Diatom fluxes in the NW Mediterranean: evidence from a 12-year sediment trap record and surficial sediments

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We examined the total diatom flux and species composition, total coccolith flux and total mass flux collected with a sediment trap between October 1993 and January 2006 in the northeastern entrance of the Gulf of Lions (North Western Mediterranean). The average daily diatom and coccolith fluxes (3×10^7 valves m^2 d^{-1} and 6.1×10^8 coccoliths m^2 day^{-1}, respectively) are comparable in magnitude with previously reported data sets in other high productivity areas of the Western Mediterranean. The temporal particle flux pattern reflected the variations in surface oceanographic conditions and primary productivity, which showed strong annual cycling. Highest diatom, coccolith and total mass fluxes always occurred during the winter–spring transition, while minima were observed during summer. Changes in the diverse diatom communities reflected the water column conditions throughout the record. The intensity of the diatom winter–spring blooms seemed to be enhanced in those years with intense and cold winds during winter, whereas years with low winter wind stress were liable to be less productive for diatoms. Coccolith fluxes exhibited a more stable interannual pattern than diatom fluxes. Significant discrepancies were found between the sediment trap and surficial sediment diatom assemblages.

KEYWORDS: diatoms; coccoliths; sediment trap; Gulf of Lions

INTRODUCTION

Diatoms are one of the main primary producers in the world's oceans. Despite their co-occurrence with other phytoplankton groups, diatoms often dominate in eutrophic environments such as upwelling regions, river mouths, equatorial divergences, spring blooms and transient open-ocean blooms triggered by wind-mixing events (Nelson et al., 1995; Ragueneau et al., 2000). Diatoms contribute significantly to opal and organic carbon export production due to their siliceous cell wall and their capacity for aggregation and rapid sinking (Smetacek, 1985). Their contribution is especially relevant on continental margins, where roughly 45 and 32–39%, respectively, of the total burial of marine organic carbon and biogenic opal occur (Hedges and Keil, 1995; Ragueneau et al., 2000). The latter characteristics allow diatom valves to be useful proxies for paleoceanographic and paleoproductivity reconstructions.

Thus, better understanding of the ecology of living diatom species and their relationships with oceanographic conditions is crucial for validating these paleoreconstructions. In this regard, sediment traps remain one of the best approaches for monitoring downward phytoplankton fluxes and comparing them to sea surface processes on a long-term basis, bridging the gap between biological oceanography and paleoceanography.

In the Mediterranean Sea, studies on pytoplankton composition and distribution have been dispersed in space and time. They have applied diverse methods and focused on different groups of organisms (Siokou-Frangou et al., 2010). Furthermore, only a few studies cover periods long enough to trace seasonal cycles or to address interannual variability (e.g. Ziveri et al., 2000; Marty et al., 2002; Rigual-Hernández et al., 2010). Four consecutive European projects (Euromarge-NB, MTPII MATER, EUROSTRATAFORM and HERMES) and the French PNEC (Programme National Environnement Côtier) have allowed the continuous monitoring of sinking particle fluxes from 1993 at two stations of the Gulf of Lions (Northwestern Mediterranean) (Heussner et al., 2006). As part of this interdisciplinary study, silicoflagellate and planktonic foraminifera fluxes have been documented using data from the initial 12 years of the time series (Rigual-Hernández et al., 2010, 2012). These studies have provided new insights into the geographical distribution and the seasonal and interannual variability of these fossilizable plankton groups in the Western Mediterranean. To complement those investigations and to provide more insights about the ecology and sedimentary processes affecting diatoms in the Gulf of Lions, we document in this paper the diatom fluxes registered at one of the stations in the Gulf of Lions from 1993 to 2006. Additionally,

total coccolith flux and total mass flux are presented and discussed. Finally, we compare the diatom content in the sediment trap with that preserved in the surface sediments to determine how seasonal fluxes over the collection period are reflected in the sedimentary record.

REGIONAL SETTING

Oceanographic and atmospheric circulation

The continental margin of the Gulf of Lions is a crescent-shaped shelf with a continental slope incised by ~10 submarine canyons. Surface water circulation in the Gulf is dominated by the Northern Current (NC), a permanent cyclonic current that flows along the slope (Millot, 1990) (Fig. 1). The NC is fed by the currents flowing on each side of Corsica: the Ligurian Current (LC) and the Tyrrhenian Current (TC) (Fig. 1). The hydrodynamics of the Gulf of Lions are largely influenced by the atmospheric circulation in the area. In winter, the cold and dry Mistral and Tramontane winds blow with intensity through the passages between the Pyrenees, the Massif Central and the Alps. These northwesterlies cause evaporation and heat loss from surface waters, inducing mixing and formation of dense water both on the shelf and offshore (Millot, 1990, 1999). From summer to spring, southeasterly winds blow with more strength over the Gulf, generating large swells and intense alongshore currents (Millot, 1990). The circulation in the North Western (NW) Mediterranean seems also to be influenced by the state of the North Atlantic Oscillation (NAO), especially during the boreal winter (Vignudelli et al., 1999; Maynou, 2008). Positive NAO winter values are coupled with warm and moist air masses conveyed toward the Northern Basin, leading to mild winters and relatively low heat loss from the sea to the atmosphere. In contrast, negative values involve colder and drier winds blowing over the NW Mediterranean that increase the evaporation and heat loss from the water column. As a result, the water transport through the Corsica Channel increases (Fig. 1), enhancing the flow of the NC (Vignudelli et al., 1999).

