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Nutrients and hydrography explain the composition of recent Mediterranean planktonic foraminiferal assemblages

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ABSTRACT

The composition of planktonic foraminiferal assemblages in surface sediments of the Mediterranean Sea shows a pronounced zonal gradient. This gradient is different from what is observed in the open ocean, indicating that the assemblage composition may respond to environmental variables other than the otherwise dominant surface water temperature. Here we make use of a dataset of census counts of 18 taxonomic categories in 124 surface-sediment samples extracted from the ForCenS database to understand the main environmental factors affecting the composition of recent Mediterranean planktonic foraminiferal assemblages. The tested explanatory variables include temperature, salinity, chlorophyll, nitrate and phosphate concentrations in the surface waters, temperature, nitrate and phosphate concentrations at depth and thermal, salinity and density vertical gradients. The composition of the assemblages is aligned along two environmental gradients and redundancy analysis reveals that the tested variables explain a large portion (>70%) of the variance in the compositional data. The first environmental gradient reflects the nutrient content in the deep waters, affecting nutrient availability in the productive zone, while the second gradient is driven by higher (northern area) and lower (southern area) upward nutrient advection due to differences in density stratification, conditioned by the regional hydrography. Although sea surface temperature is the most reconstructed environmental variable from fossil assemblages of planktonic foraminifera, it seems to play a secondary role in the Mediterranean Sea. This, has implications for reconstructions of past oceanographic conditions in this region, opening up the possibility to reconstruct productivity instead, or next to, temperature.

1. Introduction

The most direct method to identify environmental variables controlling the distribution of planktonic foraminiferal assemblages is the study of living populations using planktonic tows. Seasonal shell fluxes of different species to the seafloor could also be used for this purpose, through sediment trap studies. Although there are very few studies of living foraminifera (Cifelli, 1974; Mallo et al., 2017; Pujol and Grazzini, 1995) or time series of seasonal shell fluxes in the Mediterranean (Avnaim-Katav et al., 2020; Bárcena et al., 2004; Hernández-Almeida et al., 2011; Rigual-Hernández et al., 2012), a large number of recent surface sediments have been sampled (Hayes et al., 2005; Kontakiotis et al., 2017; Kontakiotis et al., 2021; Siccha and Kucera, 2017; Zarkogiannis et al., 2020). This record of long-term averaged shell flux preserved in the sediments also allows the study of the environmental variables controlling the distribution of planktonic foraminifera and because it is more comparable to the foraminiferal assemblages in the sedimentary record, the obtained information has a direct potential to be utilised for paleoecological reconstructions.

Planktonic foraminiferal species are not homogeneously distributed neither in the ocean surface, nor vertically in the water column, nor temporally (Jonkers and Kučera, 2015; Meilland et al., 2019; Rebotim et al., 2017; Schiebel and Hemleben, 2005). Early studies between the late 1950s and 1980s observed that species distribution in the plankton displays a latitudinal pattern that results in the emergence of five major faunal provinces: tropical, subtropical, temperate, subpolar and polar (Bé and Hutson, 1977). Although the distribution of planktonic foraminifera appeared mainly related to sea surface temperature, further

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studies of the distribution, ecology and biology of the living planktonic foraminifera identified other environmental variables that determine species distribution patterns. These variables are food availability, water column stratification, salinity, turbidity, sunlight or chlorophyll-a concentration (Bé and Tolderlund, 1971; Berger, 1971; Bijma et al., 1990; Caron et al., 1987; Erez, 1983; Erez and Luz, 1983; Giamali et al., 2021; Giamali et al., 2020; Giamali et al., 2019; Hemleben et al., 1989; Kontakiotis et al., 2017; Neil et al., 2005; Northcote and Neil, 2005; Ortiz and Mix, 1992; Ortiz et al., 1995; Rebotim et al., 2017; Schiebel and Hemleben, 2005, 2017; Schiebel et al., 2001; Siccha et al., 2009; Spindler et al., 1984; Tolderlund, 1971; Zarkogiannis et al., 2019; Zarkogiannis et al., 2022). All these environmental parameters vary on a seasonal scale conditioned by hydrographic changes that generate characteristic seasonal successions (Kroon and Ganssen, 1989). Indeed, complex seasonal patterns have been described in the Mediterranean sediment trap studies (Avnaim-Katav et al., 2020; Bárcena et al., 2004; Hernández-Almeida et al., 2011; Rigual-Hernández et al., 2012), which all seem to indicate that the assemblage composition is not driven by temperature alone.

The strong Mediterranean seasonality and its specific hydrography have an important impact on the planktonic foraminiferal assemblages within the surface sediments, which are also distinct from the neighbouring North Atlantic assemblages (Kontakiotis et al., 2021; Pujol and Grazzini, 1995; Zarkogiannis et al., 2020). For example, some common species in the sub/tropical North Atlantic are absent in the Mediterranean (Hayes et al., 2005; Pujol and Grazzini, 1995; Thunell, 1978). These species are *Globorotalia menardii, Globorotalia tumida, Globorotalia crassaformis, Pulleniatina obliquiloculata, Sphaerodinella dehiscens, Candeina nitida* and *Globorotalia hirsuta*, the latter showing a distribution extending to the Gulf of Cadiz. These differences hint at a more complex relationship between assemblage composition and environmental forcing in the Mediterranean Sea, what is likely a general pattern for isolated basins such us the Red Sea (Siccha et al., 2009), the South China Sea (Steinke et al., 2008) or the Gulf of Mexico (Antonarakou et al., 2015). The environmental control on the planktonic foraminiferal assemblages in isolated basins must be locally studied and quantitative reconstruction of past environmental conditions cannot be based on calibration dataset from outside of these seas.

Since the 1960s, planktonic foraminifera shells in surface sediments have been used to infer past physicochemical conditions of the upper ocean by analysis of species abundances in fossil sediments given their present ecological preferences. After the pioneering transfer function approach by Imbrie and Kipp (1971), sea surface temperature (SST) has been the most reconstructed variable using planktonic foraminiferal fossil assemblages due to its identification as the most explanatory variable of the variance in global-scale surface sediment assemblages (Morey et al., 2005; Rillo et al., 2019). In the Mediterranean Sea this approach has been used to reconstruct Late Pleistocene SST in many records (e.g. Hayes et al., 2005; Kallel et al., 2000; Kallel et al., 1997; Kandiano et al., 2014; Pérez-Folgado et al., 2003b; Pérez-Folgado et al., 2004). However, other studies have also related the Mediterranean planktonic foraminiferal distribution to phytoplankton productivity and the ratio of warm-oligotrophic (WO) versus cold-eutrophic (CE) species has been frequently used in the scientific literature (e.g. De Rijk et al., 1999; Geraga et al., 2010; Giamali et al., 2019; Kontakiotis, 2016; Pérez-Folgado et al., 2003a; Rohling et al., 1997; Rohling et al., 2002; Sierro et al., 2003; Sierro et al., 1999). These studies suggest that surface productivity plays an important role on the distribution of planktonic foraminifera in the Mediterranean Sea but fail to characterise this relationship quantitatively. This is because it is difficult to separate it from the temperature effect. Past temperature and surface productivity estimates obtained by the transfer function approach can only be accurately interpreted by assuming that their causality remained the same in the past compared to that of today.

In this work we aim to study surface sediments assemblage and a large suite of potential forcing variables to unravel the main environmental forcing involved in the distribution of the planktonic foraminiferal assemblages in the Mediterranean. The results from this study could clarify the limitation of current methods in the reconstruction of past environmental conditions.

2. Materials and methods

2.1. Planktonic foraminiferal dataset from the Mediterranean surface sediments

Planktonic foraminiferal relative abundances (> 150 μm) in Mediterranean surface sediments were obtained from the ForCenS database published by Siccha and Kucera (2017). Initially, the 23 taxonomical categories proposed by Hayes et al. (2005) for the Mediterranean were considered. However, due to differences in the distribution pattern of *Globorotalia truncatulinoides* dextral and sinistral coiling morphotypes (section 5.1), we considered them separately, adding a new category. On the other hand, all 'rare species' with maximum abundance always below 1% were removed (Dryden Jr, 1931; Jonkers and Kučera, 2019; Revets, 2004; Siccha et al., 2009). In this category we included *P. obliquiloculata, G. crassaformis* and the composite *G. menardii + tumida* category, which were totally absent, and *Globigerinoides conglobatus*, *S. dehiscens* and *G. hirsuta*, which were present but never reached 1% relative abundance. These latter three species were only encountered in the recent Mediterranean dataset in 3 to 7 samples and considering their low abundance it cannot be excluded that their presence is due to misidentification. Finally, samples with fewer than 300 counted specimens, and those samples that did not separate the *G. truncatulinoides* coiling morphotypes in their counting (Fig. 3), were removed. Also, one north Aegean sample has been removed because it is located close enough to the coast, which precludes the correct interpolation of deep environmental variables from the relatively coarse WOA 2005 resolution. As a result, a total of 124 samples and 18 taxonomical categories were included in the studied planktonic foraminiferal dataset.

3. Mediterranean circulation and variable selection

3.1. Surface water

The Mediterranean is a landlocked sea in which net evaporation exceeds freshwater input through rainfall and runoff (Bethoux, 1979; Lacombe et al., 1981). The water loss generates a sea level difference at the Strait of Gibraltar that initiates an Atlantic water inflow into the Mediterranean. The main branch of this Atlantic water flows eastward across the African margin and throughout the Strait of Sicily up to the easternmost Mediterranean. This surface flow is characterized by generating anticyclonic eddies in the south Mediterranean margin (Macias et al., 2019; Millot, 1999; Robinson et al., 2001; Stegner et al., 2021). In contrast, the surface circulation of the northern margin is characterized by the prevalent presence of cyclonic eddies, driven by northerly winds (Fig. 1). This contrasting surface circulation determines a different upward flow of intermediate waters. The prevailing north cyclonic circulation favours the upward flows of cold and nutrient enriched intermediate waters (Bakun and Agostini, 2001; Kontoyiannis, 2010; Salihoğlu et al., 1990; Siokou-Frangou et al., 2010), whereas in the south the pervasive presence of anticyclonic eddies prevents upwelling and induces vertical stratification (Siokou-Frangou et al., 2010). The movement of surface water towards the centre of these anticyclonic gyres and its convergence with the African margin, deepen the nutricline, keep nutrients below the euphotic zone and reduce primary productivity (Garcia-Gorriz and Carr, 2001; Heburn and La Violette, 1990; Vargas-Yáñez et al., 2002; Viúdez et al., 1998).

