation with an opposite behaviour with respect to the Atlantic Meridional Overturning Circulation (AMOC); that is, stadials were characterized by enhanced circulation and bottom ventilation and vice versa [6, 12, 13]. The significant impact on calcareous plankton assemblages has been recognized in the Sicily Channel (Figs. 2 and 5). Cold and more productive waters mark interglacial stadials, up to S25 during the last interglacial [11, 71] and within the Holocene [14]. Three different scenarios are associated with each D-O cycle of the last glacial [15]: 1) oligotrophic surface water and a deep nutricline in the early interstadials; 2) a DCM and coccolithophore winter/spring blooming in the late interstadials;

3) reduced productivity and a shallower nutricline during stadials.

The reduced productivity during stadials is also clearly indicated by geochemical and micropaleontological investigations on the Alboran Sea sedimentary record [7, 107–109]. One possible explanation of this phenomenon deals with the significant density gradient between surface and subsurface water, produced during the last glacial by global sea level fall [83, 84] and by vertical mixing disturbance due to input of fresher water of polar origin. The incursion of low-salinity waters is documented in both the Alboran Sea and the Sicily Channel by light isotopic values in planktonic foraminifera shells [17, 110, 111] during the southward shift of the Polar front and the deposition of ice rafted detritus (Heinrich events) in the North Atlantic Ocean. The high offset recorded in the isotopic values of benthic and planktonic foraminifera in the Sicily Channel suggests the possible occurrence of such a disturbance for many stadials [15].

The teleconnection between the monsoon climate system and the AMOC during the late Quaternary is well-established [e.g. 112–114] and may also have impacted the eastern Mediterranean Sea circulation. Salinity and/or temperature, speed, ventilation and the vertical location of the Levantine Intermediate Water seem to be modified across stadial/interstadial phases over the past 130 ka, both in the Sicily Channel and the Corsica Trough [11, 16, 17]. However, there is no evidence of high-frequency climate impact on calcareous plankton assemblages. It is possible that resulting hydrological variations were not able to impact surface marine ecosystems, for instance if nutricline re-locations did not reach the photic zone. Alternatively, missing evidence may be the result of a low-resolution investigation, inability to gather the millennial and centennial-scale signal, or micropaleontological studies with a different target, for instance sapropel deposition dynamics.

4 The Importance of Further Mediterranean Investigations on Planktonic Ecosystems

The Mediterranean Sea conveyor belt reproduces ocean processes that can be observed at a reasonable spatial scale and interacts with different climate systems that operate at middle and high-latitude. The plume of warm and saline water of the Mediterranean outflow enhances the North Atlantic water density and may precondition deep