The Rhone River is the main supplier of fresh water into the Gulf, the discharge mainly occurring during spring and autumn (Ulses et al., 2008). The Rhone plume is directed southwards by the general circulation and can extend over a hundred kilometers (Estournel et al., 1997).

Annual cycle of the water column and productivity

On the whole, the Mediterranean is considered to be an oligotrophic to ultra-oligotrophic sea (Antoine et al.,
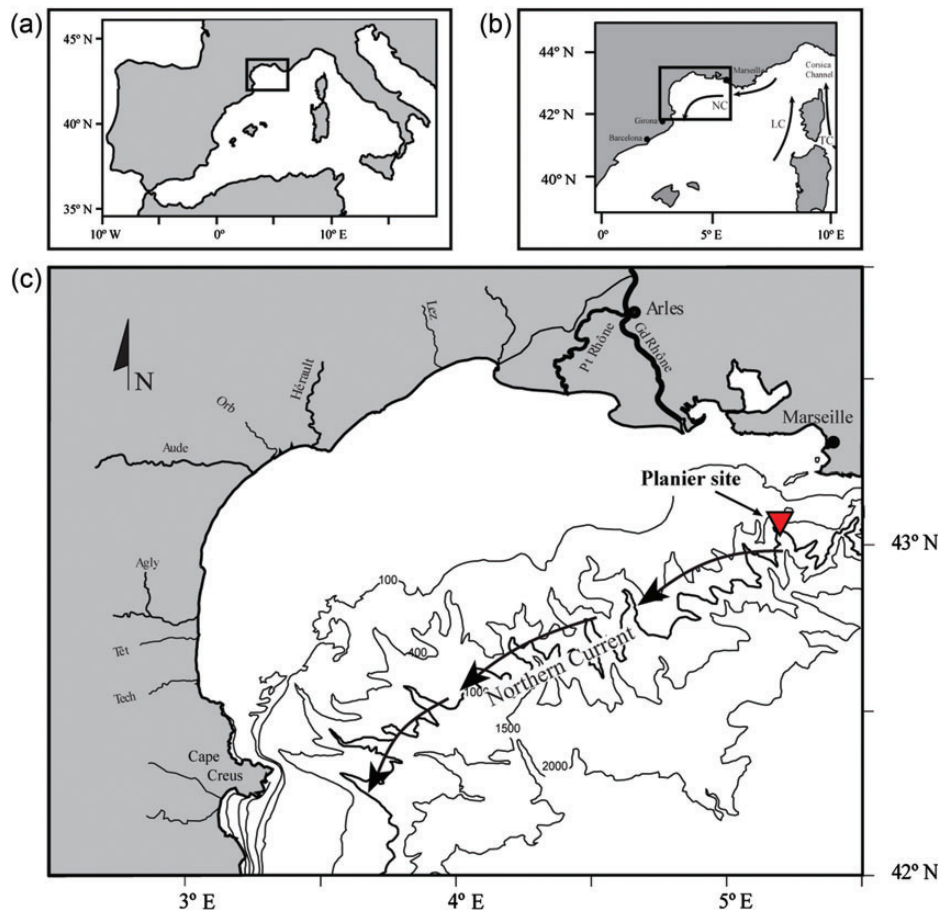
Fig. 1. Geographical setting of: (**a**) the Gulf of Lions in the NW Mediterranean and (**b**) the Mediterranean Northern Basin. NC, Northern Current; LC, Ligurian Current; TC, Tyrrhenian Current. (**c**) The Bathymetric map of the Gulf of Lions with the location of the Planier site (sediment trap and box core). Arrows represent the general surface circulation.

1995); however, it exhibits marked spatial heterogeneity. The Gulf of Lions is an exception, being one of the most productive areas of the Mediterranean (Estrada, 1996; D'Ortenzio and Ribera D'alcalá, 2009). The main fertilizing mechanisms in this area are river runoff, coastal upwelling and vertical water mixing during winter (Estrada, 1996; Millot, 1999). The annual cycle of the water column structure (Fig. 2) and primary productivity in the Gulf are closely linked and follow the seasonal evolution typical of a temperate ocean. During summer and the beginning of autumn, stratification (Fig. 2) and oligotrophic conditions prevail in the water column (Leblanc *et al.*, 2003). Around November, the thermocline breaks down, and the water column gradually starts to mix, supplying the photic zone with nutrients. In winter, the intensity of the mixing processes reaches a maximum (Fig. 2), and nutrients reach their highest concentrations (Leblanc *et al.*, 2003). In late winter to early spring, the winter–spring bloom takes place, triggered by the high nutrient

concentration in the photic zone and the onset of thermal stratification. During this period, the Gulf of Lions has the highest annual chlorophyll-*a* values in the NW Mediterranean, reaching as much as $3 \, \mu g \, L^{-1}$ (Marty *et al.*, 2002). The thermocline becomes established around late March, but it forms in stages due to frequent short-term wind events (Marty *et al.*, 2002). After spring, the cycle starts again with oligotrophic conditions and strong stratification during summer.

