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Key Points:

- Coccolithophore and alkenones underline productivity changes in a reference Early/Middle Pleistocene record from the central Mediterranean
- Productivity proxies reflect millennial-scale climate changes with low/high values during cold and drier/warm and wetter conditions
- Similarity with the Dansgaard-Oeschger oscillations scenario suggests a common regional climate forcing over productivity through time

Supporting Information:

Supporting Information may be found in the online version of this article.

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Paleoproductivity Modes in Central Mediterranean During MIS 20—MIS 18: Calcareous Plankton and Alkenone Variability

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Abstract Paleoproductivity is reconstructed across a Mediterranean benchmark record, the Early/Middle Pleistocene Montalbano Jonico section, cropping out in southern Italy. High-resolution coccolithophore and alkenone data (C_{37} and $C_{37:2}/C_{38:2}$ ratio) were collected in order to extend the data set on Mediterranean paleoproductivity pattern and forcing mechanisms. The multi-proxy record indicates low productivity during glacial and stadial phases and enhanced productivity during interglacial and interstadials. Increased surface water turbidity, cold-water temperature and polar-subpolar low salinity water incursion appear as the dominant controls for low productivity during Marine Isotope Stage (MIS) 20. Enhanced productivity during MIS 19c was sustained by warmer surface waters, coupled with a seasonal precipitation regime, providing higher nutrient availability. Productivity increases during interstadials with respect to stadials, in relation with enhanced land-derived nutrient input through river discharge during wetter winters. The productivity scenario we propose is similar to those reconstructed from deep-sea records in the central and western Mediterranean during Dansgaard-Oeschger oscillations over the last 70 ka. This indicates that similar forcing mechanisms acted on productivity dynamics on a regional scale over different times. We suggest that migration of the westerly wind system over the Mediterranean and the polar water inflow influenced productivity on a regional scale. The acquired data set provides new evidences on the environmental significance of the $C_{37:2}/C_{38:2}$ ratio and on its relation with surface water productivity.

Plain Language Summary Coccolithophores are calcifying unicellular algae and one of the most important marine phytoplankton group. In the present-day oceans their distribution strongly depends on environmental factors such as nutrient concentration, surface water temperature, sunlight availability. Therefore, changes in fossil coccolithophore assemblages are successfully used for paleoclimatic and paleoceanographic reconstructions. They are also the source of organic compounds (the alkenones), which provide estimation of paleotemperature and paleoproductivity. We used variations of coccolithophore assemblages and of alkenones to identify paleoproductivity variations in the central Mediterranean, in a nearshore environment, during a key Quaternary paleoclimate interval. Our approach benefited of other paleoenvironmental indicators such as sea surface temperature and stable oxygen and carbon isotopes available at the studied section. We find that past climate changes clearly affected coccolithophore productivity at our site. Paleoproductivity was clearly favored by warm surface waters and by seasonal nutrient availability resulting by enhanced humidity over the central Mediterranean region. Our data also provide new indications on the relation between coccolithophore assemblage and alkenone variations through climate phases which may have future implication on their use for paleoenvironmental reconstruction.

1. Introduction

Coccolithophores are a major component of oceanic phytoplankton and provide useful indications on surface water mass dynamics and particularly on primary productivity variations as well as on the relationships

between biology and oceanography (Baumann et al., 2005; Brand, 1994; Flores et al., 2003; Incarbona et al., 2013; Rickaby et al., 2010). Several sedimentary proxies are commonly used to estimate past changes in coccolithophore productivity, such as (a) variations in their absolute abundance, that is, number of coccoliths $\times$ g^{-1} of sediments (Ausín, Flores, Sierro, Bárcena, et al., 2015; Baumann & Freitag, 2004; Colmenero-Hidalgo et al., 2004; Martinez-Sanchez et al., 2019; Stolz & Baumann, 2010), (b) changes in their accumulation rate, that is, coccoliths $\times$ cm^{-2} $\times$ kyr^{-1} (Amore et al., 2012; Baumann et al., 2004; López-Otálvaro et al., 2009; Marino et al., 2014; Saavedra Pellitero et al., 2011; Steinmetz, 1994), (c) abundance of organic biomarkers produced by coccolithophores and preserved into the sediments, such as alkenones (Athanasiou et al., 2017; Emanuele et al., 2015; Quivelli et al., 2020; Sicre et al., 2000; Villanueva et al., 2001), or (d) the Sr/Ca ratio measured in the coccolith fraction (Cavaleiro et al., 2018; Mejía et al., 2014; Saavedra-Pellitero et al., 2017; Tangunan et al., 2017). The land-locked, semi-enclosed Mediterranean basin is highly sensitive to climate changes and therefore is an ideal natural laboratory for deciphering past sea-surface hydrological and productivity signals and identifying forcing mechanisms. The basin has undergone phases of enhanced surface water stratification and primary productivity events during periods of critical climate threshold, like intense humid climate conditions over the eastern Mediterranean related to minimal precession/maximal insolation (Hilgen, 1991; Lourens, 2004; Rossignol-Strick, 1985). This climate frame promoted the accumulation and preservation of organic matter at the sea floor and the formation of sapropels (e.g., Melki et al., 2009; Rohling et al., 2002, 2015; Rossignol-Strick et al., 1982; Toucanne et al., 2015). An extensive literature dealt with paleoproductivity variations associated with restricted interval of sapropel deposition in the Mediterranean, but only a few studies have focused on coccolithophore paleoproductivity over longer time windows including millennial scale climate oscillations within the Quaternary and impacting surface waters and therefore overall productivity. The available data mainly concern deep-sea records and are focused on the last glacial period, the last deglaciation and the Holocene, with a special focus to certain areas, that is, the Alboran Sea (Ausín, Flores, Sierro, Bárcena, et al., 2015; Ausín, Flores, Sierro, Cacho, et al., 2015; Bazzicalupo et al., 2020; Cacho et al., 2000, 2002; Colmenero-Hidalgo et al., 2004; Moreno et al., 2004, 2005) and the Sicily Channel (Incarbona, Di Stefano, et al., 2010; Incarbona, Martrat, et al., 2010; Incarbona et al., 2008, 2013; Sprovieri et al., 2003, 2006). The large multiproxy micropaleontological and geochemical data set available in the Alboran Sea provides a clear low/high productivity scenario matching Stadial/Interstadial phases during the Dansgaard-Oeschger oscillations (D-O) of the last glacial period, essentially related to the position and intensity of the north-westerly winds, affecting the inflow jet of Atlantic water and/or nutrient supply by climate-induced river runoff variability (Bazzicalupo et al., 2020; Cacho et al., 2000; Colmenero-Hidalgo et al., 2004; Moreno et al., 2005). The strong vertical density gradient related to Atlantic water inflow has been also considered as a forcing mechanism in weakening the vertical convection of the water column and producing a negative effect on biological productivity, during stadial phases in the Sicily Channel and on a larger scale within the Mediterranean (Incarbona et al., 2013). For the central Mediterranean and excluding the Sicily Channel area, the currently available data set remains largely incomplete and high-resolution Early to Middle Pleistocene Mediterranean records are extremely rare.

Our study aims to fill the gap of knowledge that exists on the productivity variations during the Early/Middle Pleistocene period in the central Mediterranean region, focusing across the interval from the late Marine Isotope Stage (MIS) 20 to the MIS 18 glacial inception. This interval includes MIS 19, considered a close analog of the present interglacial (Pol et al., 2010; Tzedakis et al., 2012) and which revealed orbital and millennial-scale climate variability in marine (Emanuele et al., 2015; Ferretti et al., 2015; Maiorano et al., 2016; Marino et al., 2020; Nomade et al., 2019; Sánchez Gõni et al., 2016; Toti et al., 2020; Tzedakis et al., 2012), lacustrine (Giaccio et al., 2015; Mangili et al., 2007; Regattieri et al., 2019), and ice core (Pol et al., 2010) records. We have investigated the expounded marine Ideale section in southern Italy (Figures 1A–1C), which is part of the Montalbano Jonico sequence (MJS, southern Italy) encompassing MIS 37-MIS 16. This sequence represents a world-class reference marine record for the Early-Middle Pleistocene transition (Bertini et al., 2015; Ciaranfi et al., 2010; Maiorano et al., 2010, 2016; Marino et al., 2015, 2016; Nomade et al., 2019; Petrosino et al., 2015; Simon et al., 2017). Thanks to its high sedimentation rate and well-documented supra-regional/global climate signatures (Figure 1C), the MJS offers the opportunity to gather a high-resolution data set from a shelf-upper slope environment, in a well-constrained chronological framework that is unique for the marine environment for this time period.