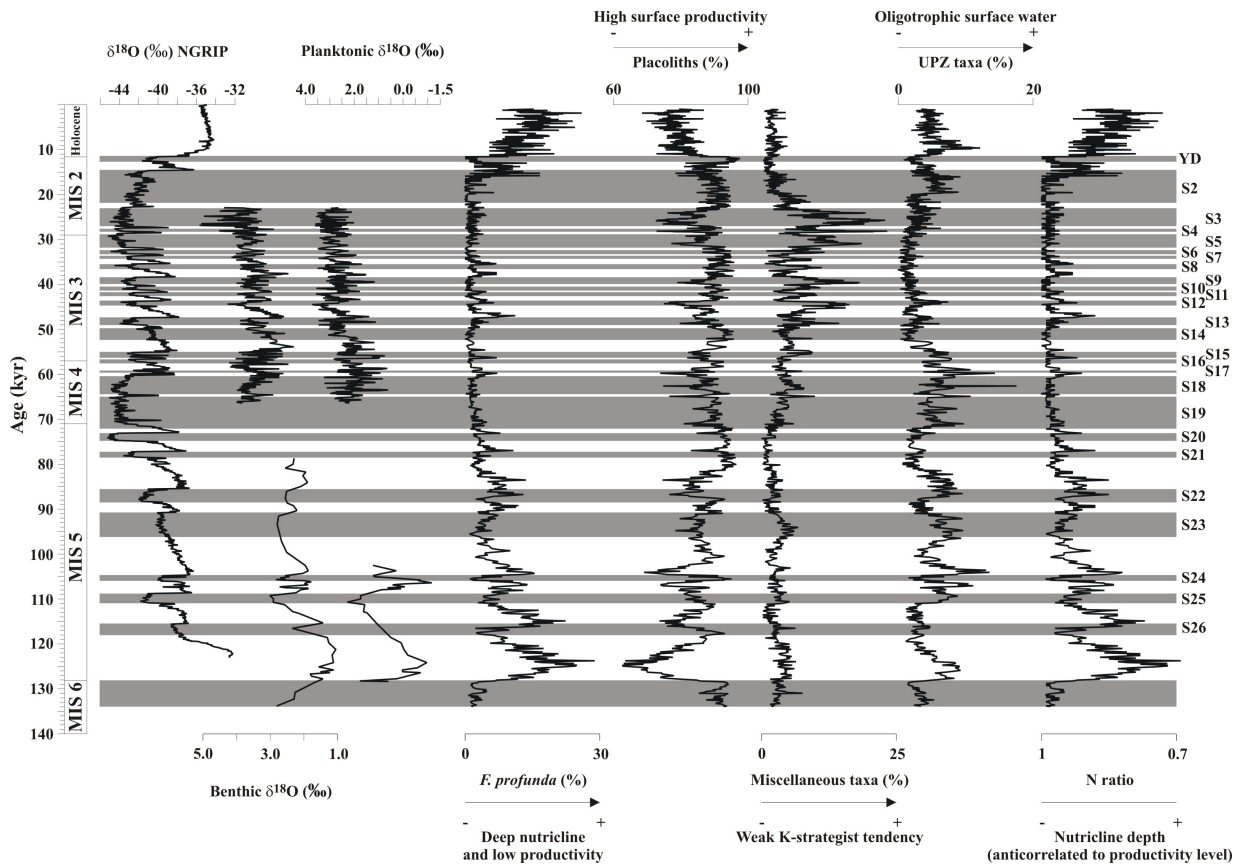


Figure 5: Downcore variations of geochemical data and coccolithophore taxa and groups at ODP Site 963, plotted versus calibrated age (kyr). From the left, oxygen isotopic record of Greenland ice cores (NGRIP members, 2004); benthic and planktonic oxygen isotopic records at ODP Site 963 [11, 17]; distribution patterns of *F. profunda*, placoliths, miscellaneous and UPZ taxa at ODP Site 963, expressed as percentage values [11, 15, 17, 80] and their ecological preference; distribution pattern of the N ratio, assessed by small placoliths / (small placoliths + *F. profunda*), following [74]. Light grey bands mark stadials, white bands mark interstadials. S26 to S2 show the sequence of stadials. YD: Younger Dryas.

water formation [115]. The enhanced water exchange at the Gibraltar Strait and the denser outflow during last glacial period cold spells may have fed the AMOC after periods of slowdown [84]. These topics justify the broad scientific interest in the Mediterranean Sea, despite the fact that it represents about 1% of the world's ocean water volume.

The planktonic community investigation from Mediterranean sedimentary archives may be equally important to understanding the biological response to climate forcing, mediated by hydrological dynamics. The present-day Mediterranean Sea primary productivity shows a wide range of seasonally-controlled trophic regimes. Productivity patterns span from 'bloom' conditions that are nearly identical to the North Atlantic Ocean, with a distinct spring maximum in the Gulf of Lions, to 'non-blooming' conditions in most of the eastern basin where a slight increase in productivity is observed in fall and winter [41]. Meso-scale permanent and semi-permanent gyres, frontal dynamics and seasonal

vertical dynamics of the water column further fragment the Mediterranean Sea environment. There is little doubt that such a variety of hydrological features and climatic and seasonal-induced variations is unique in the world's oceans. This is one of the reasons why the Mediterranean still represents one of the most appealing regions for marine biologists.

The marked trophic difference in the planktonic communities of the western and eastern (and northern and southern) Mediterranean also existed during the LGM (Fig. 4). Planktonic foraminifera and coccolithophore assemblages were immediately modified by climatic solicitations of abrupt suborbital oscillations in western-central and by sapropel dynamics in the eastern basin. Although the three-step modification described for D-O oscillations in both Sicily Channel and Alboran Sea calcareous plankton groups needs to be verified in ocean sediments to assess whether it is a local (and unique) response to climate forcing, this abrupt response

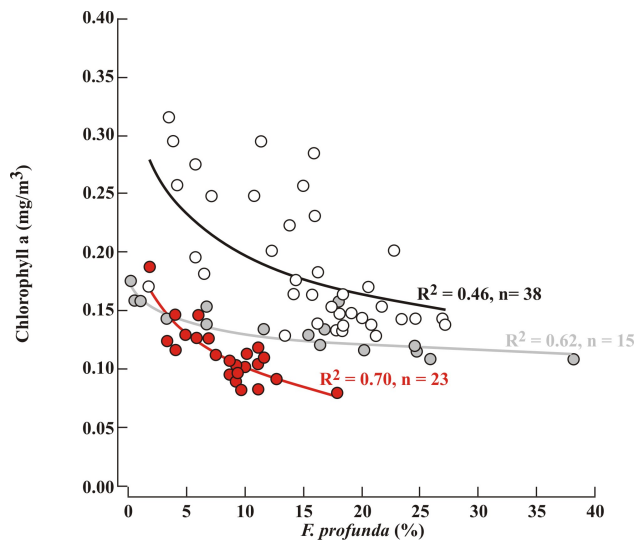


Figure 6: Plots of *F. profunda* percentage values in the eastern Mediterranean Sea [red dots 77], and in northern and southern Sicily Channel [white and grey dots 118] versus satellite-derived chlorophyll *a* values. Correlation indices are shown. The data set is available at <http://doi.pangaea.de/10.1594/PANGAEA.805695>.

to climate forcing is alarming in light of the significant impacts of global warming in the near future. Increased SST and $p\text{CO}_2$, the introduction of alien species, coastal pollution and fishing overexploitation may synergically act on planktonic communities and in turn may profoundly affect the Mediterranean Sea trophic chain. Thus, the extreme sensitivity of plankton groups found in the present study, as well as results from future high-resolution studies, will be a basic prerequisite for reliable prediction of Mediterranean Sea ecosystem transformation.