METHOD

Field experiment

A mooring line was deployed at 1000 m water depth on the axis of the Planier submarine canyon (43.02°N, 5.18°E) (Fig. 1) in the northeastern part of the Gulf of Lions. The mooring was equipped with two PPS3 Technicap sediment traps at 500 and 30 m above the
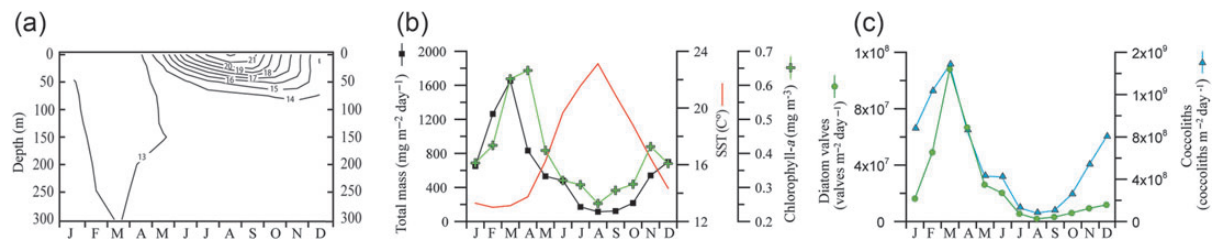
Fig. 2. (**a**) Seasonal variation in the vertical structure of temperature at the Planier station. (**b**) An average year of total mass flux, SSTs (°C) and chlorophyll-*a* concentration (mg m^3). (**c**) An average year of diatom valve (valves m^{-2} day^{-1}) and coccolith fluxes (coccolith m^{-2} day^{-1}).

bottom (hereafter designated mab) paired with current-meters (Heussner *et al.*, 2006).We present here the data recorded by the sediment trap set at 500 mab. The sampling period ranged from October 1993 until January 2006, with a sampling interval of 14 days until early 1997, and then ca. 1 month intervals until the end of the experiment. Gaps in the temporal series were due to mooring recovery periods or to problems in the operation of the sediment trap. Despite these interruptions, the data reported here represent >77% of the elapsed time.

A surficial sediment sample was recovered with an OKTOPUS Multicorer during cruise DEEP 3 (November 2009) at 989 m at the same location as the Planier mooring deployment. The diatom assemblage in the surficial sediment was compared with the assemblages obtained from the trap.

General processing of the sediment trap and surficial sediment samples

Detailed descriptions of the PPS3 sediment trap, the general sample processing used for this experiment and the determination of the total mass flux can be found in Heussner *et al.* (Heussner *et al.*, 1990, 2006). The analyses of the siliceous microplankton and calcareous nanoplankton of the sediment trap and surface sediment samples were as follows: A total of 119 sediment trap samples and 1 surficial sediment sample were processed for siliceous microplankton and planktonic foraminifera analyses. The scarcity of the sediment trap material collected obliged us to carry out both studies on the same fractions. Different fractions from the original sediment trap samples were used, most commonly 1/8, although other fractions were employed depending on availability, ranging from 1/64 to 3/4. The sediment trap and surficial sediment samples were wet-sieved on a 150-μm mesh in order to separate large foraminifera (>150 μm) from smaller foraminifera, silicoflagellates and diatoms. Detailed information on the assemblage composition of the planktonic foraminifera collected by the Planier trap can be found in Rigual-Hernández (Rigual-Hernández *et al.*, 2012). An additional sieve treatment was performed with 63-μm mesh

in order to the break up organic aggregates and to separate the 63–150-μm foraminifera fraction. The 63–150-μm fraction was visually examined, looking for diatoms and small foraminifera. The amount of siliceous microplankton in that fraction was very low or negligible in all the samples. The fraction <63 μm was acid cleaned and prepared with a standard decantation method according to the methodology outlined by Bárcena and Abrantes (Bárcena and Abrantes, 1998). Qualitative and quantitative analyses were done at ×400 and ×1000 magnifications, respectively, using a Nikon Eclipse 80i light microscope with phase-contrast illumination. The recommendations of Schrader and Gersonde (Schrader and Gersonde, 1978) were followed as the basis for counting diatom valves. A minimum of 400 diatom specimens was counted per sample. Total diatom fluxes for the sediment trap samples are given in number of valves per day and per square meter. Despite the low abundance of siliceous microplankton in the 63–150-μm fraction, large diatoms, such as some specimens of the genus *Coscinodiscus*, *Thalassiosira* or *Pleurosigma*, could have been be retained in the 63-μm mesh and therefore underrepresented in this study. With regard to the silicoflagellates, a detailed description of their abundance and assemblage composition can be found in Rigual-Hernández *et al.* (Rigual-Hernández *et al.*, 2010).