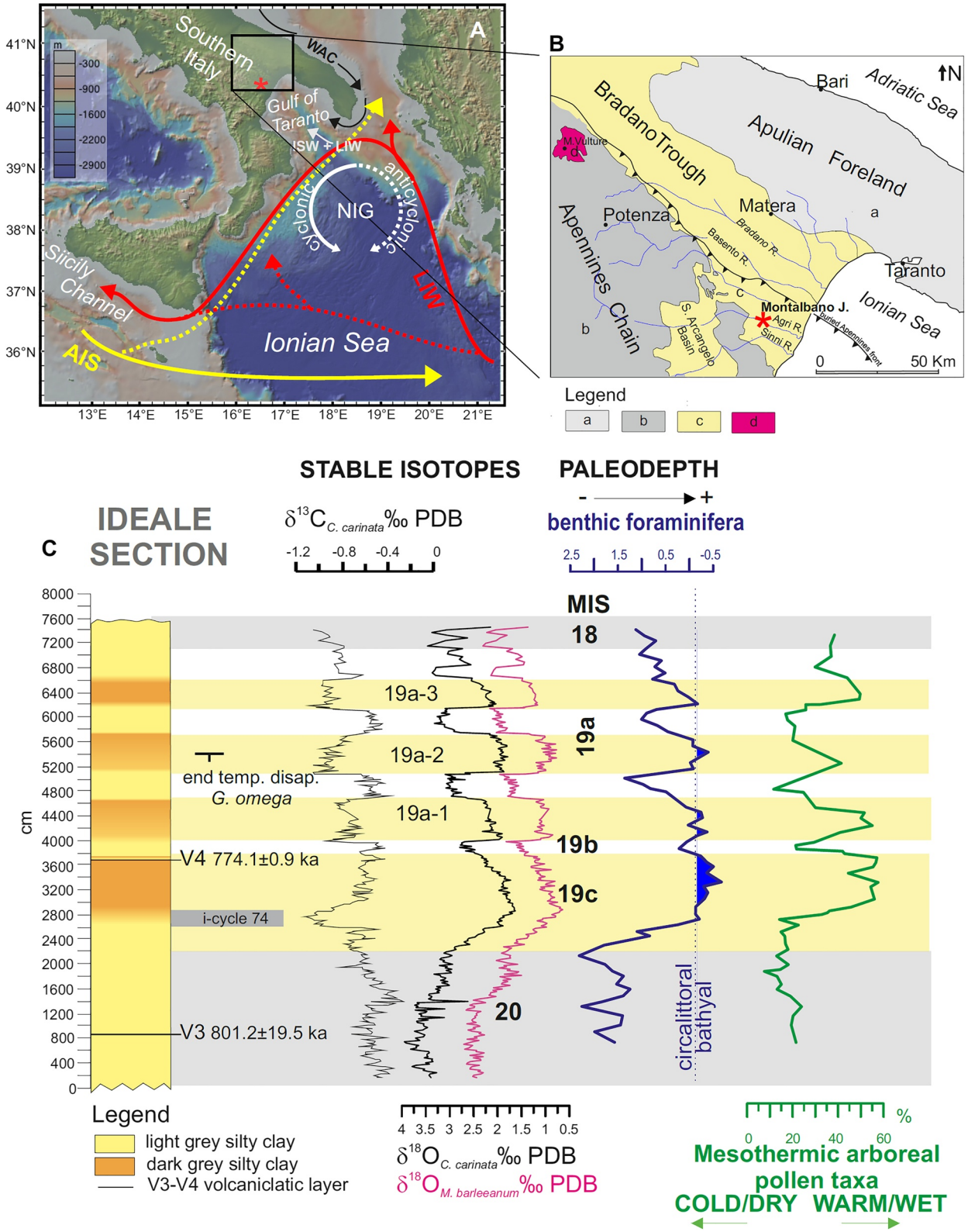

A
Southern Italy
WAC
Gulf of Taranto
ISW + LIW
cyclonic
anticyclonic
NIG
LIW
Sicily Channel
Ionian Sea
AIS
m
-300
-900
-1600
-2200
-2900
41°N
40°N
39°N
38°N
37°N
36°N
13°E
14°E
15°E
16°E
17°E
18°E
19°E
20°E
21°E
B
Bari
Adriatic Sea
N
Bradano Trough
Apulian Foreland
M.Vulture
Matera
Potenza
Bradano R.
Basento R.
Apennines Chain
Taranto
Ionian Sea
Montalbano J.
Agri R.
Sinni R.
S. Arcangelo Basin
Buried Apennines front
0
50 Km
Legend
a
b
c
d
STABLE ISOTOPES
PALEODEPTH
C
IDEALE SECTION
δ13C C. carinata ‰ PDB
-1.2 -0.8 -0.4 0
benthic foraminifera
- +
2.5 1.5 0.5 -0.5
MIS
18
19a-3
19a-2
19a-1
19a
19b
19c
20
end temp. disap.
G. omega
V4 774.1±0.9 ka
i-cycle 74
V3 801.2±19.5 ka
cm
8000
7600
7200
6800
6400
6000
5600
5200
4800
4400
4000
3600
3200
2800
2400
2000
1600
1200
800
400
0
circalittoral
bathyal
Legend
light grey silty clay
dark grey silty clay
V3-V4 volcaniclatic layer
4 3.5 3 2.5 2 1.5 1 0.5
δ18O C. carinata ‰ PDB
δ18O M. barleeanum ‰ PDB
%
0 20 40 60
Mesothermic arboreal pollen taxa
COLD/DRY WARM/WET

Figure 1.

It is important to mention here that data on paleoproductivity variation across the selected time interval are available only from the North Atlantic (Emanuele et al., 2015) and based on nannofossil accumulation rate variations. These data highlighted intra-interglacial high-frequency paleoproductivity variations related with the instability of mid-latitude North Atlantic sea surface hydrography.

Conscious that all paleoproductivity proxies suffer from ambiguities in interpretation, we take advantage of a multiproxy data set based on variations of total coccolithophore abundance (total N), total C_{37} alkenone concentration, $C_{37:2}/C_{38:2}$ ratio, distribution patterns of key coccolithophore taxa, in order to identify patterns consistent with climate-related paleoproductivity in the highly dynamic Mediterranean Sea. With the aim to identify forcing mechanisms in the study area, the data set is compared with the available multiproxy paleoclimate signals (Figure 1C), specifically with high-resolution oxygen and carbon stable isotope records (Nomade et al., 2019), alkenone-based sea surface temperature (SST) pattern and few planktonic foraminifera taxa (Marino et al., 2020) as well as pollen assemblage variations (Bertini et al., 2015; Maiorano et al., 2016).

2. Studied Area

2.1. Modern Oceanographic and Climate Setting

The studied marine sediments were deposited in the central Mediterranean, in the northern sector of the Ionian Sea and specifically in the paleo Gulf of Taranto (Figure 1A), an area very sensitive to record short-term climate variability even in the last millennia (e.g., Grauel et al., 2013; Taricco et al., 2015). The present-day surface circulation consists of the Western Adriatic Current (WAC) and the Ionian Surface Water (ISW). The WAC consists mostly of discharge from the Po River and northern Apennine rivers, thus representing a low-salinity and nutrient-rich coastal current, flowing in a narrow band from the northern Adriatic Sea into the Gulf of Taranto (Bignami et al., 2007; Poulain, 2001; Turchetto et al., 2007). Its stronger influence along the southern Italian coast and the Gulf of Taranto occurs during winter and spring (Milligan & Cattaneo, 2007; Poulain, 2001), while it is weaker during summer, due to the reduced river discharge. The WAC mixes with the warmer and more saline ISW, which enters the Gulf of Taranto from the central Ionian Sea (Figure 1A). Atlantic Water enters the Ionian Sea through the Atlantic Ionian Stream (AIS; Robinson et al., 1999) and flows along different pathways depending upon the decadal variability of the North Ionian Gyre (NIG; Figure 1A) and its cyclonic/anticyclonic circulation regime due to the interaction between the Adriatic and Ionian Seas (Civitarese et al., 2010; Gačić et al., 2010). At mid-water depth, between 200 and 600 m, the Levantine Intermediate Water (LIW) flows from the central Ionian Sea into the Gulf of Taranto (Malanotte-Rizzoli et al., 1997; Sellschopp & Álvarez, 2003). The deeper circulation of the Gulf of Taranto is associated with the Adriatic Deep Water (ADW), a dense water mass resulting from the deep convection active during late winter/early spring (Artegiani et al., 1997; Vilibić & Orlić, 2002).

The present-day Mediterranean climate is characterized by warm-dry summers and cool-wet winters, resulting from the seasonal shift of the subtropical high-pressure belt and the mid-latitude westerly system (Lionello, 2012; Lionello et al., 2006). Winter precipitations mainly derive from the southernmost location of the subtropical high, bringing rainy westerlies from the Atlantic Ocean over the Mediterranean. Summer dryness results from a prevailing anti-cyclonic atmospheric circulation over the Mediterranean, related to the northward displacement of the Hadley cell and of the Intertropical Convergence Zone (ITCZ).

Atmospheric and hydrographic conditions affect the Mediterranean trophic regime, which is among the poorest in the world's oceans (Béthoux et al., 1998) due to the semi-enclosed configuration and the anti-estuarine circulation pattern bringing nutrient depleted Atlantic waters into the basin. The nutrient

Figure 1. Location of the study area and stratigraphical/paleoclimate framework of the Ideale Section. The location of the Montalbano Jonico section is indicated by the red star. (A) Present-day sea surface and subsurface circulation in the Gulf of Taranto and Ionian Sea. AIS: Atlantic Ionian Stream; LIW: Levantine Intermediate Waters; WAC: Western Adriatic Current; ISW: Ionian Surface Water; NIG: North Ionian Gyre. Full/dashed lines denote different current pathways during cyclonic/anticyclonic regime. (B) Simplified regional geological setting of southern Italy. (a) Cretaceous Apulian Foreland units (b) Triassic-Neogene units of the Apennines Chain; (c) Plio-Pleistocene Apennines Foredeep units; (d) Quaternary volcanic units. (C): Lithological features and stratigraphical/chronological constraints of Ideale section from Ciaranfi et al. (2010), Maiorano et al. (2010) and Nomade et al. (2019). Benthic oxygen and carbon isotope data from Nomade et al. (2019); paleodepth profile from Stefanelli (2003); Mesothermic arboreal pollen taxa distribution from Bertini et al. (2015) and Nomade et al. (2019).

budget and phytoplankton biomass are related to seasonal modifications of the water column dynamics, that is, seasonal mixing providing injection of nutrients from deeper waters or, in specific areas, external nutrient being provided by river runoff and nutrient load from adjacent lands or atmospheric supply (e.g., D'Ortenzio & Ribera d'Alcalà, 2009; Ludwig et al., 2009; Richon et al., 2019). During summer, the density stratification inhibits the nutrients injection toward the surface layer, limiting autotrophic biomass. In late fall-winter, the upward mixing of underlying nutrients allows a slight but constant increase of biomass (e.g., Civitarese et al., 2010; Klein et al., 2003; Macias et al., 2015).