5 Concluding Remarks

The review of planktonic foraminifera and coccolithophore data from the Mediterranean Sea over the last 130,000 years (since the last interglacial) points to the unique importance of this area for understanding climatic, hydrological and biological interaction. The Mediterranean calcareous plankton ecosystem is extremely sensitive to climatic variations, both orbitally- and suborbitally-induced, and reveals the simultaneous impact of different climatic systems. Cold sea surface temperature and higher productivity characterize the last glacial period in the western (Alboran and Balearic Sea, Gulf of Lions), central (Sicily Channel and Tyrrhenian Sea) and northern (Adriatic and Aegean Sea) Mediterranean Sea, possibly due to strengthened Polar Vortex action. Maxima in the

Northern Hemisphere summer insolation and in the monsoon index drove calcareous plankton dynamics and led to the establishment of distinct DCM layers during eastern Mediterranean sapropel deposition.

The whole sequence of late Quaternary suborbital climatic oscillations is recorded in planktonic foraminifera and coccolithophore assemblage variations of the Sicily Channel and Alboran Sea. The in-depth examination of each D-O cycle of the last glacial period casts light on abrupt marine ecosystem modifications that can be summarized by a three-fold scenario. This again reflects teleconnection with the high-middle latitude Atlantic Ocean climatic system and possible disturbance of low-saline inflow water during relevant southward shifts of the Polar Front. So far, no evidence exists of high-frequency changes in the plankton from the ultra-oligotrophic eastern Mediterranean Sea, possibly because hydrological variations were too subtle to impact biological processes. Further research on high-resolution sedimentary records is needed to verify whether high-frequency monsoon activity may stimulate different water column and biological productivity dynamics.

The abrupt response to climate forcing of planktonic communities in the Mediterranean Sea observed in the recent past highlights the vulnerability of the basal trophic chain level to subtle environmental variations. The study of calcareous plankton in Mediterranean sedimentary archives still represents a unique opportunity to understand climatic/hydrological and biological interactions and to predict the near future marine environment evolution.

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References

- [1] Lionello P., *The Climate of the Mediterranean Region*. Elsevier, Amsterdam, The Netherlands, 2012, 1–502.
- [2] Josey S.A., Somot S., Tsimplis M., Impacts of atmospheric modes of variability on Mediterranean Sea surface heat exchange. *Journal of Geophysical Research* 2011, 116, 1–15.
- [3] Rohling E.J., Marino G., Grant K.M., Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels). *Earth-Science Reviews* 2015, 143, 62–97.
- [4] Rossignol-Strick M., African monsoons, an immediate response to orbital insolation. *Nature* 1983, 30, 446–449.
- [5] Rohling E.J., Cane T.R., Cooke S., Sprovieri M., Bouloubassi I., Emeis K.C., Schiebel R., Kroon D., Jorissen F.J., Lorre A., Kemp