A total of 131 sediment trap samples were processed for coccolith analysis. Aliquots of the sediment trap material were suspended in 250–1000 mL of tap water, depending on the amount of material. Then, the samples were thoroughly mixed and dispersed by a 30-s ultrasonic treatment. Subsamples of 5–50 mL were taken immediately afterward with a volumetric pipette and added to 200 mL of tap water in a filtration device >47 mm diameter, 0.43-μm cellulose-nitrate filters. The amount of the material on the filter varied between 0.2 and 2 mg. The pipette was thoroughly rinsed to ensure that all the materials was transferred to the filter. A membrane pump was used to draw the suspension through the filter. The filters were dried overnight at 50°C and then embedded in Canada balsam on glass slides with a cover slip. Forty fields of view were captured per sample with a Spot Insight camera and were analyzed with an automated

coccolith recognition system (SYRACO, Beaufort and Dollfus, 2004). An average of ~850 specimens was recognized by the system. Non-coccolithophore particles that might have been included in the counts were eliminated by checking the automated counts manually.

Additional data sets: environmental variables

Weekly sea surface temperatures (SSTs) from October 1993 until March 2006 (Fig. 3) were obtained from the NOAA Optimum Interpolation Sea Surface Temperature Analysis (Reynolds *et al.*, 2002). Daily wind speeds recorded by the Marseille airport weather station from July 1996 until the end of the experiment were obtained from the Weather Underground Forecast website. Major wind events are indicated by arrows in Fig. 3. Wind data were not available until summer 1996 or for the year 2000. However, a strong wind event is highlighted in Fig. 3 during early February of 2000 following the description by Leblanc *et al.* (Leblanc *et al.*, 2005). SeaWiFS satellite monthly chlorophyll-*a* concentrations from September 1997 until March 2006 (Fig. 3) were obtained from the NASA's Giovanni program (Acker and Leptoukh, 2007). The monthly concentration was averaged over a relatively small area around the mooring location ($0.2 \times 0.2°$). The monthly averages of the upper 300 m thermal structure for the 1996−2006 period (Fig. 2) were obtained for the Planier sampling location from the World Ocean Atlas 2009 (Locarnini *et al.*, 2010).

Data analysis

The Pearson correlation coefficient (*r*) was calculated to estimate the degree of dependence between the chlorophyll-*a* concentration and both diatom valve and coccolith fluxes. The statistical distributions of the studied variables are not normal but lognormal; therefore, in order to straighten the relationship between variables, a log-transformation (log $(x + 1)$) was applied to each variable before calculating the correlation coefficient. The highest chlorophyll-*a* value of the whole record (March 2001) was considered to be an outlier, and it was not included in the calculations.

Additionally, we calculated the squared-chord distances (Ortiz and Mix, 1997) between the sediment trap diatom assemblages and that of the surficial sediments as a measure of dissimilarity.

RESULTS

Sediment trap

The total particle flux registered at the 500 mab Planier sediment trap is summarized in Fig. 3. The annual maxima were generally recorded during February and March, while the magnitude of the maxima varied from year to year. The greatest particle-flux pulses were recorded during March 1999 ($3600 \text{ mg m}^{-2} \text{ day}^{-1}$), March 2004 ($3257 \text{ mg m}^{-2} \text{ day}^{-1}$) and March 1994 ($2762 \text{ mg m}^{-2} \text{ day}^{-1}$) (Fig. 3).

The opal fraction was mainly composed of diatoms and silicoflagellates. Diatoms were the dominant siliceous phytoplankton group observed during the study and were ca. 1 order of magnitude greater than the silicoflagellates (Rigual-Hernández *et al.*, 2010). Other siliceous groups also contributed to the total biogenic opal production, such as radiolarians, phytoliths and the endoskeletons of the dinoflagellate *Actiniscus pentasterias*. As a general trend, diatom fluxes showed a unimodal seasonal pattern, with the maximum fluxes during the winter−spring transition, i.e. from February to April (Fig. 2). This period included two-thirds of the total annual diatom flux. The diatom daily flux ranged between 1.7×10^5 and 3.7×10^8 valves m^2 day^{-1}, with a mean of 3×10^7. This mean at the Planier site is similar to those obtained by Bárcena *et al.* (Bárcena *et al.*, 2004) in the Western Gyre of the Alboran Sea (1.3×10^7 valves m^2 day^{-1}) and by Hernández-Almeida *et al.* (Hernández-Almeida *et al.*, 2011) in the Eastern Gyre of the Alboran Sea (12×10^7 valves m^2 day^{-1}). The annual diatom flux maxima were especially high during late March 2000 (3.7×10^8 valves m^2 day^{-1}), early April 2005 (2.7×10^8 valves m^2 day^{-1}), early March 1996 (2.6×10^8 valves m^2 day^{-1}) and March 1997 (2.1×10^8 valves m^2 day^{-1}) (Fig. 3). Smaller spring maxima were recorded in the other years, and in 1995, 2002 and 2004 the maxima were substantially lower (Fig. 3). The diatom specimens were identified to the lowest taxonomic level possible. A total of 80 diatom taxa were identified in the samples (see Supplementary Data, Taxonomic Appendix). The relative abundances of the diatom species found in the Planier sediment trap and in the surface sediments are listed in Table I. On an average, the most abundant taxa were *Skeletonema* sp. (43.7%) and *Thalassionema frauenfeldii* (19.7%). The *Chaetoceros* (Hyalochaete) Resting Spores group (14.3%) contributed a major fraction, mainly composed by *Chaetoceros diadema* (4.8%), *Chaetoceros* sp. form 1 (3.8%), *Chaetoceros seychelarum* (2%) and *Chaetoceros affinis* (1.8%). In addition, *Chaetoceros* sp. (2.9%), *Thalassiosira* sp. (1.7%), *Ditylum brightwellii* (1.6%), *Nitzschia bicapitata* (1.5%), *Cocconeis* spp. (1.44%), *Nitzschia braarudii* (1.33%) and *Thalassionema nitzschioides* var. *parvum* (1.2%) exhibited high relative abundances (Table I). Scanning electron microscope (SEM) pictures of some of these dominant taxa can be seen in Fig. 4.