2.2. Stratigraphy and Paleoclimate Framework of the Ideale Section

The Ideale section (IS) deposited on the south-western margin of the Bradanic Trough (Casnedi, 1988), located between the Apennines Chain to the west and the Apulia foreland eastward (Figure 1B; 40°17′29.52″N, 16°33′10.58″E). The section is part of the Pleistocene Apennines Foreland unit. It is about 80 m thick, and consists of clays and silty-clays (Figure 1C) deposited in an upper circalittoral-upper bathyal setting (Ciaranfi & D'Alessandro, 2005; D'Alessandro et al., 2003; Stefanelli, 2003). Two volcaniclastic layers, V3 (at about 800 cm) and V4 (at about 3,620 cm), have been radiometrically dated and give $^{40}Ar/^{39}Ar$ ages of 801.2 ± 19.5 ka (Maiorano et al., 2010), and 773.9 ± 1.3 ka (Petrosino et al., 2015; 774.1 ± 0.9 ka, Nomade et al., 2019), respectively (Figure 1C). The very high resolution of recently generated benthic (*Cassidulina carinata* and *Melonis barleeanum*) $\delta^{18}O$ records allowed to obtain a precise stratigraphical and chronological framework for the IS which is described in detail in Nomade et al. (2019) and Simon et al. (2017), from MIS 20 to early MIS 18 (Figure 1C). The adopted age model includes both astronomical tie-points and dated tephra layers interbedded in the IS section, which represents the age-model strategy that better resolve the timing of MIS 19 (Nomade et al., 2019). The sedimentation rates are very high, ranging between 90 and 200 cm/ky (Nomade et al., 2019). The dark gray bands (Figure 1C), during interglacial MIS 19c and MIS 19a interstadials (19a-1, 19a-2, and 19a-3) correspond to dark silty-clays enriched in kaolinite and smectite content (Maiorano et al., 2016). They deposited during wetter conditions promoting chemical weathering on land and enhanced continental fresh water input (Bertini et al., 2015; Maiorano et al., 2016; Nomade et al., 2019). Conversely, the light gray bands are related to quartz and dolomite increases associated with enhanced supplies of the coarser grain size fraction supply during more arid climatic conditions (Bertini et al., 2015; Maiorano et al., 2016), from those rivers (Sinni, Agri, Cavone, Basento, and Bradano) representing the major tributary for the study area (Figure 1B). The dark and light intervals correspond to lower (interglacial, interstadials) and higher (glacial, stadials) benthic $\delta^{18}O$ values (Ciaranfi et al., 2010; Nomade et al., 2019), respectively, associated with higher (~180 m depth) and lower (~100 m depth) sea level (Aiello et al., 2015; Bertini et al., 2015; D'Alessandro et al., 2003; Marino et al., 2015; Stefanelli, 2003), suggesting a glacio-eustatic/climate control on sedimentary features of the IS. The lower values of benthic (*C. carinata*) $\delta^{13}C$ during full interglacial and interstadial phases have been interpreted as reflecting higher organic matter arrival/preservation at the sea bottom, likely in relation to higher primary productivity and water column stratification or organic matter influx from land (Marino et al., 2020; Nomade et al., 2019). The paleoenvironmental/paleoceanographic setting based on the $\delta^{13}C$ minima during the earliest MIS 19c (Nomade et al., 2019) together with co-registered micropaleontological evidences (Maiorano et al., 2016; Marino et al., 2020) support the interpretation of a sapropelic layer from 2,620 to 2,840 cm (Figure 1C) associated with insolation cycle 74 (i-c 74, 784 ka, Lourens, 2004; 785 ka, Konijnendijk et al., 2014).

3. Methods

3.1. Calcareous Plankton

One hundred sixty-six samples were investigated with a sample spacing of about 40 cm, providing a temporal resolution of ~200 years. Slides for coccolithophore analysis were prepared following Flores and Sierro (1997) to estimate absolute coccolith abundances (# coccoliths/g). Quantitative analyses were performed using a polarized light microscope at 1,000 × magnification. Abundances were determined by counting at least 500 coccoliths of all sizes. Reworked calcareous nannofossils, that is, taxa belonging to older (Mesozoic and Paleogene-Neogene) stratigraphic intervals, were estimated separately during this counting. Variations in the assemblage were assessed using percentages and number of coccoliths/g of

sediment. *Umbilicosphaera sibogae* s.l., *Calciosolenia* spp., *Discosphaera tubifera*, *Rhabdospaera clavigera*, *Umbellosphaera* spp., and *Oolithotus* spp., were here grouped as warm-water coccolith taxa (WWCT) according to their ecological preferences (Baumann et al., 2004; Boeckel & Baumann, 2004; McIntyre & Bé, 1967; Saavedra-Pellitero et al., 2010 Winter et al., 1994; Ziveri et al., 2004). The coccolith dissolution index (DI) was estimated using the method of Dittert et al. (1999) modified by Amore et al. (2012) according to the following ratio: DI = small *Gephyrocapsa*/(small *Gephyrocapsa* + *Calcidiscus leptoporus*). High values of DI indicate good preservation. Species dominance of the coccolithophore assemblage has been obtained using PAleontological STatistics Software 4.02 (Hammer et al., 2001) and is equivalent to 1-Simpson index. With regard to the taxonomy of gephyrocapsids, which are a major component of the assemblage, we followed the criteria adopted in Maiorano et al. (2013) separating small *Gephyrocapsa* < 3 μm, *Gephyrocapsa oceanica* > 3 μm with angle bridge > 50°, and *Gephyrocapsa caribbeanica* > 3 μm and closed central area. The identification of taxa other than gephyrocapsids refers to Jordan et al. (2004) and Young et al. (2003).

We also rely on the relative abundances of two key target planktonic foraminifera taxa, presented in more detail in a different study (Marino et al., 2020), that are, the herbivorous *Globigerina bulloides* and the polar-subpolar *Neogloboquadrina pachyderma* (sensu Darling et al., 2006). *Globigerina bulloides*, due to its opportunistic behavior (Schiebel & Hemleben, 2005; Schiebel et al., 1997), is used as an indicator of high nutrient content in surface water. In recent Mediterranean, *G. bulloides* is abundant during periods characterized by high productivity in surface waters related to upwelling, strong seasonal mixing (Bárcena et al., 2004; Hernández-Almeida et al., 2011; Mallo et al., 2017; Pujol & Vergnaud-Grazzini, 1995) or fertilization by river input (Rigual-Hernández et al., 2012) at the winter-early summer. The eutrophic affinity of *G. bulloides* in the fossil record has been also widely documented in different Mediterranean geological settings (e.g., Rohling et al., 1997 and references therein; Zachariasse et al., 1997; Kontakiotis, 2016 and references therein). *Neogloboquadrina pachyderma*, a polar-subpolar species (Darling et al., 2006; Hemleben et al., 1989) is used as a proxy of Atlantic cold (melt) water influx into Mediterranean (Bazzicalupo et al., 2018; Cacho et al., 1999; Capotondi et al., 2016; Girone et al., 2013; Marino et al., 2018, 2020; Pérez-Folgado et al., 2003; Sierro et al., 2005; Toti et al., 2020).

3.2. Alkenone Analysis

We analyzed 162 samples every 40–60 cm (average temporal resolution of ~200/300 years) in the same sediment layers sampled for calcareous plankton, stable isotopes and pollen. Alkenone extraction followed freeze-drying ~5 g of homogenized dry sediment, using 100% Dichloromethane (DCM) and a Dionex 200 Accelerated Solvent Extractor (ASE). Prior to quantification, extracts were evaporated with nitrogen and reconstituted with 200 μL of toluene spiked with n-hexatriacontane (C_{36}) and n-heptatriacontane (C_{37}) internal standards. Samples were purified by silica gel flash column chromatography to further isolate the ketone fraction. The silica gel was conditioned in glass pipettes with 6 ml of hexane, then eluted with 4 ml hexane, followed by 4 ml dichloromethane (ketone fraction). Alkenone concentrations ($C_{37:2}$, $C_{37:3}$, $C_{38:3}$ ethyl, $C_{38:3}$ methyl, $C_{38:2}$ 2ethyl, and $C_{38:2}$ methyl ketones, resolved to baseline under our chromatographic conditions) were determined using an Agilent Technologies 6890 gas chromatograph-flame ionization detector (GC-FID), with Agilent Technologies DB-1 column (60 m, 0.32 mm diameter, and 0.10 mm film thickness). Procedure entailed a 1-μl injection, initial temperature 90°C, increased to 255°C with 40°C/min rate, increased by 1°C/min to 300°C, increased by 10°C/min to 320°C, and an isothermal hold at 320°C for 11 min. The C_{37} total (ng/gram dry weight sediment) was derived by normalizing these areas to the peak areas of the internal C_{36} and C_{37} n-alkane standards and dividing by the weight of the sample extracted. Gas chromatography and column conditions were optimized to allow for accurate quantification of the four C_{38} alkenones (we found that daily trimming of the chromatographic column and regular maintenance of the GC inlet is essential to avoid "drift" in the column retention of C_{38} alkenones relative to the C_{37} alkenones). Long-term laboratory analytical error, estimated from replicate extractions and gas chromatographic analyses of a composite sediment standard is equivalent in temperature to ±0.1°C and to a relative error of 10% in quantifying C_{37}. The relative reproducibility of the C_{37}:C_{38} indices was approximately 3% (N = 12 replicates).