The Atlantic water flowing eastward along the north Africa, typically at 15–16 °C and salinities between 36 and 37 ‰, is exposed to the Mediterranean freshwater and heat forcing to reach over 28 °C and 39 ‰ in the easternmost Levant margin (Antonov et al., 2006; Locarnini et al.,

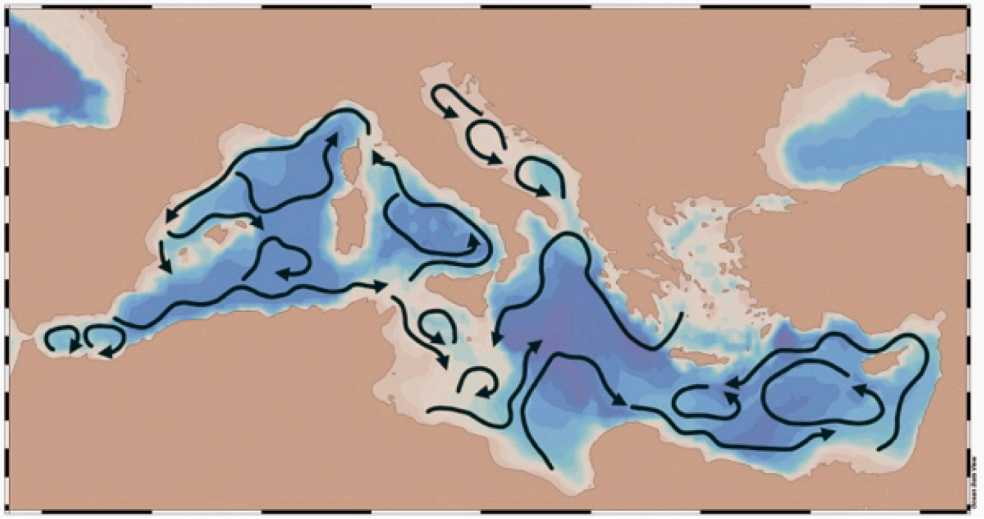

Fig. 1. Mediterranean Sea map with main surface currents (Macias et al., 2019) represented by black arrows.

2006). Then, due to its isolation from the Atlantic ocean, the Mediterranean Sea has a specific hydrography with large temperature, salinity and nutrient availability gradients occurring across a relatively short geographical distance (Thunell, 1978).

In order to evaluate both meridional and longitudinal surface differences, and their influence in the Mediterranean planktonic foraminiferal distribution, five potential explanatory environmental variables were analysed at the surface: temperature, salinity, chlorophyll, nitrates and phosphates content. These surface variables were taken at 10 m water depth as recommended by Kucera et al. (2005a). SSTs were taken from the World Ocean Atlas (WOA) 2005 (Locarnini et al., 2006).

SST has been identified as the key variable in the global distribution of different species of zooplankton groups, including foraminifera (Mackas et al., 2012; Morey et al., 2005; Richardson, 2008; Rillo et al., 2019) and therefore, its effect has been one of the most studied variables in the Mediterranean Sea (e.g. Kontakiotis, 2016; Mallo et al., 2017; Pujol and Grazzini, 1995; Thunell, 1978). Although most of the planktonic foraminiferal species have a temperature optimum, they have an eurythermal behaviour surviving in a wide range of temperatures (Bijma et al., 1990; Hemleben et al., 1989; Lombard et al., 2011; Schiebel and Hemleben, 2017; Tolderlund, 1971). In view of their broad temperature tolerance, the Mediterranean thermal gradient is likely not sufficient to explain the large-scale pattern in species distribution in this basin (Mallo et al., 2017; Pujol and Grazzini, 1995). Moreover, the high correlation between temperature and other environmental variables such as salinity, or chlorophyll concentration, especially within the Mediterranean, prevents direct demonstration of the temperature effect on species distribution and its decoupling from the effect of other variables.

Although some species of planktonic foraminifera have been described to be sensitive to salinity (Bé and Tolderlund, 1971; Thunell, 1978), the physiological limits of species are much broader than the natural salinity range (Bijma et al., 1990) and it is likely that this effect is indirect. Indeed, previous studies concluded that the surface salinity Mediterranean gradient cannot explain most of the species variability (Mallo et al., 2017; Pujol and Grazzini, 1995). In this study this variable was considered due to its determinant influence on density, a decisive oceanographic variable in stratification/mixing processes that have been proposed to affect planktonic foraminiferal species distribution within other marginal seas such as in the Red Sea (Siccha et al., 2009). Salinities were taken from the WOA 2005 (Antonov et al., 2006).

Unlike salinity, trophic conditions play a major role in phytoplankton productivity and thus should have a direct effect on the planktonic foraminiferal species stocks and distribution (Giamali et al., 2021; Mallo et al., 2017; Pujol and Grazzini, 1995; Siccha et al., 2009). To study the effect of nutrient conditions, we used surface nitrate and phosphate concentrations to approximate the upper-ocean nutrient content and surface trophic conditions, as well as the surface chlorophyll-a concentration as an approximation of nutrient uptake by the phytoplankton. Nutrients were taken from the WOA 2005 (Garcia et al., 2006), while the chlorophyll-a concentration was obtained from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (data downloaded from http://oceancolor.gsfc.nasa.gov/).

Monthly values of all variables were interpolated to the position of the analysed sediment samples as area-weighted averaged within a 100 km radius around each site. The seasonal variables were then calculated by averaging monthly values: January, February and March for winter, April, May and June for spring, July, August and September for summer and October, November and December for autumn. Annual variables were obtained averaging the 12 monthly values. The seasonality values were also calculated as the difference between the maximum and the minimum monthly values.

3.2. *Intermediate and deep waters*

Because of its exposure to the Mediterranean negative freshwater budget, the modified Atlantic water (MAW) increases its density as it moves eastward, thus generating a vertical density gradient that triggers surface water sinking in the eastern Mediterranean to form the Intermediate Levantine Water (LIW) (Bethoux, 1979; Emelianov et al., 2006; Lacombe et al., 1981; Millot and Taupier-Letage, 2005) (Fig. 2). Deep Mediterranean water is formed in the northern margins induced by surface water cooling and mixing due to the prevailing northerly winds during winter (Gascard, 1978; Tziperman and Speer, 1994). Both intermediate and deep waters are exported to the North Atlantic Ocean throughout the Gibraltar strait (Font et al., 2007; Robinson et al., 2001). This general overturning circulation pattern determines the distribution of nutrients, temperature and salinity in the deep and intermediate waters (Fig. 2).

As may be seen in Fig. 2, the temperature of subsurface waters in the eastern and western Mediterranean is relatively constant, being the intermediate-deep-waters in the western Mediterranean (13.0 to ~13.75 °C) cooler than their equivalents in the eastern basin (13.75 up to 14.5 °C) (Locarnini et al., 2018). This is due to the different winter temperatures in the areas of deep and intermediate water formation, that is the Aegean and Levantine seas in the eastern Mediterranean and the Gulf of Lion in the western Mediterranean.

Salinity and nutrients of intermediate and deep waters in the eastern Mediterranean are also relatively similar, but different from those of the

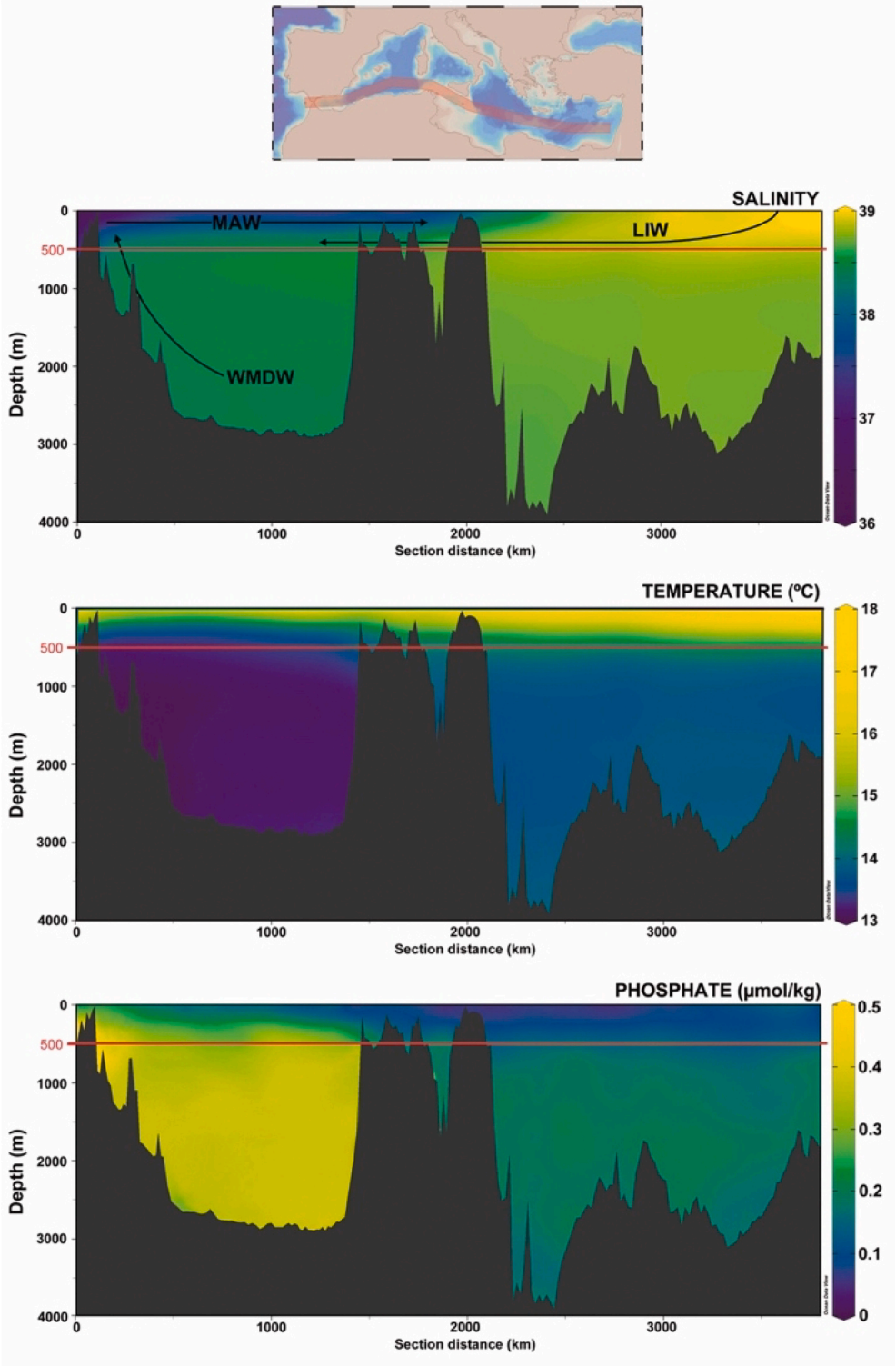

Fig. 2. Mediterranean vertical profiles of salinity, temperature and phosphate concentration (WOA 2018) (Garcia et al., 2019; Locarnini et al., 2018; Zweng et al., 2019). The profiles show a west-east transect indicated in the upper map of the figure. The red line identified the 500 m water depth taken as representative of the intermediate water conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

western Mediterranean, being the last one fresher and more enriched in nutrients (Fig. 2). This distinct configuration is due to the antiestuarine circulation between both basins and the export of nutrients and salt from the eastern to the western basin through the Strait of Sicily (Bethoux, 1979, 1980; Krom et al., 2010; Krom et al., 2004; Krom et al., 1991; Lacombe et al., 1981).