- A.E.S., African monsoon variability during the previous interglacial maximum. *Earth and Planetary Science Letters*, 2002, 202, 61–75.
- [6] Cacho I., Grimalt J.O., Pelejero C., Canals M., Sierro F.J., Flores J.A., Shackleton N., Dansgaard-Oeschger and Heinrich event imprints in Alboran Sea paleotemperatures. *Paleoceanography* 1999, 14, 698–705.
- [7] Cacho I., Grimalt J.O., Sierro F.J., Shackleton N., Canals M., Evidence for enhanced Mediterranean thermohaline circulation during rapid climatic coolings. *Earth and Planetary Science Letters* 2000, 183, 417–429.
- [8] Cacho I., Grimalt J.O., Canals M., Sbaiffi L., Shackleton N.J., Schoenfeld J., Zahn R., Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climate changes. *Paleoceanography*, 2001, 16, 40–52.
- [9] Cacho I., Grimalt J.O., Canals M., Response of the Western Mediterranean Sea to rapid climatic variability during the last 50,000 years: a molecular biomarker approach. *Journal of Marine Systems*, 2002, 33, 253–272.
- [10] Sprovieri R., Di Stefano E., Incarbona A., Gargano M.E., A high-resolution record of the last deglaciation in the Sicily Channel based on foraminifera and calcareous nannofossil quantitative distribution. *Palaeogeography Palaeoclimatology Palaeoecology*, 2003, 202, 119–142.
- [11] Sprovieri R., Di Stefano E., Incarbona A., Oppo D.W., Suborbital climate variability during Marine Isotopic Stage 5 in the central Mediterranean Basin: evidence from calcareous plankton. *Quaternary Science Reviews*, 2006, 25, 2332–2342.
- [12] Martrat B., Grimalt J.O., Lopez-Martinez C., Cacho I., Sierro F.J., Flores J.A., Zahn R., Canals M., Curtis J.H., Hodell D.A., Abrupt Temperature Changes in the Western Mediterranean over the Past 250,000 Years. *Science*, 2004, 306, 1762–1765.
- [13] Frigola J., Moreno A., Cacho I., Canals M., Sierro F.J., Flores J.A., Grimalt J.O., Evidence of abrupt changes in Western Mediterranean Deep Water circulation during the last 50 kyr: A high-resolution marine record from the Balearic Sea. *Quaternary International*, 2008, 181, 88–104.
- [14] Incarbona A., Di Stefano E., Patti B., Pelosi N., Bonomo S., Mazzola S., Sprovieri R., Tranchida G., Zgozi S., Bonanno A., Holocene millennial-scale productivity variations in the Sicily Channel (Mediterranean Sea). *Paleoceanography*, 2008, 23, 1–18.
- [15] Incarbona A., Sprovieri M., Di Stefano A., Di Stefano E., Salvaggio Manta D., Pelosi N., Ribera d'Alcalà M., Sprovieri R., Ziveri P., Productivity modes in the Mediterranean Sea during Dansgaard-Oeschger (20,000–70,000 yr ago) oscillations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2013, 392, 128–137.
- [16] Toucanne S., Jouet G., Ducassou E., Bassetti M.-A., Dennielou B., Angue Minto'o C.M., Lahmi M., Touyet N., Charlier K., Lericola G., Mulder T., A 130,000-year record of Levantine Intermediate Water flow variability in the Corsica Trough, western Mediterranean Sea. *Quaternary Science Reviews*, 2012, 33, 55–73.
- [17] Sprovieri M., Di Stefano E., Incarbona A., Salvaggio Manta D., Pelosi N., Ribera d'Alcalà M., Sprovieri R., Centennial-to millennial-scale climate oscillations in the Central-Eastern Mediterranean Sea between 20,000 and 70,000 years ago: Evidence from a high-resolution geochemical and micropaleontological record. *Quaternary Science Reviews*, 2012, 46, 126–135.
- [18] Ausín B., Hernández-Almeida I., Flores J.-A., Sierro F.-J., Grosjean M., Francés G., Alonso B., Development of coccolithophore-based transfer functions in the western Mediterranean sea: a sea surface salinity reconstruction for the last 15.5 kyr. *Climate of the Past*, 2015, 11, 1635–1651, doi:10.5194/cp-11-1635-2015.
- [19] Kemp A.E.S., Pearce R.B., Koizumi I., Pike J., Rance S.J., The role of mat-forming diatoms in the formation of Mediterranean sapropels. *Nature*, 1999, 398, 57–61.
- [20] Rio D., Raffi I., Villa G., Pliocene-Pleistocene calcareous nannofossil distribution patterns in the western Mediterranean. In Kastens K.A. (Ed.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 1990, 107, 513–533.
- [21] Sprovieri R., Pliocene-early Pleistocene astronomically forced planktonic foraminifera abundance fluctuations and chronology of Mediterranean calcareous plankton bio-events. *Rivista Italiana di Paleontologia e Stratigrafia*, 1993, 99, 371–414.
- [22] Raffi I., Mozzato C., Fornaciari E., Hilgen F.J., Rio D., Late Miocene calcareous nannofossil biostratigraphy and astrobiochronology for the Mediterranean region. *Micropaleontology*, 2003, 49, 1–26.
- [23] Knappertsbusch M., Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea. *Marine Micropaleontology*, 1993, 21, 219–247.
- [24] Pujol C., Vergnaud-Grazzini C., Distribution patterns of live planktonic foraminifera as related to regional hydrography and productive system of the Mediterranean Sea. *Marine Micropaleontology*, 1995, 25, 187–217.
- [25] Rigual-Hernández A.S., Sierro F.J., Bárcena M.A., Flores J.-A., Heussner S., Seasonal and interannual changes of planktonic foraminiferal fluxes in the Gulf of Lions (NW Mediterranean) and their implications for paleoceanographic studies: Two 12-year sediment trap records. *Deep-Sea Research I*, 2012, 66, 26–40.
- [26] Krom M.D., Emeis K.-C., Van Cappellen P., Why is the Eastern Mediterranean phosphorus limited? *Progress in Oceanography*, 2010, 85, 236–244.
- [27] Ziveri P., Rutten A., De Lange G.J., Thomson J., Corselli C., Present-day coccolith fluxes recorded in central eastern Mediterranean sediment traps and surface sediments. *Palaeogeography Palaeoclimatology Palaeoecology*, 2000, 158, 175–195.
- [28] Cros L., Fortuño J.M., Atlas of Northwestern Mediterranean Coccolithophores. *Scientia Marina*, 2002, 66, 1–186.
- [29] Malinverno E., Ziveri P., Corselli C., Coccolithophorid distribution in the Ionian Sea and its relationship to eastern Mediterranean circulation during late fall to early winter 1997. *Journal of Geophysical Research*, 2003, 108, doi:10.1029/2002JC001346.
- [30] Malinverno E., Dimiza M.D., Triantaphyllou M.B., Dermizakis M.D., Corselli C., Coccolithophores in the Eastern Mediterranean. ION Publishing Group, Athens, 2008, 1–188.
- [31] Malinverno E., Triantaphyllou M.V., Stavrakakis S., Ziveri P., Lykousis V., Seasonal and spatial variability of coccolithophore export production at the South-Western margin of Crete (Eastern Mediterranean). *Marine Micropaleontology*, 2009, 71, 131–147.
- [32] Malinverno E., Maffioli P., Corselli C., De Lange G.J., 2014, Present-day fluxes of coccolithophores and diatoms in the pelagic Ionian Sea. *Journal of Marine System*, 2014, 132, 13–27.
- [33] Bárcena M.A., Flores J.A., Sierro F.J., Pérez-Folgado M., Fabres J., Calafat A., Canals M., Planktonic response to main oceanographic changes in the Alboran Sea (Western Mediterranean) as