Alkenone paleothermometry relies on the temperature dependence of the degree of unsaturation (number of double bonds) observed in the suite of organic compounds ($C_{37:3}$ and $C_{37:2}$ alkenones) synthesized by marine surface-dwelling haptophyte algae (Marlowe et al., 1984; Prahl & Wakeham, 1987). There are several choices concerning which calibration to use to translate alkenone unsaturation ratio ($U^{k'}_{37}$) to SST (Conte et al., 2006; Müller et al., 1998; Prahl & Wakeham, 1987; Tierney & Tingley, 2018), but all give very similar estimates in the range of $U^{k'}_{37}$ encountered in the Ideale section. For this work, we used the Müller et al. (1998) calibration to translate $U^{k'}_{37}$ to SST. The whole alkenone-based SST record (Figure 2b) is already presented in Marino et al. (2020) and thus not introduced in the following result section. However, in Table S1, we also supply the Bayesian estimate and arguments (Text S1) for choosing the Müller et al. (1998) calibration.

4. Results

4.1. Calcareous Plankton

Total coccolithophore abundance (Total N) ranges between ~11×10^7 and ~102×10^7 (coccoliths/g; Figure 2c), with maximum values occurring during MIS 19c (783.7–773.1 ka). In contrast to their scanty present-day distribution in the Ionian Sea with respect to western Mediterranean (Knappertsbusch, 1993; Malinverno et al., 2003), gephyrocapsids represent the dominant taxa in the IS assemblage, with abundance ranging between 70% and 95% (Figure 2e), thus suggesting a different biogeography through time, although the rising of dominant *Emiliania huxleyi* among Noelaerhabdaceae lineage in the modern Mediterranean coccolithophore communities should be also considered. Small gephyrocapsids dominate during glacial MIS 20 and from MIS 19b upwards, with relative values ranging between 50% and 85%. Their lower abundances (~30%) characterize MIS 19c (~777–784 ka), while increases occur during interstadials MIS 19a-1 to 19a-3. Medium-sized gephyrocapsids (>3 μm), *G. caribbeanica* and *G. oceanica,* are rare (generally lower than 10%–15%) throughout the record, while noticeably relative abundance increase occurs during MIS 19c, reaching about 70% of the assemblage (Figure 2d). Among subordinate taxa, *Helicosphaera carteri* has percentage values no greater than ~7% (Figure 2f), with the highest abundance during MIS 20-earliest MIS 19c and at the onset of MIS 18. Minimum values are noticed during most of MIS 19c, between 783.7 and 773.1 ka. Distinct short-terms increases of *H. carteri* occur at the stadial phases of MIS 19a. *Florisphaera profunda* has a strongly fluctuating pattern (Figure 2g), with relative abundance generally not greater than 8% (occasionally reaching 11%) and the highest values during MIS 19c and at the base of MIS 19a-1. WWCT have rather low abundances (generally <1%) all through the section with the exclusion of a first slight increase at 784 ka and higher relative increase during the warm oscillation of MIS 19a-2 (Figure 2h). Reworked coccoliths reach 40% with respect to the indigenous taxa (Figure 2i), with the highest values during MIS 20 and earliest MIS 19 as well as distinct short-term increases tracing most of the stadial phases. The calcareous nannofossil dissolution index has values close to 1 through the entire section (Figure 3f), thus suggesting that dissolution was insignificant. Within the planktonic foraminifera assemblage *G. bulloides* is continuously present throughout the IS with several brief decreases/increases and a long-term increase from MIS 19b upwards (Figure 3h). *Neogloboquadrina pachyderma* occurs mainly during late MIS 20, with percentages never exceeding 5% of total assemblages (Figure 3i), and a brief incursion of the taxon is also recorded during the stadial part of MIS 19a-2. The coccolithophore data set is provided in Tables S2 and S3.

4.2. C_{37} Alkenone Concentration

Through the investigated interval, the total C_{37} alkenone concentration varies between 20 and 470 ng/gram (Figure 3d). The lowest values are recorded during MIS 20 and from 19a-2 upwards. An interval of marked increase is observed during most of MIS 19c, starting from about 784 ka, and sharp peaks also occur during 19b and 19a-1. The $C_{37:2}/C_{38:2}$ ratio has the lowest values (about 0.9) during MIS 20 (Figure 3b), while it reaches its maximum increase (about 1.1) during most of MIS 19c. Fluctuating values of the $C_{37:2}/C_{38:2}$ characterize the upper portion of the section, from MIS 19b upwards and showing increase/decrease during interstadials/stadials, with a prominent decrease at the cold oscillation between MIS 19a-2 and 19a-3 (Figure 3b). Note that both the C_{37} total and the $C_{37:2}/C_{38:2}$ ratio rather strongly mirror changes in the total coccolith abundance (Figure 3e). Alkenone concentrations are provided in Table S4.

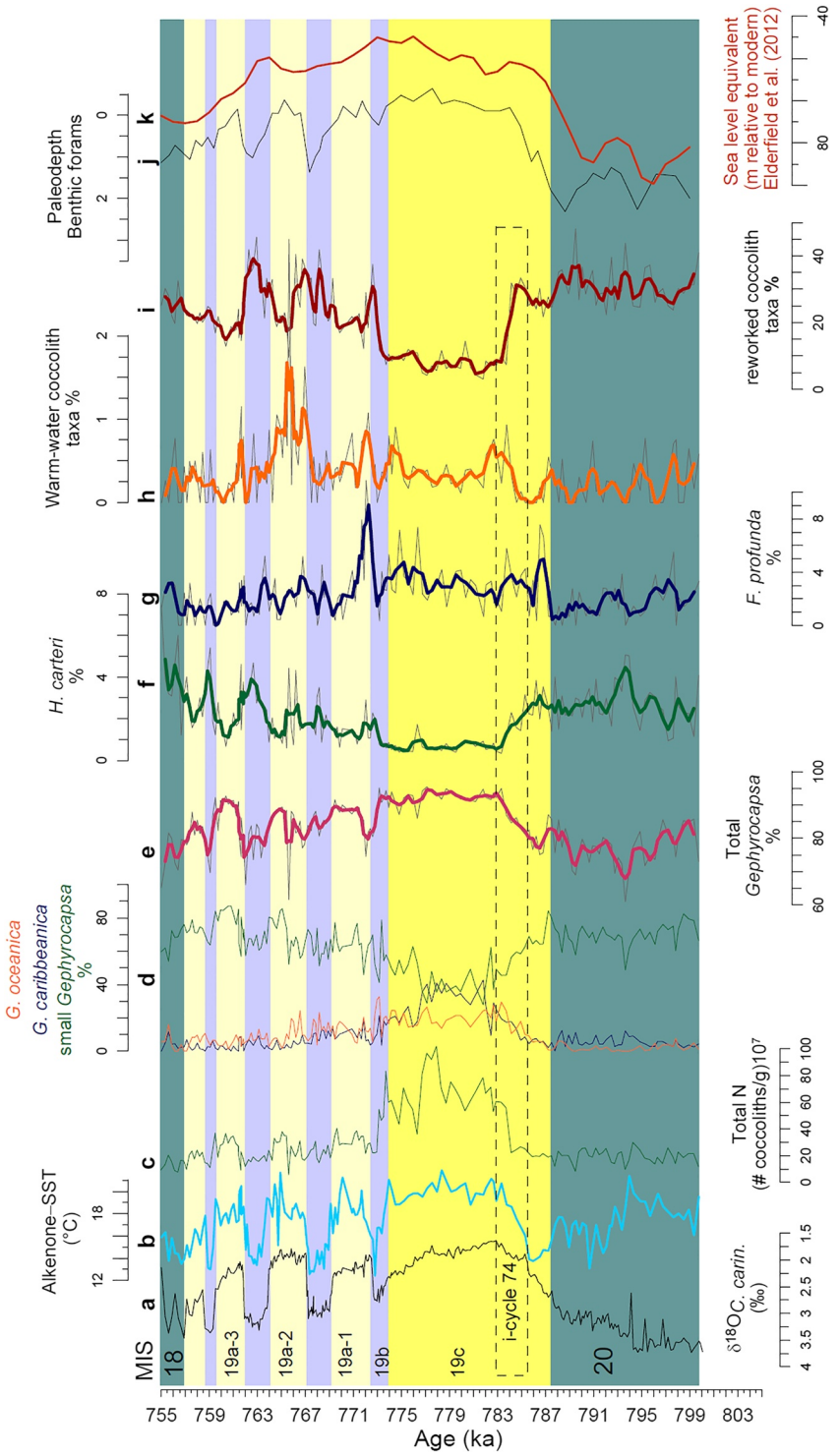


Figure 2. Benthic oxygen isotope (a) from Nomade et al. (2019) and alkenone-sea surface temperature (SST) records (b) from Marino et al. (2020) are compared with absolute (c) and relative (d)–(h) coccolithophore abundance at the Ideale section. Reworked coccolith taxa (i) are also shown and compared with paleodepth profile (j) at Ideale section (IS) (Stefanelli, 2003) and global sea level reconstruction plotted as sea level equivalent (m relative to modern) (k) from Elderfield et al. (2012). Dashed rectangle marks the sapropelic layer i-cycle 74 according to Maiorano et al. (2016) and Nomade et al. (2019).