As previously mentioned, planktonic foraminifer growth is greatly affected by stratification/mixing processes in the water column and its consequent influence on surface productivity. The surface productivity, which is described in other marginal seas as the main environmental factor controlling the foraminiferal assemblage (Siccha et al., 2009), is strongly enhanced by the nutrient content transferred from the depths to the surface by the upward water.

Although planktonic foraminifera mainly live in the upper 200 m,

following this hypothesis that upwelled waters are perhaps important, nutrients, temperature and salinity at 500 m were selected as potential explanatory variables. This depth was not taken arbitrarily but was selected as the shallowest depth capable of representing the more or less stable deep values, reflecting approximately the different mean values of each basin (Fig. 2) while retaining sediment samples from shallower areas for the analysis. Nutrients, salinity and temperature at 500 m were taken from the WOA 2005 (Antonov et al., 2006; Garcia et al., 2006; Locarnini et al., 2006).

In order to estimate vertical mixing or stratification processes, salinity, temperature and density vertical differences were estimated as the difference between 500 and 10 m depth. Density was estimated using Gibbs seawater equations included in the GSW Package v1.0–6 (Kelley and Richards, 2015) and the Analysis of Oceanographic Data Package v1.4–0 (Kelley, 2018) for R software (R Core Team, 2020). Both for deep variables and vertical gradients, monthly, annual and season variables were interpolated as previously explained for surface ones.

Beyond the considered environmental variables, there are other parameters related with the seawater carbonate properties such as the alkalinity, pH, dissolved inorganic carbon, pCO2 and [CO32-]. These variables were excluded from the analysis due to its identification as second role parameters in the planktonic foraminiferal species distribution within the Mediterranean (Mallo et al., 2017).

3.3. Seasonal planktonic foraminiferal fluxes and variables

Sediment trap studies, which can approximate the flux of planktonic foraminiferal specimens exported from the upper-ocean to the ocean surface sediments (e.g. Asahi and Takahashi, 2007; Deuser et al., 1981; Jonkers et al., 2019; King and Howard, 2003; Rigual-Hernández et al., 2012; Thunell and Reynolds, 1984), indicate strong annual cycles and seasonal flux variation both in the western and eastern Mediterranean basins. During summer and autumn, the planktonic foraminiferal fluxes in the Mediterranean are dramatically reduced and can reach near-zero values (Bárcena et al., 2004; Hernández-Almeida et al., 2011; Rigual-Hernández et al., 2012). In the eastern Mediterranean, recent sediment traps studies from the Levantine basin identified a second minor flux peak (> 125 μm) in late summer and early autumn (Avnaim-Katav et al., 2020). Overall, summer-autumn flux seems to be so low throughout the Mediterranean, that the contribution of these seasonal assemblages to the annual foraminiferal accumulation rates is probably negligible (Bárcena et al., 2004; Rigual-Hernández et al., 2012). Rigual-Hernández et al. (2012) calculated that the winter-spring flux represents >80% of the Gulf of Lion annual flux and thus, the foraminiferal assemblages in the surface sediments represent mainly the winter-spring assemblage. Therefore, this study was focused on the environmental variables of the most representative periods of the surface sediments assemblages, i.e. annual, winter and spring.

4. Statistical analyses

Planktonic foraminiferal abundances in the statistical analyses were analysed as relative proportions. Detrended correspondence analysis (DCA) was performed on the planktonic foraminiferal dataset to estimate the length of the sampled environmental gradient and determine whether linear or unimodal models are more appropriate for ordination analyses. The sea surface environment of the Mediterranean Sea is characterized by a steep environmental gradient in many key parameters (e.g. temperature and salinity), which is unusually strong compared to the small size of the basin (Thunell, 1978). Nevertheless, the length of the first DCA axis is <3 standard deviations (2.65), suggesting that the environmental gradient remains short compared to the dispersion distance of the complete ocean environmental gradient (Lepš and Šmilauer, 2003), resulting in a linear response of the planktonic foraminiferal species. Therefore, principal component analysis (PCA) and redundancy analysis (RDA) as linear ordination methods are most suitable to analyse the response of Mediterranean planktonic foraminiferal assemblages to environmental forcing (Lepš and Šmilauer, 2003).

PCA was performed on the planktonic foraminiferal dataset to identify species that contribute the most to the variability of the Mediterranean assemblages. Redundancy analysis (RDA) is a series of linear analyses that displays and explains variation in a set of response variables constrained by a set of predictor variables (Borcard et al., 2018; Legendre and Gallagher, 2001; Legendre and Legendre, 2012; Lepš and Šmilauer, 2003). In this study, RDA was used to decompose the variation in the Mediterranean planktonic foraminiferal assemblages into variation associated to the environmental variables. Initially, an individual RDA was performed for each variable to evaluate its individual effect (marginal effect). Through a permutation ANOVA-like test (Legendre et al., 2011), all variables that appear to explain a significant ($p < 0.01$) amount of variability in species proportions were identified. Then, RDA with annual and seasonal variables were performed using only the significant variables in order to evaluate the seasonal aspect of the tested parameters that explains most variance in planktonic foraminiferal assemblages and estimate the conditional effect of the variables. Ordination analyses were performed using the *vegan: Community Ecology Package* v.2.5–7 (Oksanen et al., 2020) for R software (R Core Team, 2020).

5. Results

5.1. Geographical distribution of planktonic foraminiferal assemblages in the Mediterranean Sea

The five most abundant species (*Globigerinoides ruber* (white + pink), *Neogloboquadrina incompta, Globoconella inflata, Globigerina bulloides* and *Globorotalia truncatulinoides* (dextral + sinistral)) together account for 62 to 100% of the planktonic foraminiferal assemblages in core top samples in the Mediterranean (Fig. 3). The species *G. ruber* and *G. bulloides* are present in all samples.

The species *G. ruber* is the most frequent in sub/tropical environments (e.g. Bé and Hutson, 1977; Kontakiotis et al., 2017; Zarkogiannis et al., 2020). Both white and pink subspecies (Morard et al., 2019) are largely constrained to the eastern and central basins in the recent Mediterranean (Caddy et al., 1995; Kontakiotis et al., 2021) where their abundance ranges between 30% and 81% (Fig. 3 b). In contrast, *G. ruber* in the western basin rarely reaches 30% with an average abundance of 15%. This inter-basin contrast is opposite in *N. incompta*, *G. truncatulinoides* and *G. inflata*. These three species show their maximum abundances in the western basin and are rare or absent in the eastern Mediterranean.

The species *G. truncatulin*oides shows almost an exclusive distribution in the western basin although it is absent in the Alboran Sea (Fig. 3 f and g). The Mediterranean *G. truncatulinoides* specimens are genetic Type II, which is the only genotype with both right and left coiling morphotypes (Darling and Wade, 2008; Ujiié et al., 2010). Although this species is described as a deep-dwelling species (Hemleben et al., 1989; Schiebel and Hemleben, 2017), both morphotypes have been identified in the Mediterranean sediments with remarkably different distributions that could correspond to different ecological preferences as described in the Atlantic Ocean (Darling and Wade, 2008; de Vargas et al., 2001; Ujiié et al., 2010). The dextral morphotype of *G. truncatulinoides* spreads exclusively in the central western basin while the sinistral morphotype inhabits the areas of lower abundance of the dextral form. The species *G. bulloides* reaches proportions of up to 20% in the cooler and in winter well mixed Gulf of Lion (Fig. 3 f and g). Due to this difference in the distribution of both morphotypes, in this study we considered them as separated taxonomical categories in the analyses.

The species *G. inflata* and *N. incompta* are also almost exclusive to the western basin. *N. incompta,* described as a temperate and subpolar species, is absent in most of the Mediterranean (Cifelli, 1973, 1974; Schiebel and Hemleben, 2017). However, higher abundances occur in