The biogenic calcareous fraction mainly comprised coccoliths and planktonic foraminifera (Rigual-Hernández
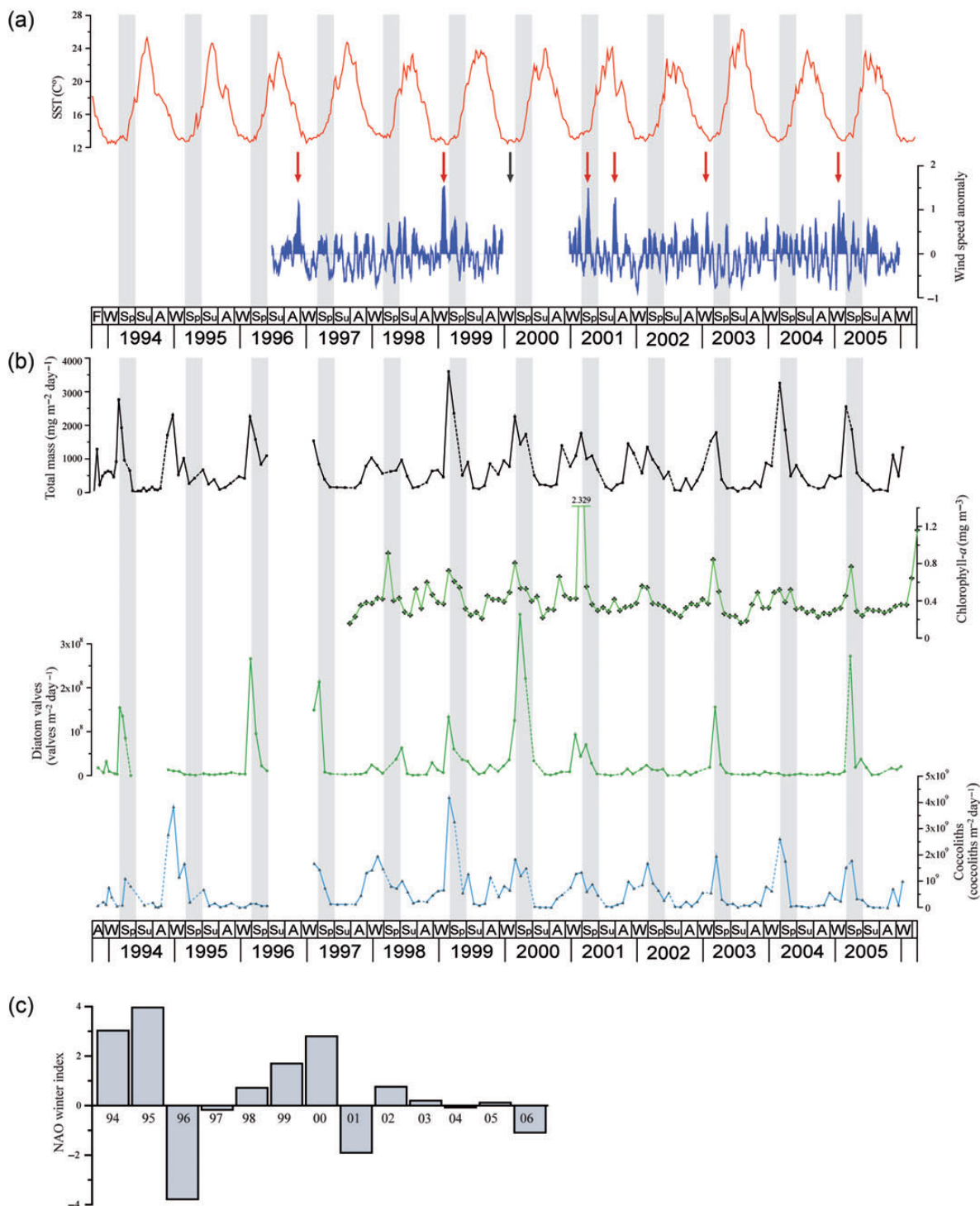
Fig. 3. (**a**) Temporal changes in SST (°C) and wind speed anomaly. Intense wind events are indicated with arrows. No wind data were available for 2000; however a major wind event during this year is indicated with a black arrow following the description by Leblanc *et al.* (Leblanc *et al.*, 2005). (**b**) Temporal changes in the flux of total particles (mg m^{-2} day^{-1}), chlorophyll-*a* concentration (mg m^3), diatom valve flux (valves m^{-2} day^{-1}) and coccolith flux (coccolith m^{-2} day^{-1}). Small gaps in the time series are represented by a dotted line. Gray shading highlights spring. (**c**) NAO Winter index.