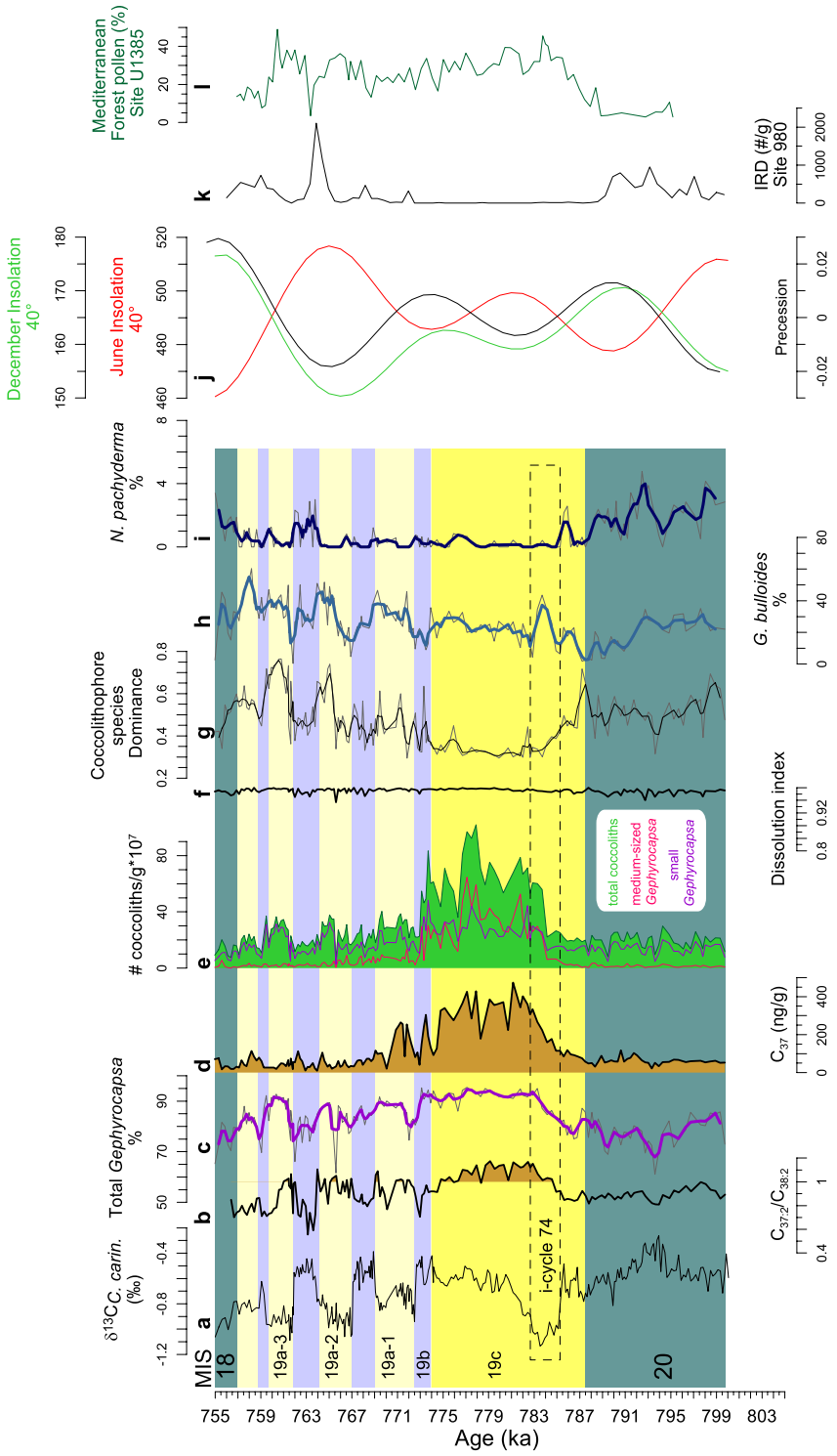


Figure 3. Carbon isotope record (a) from Nomade et al. (2019) compared with alkenone $C_{37:2}/C_{38:2}$ (b) and C_{37} patterns (d), coccolithophore relative (c) and absolute (e) abundances, dissolution index (f) and species dominance (g). *Globigerina bulloides* and polar-subpolar *Neogloboquadrina pachyderma* patterns at the Ideale section (h)–(i) are from Marino et al. (2020). Precession and insolation curves (j) are according to Laskar et al. (2004). Ice rafted debris (IRD) at ODP Site 980 (k) is from Wright and Flower (2002); Mediterranean forest pollen taxa record at IODP Site U1385 (l) is from Sánchez Gõni et al. (2016). Colored bands trace glacial-interglacial and stadial-interstadial phases across late Marine Isotope Stage (MIS) 20 and early MIS 18 according to Nomade et al. (2019). Dashed rectangle marks the sapropelic layer i-cycle 74 according to Maiorano et al. (2016) and Nomade et al. (2019).

5. Discussion

5.1. Paleoproductivity Proxies: Potential Interferences From Preservation/Dilution

Coccolith absolute abundance in the sediments may provide information on coccolithophore productivity in surface waters, although the effect of dissolution in water and/or at the sediment/water interface should be also considered (Flores et al., 2012). In the hemipelagic setting of the IS, variations in terrigenous input must also be considered. Similarly, changes in the concentrations of organic compounds can be controlled by preservation and/or terrigenous sediment dilution. The data set compiled here allows us to assess whether these complications override paleoproductivity signals, because they contain independent information of concentrations. As mentioned above, dissolution can be considered as negligible in the study section. In addition, changes in alkenone abundances (total C_{37}) mirror variations in the concentration of total coccoliths (Figures 3d and 3e), and, more specifically, of gephyrocapsids, likely the main producer of alkenones, suggesting that alkenone abundance mainly records past changes in alkenone accumulation rather than changes in the preservation of these biomarkers over time. In the modern ocean, alkenones are synthesized by a small group of haptophyte algae, restricted to the Noelaerhabdaceae family and specifically to *Emiliania huxleyi* and *G. oceanica* (Marlowe et al., 1990; Volkman et al., 1980, 1995), while in the Cenozoic record the topic on alkenone precursors is still debated (e.g., Athanasiou et al., 2017; Beltran et al., 2011; Plancq et al., 2012; Sicre et al., 2000; Villanueva et al., 2002). In the IS, *E. huxleyi* is absent due to the later appearance of the taxon, which occurs in the upper part of the Middle Pleistocene and thus the total N is mostly composed of gephyrocapsids that are mainly represented by small gephyrocapsids (small *G. caribbeanica* and small *Gephyrocapsa* with open central area) during MIS 20 and 19b-a (Figures 4a and 4d), and by medium-size *Gephyrocapsa* (*G. caribbeanica* and *G. oceanica* > 3 μm) during MIS 19c (Figures 4b and 4c). Despite the subject it is out of the main aim of the present study and conscious of the possible factors such as degradation, ecological conditions and alkenone contribution from non-calcifying species possibly involved in the relation between alkenone concentration and abundance of taxa (Beltran et al., 2011; Malinverno et al., 2008; Plancq, 2015; Prahl et al., 1989), we point out that the pattern of absolute abundance of *G. oceanica* and of *G. caribbeanica* displays similarities with that of total alkenone concentration, supported by positive correlations ($r = +0.80$ and $+0.82$, respectively; Figures 5c and 5d). This may imply, although not necessarily demonstrate, that these taxa are both the main alkenone producers during the studied interval, in agreement with recent data from the southern Indian Ocean during MIS 8 (Tangunan et al., 2021).

The good visual correspondence between alkenone concentration and total coccoliths through the record, although less evident at lower values, is associated with a high Pearson correlation coefficient ($r = +0.82$; Figure 5a). This is in agreement with previous observations made during the Holocene (Schwab et al., 2012; Weaver et al., 1999) and in the Pleistocene (Maiorano et al., 2015; Palumbo et al., 2013). The good correlation between the two proxies suggests that they can be used to reflect paleoproductivity variations in the IS.

A closer look at C_{37} and Total N shows that during MIS 20, and from MIS 19b upwards, C_{37} has rather low concentration with respect to the Total N (Figures 3d and 3e). It is noteworthy that alkenone concentration, although highly resistant, could be affected by degradation in the water column and in the sediment (Cacho et al., 2000; Grimalt et al., 2000; Madureira et al., 1995; Prahl et al., 1989, 1993, 2001; Sachs et al., 2000). A certain degree of degradation of C_{37} into the sediment has been observed during early diagenesis, depending on different oxygen content (Gong & Hollander, 1999; Rontani & Volkman, 2005). We cannot exclude the possibility that the lower concentration of C_{37} during MIS 20 and 19a may be related to enhanced degradation at the sea bottom, due to improved mixing/ventilation, as testified by the concomitant higher and/or strongly fluctuating $\delta^{13}C$ values (Nomade et al., 2019) (Figure 3a). However, studies on alkenone degradation do not find evidence of selective preservation of C_{37} relative to C_{38} alkenones (Prahl et al., 1989; Sinninghe Damsté et al., 2002).