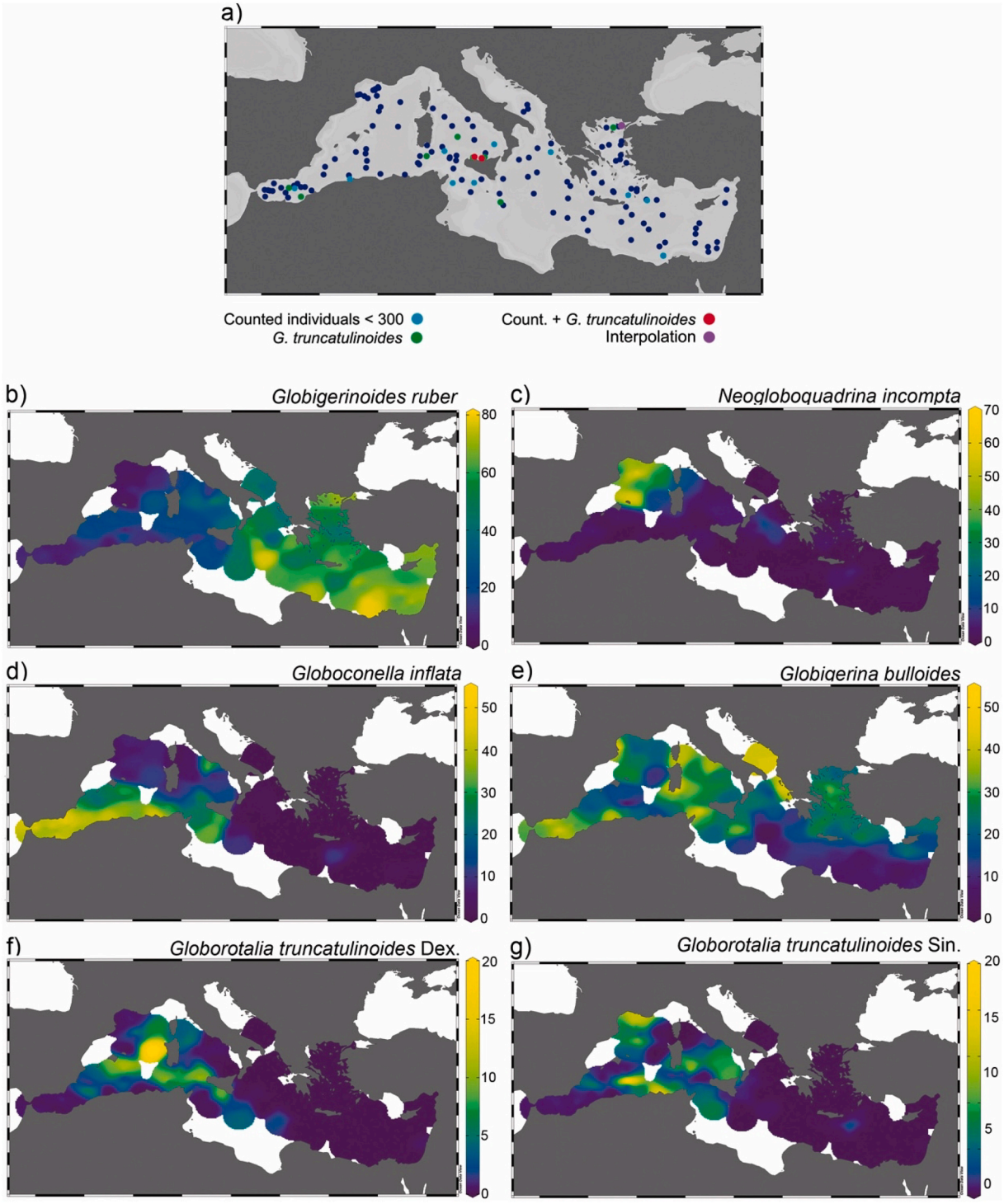

Fig. 3. Major species distribution maps. a) In dark blue, location of the Mediterranean surface sediment samples included in this study. Census counts excluded are identified with colours according to the exclusion criteria. Panel b to g) Distribution maps showing the relative abundances (%) of *G. ruber* (white + pink), *N. incompta, G. inflata, G. bulloides, G. truncatulinoides* dextral and *G. truncatulinoides* sinistral coiling based on ForCenS database (Siccha and Kucera, 2017). The software Ocean Data View (Schlitzer, 2018) was used to generate this and the other Mediterranean Sea figures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the north western basin where it represents up to 71% of the surface sediment assemblage (Fig. 3 c). The species *G. inflata* is largely restricted to the south of the western basin and its distribution in the Mediterranean seems to follow the inflow of Atlantic waters (Fig. 3 d). In the modern global ocean, *G. inflata* has been described as an opportunistic species abundant in mesotrophic waters associated with hydrologic fronts (Chapman, 2010; Lončarić et al., 2007; Retailleau et al., 2011; Schiebel and Hemleben, 2017; Storz et al., 2009). The areas of higher abundances of *G. inflata* and *N. incompta* are clearly separated, the first one preferentially lives in the south western Mediterranean while the second shows highest relative abundances in the north-western region. The divide between these two regions is defined near the North Balearic front (Millot and Taupier-Letage, 2005).

While the previous species distributions are virtually restricted to the

western or eastern Mediterranean, *G. bulloides* is common in both basins (Fig. 3 e). The species *G. bulloides* shows.

a transitional and subpolar distribution with highest abundances in upwelling regions and other eutrophic settings (Bé and Hutson, 1977; Bé and Tolderlund, 1971; Naidu and Malmgren, 1996; Schiebel et al., 1997; Schiebel and Hemleben, 2017). In the Mediterranean, the highest abundances are found along the northern margins, with maxima in the Alboran, Tyrrhenian and Adriatic seas. Significant *G. bulloides*, abundances of up to 65%, have also been reported in the north Aegean Sea due to coastal upwelling and freshwater inflows from the Black Sea, which is indicative of high nutrient concentrations in this area (Kontakiotis, 2016).

The especies showing minor abundances (Fig. 4) are: *Orbulina universa, Neogloboquadrina dutertrei, Trilobatus sacculifer, Globigerinella siphonifera and Globigerinella calida, Globigerinita glutinata, Globigerina falconensis, Turborotalita quinqueloba, Globotuborotalita rubescens, Globorotalia scitula, Globigerinoides tenellus, Beella digitata* and *Neogloboquadrina pachyderma.* Among these are the tropical species such as *T. sacculifer, G. siphonifera* + *G. calida, G. tenellus*, *G. rubescens*, and *B. digitata* (Be et al., 1985; Bé and Hutson, 1977; Conan and Brummer, 2000; Ortiz et al., 1995; Parker, 1962; Retailleau et al., 2012; Schmuker, 2000; Schmuker and Schiebel, 2002; Yamasaki et al., 2008), which all show higher abundances in the eastern basin, particularly along the southern margin (Avnaim-Katav et al., 2020; Zarkogiannis et al., 2020).

The species *N. dutertrei* is frequent in tropical to subtropical areas and in temperate waters during the summer (Bé and Hutson, 1977; Hilbrecht, 1997; Schiebel and Hemleben, 2000, 2017). In contrast, the only higher abundances in the Mediterranean dataset are recorded in the coldest NW area (Fig. 4). No individuals of *N. dutertrei* have been reported in sediment traps studies in the Gulf of Lion (Rigual-Hernández et al., 2012) and only abundances below 1% in the Levantine basin (Avnaim-Katav et al., 2020). Because of the low abundance and due to the morphological similarity with *N. incompta*, individuals identified as *N. dutertrei* in the Mediterranean may correspond to *N. incompta* with more than four chambers in the last whorl, akin to the Pachyderma-Dutertrei intergrades category established by Kipp (1976), now considered to likely *refer to N. incompta* (Kucera et al., 2005a, 2005b).

A similar circumstance may hold for *N. pachyderma*. Although its abundance is consistently low, the maximum abundance is higher than 1% and consequently the species could not be removed using the rare species criterion. However, *N. pachyderma* is a typical polar species (Bé and Hutson, 1977) and its presence, especially in the eastern basin, is inconsistent with its Atlantic ocean ecology. Therefore, we believe it is possible that these specimens correspond to rare specimens of *N. incompta* sinistral. The rare abundances of sinistral specimens representing aberrant coiling rather than *N. pachyderma* would be consistent with the dominance of the dextral morphotype (Darling et al., 2006; Oda and Domitsu, 2009; Sagawa et al., 2013) and this conclusion is supported by the high positive correlation ($r = 0.5$) between the relative abundance of *N. pachyderma* and *N. incompta* in the analysed dataset.

5.2. Variability in modern Mediterranean planktonic foraminiferal assemblages explained by the environmental variables

The covariance-based principal component analysis revealed that *G. ruber, G. inflata, G. bulloides* and *N. incompta* are the major

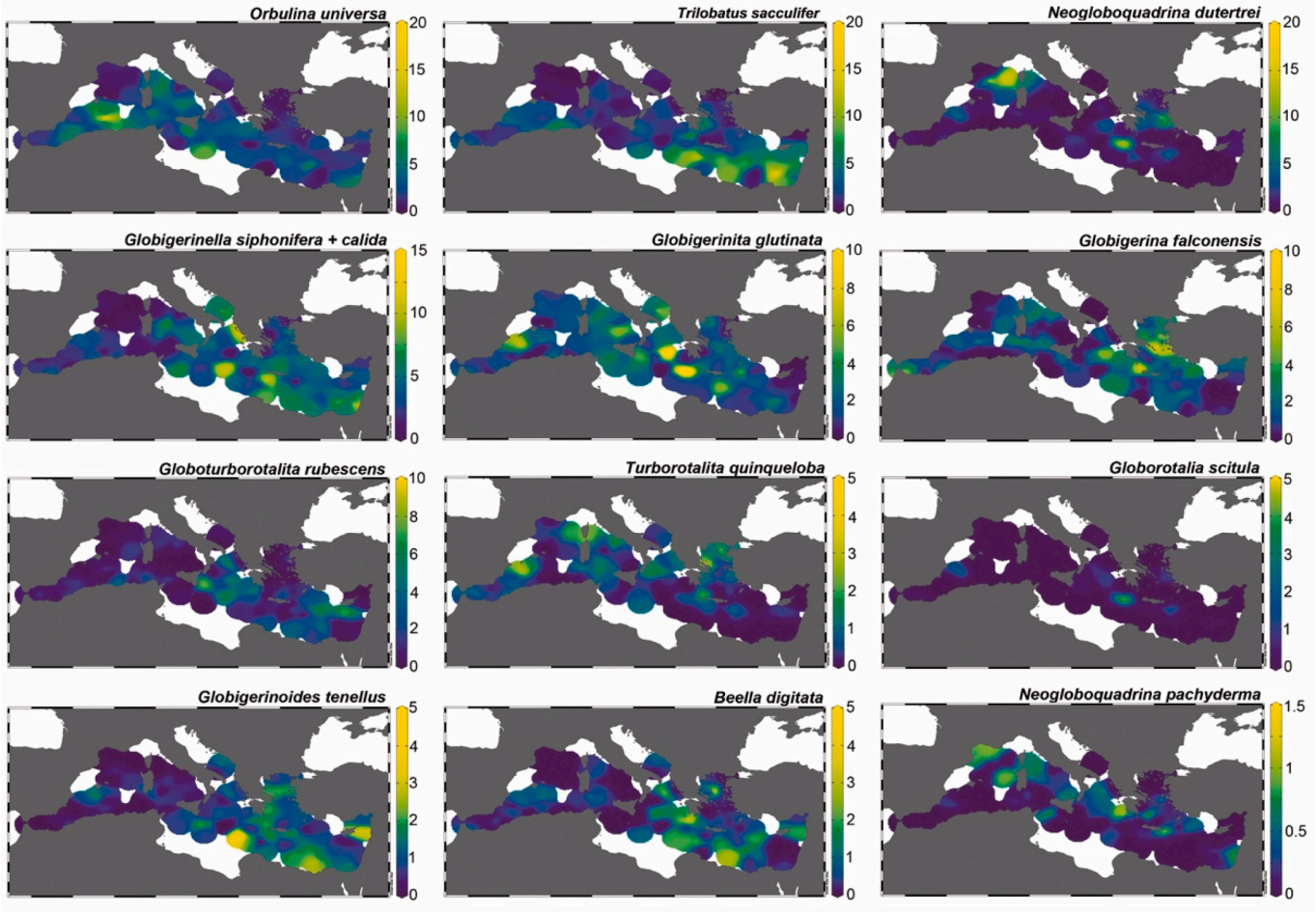

Fig. 4. Distribution maps of the species showing minor abundances *O. universa, T. sacculifer, N. dutertrei, G. siphonifera* + *G. calida, G. glutinata, G. falconensis, G. rubescens, T. quinqueloba, G. scitula, G. tenellus, B. digitata* and *N. pachyderma* based on ForCenS database (Siccha and Kucera, 2017).

contributors to the first two factors (PC1 and PC2) controlling the variability of the assemblages, while the other species show much lower loadings, which indicates that their abundance may be related to other environmental factors or represent noise due to low counts (Table 1). PC1 explains 64% of the total variance within the dataset and is highly associated to the relative abundances of *G. ruber* (Fig. 5 a) while PC2 explains 21%, correlating with *G. inflata* and anticorrelating with *N. incompta*.