- documented in sediment traps and surface sediments. *Marine Micropaleontology*, 2004, 53, 423–445.
- [34] Triantaphyllou M.V., Ziveri P., Tselepidis A., Coccolithophore export production and response to seasonal surface water variability in the oligotrophic Cretan Sea (NE Mediterranean). *Micropaleontology*, 2004, 50, 127–144.
- [35] Balestra B., Marino M., Monechi S., Marano C., Locaiono F., Coccolithophore communities in the Gulf of Manfredonia (Southern Adriatic Sea): Data from water and surface sediments. *Micropaleontology*, 2008, 54, 377–396.
- [36] Dimiza M.D., Triantaphyllou M.V., Dermitzakis M.D., Seasonality and ecology of living coccolithophores in Eastern Mediterranean coastal environments (Andros Island, Middle Aegean Sea). *Micropaleontology*, 2008, 54, 159–175.
- [37] Hernández-Almeida I., Bárcena M.A., Flores J.A., Sierro F.J., Sanchez-Vidal A., Calafat A., Microplankton response to environmental conditions in the Alboran Sea (Western Mediterranean): One year sediment trap record. *Marine Micropaleontology*, 2011, 78, 14–24.
- [38] Bonomo S., Cascella A., Alberico I., Ferraro L., Giordano L., Lirer F., Vallefuoco M., Marsella E., Coccolithophores from near the Volturno estuary (central Tyrrhenian Sea). *Marine Micropaleontology*, 2014, 111, 26–37.
- [39] Bonomo S., Grelaud M., Incarbona A., Malinverno E., Placenti F., Bonanno A., Di Stefano E., Patti B., Sprovieri M., Ziveri P., Genovese S., Rumolo P., Mazzola S., Zgozi S., Living Coccolithophores from the Gulf of Sirte (Southern Mediterranean Sea) during the summer of 2008. *Micropaleontology*, 2012, 58, 487–503.
- [40] Klein P., Coste P., Effects of wind stress variability on nutrient transport into the mixed layer. *Deep-Sea Research*, 1984, 31, 21–37.
- [41] D’Ortenzio F., Ribera d’Alcalà M., On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosciences*, 2009, 6, 139–148.
- [42] Pérez-Folgado M., Sierro F.J., Flores J.-A., Cacho I., Grimalt J.O., Zahn R., Western Mediterranean planktonic foraminifera events and climatic variability during the last 70 kyr. *Marine Micropaleontology*, 2003, 48, 49–70.
- [43] Pérez-Folgado M., Sierro F.J., Flores J.-A., Grimalt J.O., Zahn R., Paleoclimatic variations in foraminifer assemblages from the Alboran Sea (Western Mediterranean) during the last 150 ka in ODP Site 977. *Marine Geology*, 2004, 212, 113–131.
- [44] Hemleben C., Spindler M., Anderson O.R., *Modern planktonic foraminifera*. Springer-Verlag, New York, 1989, 1–363.
- [45] Žarić S., Donner B., Fischer G., Mulitz S., Wefer G., Sensitivity of planktic foraminifera to sea surface temperature and export production as derived from sediment trap data. *Marine Micropaleontology*, 2005, 55, 75–105.
- [46] Rohling E.J., Hayes A., De Rijk S., Kroon D., Zachariasse W.J., Eisma D., Abrupt cold spells in the northwest Mediterranean. *Paleoceanography*, 1998, 13, 316–322.
- [47] Capotondi L., Borsetti A.M., Morigi C., Foraminiferal ecozones, a high resolution proxy for the late Quaternary biochronology in the central Mediterranean Sea. *Marine Geology*, 1999, 153, 253–274.
- [48] Hayes A., Rohling E.J., De Rijk S., Zachariasse W.J., Mediterranean planktonic foraminiferal faunas during the last glacial cycle. *Marine Geology*, 1999, 153, 239–252.