Finally, considering the near-shore depositional setting of the IS, a dilution scenario for C_{37} alkenones and total coccolith abundance should be also discussed. In the IS, intervals of enhanced erosional processes and terrigenous input have been recorded during colder phases and low sea level (Maiorano et al., 2016). In this regard, we also examined changes in the relative proportions of $C_{37:2}/C_{38:2}$ as a potential paleoproductivity proxy. The $C_{37:2}/C_{38:2}$ ratio does not depend on the preservation or dilution controls that might affect total C_{37} alkenone concentrations. The $C_{37:2}/C_{38:2}$ ratio is chosen because both are diunsaturated methyl ketones

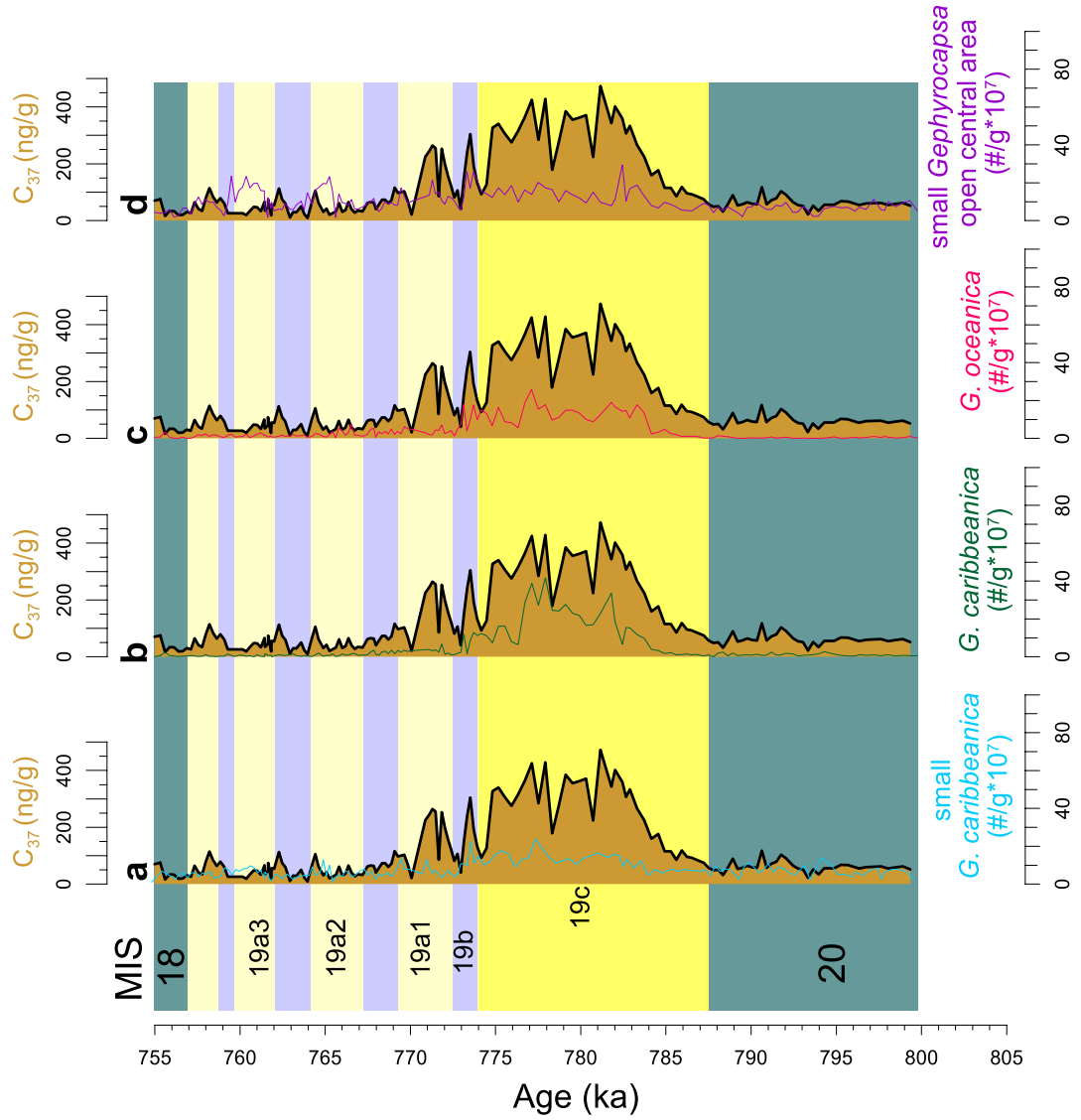


Figure 4. Gephyrocapsid absolute abundances (#/g) plotted against C_{37} concentration at the Ideale section. Colored bands trace glacial-interglacial and stadial-interstadial phases across late Marine Isotope Stage (MIS) 20 and early MIS 18 according to Nomade et al. (2019).

(there is also a $C_{38:3}$ ethyl ketone measured). Because these are homologous (methyl ketone) compounds, they should have similar temperature dependence as shown by the tight covariance of the U^k_{37} and U^k_{38} (methyl) unsaturation indices (Herbert, 2014; Figure 2). Therefore any variation in the $C_{37:2}/C_{38:2}$ ratio does not arise from a temperature control, but instead from a physiologically driven change in allocation of chain length during alkenone synthesis. Paleoecological factors involved in changing the ratio are not clear and could arise from changes in the alkenone producers over time, or from physiological reasons for changing contribution in C_{37} to C_{38} alkenone synthesis in response to environmental factors. The index seems to correspond to well-known oligotrophic-eutrophic cycles in the Plio-Pleistocene of the Eastern Mediterranean (Herbert et al., 2015). The IS record displays a positive, although moderate correlation ($r = +0.59$) between $C_{37:2}/C_{38:2}$ ratio and the total number of coccoliths as well (Figure 5b) suggesting that, although a dilution effect likely occurred in the study section, the primary signal was conserved. This alkenone ratio and its comparison with total coccolith abundance is the first of its kind documented so far in the literature. Its positive correlation with changes in total coccolith abundance (mainly with placolith-bearing taxa) may indicate a relation with paleoecological conditions and encourage future investigations on the usefulness

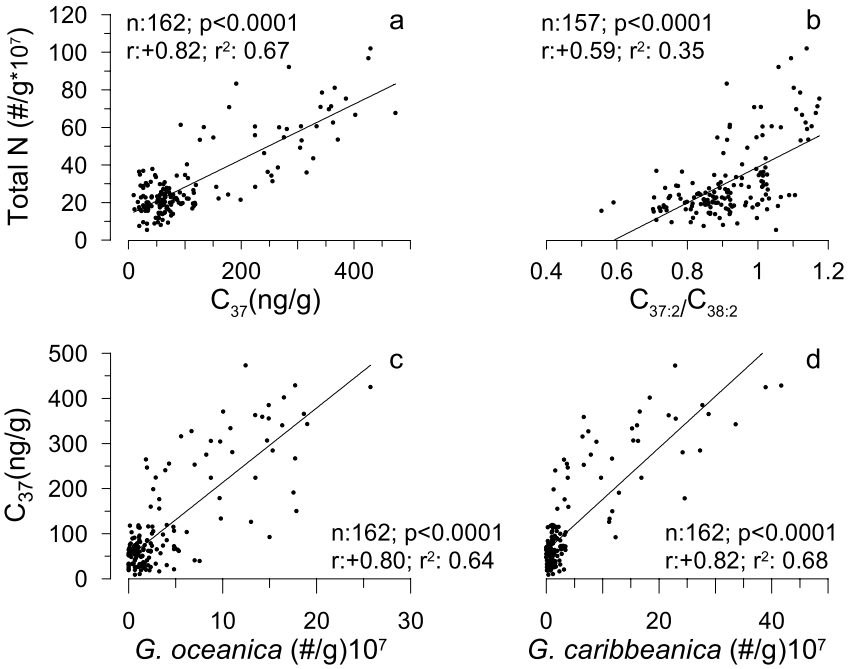


Figure 5. Scattered plot of total coccolithophore abundance (Total N) versus C_{37} (a) and $C_{37:2}/C_{38:2}$ (b) and of gephyrocapsid absolute abundances versus C_{37} (c)–(d) based on Pearson correlation results.

of this proxy. Taking into account potential interferences, the independent micropaleontological (Total N) and organic (C_{37} and $C_{37:2}/C_{38:2}$) paleoproductivity proxies, through the IS, highlight low productivity values during MIS 20 (Figures 3b, 3d and 3e), increased productivity during most of MIS 19c and fluctuating values during MIS 19a, following interstadial-stadial oscillations, the latter primarily marked by the pattern of Total N and $C_{37:2}/C_{38:2}$ ratio.