In the dimensional reduction obtained from PCA there is an evident spatial clustering among the samples (Fig. 5 b) and thus three distinct regions can be defined: (1) the eastern Mediterranean and the middle-Tyrrhenian Sea, (2) the north-western Mediterranean and (3) southern and eastern regions of the western basin, excluding the portion of the Tyrrhenian Sea attached to the eastern basin. To further investigate their influence, the annual, winter, spring and seasonality values of the environmental variables were tested carrying out an RDA individually for each variable. These analyses revealed that most of the proposed variables are significant ($p < 0.01$) in the explanation of the variation in the composition of the foraminiferal assemblages (Table 2).

In general, the significance of the seasonal variables is notably lower, with surface temperature and the salinity gradient becoming not significant in the explanation of the variance in the foraminiferal distribution in the Mediterranean (Table 2). Of the remaining variables, the highest proportion of variance is explained by the surface nutrients, both nitrates and phosphates, and especially the seasonality of the surface concentration of chlorophyll. These parameters seem to be involved in the main structure of the environmental W-E and N-S gradients defining the distribution of planktonic foraminiferal species. As both nutrients and chlorophyll surface show their annual maxima concentrations during winter and spring (e.g. Krom et al., 2010; Krom et al., 2004), the subsequently analyses of these seasonal variables will serve as a reference for their seasonality study.

To explore the link between these significant environmental variables and the distribution patterns of planktonic foraminiferal assemblages in the Mediterranean, we carried out an RDA. The geographic distribution of the loadings and the three RDA (annual, winter and spring) are shown in Fig. 6. In the RDA triplots (scaling 2) (Fig. 6 b to d), the lower the angles formed between vectors, either species or environmental variables, the higher the correlation between them (Legendre and Legendre, 1998; Lepš and Šmilauer, 2003; Ter Braak, 1994; Zuur et al., 2007).

In the annual, winter and spring RDA analyses, RDA1 explains between 55.10 and 55.89% of the constrained variance while RDA2 explains 15.66 to 16.25%. RDA1 and RDA2 show similar patterns as PC1 and PC2 evidencing that the planktonic foraminiferal species abundance dataset is strongly structured by the proposed and analysed environmental variables. With the exception of the surface phosphate, which shows the greatest difference between the RDAs (Fig. 6 b to d), the environmental variables do not show major differences between the annual, the spring and the summer analyses, which allows establishing general environmental patterns for RDA1 and RDA2. While the eastern Mediterranean displays negative scores for RDA1, the western basin sites show positive values. In the eastern Mediterranean surface sediment assemblages are mainly defined by higher relative abundances of *G. ruber*, whereas the western basin ones are defined by higher abundances of *G. inflata, G. bulloides* and *N. incompta*, and hence, lower abundances of *G. ruber*. According to the RDA results the proportion of *G. ruber* and the other major contributor species is closely linked to temperature at 500 m water depth and negatively correlated to surface chlorophyll and nutrient content, especially both surface and deep nitrates. The correlation of the negative scores of RDA1 with higher surface temperature and salinity is lower.

RDA2, which shows the direction of the second most variation, expresses the difference between the northern and southern regions of the western basin, excluding the portion of the Tyrrhenian Sea attached to the eastern basin (Fig. 6 b to d). Although there is a sign inversion in the spring RDA2 to the annual and winter ones, species and variables cooccur in the same quadrants. Higher relative abundances of *N. incompta* are characteristic of the north-western region, which is closely linked to surface phosphate, deep nitrate and surface chlorophyll (Fig. 6 b to d). In contrast, assemblages rich in *G. inflata* are characteristic of the southern region that are closely linked to the salinity vertical gradient (Fig. 6 b to d). The eastern basin displays scores for RDA2 that are close to zero.

Table 1
Loadings of the species in the PCA.

Species	PC1	PC2
B. digitata	0.01	0.00
G. bulloides	**−0.21**	0.11
G. glutinata	0.00	0.00
G. falconensis	0.01	0.02
G. inflata	**−0.40**	**0.60**
G. ruber	**0.85**	0.06
G. rubescens	0.02	0.01
G. scitula	0.00	0.00
G. siphonifera + G. calida	0.05	0.02
G. tenellus	0.02	0.00
G. truncatulinoides Dex.	−0.03	0.03
G. truncatulinoides Sin.	−0.09	−0.11
N. dutertrei	−0.01	−0.02
N. incompta	**−0.25**	**−0.78**
N. pachyderma	0.00	−0.01
O. universa	−0.01	0.05
T. quinqueloba	0.00	0.00
T. sacculifer	0.04	0.03

6. Discussion

6.1. Nutrients and hydrography control the modern Mediterranean planktonic foraminiferal assemblages

The higher correlation of RDA1 with deep-water temperature and nitrate content (Fig. 6 b to d), indicates that in addition to surface conditions, deep-water properties of the eastern and western Mediterranean exert an important control on the distribution of recent planktonic foraminifera. Because planktonic foraminifera are considered to grow mainly near the ocean surface, it would be expected the highest correlation with surface productivity inferred from chlorophyll concentration. However, the obtained results point that the distribution pattern of the planktonic foraminiferal species in recent Mediterranean sediments is mainly controlled by the productivity throughout the water column that rely on nutrient storage at depth, and their advection into the surface layer. While PC1 and RDA1 scores, which follow a western-eastern pattern, are driven by the differential deep nutrient storage between the two basins, PC2 and RDA2 follow a meridional direction between the northern and southern regions of the western Mediterranean reflecting differences in advection of the deep nutrient reservoirs to the surface. Both environmental factors (nutrient storage at depth, and their advection into the surface layer) are tightly linked to the hydrographic regime of the Mediterranean Sea.

6.1.1. Eastern warm-oligotrophic versus western cold-eutrophic planktonic foraminifera

Surface temperature and salinity, as well as phosphate concentration, especially in subsurface waters, are also related to RDA1 (Fig. 6 b to d). The spatial distributions of these surface variables (Fig. 7) are similar to that of PC1. The good correlation between PC1 and RDA1 with deep-water properties (temperature and nutrient contents) are the result of the distinct heat and nutrient contents of the western and eastern Mediterranean and their impact (nutrient and heat upward transfer) on the surface properties of both basins. A lower nutrient and higher heat content (warmer water at depth) of the eastern Mediterranean interior water is responsible for the higher sea surface temperatures and lower

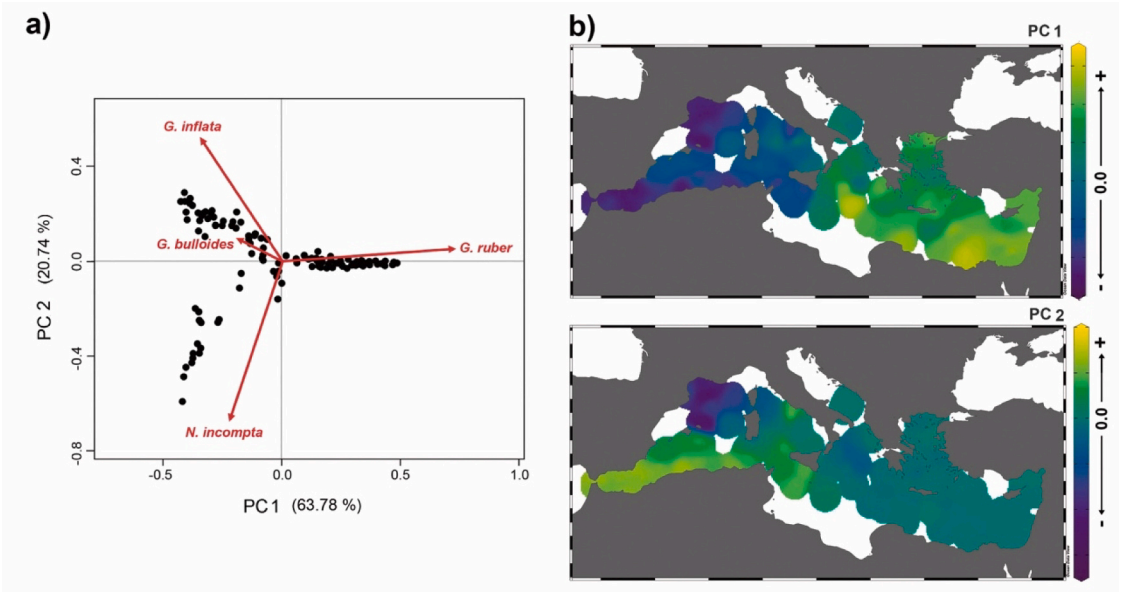

Fig. 5. Covariance-based PCA results. A) PCA biplot (scaling =1) with species represented by their contribution vector and sites by dots and b) PC1and PC2 loadings distribution maps.

Table 2
Proportion of variance explained individually by each variable (constrained axis) versus the proportion of variance explained by unconstrained axis.

Environmental variable	% explained variance by first constrained and unconstrained axis							
	Annual		Winter		Spring		Seasonality	
	Constrained	Unconstrained	Constrained	Unconstrained	Constrained	Unconstrained	Constrained	Unconstrained
Nitrate (S)	45.55	26.59	34.46	30.31	14.50	51.86	38.91	32.47
Salinity (S)	45.36	31.86	45.02	33.61	46.23	31.06	6.07*	58.24
Temperature (D)	41.95	23.57	40.96	25.62	42.01	23.16	3.91*	61.5
Phosphate (D)	41.09	28.81	31.42	36.61	4.64	60.6	21.08	45.76
Temperature (S)	37.32	34.38	34.89	38.03	40.54	32.22		
Salinity gradient	36.47	41.65	37.25	42.01	39.97	38.02		
Nitrate (D)	33.39	32.97	40.13	28.52	38.79	26.66	16.92	47.13
Chlorophyll (S)	31.32	34.02	38.59	26.51	28.03	40.64	41.12	30.76
Thermal gradient	25.65	44.54	19.18	50.20	25.45	40.80	3.94*	60.43
Density gradient	22.50	55.65	25.92	52.88	25.51	52.46	4.77*	59.21
Phosphate (S)	20.46	49.49	31.30	36.94	6.06*	62.38	34.97	29.61

Significant variables ($p < 0.001$).
(S) in surface (10 m)
(D) in depth (500 m)
* Significant variables ($p < 0.01$).

nutrient contents in this basin when compared with the deep western Mediterranean. This, favours warm-oligotrophic foraminifera in the east and cool-eutrophic foraminifera in the west.