Table I: Relative abundance (%) of the diatom taxa found in the Planier sediment trap (12-year integrated assemblage) and in the surficial sediments below the trap

	Sediment trap	Surficial sediment		Sediment trap	Surficial sediment
Skeletonema spp.	43.7092	0.0000	*Alveus marinus*	0.0840	1.2407
Thalassionema frauenfeldii	19.7064	38.2134	*Aulacoseira granulata*	0.0825	2.4814
Chaetoceros RS group	14.2766	31.0174	*Thalassiosira angustelineata*	0.0784	0.0000
Chaetoceros affinis (>15 μm) RS	0.1287	0.4963	*Asteromphalus hyalinus*	0.0464	0.0000
Chaetoceros affinis RS	1.8157	0.9926	*Achnanthes* sp.	0.0460	0.0000
Chaetoceros diadema RS	4.8783	12.6551	*Thalassiosira symmetrica*	0.0423	1.4888
Chaetoceros sp. form 1 RS	3.8012	8.6849	*Thalassiotrix* sp.	0.0403	0.0000
Chaetoceros lauderi RS	0.0176	0.0000	*Toxarium* sp.	0.0307	0.4963
Chaetoceros mitra RS	0.0047	0.0000	*Hantzschia* sp.	0.0271	0.2481
Chaetoceros seychelarum RS	2.0539	4.9628	*Actinocyclus* sp.	0.0267	0.0000
Chaetoceros spp. RS	1.5735	3.2258	*Actinocyclus octonari* s	0.0231	0.2481
Chaetoceros vanheurckii RS	0.0029	0.0000	*Thalassiosira rotula*	0.0205	0.0000
Chaetoceros sp.	2.9409	0.0000	*Synedra* sp.	0.0173	0.0000
Thalassiosira sp.	1.6763	3.4739	*Diatoma* sp.	0.0164	0.0000
Ditylum brightwellii	1.5642	0.9926	*Amphora bigibba*	0.0154	0.0000
Nitzschia bicapitata	1.5312	0.0000	*Rhopalodia* sp.	0.0151	0.0000
Cocconeis spp.	1.4412	0.9926	*Raphoneis* sp.	0.0123	0.7444
Nitzschia braarudii	1.3395	3.9702	*Surinella* sp.	0.0095	0.0000
Thalassionema nitzschoides			*Entomoneis* sp.	0.0086	0.0000
var. *parvum*	1.1865	0.9926	*Leptocylindrus danicus*	0.0084	0.0000
Bacteriastrum spp.	0.9652	0.0000	*Thalassionema nitzschoides*		
Psammodictyon panduriforme	0.7581	0.2481	var. *capitulata*	0.0081	0.0000
Odontella sp.	0.7126	0.0000	*Triceratium* sp.	0.0056	0.0000
Navicula sp.	0.7122	0.0000	*Amphiprora* sp.	0.0047	0.0000
Nitzschia sp.	0.6748	0.0000	*Thalassionema bacillaris*	0.0044	0.0000
Rhizosolenia spp.	0.5381	0.9926	*Podocystis* sp.	0.0038	0.0000
Thalassiosira lineata	0.4900	0.0000	*Rhoicosphenia* sp.	0.0037	0.0000
Amphora spp.	0.4872	0.7444	*Hannaea* sp.	0.0036	0.0000
Thalassiosira eccentrica	0.3109	0.2481	*Paralia sulcata*	0.0032	0.0000
Coscinodiscus spp.	0.2733	2.9777	*Thalassiosira oestrupii*	0.0023	0.0000
Thalassiosira tenera	0.2608	0.2481	*Bidulphia pulchella*	0.0019	0.0000
Mastogloia sp.	0.2325	0.2481	*Pleurosygma directum*	0.0018	0.0000
Cyclotella spp.	0.2289	0.9926	*Licmophora* sp.	0.0017	0.0000
Diploneis bombus	0.1845	0.2481	*Gyrosigma* sp.	0.0012	0.0000
Fallacia sp.	0.1724	0.2481	*Actinocyclus curvatulus*	0.0009	0.0000
Pleurosygma sp.	0.1659	0.2481	*Actinoptychus* sp.	0.0006	0.0000
Hemidiscus cuneiformis	0.1398	0.9926	*Opephora* sp.	0.0005	0.0000
Nitzschia sicula	0.1211	0.2481	*Cymbella* sp.	0.0004	0.0000
Pleurosygma normanii	0.1199	0.0000	*Roperia tesselata*	0.0002	0.0000
Trachyneis aspera	0.1116	0.0000	*Thalassiosira gravida*	0.0001	0.0000
Grammatophora sp.	0.1078	0.9926	No identified diatoms	2.0566	3.7221
Azpeitia sp.	0.1041	0.0000			

et al., 2012). However, other calcareous organisms were found at very low abundances, such as small bivalves, gastropods and benthic foraminifera. Numerically, calcareous plankton fluxes were dominated by coccoliths. The average year of the coccolith fluxes revealed a unimodal distribution, with a maximum from November to April (Fig. 2) that was more prolonged than the average diatom peak. Half (48%) of the flux occurred from February to April, and one-third (30%) from November to January (Fig. 2).