5.2. Main Shifts in the Coccolithophore Community: Productivity Versus Turbidity

We compared the paleoproductivity proxies with the relative abundance of the most important component of the coccolithophore assemblage, that is, the placoliths-bearing taxa belonging to the genus *Gephyrocapsa* (Figure 3c). Placoliths are r-strategist taxa that bloom after nutrient fertilization and their abundance variation is considered a proxy of high productivity conditions (Broerse et al., 2000; Flores et al., 2000; López-Otálvaro et al., 2008; Young, 1994). They are characteristic of meso to eutrophic environments, such as upwelling areas and shelf seas (Baumann et al., 2005). In order to avoid here again potential dilution effect, we solely relied on the relative abundance of specific taxa that provides biological information independently from sedimentological effect (Gibbs et al., 2012). The oscillating distribution pattern of the total gephyrocapsids (Figure 3c) indicates that the parameters controlling their proliferation frequently switched through time, with persistent low/high productivity occurring during MIS 20/MIS 19c, and a fluctuating pattern from MIS 19b upwards, with enhanced productivity during warmer and wetter interstadials. The total gephyrocapsid distribution through time (Figure 3c) parallels fluctuations of the $C_{37:2}/C_{38:2}$ ratio (Figure 3b). From a paleoecological point of view, placolith relative increases alternate with those of *H. carteri* (Figure 2f), as shown by their strong inverse correlation ($r = -0.82$; Figure S2). *H. carteri* benefits from turbid upper water layer (Bonomo et al., 2014, 2021; Colmenero-Hidalgo et al., 2004; Maiorano et al., 2019) and is a species with neritic affinity (Aizawa et al., 2004; Dimiza et al., 2014; Okada, 1992). Thus, decreased placolith abundances versus increase of *H. carteri* during cold phases may reflect enhanced turbidity and decrease in the light intensity in surface water. The positive, although moderate correlation of *H. carteri* with reworked coccoliths ($r = +0.55$; Figure S2), a valuable proxy of higher continental input (Bonomo et al., 2016; Colmenero-Hidalgo et al., 2004; Flores et al., 1997; Maiorano et al., 2016) supports the relation of the taxon with turbid surface water. In the Montalbano Jonico section, more specifically, the abundance of reworked coccoliths is related with the pattern of local paleodepth changes (Figure 2j) and global

sea level reconstruction (Figure 2k), with increasing values during low sea level phases (i.e., during drier glacial/stadial phases) when more efficient erosion on land prevailed (Maiorano et al., 2016). The results indicate that increased land-derived nutrient from river input, during warm and wetter conditions, and enhanced turbidity consequent of improved continental erosion during colder and drier climate were important forcing mechanism modulating coccolithophore productivity in the near-shore depositional setting of the IS. However, within the placolith-bearing taxa, prominent shifts between small and medium-sized taxa did occur over time (Figure 2d) and were likely forced by climate-induced paleoenvironmental variations.

5.3. Glacial-Interglacial Productivity Mode

Productivity in the IS mainly shifts between a cold-low productivity to warm-high productivity scenario, with a distinct change in terms of assemblage variations occurring between glacial MIS 20 and full interglacial MIS 19c. During MIS 20, small *Gephyrocapsa* largely dominate among the placoliths (Figure 2d), representing the most important group within the total coccolith abundance (Figure 3e). It is well known that small *Gephyrocapsa*, which inhabit the upper photic zone, are opportunistic taxa showing a rapid response to nutrients availability and provide a proxy of high productivity and unstable surface waters (Gartner, 1988; Hernández-Almeida et al., 2011; Knappertsbusch, 1993; Marino et al., 2011, 2018; Takahashi & Okada, 2000). Therefore, the dominance of small *Gephyrocapsa* at the IS during MIS 20 (Figure 2d) suggests high-nutrient availability and water-mixing in surface water; low relative abundances of the deep dwelling taxon *F. profunda* (Figure 2g) in the same interval, support nutrient availability in surface water, shallow nutricline and reduced seasonal stratification as the dominant controls on productivity (Beaufort et al., 1997, 2001; McIntyre & Molfino, 1996; Molfino and McIntyre, 1990a, 1990b). The occurrence of *G. bulloides* (Figure 3h) is consistent with nutrient availability in surface water related to wind-induced vertical mixing during cold and arid climate, while the presence of *N. pachyderma* (Figure 3i) suggests polar-subpolar water incursion into the Mediterranean (Cacho et al., 1999; Capotondi et al., 2016; Girone et al., 2013; Marino et al., 2018; Pérez-Folgado et al., 2003; Sierro et al., 2005) and at the site location. Both marine and continental proxies support colder-drier conditions during MIS 20 in the IS (Figure 1C; Bertini et al., 2015; Maiorano et al., 2016; Marino et al., 2020; Nomade et al., 2019), which are likely related to enhanced north-westerly winds, adequate mixing and nutrient availability in surface water. Despite the flourishing of the highly productive small *Gephyrocapsa* group (Figure 2d), Total N, C_{37} and $C_{37:2}/C_{38:2}$ indicate that coccolithophore productivity in surface waters remains rather low during this phase (Figures 3b, 3d and 3e), with respect to other periods. Less negative $\delta^{13}C$ values during this part of the record also support reduced carbon supply and enhanced ventilation at the seafloor (Figure 3a). It is reasonable to hypothesize that colder glacial conditions and polar water influx (increase of *N. pachyderma*—Figure 3i), likely combined with surface water turbidity (increased abundance of *H. carteri*—Figure 2f) created unfavorable environmental conditions that prevented the proliferation of the coccolithophores during late MIS 20 as indicated by low values of total coccolithophore abundance.

On the other hand, Total N, C_{37} and $C_{37:2}/C_{38:2}$ ratio reach maximum values during most of MIS 19c (Figures 3b, 3d and 3e), that is, the climatically stable part of interglacial MIS 19 in the IS (Nomade et al., 2019), indicating a marked increase of coccolithophore productivity. In fact, total gephyrocapsids reach their highest relative and absolute abundances during this phase as well (Figures 3c and 3e). The most significant shift in the assemblage is marked by the recovery of medium-sized *Gephyrocapsa* and a strong reduction in the species dominance (Figure 3g) suggesting a well-diversified coccolithophore community. Within the medium-sized group, *G. oceanica* is a common component of low-latitude assemblages (Baumann et al., 2005; Boeckel & Baumann, 2004; Haidar & Thierstein, 2001; Winter et al., 1994; Ziveri et al., 2004) and related to less saline Atlantic inflow in the Mediterranean Sea (Álvarez et al., 2010; Bárcena et al., 2004; Bazzicalupo et al., 2018, 2020; Knappertsbusch, 1993; Oviedo et al., 2017) especially during sea level highstand. On the other hand, *G. caribbeanica* is considered a cosmopolitan taxon (Baumann & Freitag, 2004; Flores et al., 2012; Saavedra-Pellitero et al., 2017) with a more questionable ecology since it has been related to oligotrophic and warm surface waters (Bollmann, 1997; Bollmann et al., 1998; Toti et al., 2020), to seasonally nutrient-enriched subpolar to subtropical waters (Baumann & Freitag, 2004). This species is capable of seasonal bloom (Baumann et al., 2005; Flores et al., 2012), and usually used as a proxy for high paleoproductivity (González-Lanchas et al., 2020; López-Otálvaro et al., 2008; Maiorano et al., 2013; Quivelli et al., 2020). The increase of medium-sized *Gephyrocapsa* and their significant contribution to

coccolithophore abundance during MIS 19c, with respect to MIS 20 can be interpreted as a marked change in the paleoenvironment and specifically associated with a persistent warmer environment (SSTs are persistently at their maxima values, with mean values of about 18.5°C; Figure 2b) as well as adequate, seasonal nutrient availability that sustained placolith spring/winter blooming. Nutrients were likely replenished from continental supply through precipitations and vertical mixing during winter.

The persistent occurrence of *G. bulloides* (Figure 3h) supports seasonal sea surface water nutrient availability, likely related to river run-off during the winter-spring period, that is, when *G. bulloides* proliferates. It is noteworthy that thanks to the high-sedimentation rate and the sampling resolution it is possible to observe that the onset of the enhanced coccolithophore productivity during MIS 19c does not develop earlier than the upper portion of the sapropelic layer related to i-cycle 74 (Figure 3), as testified by the gradual increase of Total N, C_{37} and $C_{37:2}/C_{38:2}$. This is likely in relation with enhanced turbidity associated with the increase in precipitation/river runoff accompanying the lowermost sapropel portion during insolation maximum (Marino et al., 2020). This hypothesis is supported by the prominent peak of reworking (Figure 2i) and also of *G. bulloides* (Figure 3h) that, thanks to its opportunistic behavior, likely exploited enhanced nutrient from land during increased river input. The scenario during MIS 19c is in agreement with the climate framework reconstructed at the IS during this time period, which is characterized by climate improvement on land as suggested by the main expansion of temperate forest, dominated by broad-leaved trees typical of a (warm) temperate and relatively humid climate, with mild winters and warm summers and a seasonal precipitation regime (Bertini et al., 2015; Maiorano et al., 2016; Nomade et al., 2019). The latter provided adequate seasonal external input of nutrients from river runoff which, together with warmer surface water conditions, ensured the highest coccolithophore productivity.