The anti-estuarine circulation of the eastern basin with regards to the western basin results in nutrient impoverishment of the eastern Mediterranean, where the circulation exports remineralised nutrients in deep-water through the Strait of Sicily into the western Mediterranean. As a result, the Mediterranean surface conditions range from oligotrophic in the west to ultra-oligotrophic in the east (Crise et al., 1999; de Fommervault et al., 2015; Krom et al., 1992; Krom et al., 2010; Krom et al., 2004; Krom et al., 1991; Lazzari et al., 2012; Mallo et al., 2017; Sournia, 1973; Thingstad et al., 2005; Van Cappellen et al., 2014). The response of the planktonic foraminifera to the western Mediterranean higher chlorophyll and nutrient content of surface waters can be examined by considering the pattern of shell flux in sediment traps of both basins. To facilitate a comparison with the composition of sedimentary assemblages, we here consider the annual mean fluxes. In the western Mediterranean, the mean annual flux is mainly composed of spring-growing species such as *G. bulloides, N. incompta, G. truncatulinoides, G. inflata* (Bárcena et al., 2004; Rigual-Hernández et al., 2012), which are characteristic of cooler and nutrient-enriched waters and belong to the cold-eutrophic (CE) water species cluster (De Rijk et al., 1999; Rohling et al., 1997; Rohling et al., 2002; Schiebel and Hemleben, 2017; Schiebel et al., 2018; Sierro et al., 2003). The fluxes of warm-water species like *G. ruber* (white), *T. sacculifer* and *O. universa* increase towards the summer-autumn but the fluxes are too small, resulting in low relative abundances in sedimentary assemblages. In the eastern Mediterranean, sediment trap studies from the Levantine basin also observed the highest foraminiferal shell flux (> 125 μm) during late winter and early spring (Avnaim-Katav et al., 2020). However, the late winter-early spring foraminiferal assemblage is composed of *G. ruber* (~60%) and *G. rubescens* (~20%) with minor contribution of less abundant species such as *G. tenellus*, *G. calida*, *G. ruber* pink (Avnaim-Katav et al., 2020). In contrast, the annual fluxes of the CE species such as *G. bulloides*, which are high in the western Mediterranean, are very low here and some species like *N. incompta* are completely absent. As a result, the warm-oligotrophic (WO) species *G. ruber, G. rubescens, G. tenellus* and *G. ruber* pink, constitute up to 97.2% of the total assemblage

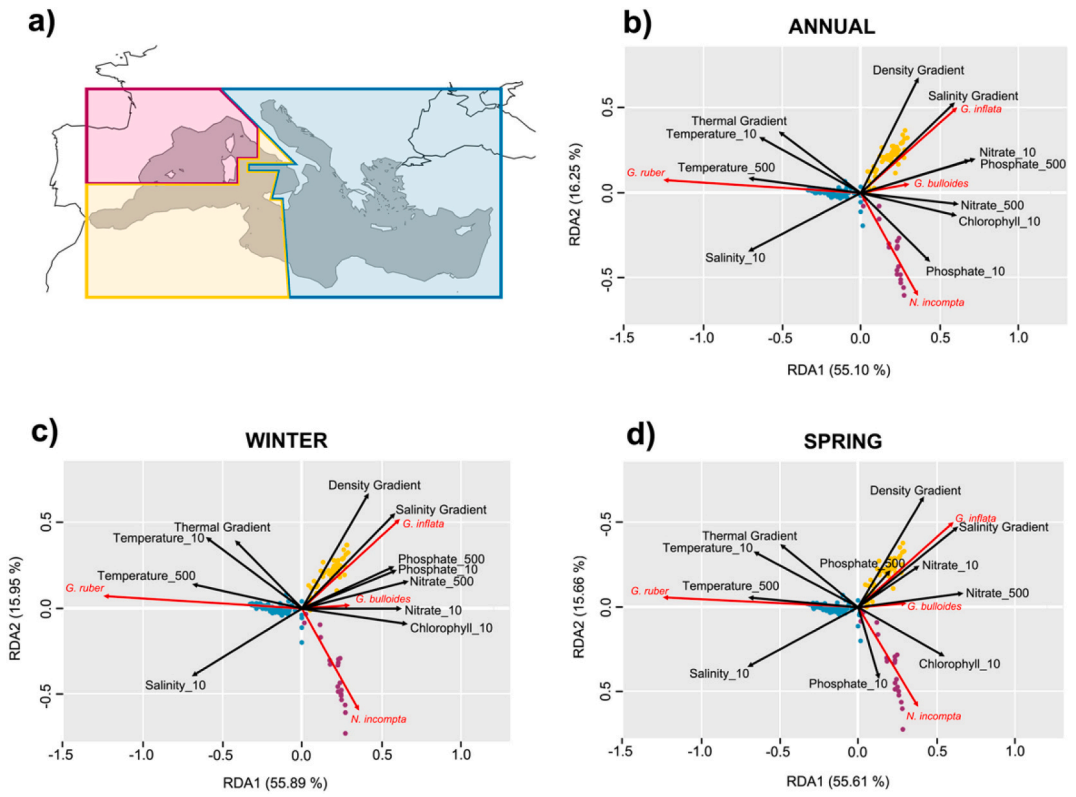

Fig. 6. a) Mediterranean Sea with coloured polygons defining the three main regions based on the loadings distribution in Fig. 3b. RDA triplots scaling 2 with site scores as weighted sums of species (wa) for annual (b), winter (c) and spring (d) explanatory environmental variables.

(Fig. 7 h). These spinose and photosynthetic symbiont-bearing species are known to be associated with warm and nutrient-depleted (oligotrophic) waters (De Rijk et al., 1999; Rohling et al., 1997; Rohling et al., 2002; Schiebel and Hemleben, 2017; Schiebel et al., 2018; Sierro et al., 2003), which coincide with lower planktonic foraminiferal production environments (Schiebel and Hemleben, 2017; Schiebel et al., 2018). Therefore, the proportions of WO species in the modern Mediterranean are also highly correlated with PC1 and RDA1 (r 0.99) and coincides with previous observations (Kontakiotis et al., 2021; Mallo et al., 2017; Thunell, 1978; Zarkogiannis et al., 2020).

Beyond the relative abundances of the different species, the difference in primary productivity between the two basins can be seen in the magnitude of the foraminiferal fluxes. While in the western Mediterranean, especially in the Gulf of Lion, the flux can reach >4000 shells m^{-2} d^{-1}, coinciding with times of high abundance of the CE species (Rigual-Hernández et al., 2012), fluxes of these species are negligible in the Levantine basin (max. 10 shells m^{-2} d^{-1} *G. bulloides* and *T. quinqueloba* in the >125 μm fraction) (Avnaim-Katav et al., 2020). Furthermore, the flux of *G. ruber* and *G. rubescens*, which are the dominant WO species in the Levantine basin, only reach between 300 and 150 shells m^{-2} d^{-1}, respectively (Avnaim-Katav et al., 2020).

6.1.2. Meridional hydrographic control on the distribution of planktonic foraminiferal species

The composition of planktonic foraminiferal assemblages from the north and south western Mediterranean differs and the pattern is visible in the PC2 and RDA2 (Fig. 5 and Fig. 6). The species loadings are dominated by *N. incompta* and *G. inflata*, which are anticorrelated. There is a good correlation of RDA2 with salinity and density vertical gradients in anticorrelation with surface salinity and surface phosphate annually, and with the spring chlorophyll (Fig. 6 b to d). This points to a common hydrographic forcing as the underlying factor behind the environmental gradient RDA2.

The vertical thermal, salinity and density gradients follow a clear meridional pattern (Fig. 8 a to c). Weaker gradients occur in the northern areas while stronger gradients are seen towards the south. This meridional pattern in the vertical gradients is seen both in the western and eastern Mediterranean. This phenomenon is caused by the Mediterranean surface circulation, which is characterized by anticyclonic eddies in the south and prevalent cyclonic eddies in the north (Fig. 1), the latter favouring the upward flow of subsurface waters and the homogenization of the water column (Bakun and Agostini, 2001; Kontoyiannis, 2010; Salihoğlu et al., 1990; Siokou-Frangou et al., 2010). The intensity of these cyclonic eddies is driven by northerly winds that promote upward water mixing in winter. The lower vertical salinity and density gradients seen in the Gulf of Lion (Fig. 8) undoubtedly reflect this mixing process triggered by cold northern winds that break autumn-summer stratification. Thus, differences in planktonic foraminiferal assemblages within the western Mediterranean basin are driven by the differences in surface circulation. The anomalies recorded in the northern Aegean Sea are driven by the much less saline and relatively cold water inflow from the Black Sea.

In the southern regions, the upwelling is reduced due to the pervasive presence of anticyclonic eddies (Siokou-Frangou et al., 2010). The movement of surface water towards the centre of these anticyclonic gyres and its convergence with the African margin deepen the nutricline, keeping nutrients below the euphotic zone and reducing primary productivity (Garcia-Gorriz and Carr, 2001; Heburn and La Violette, 1990; Vargas-Yáñez et al., 2002; Viúdez et al., 1998). The preferential flow of the low saline modified Atlantic water along the southern margin of the western Mediterranean, and the strong contrast with the underlaying more saline Mediterranean intermediate water (Millot and Taupier-Letage, 2005; Viúdez et al., 1998; Wüst, 1961) also favour the stratification of the water column. In addition, the surface temperature in the SW Mediterranean during winter is 1 to 1.5 °C cooler than the Atlantic inflowing waters enhancing the stratification, for example in the