- [49] Sbaffi L., Wezel F.C., Kallel N., Paterne M., Cacho I., Ziveri P., Shackleton N., Response of the pelagic environment to palaeoclimatic changes in the central Mediterranean Sea during the Late Quaternary. *Marine Geology*, 2001, 178, 39–62.
- [50] Sbaffi L., Wezel F.C., Curzi G., Zoppi U., Millennial- to centennial-scale palaeoclimatic variations during Termination I and the Holocene in the central Mediterranean Sea. *Global and Planetary Change*, 2004, 40, 201–217.
- [51] Buccheri G., Capretto G., Di Donato V., Esposito P., Ferruzza G., Pescatore T., Russo Ermolli E., Senatore M.R., Sprovieri M., Bertoldo M., Carella D., Madonia G., A high resolution record of the last deglaciation in the southern Tyrrhenian Sea: environmental and climatic evolution. *Marine Geology*, 2002, 181, 3–34.
- [52] Incarbona A., Di Stefano E., Sprovieri R., Bonomo S., Censi P., Dinarès-Turell J., Spoto S., Vertical structure variability of the water column and Paleoproductivity reconstruction in the Central-Western Mediterranean during the Late Pleistocene. *Marine Micropaleontology*, 2008, 69, 26–41.
- [53] Rouis-Zargouni I., Turon J.-L., Londeix L., Essallami L., Kallel N., Sicre M.-A., Environmental and climatic changes in the central Mediterranean Sea (Siculo–Tunisian Strait) during the last 30 ka based on dinoflagellate cyst and planktonic foraminifera assemblages. *Palaeogeography Palaeoclimatology Palaeoecology*, 2010, 285, 17–29.
- [54] Siani G., Paterne M., Colin C., Late glacial to Holocene planktic foraminifera bioevents and climatic record in the South Adriatic Sea. *Journal of Quaternary Science*, 2010, 25, 808–821.
- [55] Rohling E.J., Jorissen F.J., Vergnaud-Grazzini C., Zachariasse W.J., Northern Levantine and Adriatic Quaternary planktic foraminifera; Reconstruction of paleoenvironmental gradients. *Marine Micropaleontology*, 1993, 21, 191–218.
- [56] Principato M.S., Giunta S., Corselli C., Negri A., Late Pleistocene–Holocene planktonic assemblages in three box-cores from the Mediterranean Ridge area (west-southwest of Crete): palaeoecological and palaeoceanographic reconstruction of sapropel S1 interval. *Palaeogeography Palaeoclimatology Palaeoecology*, 2003, 190, 61–77.
- [57] Triantaphyllou M.V., Antonarakou A., Kouli K., Dimiza M., Kontakios G., Papanikolaou M.D., Ziveri P., Mortyn P.G., Lianou V., Lykousis V., Dermitzakis M.D., Late Glacial–Holocene ecotratigraphy of the south-eastern Aegean Sea, based on plankton and pollen assemblages. *Geo-Marine Letters*, 2009, 29, 249–267.
- [58] Hayes A., Kucera M., Kallel N., Sbaffi L., Rohling E.J., Glacial Mediterranean sea surface temperatures reconstructed from planktonic foraminiferal assemblages, *Quaternary Science Reviews*, 2005, 24, 999–1016.
- [59] De Rijk S., Hayes A., Rohling E.J., Eastern Mediterranean sapropel S1 interruption: an expression of the onset of climatic deterioration around 7 ka BP. *Marine Geology*, 1999, 153, 337–343.
- [60] Geraga M., Tsaila-Monopolis S., Ioakim C., Papatheodorou G., Ferentinos G., Short-term climate changes in the southern Aegean Sea over the last 48,000 years. *Palaeogeography Palaeoclimatology Palaeoecology*, 2005, 220, 311–332.
- [61] Geraga M., Mylona G., Tsaila-Monopoli St., Papatheodorou G., Ferentinos G., Northeastern Ionian Sea: Palaeoceanographic variability over the last 22 ka. *Journal of Marine System*, 2008, 74, 623–638.