Daily coccolith fluxes ranged between 4.3×10^6 and 4.1×10^9, with a mean of 6.1×10^8 coccoliths m^{-2} day^{-1}. These fluxes at the Planier site are comparable to those reported by Hernández-Almeida (Hernández-Almeida, 2010) (10×10^8 coccoliths m^2 day^{-1}) and by Bárcena *et al.* (Bárcena *et al.*, 2004) (31×10^8 coccoliths m^2 day^{-1}) from the Alboran Sea. In the central Eastern Mediterranean, Ziveri *et al.* (Ziveri *et al.*, 2000) registered coccolith fluxes an order of magnitude lower (0.3×10^8 coccoliths m^2 day^{-1}). Coccolith fluxes at the Planier site showed more stable and repetitive interannual fluctuations than those of diatoms (Fig. 3). The greatest coccolith fluxes were recorded during early March 1999 (4.1×10^9 coccoliths m^2 day^{-1}), the end of December 1994 (3.8×10^9 coccoliths m^2 day^{-1}) and early on in 2004 (2.6×10^9 coccoliths m^2 day^{-1}) (Fig. 3). The main contributors to the total coccolith flux were *Emiliania huxleyi* (Meier *et al.*, subm.) and *Gephyrocapsa* spp. Further taxonomic detail of the coccolith flux is not available, as the automated system SYRACO recognizes only major species.

Surficial sediment

Remarkable differences were found between the sediment trap and surficial sediment diatom assemblages. Some of the most abundant species in the sediment trap record, such as, *Skeletonema* spp., *Chaetoceros* spp., *N. bicapitata* and *Bacteriastrum* spp. were not found in the surficial sediment sample, while other taxa, such as, *T. frauenfeldii* and *Chaetoceros* Resting Spore group had values about double those in the sediment trap assemblage (Table I).

Data analysis

Correlation was significant between diatom valves and chlorophyll-*a* ($r = 0.58$***, $n = 86$), coccoliths and chlorophyll-*a* ($r = 0.54$***, $n = 93$) and total mass flux and chlorophyll-*a* ($r = 0.62$***, $n = 93$) (Fig. 5), despite several biases in this calculation, including the presence of other phytoplankton groups in the water column, variability in the chlorophyll-*a* content of different diatom and coccolithophore species, the intrinsic biases of the measurement tools (i.e. satellite and sediment trap biases), different sampling resolutions and silica dissolution processes.

Previous studies (e.g. Ortiz and Mix, 1997) suggest that squared-chord distance values <0.25 yield reliable analogs. In this work, the calculated squared-chord distance between the sediment trap diatom assemblage and that of the surficial sediments is 1.00, indicating strong dissimilarity between samples.

DISCUSSION

Particle flux seasonal variability

The main origins of newly introduced particulate matter in the Gulf of Lions are river discharge and surface biological production (Heussner *et al.*, 2006). The atmospheric deposition in the Gulf of Lions shelf and slope area is considered negligible, since it represents <2% of the Rhone River input (average: $12 \times 10^6 \, T y^{-1}$) (Heussner *et al.*, 2006). This contrasts with other sediment trap studies in the Mediterranean Sea, where the eolian deposition has been a notable contributor to the particle flux (e.g. Ziveri *et al.*, 2000; Bárcena *et al.*, 2004). Sediment resuspension provides an additional input of the material. However, the 500-m Planier site trap experiences the lowest influence of particle inputs from the shelf of all the monitored sites in the Gulf of Lions (Heussner *et al.*, 2006).

The total mass, diatom valve and coccolith fluxes recorded at the Planier site exhibited a strong seasonal pattern with a general increase in late winter–early spring and minimum values from summer to mid-autumn, a cycle that matches that of primary productivity as reflected by satellite chlorophyll-*a* estimates (Figs 2 and 3). Seasonal variability in particle transfer in open-ocean environments has often been attributed to seasonal changes in the productivity in the photic zone (e.g. Deuser *et al.*, 1983; Jickells *et al.*, 1996; Waniek *et al.*, 2005; Loncaric *et al.*, 2007). At the nearby DYFAMED site, seasonal variability of particle flux has been suggested to be largely controlled by the pelagic production and increased during winter vertical mixing (Miquel *et al.*, 1994). The Planier sediment trap was located over the continental slope (500 mab), and was exposed to a higher particle input from the shelf than DYFAMED. Despite this more complex scenario at the Planier site, the good correlation between the total mass flux and the satellite chlorophyll-*a* (Fig. 5) suggests that primary producers may play an important role in the particle sedimentation at Planier.

Diatom and coccolith flux seasonal variability

Several facts demonstrate that biogenic particle fluxes at the Planier sediment trap site reflect changes of the photic-zone plankton assemblage and are little influenced by resuspension: (i) seasonal variability of diatom and coccolith fluxes follow patterns similar to those described by Marty *et al.* (Marty *et al.*, 2002) at the DYFAMED site based on pigment profiles and are significantly correlated with the chlorophyll-*a* concentration (Fig. 5); (ii) diatom and coccolith fluxes are comparable in magnitude to previously reported data sets in other area of high productivity in the Western Mediterranean, i.e. the Alboran Sea (Bárcena *et al.*, 2004; Hernández-Almeida *et al.*, 2011); (iii) benthic foraminifera fluxes are negligible in the sediment trap samples (Rigual-Hernández *et al.*, 2012) and (iv) the diatom species with the highest fluxes of the record, *Skeletonema* sp., is absent in the surface sediments of the continental slope (Table I).