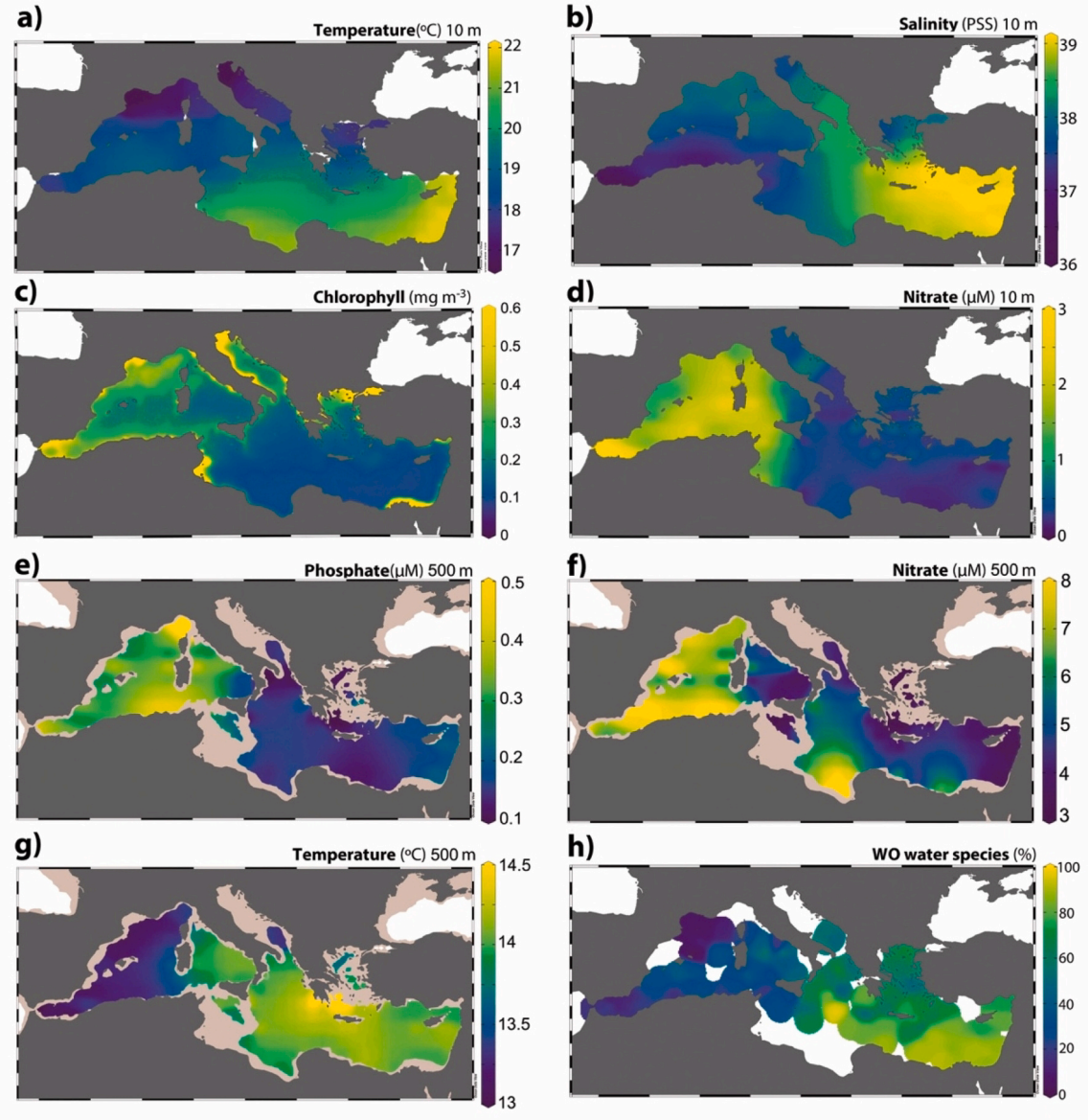

Fig. 7. Variables associated to the first environmental factor. Annual surface water temperature (a) and salinity (b), chlorophyll (c) surface water nitrate concentration (d). Phosphate concentration at 500 m water depth (e), nitrate concentration at 500 m water depth (f) (Garcia et al., 2006) and deep-water temperature at 500 m water depth (g) (Locarnini et al., 2006). Warm-oligotrophic (WO) planktonic foraminiferal relative abundances in the recent Mediterranean sediments (h) (Siccha and Kucera, 2017).

Alboran Sea (Bárcena et al., 2004). Indeed, *G. inflata* abundance (Fig. 3 d), higher PC2 values (Fig. 5) and the southwestern sample component distributions match almost perfectly with the Atlantic inflow jet course up to the Strait of Sicily. This latitudinal difference in the mixing intensity and its consequent upward advection of nutrients within the western Mediterranean, drive differences in primary productivity during spring and hence in the foraminiferal fluxes and the assemblage composition.

On the other hand, the uplift of nutrient-enriched deep waters in the Gulf of Lion explains the growth of *N. incompta, G. truncatulinoides* sinistral and *G. bulloides* (Rigual-Hernández et al., 2012). Although strong winds can affect large areas of the Alboran Sea and cause an extensive bloom regime (Garcia-Gorriz and Carr, 2001; Hernández-Almeida et al., 2011; Sanchez-Vidal et al., 2004), most of the SW basin does not experience important mixing processes and continues with higher thermal gradient values during most of the year. Therefore, the SW Mediterranean assemblages are dominated by the mesotrophic opportunistic species *G. inflata,* which accounts for up to the 100% of the foraminiferal flux during winter and early spring in the Alboran Sea sediments traps (Bárcena et al., 2004).

Although the eastern Mediterranean is more prone to stratification throughout the year, some mixing processes occur during winter in the northern seas of this basin, where intermediate and deep water are formed (Font et al., 2007; Millot and Taupier-Letage, 2005; Robinson et al., 2001). Assuming that winter vertical mixing is equivalent in the northern areas of the eastern and western basins, the higher abundance of WO water species in the east (Fig. 7 h) can only be explained if the waters rising to the surface in the eastern Mediterranean are nutrient-poor compared to their equivalents in the western basins, as discussed above. The highest relative abundances of CE species in the eastern Mediterranean are found in the Adriatic Sea. In this region *G. bulloides* can reach ~40% (Fig. 3 e). As seen in the RDA results (Fig. 6), the vector of *G. bulloides* is totally opposed to that of *G. ruber*, evidencing the importance of this CE species in diluting *G. ruber* relative abundances, and those of the WO species group in general. However, these abundances do not reach values comparable to those of the northern margin

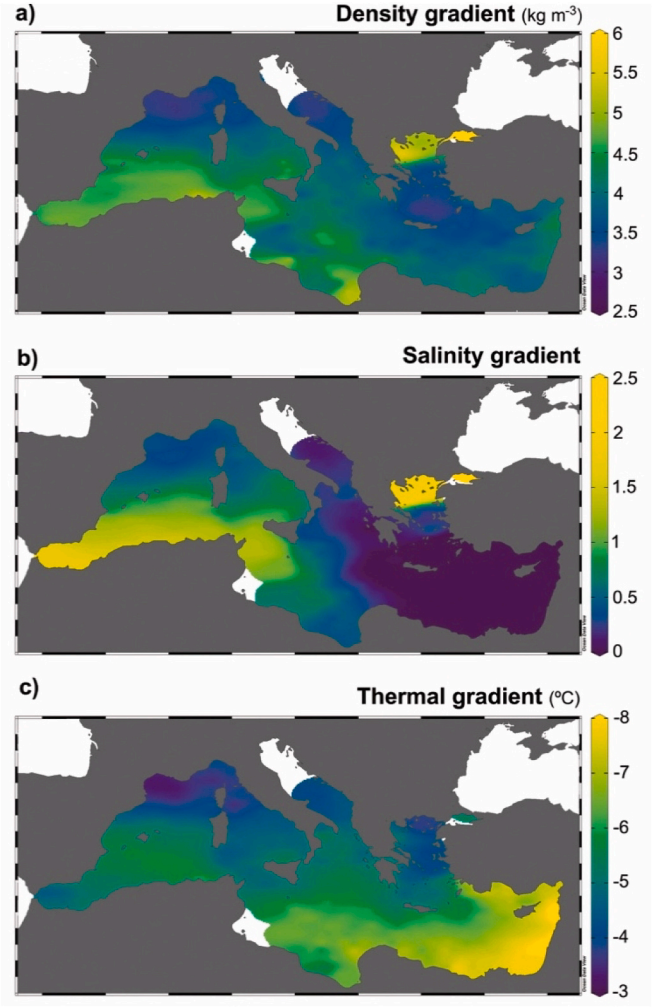

Fig. 8. Variables associated with the second environmental gradient. Annual density (a), salinity (b) (Antonov et al., 2006) and thermal (c) (Locarnini et al., 2006) vertical gradients in the upper 500 m of the water column.

of the western basin, where CE species account for 80 to 100% of the assemblages. Therefore, the overall low nutrient content of the upwelled deep-water during winter mixing in the northern seas of the eastern Mediterranean does not stimulate the high rates of phytoplankton productivity, typical of the western Mediterranean, and the growth of CE planktonic foraminiferal species, leading to much lower increases in the proportion of WO species.

6.2. *The role of deep and surface temperature in the distribution of recent Mediterranean planktonic foraminiferal assemblages*

As previously discussed, the deep nutrient content and its seasonal surface availability (conditioned by vertical density gradients) appear to be the main controlling factors for the distribution of planktonic foraminiferal assemblages in the Mediterranean. However, SST has been the most reconstructed variable from fossil foraminiferal assemblages in the Mediterranean (e.g. Azibeiro et al., 2021; Hayes et al., 2005; Kallel et al., 2000; Kallel et al., 1997; Kandiano et al., 2014; Kontakiotis et al., 2019; Kontakiotis et al., 2022; Kucera et al., 2005b; Pérez-Folgado et al., 2004; Vasiliev et al., 2019; Zachariasse et al., 2021). Our results show an apparently significant and strong link between temperature and assemblage composition as well, but this relationship is clearly coincidental and not causal. For example, the results in this study show that variability in the deep-water (500 m) temperature of the Mediterranean Sea explains more variability in recent planktonic foraminiferal assemblages than the surface temperature (Fig. 6, Table 2). Because most planktonic foraminifera live above 250 m, the strong explanatory power of the deep-water temperature implies that the relationship is due to the strong negative correlation between nutrient content and temperature at depth. The same phenomenon explains the counter-intuitive observation that, in general, surface primary productivity has a stronger negative correlation with deep temperature than with surface temperature (Table 3), especially during winter when the greatest vertical mixing and upwelling of cold, nutrient-rich deep-water occurs. This correlation with deep-water temperature comes from the strong link between deep-water temperature and nutrient contents and their respective influence on surface waters.

The processes of winter mixing, and the associated vertical heat flows, homogenise the temperature of the water column decreasing the surface temperature, but this decrease is limited by the temperature of the intermediate-deep Mediterranean water, which is different in the eastern and western Mediterranean and is well correlated with their respective intermediate-deep nutrient contents (Fig. 7).

The chlorophyll and surface temperature anticorrelation is clearly seen in Fig. 9. The Alboran sites display, during spring, a different behaviour showing relatively high temperatures with high chlorophyll contents. This pattern is related to the special role that the Alboran Sea plays on the water exchange, including nutrients and heat, with the Atlantic Ocean. During spring, coinciding with intense episodes of fertilization of surface water and hence high chlorophyll contents, the relatively higher temperatures of the Alboran Sea, compared to the rest of the Western basin, are linked to the inflow of warmer Atlantic waters. This negative correlation between SST and chlorophyll confirms the pattern observed in the foraminiferal assemblages and displayed by the RDA analysis (Fig. 6). The southern assemblages of the western basin, with intermediate values of temperature and chlorophyll, are dominated by mesotrophic and temperate waters species such as *G. inflata*.

If we assume that planktonic foraminiferal assemblages are mainly controlled by the deep nutrient content and its availability in surface waters, controlling the primary productivity and thus the surface chlorophyll concentration as it was concluded in the previous section, the correlation between the distribution of planktonic foraminiferal assemblages and SST seems to derive from the anticorrelation between the surface chlorophyll concentration and SST. This anticorrelation is strongly linked to the hydrographic processes that transfer cold, nutrient-enriched subsurface water to the surface, decreasing SST and favouring phytoplankton growth (chlorophyll concentration increase). Wherever these processes occur, surface waters will be cold and rich in chlorophyll, while this will be scarce in regions with prevailing stratification and higher SSTs. Only a few outlier sites deviate from the general Mediterranean chlorophyll-SST pattern showing higher chlorophyll concentrations than expected based on their surface temperature (Fig. 9). These locations probably correspond to sites where there is an external supply of nutrients unrelated to the hydrodynamic vertical mixing.