5.4. Stadial/Interstadial Productivity Variations

From MIS 19b onwards, alternating warm-cold paleoproductivity scenario is observed on a short-term time scale as well, matching stadial-interstadial variations. It has been documented that in this part of the section marked millennial-scale drying and cooling events alternate with wetter and warmer phases, as proved by distinct shifts in the Mesothermic arboreal pollen taxa (Figure 1C) coupled with sharp SST and oxygen and carbon isotope changes (Maiorano et al., 2016; Marino et al., 2020; Nomade et al., 2019). They reflect not only local environmental changes but also short-term climate instability recorded on a global scale, during the transition toward the MIS 18 glacial inception in North Atlantic (Emanuele et al., 2015; Ferretti et al., 2015; Kleiven et al., 2011), at the Iberian margin (Sánchez Gõni et al., 2016) and in the Mediterranean region, in both marine (Marino et al., 2015, 2016; Nomade et al., 2019; Toti et al., 2020) and continental records (Giaccio et al., 2015; Mangili et al., 2007; Regattieri et al., 2019). The millennial-scale productivity changes we observe during MIS 19a points toward enhanced productivity during interstadials relative to stadials. This pattern is less evident in the C_{37} profile, likely due to the low concentration of total alkenones and the potential effects of preservation and/or dilution of biomarkers as discussed above. A rapid shift in the coccolithophore community occurred as shown by the increase of small *Gephyrocapsa* and of species dominance (Figure 3g), indicating a rather unstable, nutrient-rich surface water environment developed during interstadials. Indeed, the contribution of medium-sized *Gephyrocapsa* to Total N during MIS 19a warm oscillations is negligible, if compared with MIS 19c warm scenario, as shown by their rather low absolute abundances (Figure 3e). Despite the relevant shift in terms of gephyrocapsid assemblage, surface water temperature did not change significantly between MIS 19c and MIS 19a interstadials (Figure 2b), thus suggesting that temperature was not the primary parameter hampering or reducing the proliferation of medium-sized *Gephyrocapsa* in the assemblage during warm episodes of MIS 19a. Within the foraminiferal assemblage, the long-term increasing trend of *G. bulloides* during MIS 19a, and at shorter scale during interstadials (Figure 3h), supports enhanced nutrient availability in surface water. It is noteworthy that MIS 19a occurs when precession index is at minimum (Figure 3i), an orbital configuration leading to northward penetration of the ITCZ promoting intensified summer aridity and enhanced winter precipitation in the region (e.g., Milner et al., 2012; Nomade et al., 2019; Regattieri et al., 2015; Tzedakis, 2007; Wagner et al., 2019). It is therefore likely that enhanced productivity during interstadials was primarily promoted by the increased land-derived nutrient availability through river discharges from neighboring land, during more pronounced wetter winters, rapidly exploited by r-strategist small *Gephyrocapsa* group. In this scenario, an increased influence of the WAC may have also contributed to the nutrient delivery in the study area.

A contribution from local upwelling resulting from improved advection of Atlantic water during sea level rise that goes along with interstadials (Figure 1C), as occurs today at the periphery of the anticyclonic NIG (Batistić et al., 2014, 2017; Civitarese et al., 2010), cannot be also excluded.

Looking in more detail at the evolution of MIS 19 interstadials, their earlier portions are generally marked by a slight increase in the abundance of *F. profunda* (Figure 2g), suggesting deeper nutricline and lower productivity in surface water (e.g., Beaufort et al., 1997; Molfino & McIntyre, 1990a, 1990b). It is likely that the abrupt shift in SST accompanying the onset of each interstadial (Figure 2b) promoted strong summer thermocline favoring *F. profunda* and low nutrient contents at sea surface waters, as indicated by low abundances of *G. bulloides* (Figure 3h). Then, a shallowing in the nutricline depth, from a distinct Deep Chlorophyll Maximum (DCM) to highly productive surface water is observed in the course of each interstadial (slight decrease of *F. profunda*, increase of Total N, small *Gephyrocapsa* and *G. bulloides*), likely reflecting the land-derived nutrient enrichment in surface water and possible local upwelling. A similar pattern in the interstadial evolution has been also observed in the Sicily Channel (Incarbona et al., 2013). On the other hand, during stadial phases, the pronounced SST decrease (Figure 2b), reaching minima of 12–13°C at the IS, coupled with enhanced surface water turbidity (marked increase of *H. carteri* and reworking) occurring during drier phases, were likely unfavorable conditions even for small gephyrocapsids and may explain the reduction in total coccolithophore productivity.

Exacerbated summer aridity likely developed during MIS 19a-2, at the precession minimum peak (Figure 3j). Differently from the other interstadials, MIS 19a-2 records a marked increase of WWCT (Figure 2h). The more oligotrophic conditions in surface waters developed during maximum summer aridity on land (reduced nutrient supply from land), favoring the vertical taxon zonation in the Mediterranean (Knappertsbusch, 1993; Oviedo et al., 2015) and the increase of WWCT that benefit from warm and oligotrophic waters (Baumann et al., 2004; Boeckel & Baumann, 2004; McIntyre & Bé, 1967; Palumbo et al., 2013; Saavedra-Pellitero et al., 2010; Winter et al., 1994; Ziveri et al., 1995, 2004). It is worth noticing the stadial part of MIS 19a-2, that is characterized by the distinct increase of *N. pachyderma* with respect to the other stadials (Figure 3i). The incursion of the polar taxon clearly marks enhanced arrival of cold polar water in the Mediterranean and in the Ionian basin, likely related to ice-sheet instability in the North Atlantic. This hypothesis is strengthened by the increase of *N. pachyderma* in the western Mediterranean at ODP Site 975 (Quivelli, 2020) during the same stadial phase. Finally, this cold water arrival is probably linked to the Ice Rafted Debris (IRD) peak recorded at ODP Site 980 in North Atlantic (Wright & Flower, 2002), as well as enhanced freshwater pulse at the Iberian Margin (Rodrigues et al., 2017). This phase is also marked by a peak of Mediterranean forest pollen taxa decrease (Sánchez Gõni et al., 2016; Figure 3l), suggesting aridity on land and the worldwide relevance of this iceberg discharge event. At the IS the sharp coeval depletion observed in the $C_{37:2}/C_{38:2}$ ratio (Figure 3b) may reflect a relevant impact of this event on coccolithophore productivity in relation with enhanced arrival of cold and low salinity surface water, hampering biological productivity as observed during the last glacial stadial phases (Colmenero-Hidalgo et al., 2004; Incarbona et al., 2013).

The observed warm-cold millennial-scale productivity mode in the IS during MIS 19a appears rather comparable to the pattern observed in the Alboran Sea (Cacho et al., 2000; Colmenero-Hidalgo et al., 2004; Moreno et al., 2005) and in the Sicily Channel (Incarbona et al., 2013) during Dansgaard-Oeschger oscillations of the last 70 kyr, indicating a similar productivity dynamic in different areas, depositional settings and time intervals. It is noteworthy that both in the Alboran Sea and in the Sicily Channel the stadial/low productivity and interstadial/high productivity pattern in the last glacial period is marked by relative increase of small placoliths during Interstadials and of *H. carteri* and *Syracosphaera* spp. during Stadials and Heinrich events (Colmenero-Hidalgo et al., 2004), similarly to the result in the IS. The strong relation between placoliths and *H. carteri* at the IS, the documented vegetation changes, consistent with the climate framework in southern Europe at Site U1385 (Sánchez Gõni et al., 2016), in central (Regattieri et al., 2019) and northern Italy (Moscariello et al., 2000; Rossi, 2003), as discussed by Nomade et al. (2019), suggests that the productivity pattern in the IS was the local response to the basin-wide warmer and wetter conditions during MIS 19 interstadials, resulting from the southward positions of the westerlies, which provided enhanced humidity over the Mediterranean region. This pattern would have promoted a shift from low basinal nutrient inventory during cold and arid phases to a higher nutrient budget in warm and humid

periods. This productivity scenario appears also in line with the modern seasonal variability observed in the coccolithophore export production in the eastern Mediterranean, which documents enhanced productivity during the late winter-spring season, associated with water column mixing and increased rainfall rate (Malinverno et al., 2009; Triantaphyllou et al., 2010).

6. Conclusion

We obtained a high temporal resolution data set of coccolithophores and organic biomarkers, which provides evidence of climate-induced productivity variations in the central Mediterranean at millennial-scale in a near-shore environment. The patterns of Total N, alkenone parameters, that is, C_{37} and $C_{37:2}/C_{38:2}$ ratio, compared with the relative abundance of coccolithophore blooming species (gephyrocapsids), *H. carteri*, reworked coccolith taxa and few planktonic foraminifera species, make it possible to propose a paleoproductivity scenario from late MIS 20 to earliest MIS 18. Our main results include not only the first Mediterranean documentation of C_{37} total concentration during the late MIS 20-early MIS 18, but also the use of $C_{37:2}/C_{38:2}$ ratio as a paleoenvironmental proxy. The pattern of this ratio mirrors the profiles of those taxa related to productivity, thus encouraging future investigations in different depositional settings. Potential interferences from dilution and degradation phenomena have been taken into account and cannot fully be excluded in the study section. However, a primary ecological signal is recognizable in our record since the integrated data set shows consistent patterns, which sustain their use as paleoproductivity signals in a near-shore environment. The resulting cold/low- to warm/high- productivity scenario matches glacial-interglacial and stadial-interstadial variations. Low productive surface water resulted from enhanced surface water turbidity developing during prevalent erosion process on land and low sea level and from cold-water conditions and polar-subpolar low salinity water incursion into the Mediterranean. The higher coccolithophore productivity during warm MIS 19c was sustained by persistent warmer surface waters coupled with a seasonal precipitation regime and consequent nutrient availability. Millennial-scale low-high productivity variations mirror stadial-interstadial phases. Enhanced productivity during interstadials was likely promoted by the increased land-derived nutrients through river discharge during more pronounced wetter winters. Specifically, increased SST firstly developed a summer thermocline and oligotrophic surface water conditions at the onset of each interstadial, while enhanced nutrient supply from land and local upwelling promoted a shallow nutricline and highly productive surface water during the late interstadials. This short-term scenario is rather very similar to evidences brought from deep-sea records from central and western Mediterranean during Dansgaard-Oeschger oscillations of the last 70 kyr, highlighting a comparable productivity dynamic in different time intervals and depositional settings. Our results suggest a common regional forcing over time that mirrors the changing westerlies position and related humidity over the Mediterranean region and the periodic North Atlantic water inflow of polar origin. Finally, comparison of alkenone patterns with that of the coccolithophore assemblages suggests the gephyrocapsid group, essentially the medium-size morphotypes, as the main alkenone contributor in the studied interval.

Data Availability Statement

In the present version, data are available via supplements. The new data supporting figures of the present manuscript are deposited on https://data.mendeley.com/datasets/38rvfnvmt3/1.

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