- [62] Geraga M., Ioakim C., Lykousis V., Tsaila-Monopolis S., Mylona G., The high-resolution palaeoclimatic and palaeoceanographic history of the last 24,000 years in the central Aegean Sea, Greece. *Palaeogeography Palaeoclimatology Palaeoecology*, 2010, 287, 101–115.
- [63] Rossignol-Strick M., Mediterranean Quaternary sapropels, an immediate response of the African Monsoon to variation of insolation. *Palaeogeography Palaeoclimatology Palaeoecology*, 1985, 49, 237–263.
- [64] Hilgen F.J., Astronomical calibration of Gauss to Matuyama sapropels in the Mediterranean and implication for the geomagnetic polarity time scale. *Earth and Planetary Science Letters*, 1991, 104, 226–244.
- [65] Lourens L.J.A., Antonarakou F.J., Hilgen F.J., Van Hoof A.A.F., Vergnaud Grazzini C., Zachariasse W.J., Evaluation of the Plio-Pleistocene astronomical time scale. *Paleoceanography*, 1996, 11, 391–431.
- [66] Osborne A.H., Vance D., Rohling E.J., Barton N., Rogerson M., Fello N., A humid corridor across the Sahara for the migration of early modern humans out of Africa 120,000 years ago. *Proceedings of the National Academy of Sciences of the United States of America*, 2008, 105, 16444–16447.
- [67] Rohling E.J., Review and new aspects concerning the formation of Mediterranean sapropels. *Marine Geology*, 1994, 122, 1–28.
- [68] Myers P., Haines K., Rohling E.J., Modelling the paleocirculation of the Mediterranean: The last glacial maximum and the Holocene with emphasis on the formation of sapropel S1. *Paleoceanography*, 1998, 13, 586–606.
- [69] Rohling E.J., Gieskes W.W.C., Late Quaternary changes in Mediterranean Intermediate Water density and formation rate. *Paleoceanography*, 1989, 4, 531–545.
- [70] Di Stefano E., Incarbona A., High resolution paleoenvironmental reconstruction of the ODP-963D Hole (Sicily Channel) during the last deglaciation, based on calcareous nanofossils. *Marine Micropaleontology*, 2004, 52, 241–254.
- [71] Incarbona A., Bonomo S., Di Stefano E., Sprovieri R., Pelosi N., Sprovieri M., Millennial-scale paleoenvironmental changes in the central Mediterranean during the Last Interglacial: comparison with European and Mediterranean records. *Geobios*, 2010, 43, 111–122.
- [72] Young J.R., Functions of coccoliths. In: Winter, A., Siesser, W.G., (Eds.), *Coccolithophores*, Cambridge University Press, Cambridge, 1994, 63–82.
- [73] Broerse A.T.C., Ziveri P., van Hinte J.E., Honjo S., Coccolithophore export production, species composition, and coccolith-CaCO₃ fluxes in the NE Atlantic (34°N 21°W and 48°N 21°W). *Deep-Sea Research II*, 2000, 47, 1877–1905.
- [74] Flores J.-A., Bárcena M.A., Sierro F.J., Ocean-surface and wind dynamics in the Atlantic Ocean off Northwest Africa during the last 140,000 years. *Palaeogeography Palaeoclimatology Palaeoecology*, 2000, 161, 459–478.
- [75] Molfino B., McIntyre A., Precessional forcing of nutricline dynamics in the Equatorial Atlantic. *Science*, 1990, 249, 766–769.
- [76] Beaufort L., Lancelot Y., Camberlin P., Cayre O., Vincent E., Bassinot F., Labeyrie L., Insolation Cycles as a Major Control of Equatorial Indian Ocean Primary Production. *Science*, 1997, 278, 1451–1454.
- [77] Grelaud M., Marino G., Ziveri P., Rohling E.J., Abrupt shoaling of the nutricline in response to massive freshwater flooding at the onset of the last interglacial sapropel event. *Paleoceanography*, 2012, 27, DOI: 10.1029/2012PA002288.
- [78] Andruleit H., Stäger S., Rogalla U., Cepek P., Living coccolithophores in the northern Arabian Sea: ecological tolerances and environmental control. *Marine Micropaleontology*, 2003, 49, 157–181.
- [79] Boeckel B., Baumann K.-H., Distribution of coccoliths in surface sediments of the south-eastern South Atlantic Ocean: ecology, preservation and carbonate contribution. *Marine Micropaleontology*, 2004, 51, 301–320.
- [80] Incarbona A., Ziveri P., Di Stefano E., Lirer F., Mortyn G., Patti B., Pelosi N., Sprovieri M., Tranchida G., Vallefuoco M., Albertazzi S., Bellucci L.G., Bonanno A., Bonomo S., Censi P., Ferraro L., Giuliani S., Mazzola S., Sprovieri R., The Impact of the Little Ice Age on coccolithophores in the Central Mediterranean Sea. *Climate of the Past*, 2010, 6, 795–805.
- [81] López-Otálvaro G.E., Flores J.A., Sierro F.J., Cacho I., Variations in coccolithophorid production in the Eastern Equatorial Pacific at ODP Site 1240 over the last seven glacial–interglacial cycles. *Marine Micropaleontology*, 2008, 69, 52–69.
- [82] Flores J.-A., Sierro F.J., Francés G., Vázquez A., The last 100,000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. *Marine Micropaleontology*, 1997, 29, 351–366.
- [83] Mikolajewicz U., Modeling Mediterranean Ocean climate of the Last Glacial Maximum. *Climate of the Past*, 2011, 7, 161–180.
- [84] Rogerson M., Rohling E.J., Bigg G.R., Ramirez J., Paleogeography of the Atlantic-Mediterranean exchange: Overview and first quantitative assessment of climatic forcing. *Reviews of Geophysics*, 2012, 50, DOI: 10.1029/2011RG000376.
- [85] Incarbona A., Ziveri P., Sabatino N., Salvaggio Manta D., Sprovieri M., Conflicting coccolithophore and geochemical evidence for productivity levels in the Eastern Mediterranean sapropel S1. *Marine Micropaleontology*, 2011, 81, 131–143.
- [86] Astraldi M., Balopoulos S., Candela J., Font J., Gačić M., Gasparini G.P., Manca B., Theocharis A., Tintorè J., The role of straits and channels in understanding the characteristics of Mediterranean circulation. *Progress in Oceanography*, 1999, 44, 65–108.
- [87] Astraldi M., Gasparini G.P., Vetrano A., Vignudelli S., Hydrographic characteristics and interannual variability of water masses in the central Mediterranean: a sensitivity test for long-term changes in the Mediterranean Sea. *Deep-Sea Research I*, 2002, 49, 661–680.
- [88] Castradori D., Calcareous nanofossils and the origin of eastern Mediterranean sapropels. *Paleoceanography*, 1993, 8, 459–471.
- [89] Negri A., Capotondi L., Keller J., Calcareous nanofossils, planktonic foraminifera and oxygen isotopes in the late Quaternary sapropels of the Ionian Sea. *Marine Geology*, 1999, 157, 89–103.
- [90] Giunta S., Negri A., Maffioli P., Sangiorgi F., Capotondi L., Morigi C., Principato M.S., Corselli C., Phytoplankton dynamics in the eastern Mediterranean Sea during Marine Isotope Stage 5. *Palaeogeography Palaeoclimatology Palaeoecology*, 2006, 235, 28–47.
- [91] Principato M.S., Crudeli D., Ziveri P., Slomp C.P., Corselli C., Erba E., De Lange G.J., Phyto- and zooplankton paleofluxes during the deposition of sapropel S1 (eastern Mediterranean): Biogenic carbonate preservation and paleoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2006, 235, 8–27.