Then, although the SST is the most frequently reconstructed oceanographic variable through fossil assemblages, as discussed above, in the recent Mediterranean it is not the main factor determining their modern distribution. The importance of environmental variables other than SST has been highlighted in planktonic foraminiferal distribution studies in the surface sediments of the east Mediterranean (Giamali et al., 2021;

Table 3
Chlorophyll and temperature correlation coefficients. (An) annual, (W) winter and (Sp) spring.

		Deep temperature			Surface temperature		
		W	**An**	**Sp**	**W**	**An**	**Sp**
Chlorophyll	**Sp**	−0.78	−0. 74	−0.72	−0.56	−0.74	−0.69
	An	−0.83	−0.80	−0.79	−0.54	−0.73	−0.68
	W	−0.87	−0.85	−0.84	−0.63	−0.76	−0.74

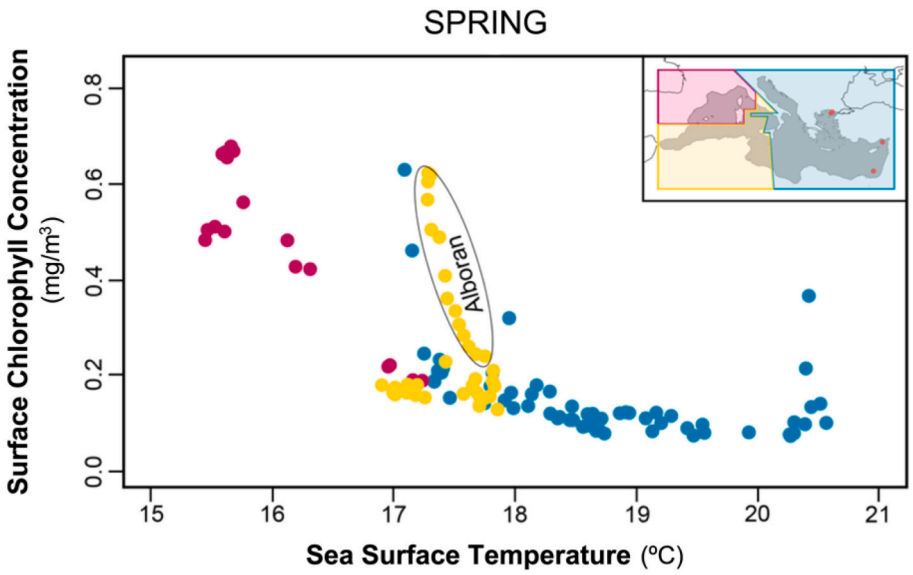

Fig. 9. Position of the Mediterranean sites in a plot of spring surface chlorophyll concentration (SeaWifs) and SST (Locarnini et al., 2006). The sites are coloured according to their location within the georeferenced areas. Samples with outliers are highlighted in red in the upper left map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Zarkogiannis et al., 2020) and other marginal basins such as the Red Sea. Siccha et al. (2009), which identifies productivity, approximated by surface chlorophyll concentration, as the fundamental factor in line with the conclusions of this study. Thus, both in the Red and the Mediterranean Seas, SST seems to play a secondary role in controlling the distribution of planktonic foraminiferal species. For example, both *G. bulloides* and *N. incompta* are highly abundant in recent assemblages from high nutrient content areas and tend to grow in spring (Bárcena et al., 2004; Rigual-Hernández et al., 2012). Surface sediment assemblages of the Alboran Sea are dominated by *G. bulloides*, and to a lesser extent those of the Adriatic, while *N. incompta* is present in NW sites, especially in the Gulf of Lion (Fig. 3c and e). Then, past surface temperature reconstruction in the Mediterranean based on the composition of fossil assemblages could be biased by nutrient and primary productivity variations.

It seems that, in high chlorophyll scenarios, the dominance of *G. bulloides* or *N. incompta* is determined by SST. In the high chlorophyll regions of the north Atlantic and Mediterranean (Fig. 10), *N. incompta* reaches the highest relative abundances with spring SSTs between 6 and 14 °C. However, *G. bulloides,* which is also characteristic of the CE assemblage, seems to be more tolerant to a wide temperature range from 4 to 18 °C. In particular, the relative abundance of *G. bulloides* is lower at water temperatures between 6 and 14 °C, because it is diluted by *N. incompta,* but reaches the highest proportions between 15 and 18 °C, when *N. incompta* decreases. The dominance of *G. bulloides* in the Alboran sea may be due to the spring SST around 16 °C while the presence *of N. incompta* restricted to the Gulf of Lion may be due to the lower spring SST (14 °C). Similarly, in the eastern Mediterranean, where CE species are relatively frequent in the northern sites characterized by slightly higher sea surface chlorophyll concentrations, *G. bulloides* is always the dominant species within the CE cluster because spring temperatures are higher than 15 °C.

7. Conclusions

The multivariate analysis of planktonic foraminiferal assemblages from surface sediments leads us to conclude that recent Mediterranean assemblages are mainly controlled by productivity and therefore food

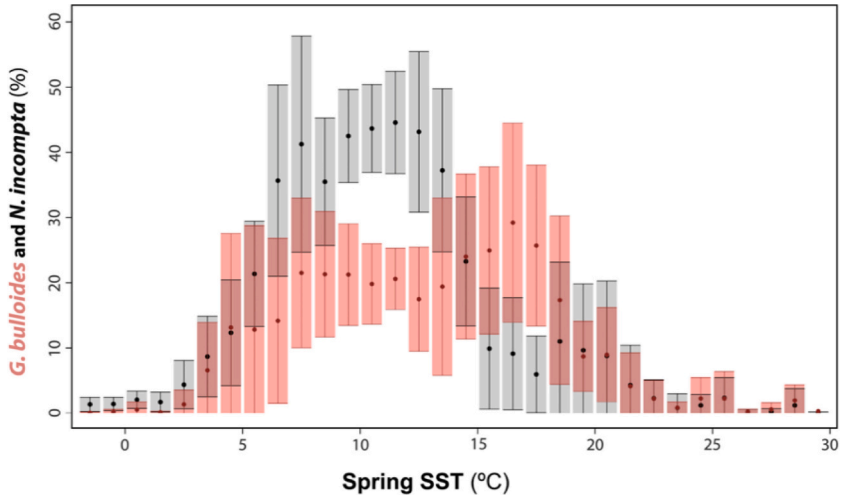

Fig. 10. Plot showing the average relative abundances (dots) of *G. bulloides* (orange) and *N. incompta* (grey), with its standard deviation (bars) (Siccha and Kucera, 2017), against the SST (Locarnini et al., 2006) in the Mediterranean and North Atlantic.

availability in the upper layer. The variability is mainly controlled by the zonal deep nutrient content, that follows an *E*-W direction, and the availability of those nutrients at the surface due to advection, that separate the northern and southern assemblages especially in the western basin.

The meridional variability is driven by surface circulation. While the northern margin is characterized by cyclonic eddies that favour the upward advection of deep nutrients, the southern margin is dominated by anticyclonic eddies and surface convergence with the African margin, which tend to deepen the nutricline. This contrasting behaviour causes phytoplankton blooms in the north resulting in higher fluxes of CE species, such as *N. incompta*, to the seafloor during winter-spring and hindering phytoplankton growth in the southern margins, favouring the development of mesotrophic species, such as *G. inflata*.

In contrast, the zonal variability is controlled by the different size of the eastern and western Mediterranean nutrient deep reservoirs due to the antiestuarine circulation. This variability factor controls the balance between the relative proportions of WO and CE species, separating the eastern basin and eastern Tyrrhenian Sea assemblages, dominated by the WO species, from other western assemblages, dominated by the CE species. Although low surface nutrient availability can also be explained by surface water stratification, which may be permanent in the southern margin of the eastern Mediterranean, winter mixing in the northern Aegean and Adriatic Seas should promote phytoplankton growth like in the northern areas of the western Mediterranean. However, the low chlorophyll and relative low proportions of the CE species in these areas attest to the low nutrient content of the upwelled waters. This is supported by the good correlation between the distribution of the WO-CE species, the Mediterranean nutrient content at 500 m water depth and the sea surface chlorophyll.

Although SST is the most reconstructed environmental variable from fossil assemblages even in the Mediterranean, our analysis reveals that the relationship between SST and planktonic foraminiferal assemblage composition is secondary. These results allow us to better understand biases of transfer functions in paleoclimatic reconstructions as well as open the door to the reconstruction of productivity in the Mediterranean Sea.

CRediT authorship contribution statement

Lucia A. Azibeiro: Writing – original draft, Conceptualization, Methodology, Formal analysis, Software, Writing – review & editing. **Michal Kučera:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration. **Lukas Jonkers:** Conceptualization, Methodology, Software, Formal analysis, Resources, Writing – review & editing. **Angela Cloke-Hayes:** Resources, Conceptualization, Writing – review & editing. **Francisco J. Sierro:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data were taken from previous studies cited and referenced in the paper.

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Appendix I

Planktonic foraminiferal species cited in the text and figures, sorted by genus, including author and year of first description:

Beella digitata (Brady 1879)
Candeina nítida (d'Orbigny 1839)
Globigerina bulloides (d'Orbigny 1826)
Globigerina falconensis (Blow 1959)
Globigerinella calida (Parker, 1962)
Globigerinella siphonifera (d'Orbigny 1839)
Globigerinita glutinata (Egger 1893)
Globigerinoides conglobatus (Brady 1879)
Globigerinoides ruber (d'Orbigny 1839).
Globigerinoides tenellus (Parker 1958)
Globoconella inflata (d'Orbigny 1839)
Globorotalia crassaformis (Galloway and Wissler 1927)
Globorotalia hirsuta (d'Orbigny 1839)
Globorotalia menardii (Parker, Jones and Brady 1865)
Globorotalia scitula (Brady 1882)
Globorotalia truncatulinoides (d'Orbigny 1839)
Globorotalia tumida (Brady 1877)
Globotuborotalita rubescens (Hofker 1956)
Neogloboquadrina dutertrei (d'Orbigny 1839)
Neogloboquadrina incompta (Cifelli 1961)
Neogloboquadrina pachyderma (Ehrenberg 1861)
Orbulina universa (d'Orbigny 1839)
Pulleniatina obliquiloculata (Parker and Jones 1865)
Sphaerodinella dehiscens (Parker and Jones 1865).
Trilobatus sacculifer (Brady 1877)
Turborotalita quinqueloba (Natland 1938)

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