- [92] Triantaphyllou M.V., Antonarakou A., Dimiza M., Anagnostou C., Calcareous nannofossil and planktonic foraminiferal distributional patterns during deposition of sapropels S6, S5 and S1 in the Libyan Sea (Eastern Mediterranean). *Geo-Marine Letters*, 2010, 30, 1–13.
- [93] Van Santvoort P.J.M., De Lange G.J., Thomson J., Cussen H., Wilson T.R.S., Krom M.D., Ströhle K., Active post-depositional oxidation of the most recent sapropel (S1) in sediments of the eastern Mediterranean Sea. *Geochimica et Cosmochimica Acta*, 1996, 60, 4007–4024.
- [94] Sachs J.P., Repeta D.J., Oligotrophy and nitrogen fixation during eastern Mediterranean sapropel events. *Science*, 1999, 286, 2485–2488.
- [95] Rutten A., De Lange G.J., A novel selective extraction of barite, and its application to eastern Mediterranean sediments. *Earth and Planetary Science Letters*, 2002, 198, 11–24.
- [96] Arnaboldi M., Meyers P.A., Patterns of organic carbon and nitrogen isotopic compositions of latest Pliocene sapropels from six locations across the Mediterranean Sea. *Palaeogeography Palaeoclimatology Palaeoecology*, 2006, 235, 149–167.
- [97] Arnaboldi M., Meyers P.A., Trace element indicators of increased primary production and decreased water-column ventilation during deposition of latest Pliocene sapropels at five locations across the Mediterranean Sea. *Palaeogeography Palaeoclimatology Palaeoecology*, 2007, 249, 425–443.
- [98] De Lange G.J., Thomson J., Reitz A., Slomp C.P., Speranza Principato M., Erba E., Corselli C., Synchronous basin-wide formation and redox-controlled preservation of a Mediterranean sapropel. *Nature Geoscience*, 2008, 1, 606–610.
- [99] Margalef R., Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, 1978, 1, 493–509.
- [100] Bond G., Broecker W., Johnson S., Jouzel J., Labeyrie L., McManus J., Bonani G., Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature*, 1993, 365, 143–147.
- [101] Grootes P.M., Stuiver M., White J.W.C., Johnsen S., Jouzel J., Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature*, 1993, 366, 552–554.
- [102] Voelker A.H.L., SCOR-IMAGES workshop participants, Global distribution of centennial-scale records for marine isotope stage (MIS) 3: a database. *Quaternary Science Reviews*, 2002, 21, 1185–1212.
- [103] Rohling E.J., Mayewsky P.A., Challenor P., On the timing and mechanism of millennial-scale climate variability during the last glacial cycle. *Climate Dynamics*, 2003, 20, 257–267.
- [104] Oppo D.W., Horowitz M., Lehman S.J., Marine core evidence for reduced deep water production during Termination II followed by a relatively stable substage 5e (Eemian). *Paleoceanography*, 1997, 12, 51–63.
- [105] Oppo D.W., Keigwin L.D., McManus J.F., Persistent suborbital climate variability in marine isotope stage 5 and Termination II. *Paleoceanography*, 2001, 16, 280–292.
- [106] NGRIP - North Greenland Ice Core Project members, High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature*, 2004, 431, 148–151.
- [107] Colmenero-Hidalgo E., Flores J.-A., Sierro F.J., Bárcena M.A., Löwemark L., Schönfeld J., Grimalt J.O., Ocean surface water response to short-term climate changes revealed by coccolithophores from the Gulf of Cadiz (NE Atlantic) and Alboran Sea (W Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2004, 205, 317–336.
- [108] Moreno A., Cacho I., Canals M., Grimalt J.O., millennial-scale variability in the productivity signal from the Alboran Sea record. *Palaeogeography Palaeoclimatology Palaeoecology*, 2004, 211, 205–219.
- [109] Moreno A., Cacho I., Canals M., Grimalt J.O., Sánchez-Goñi M.-F., Shackleton N., Sierro F.J., Links between marine and atmospheric processes oscillating on a millennial time-scale. A multi-proxy study of the last 50,000 yr from the Alboran Sea (Western Mediterranean Sea). *Quaternary Science Reviews*, 2005, 24, 1623–1636.
- [110] Sierro F.J., Hodell D.A., Curtis J.H., Flores J.-A., Reguera I., Colmenero-Hidalgo E., Bárcena M.A., Grimalt J.O., Cacho I., Frigola J., Canals M., Impact of iceberg melting on Mediterranean thermohaline circulation during Heinrich Events. *Paleoceanography*, 2005, 20, DOI: 10.1029/2004PA001051.
- [111] Rogerson M., Colmenero-Hidalgo E., Levine R.C., Rohling E.J., Voelker A.H.L., Bigg G.R., Schönfeld J., Cacho I., Sierro F.J., Löwemark L., Reguera M.I., de Abreu L., Garrick K., Enhanced Mediterranean-Atlantic exchange during Atlantic freshening phases. *Geochemistry, Geophysics, Geosystems*, 2010, 11, DOI: 10.1029/2009GC002931.
- [112] Sirocko F., Sarnthein M., Erlenkeuser H., Lange H., Arnold M., Duplessy C., Century-scale events in monsoonal climate over the past 24,000 years. *Nature*, 1993, 364, 322–324.
- [113] Sirocko F., Garbe-Schönberg D., McIntyre A., Molfino B., Teleconnections between the subtropical monsoons and high-latitude climates during the last deglaciation. *Science*, 1996, 272, 526–529.
- [114] Leuschner D.C., Sirocko F., The low-latitude monsoon climate during Dansgaard-Oeschger cycles and Heinrich Events. *Quaternary Science Reviews*, 2000, 19, 243–254.
- [115] Bigg G.R., Jickells T.D., Liss P.S., Osborn T.J., The role of the oceans in climate. *International Journal of Climatology*, 2003, 23, 1127–1159.
- [116] POEM group, General circulation of the Eastern Mediterranean. *Earth-Science Reviews*, 1992, 32, 285–309.
- [117] Pinardi N., Masetti E., Variability of the large scale general circulation of the Mediterranean Sea from observations and modelling: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2000, 158, 153–174.
- [118] Incarbona A., Bonomo S., Di Stefano E., Zgozi S., Essarbout N., Talha M., Tranchida G., Bonanno A., Patti B., Placenti F., Buscaino G., Cuttitta A., Basilone G., Bahri T., Massa F., Censi P., Mazzola S., Calcareous nannofossil surface sediment assemblages from the Sicily Channel (central Mediterranean Sea): palaeoceanographic implications. *Marine Micropaleontology*, 2008, 67, 297–309.