The diatom valve and coccolith seasonal fluxes exhibit a unimodal pattern that reflects the changes in the upper water column and atmosphere dynamics of the Gulf of Lions. Diatom and coccolith fluxes show maxima during the winter–spring transition lasting 3 and 4 months, respectively. The maximum primary productivity is also registered during this period (Fig. 2). This seasonal cycle is unique in the Mediterranean Sea and a characteristic feature of its NW sector (D'Ortenzio and Ribera D'alcalá, 2009; Siokou-Frangou *et al.*, 2010). During the winter–spring bloom, i.e. from February to April, two-thirds (67%) of the annual diatom flux is recorded (Fig. 2). The well-mixed water column and nutrient-rich conditions during this period favor increase of this opportunistic phytoplankton group (Fogg, 1991). Our
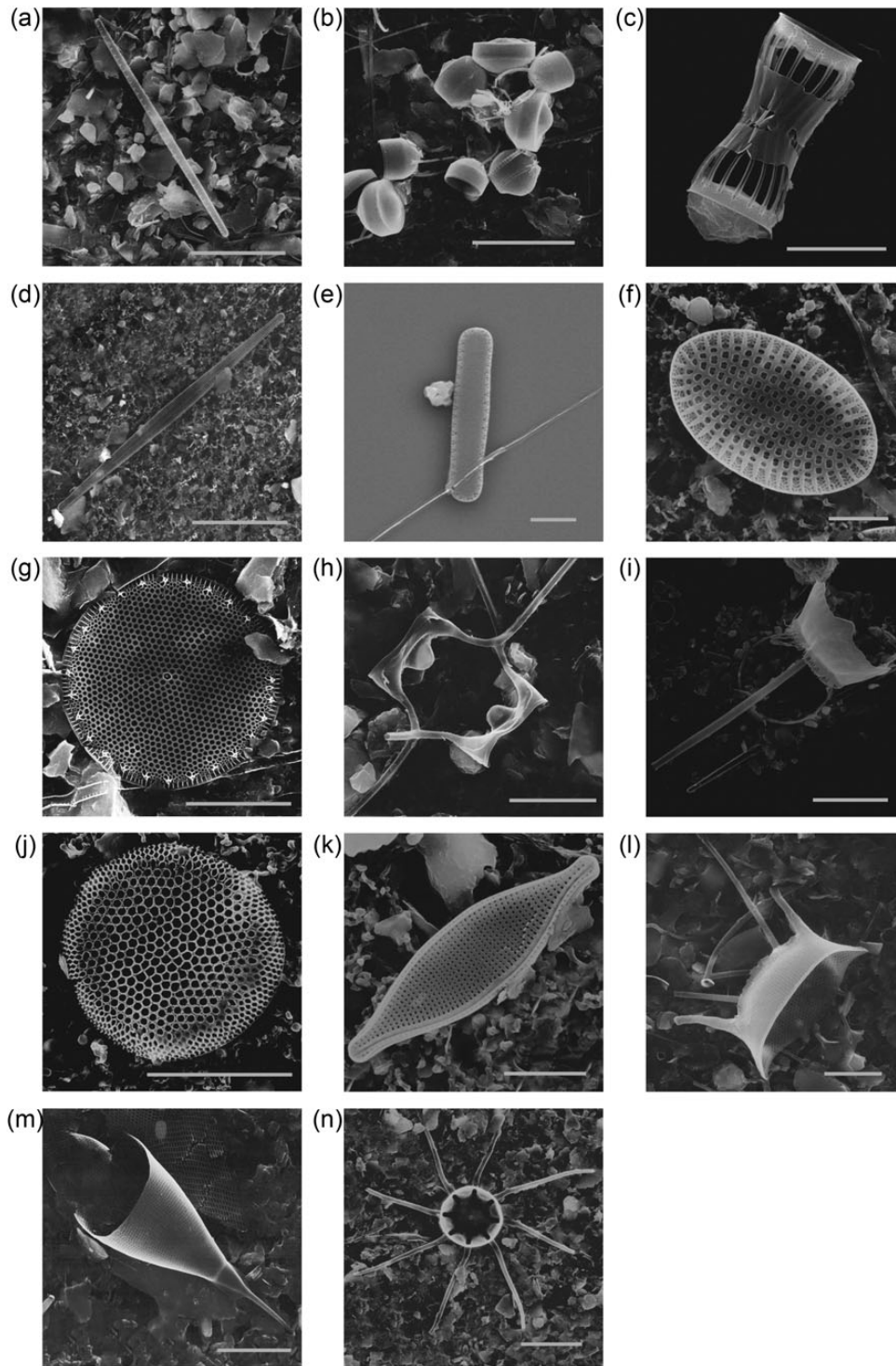
Fig. 4. SEM photos of some of the most relevant diatom taxa found in Planier sediment trap. (**a**) *Thalassionema frauenfeldii*, (**b**) *Chaetoceros* spp. resting spores, (**c**) *Skeletonema* spp. (**d**) *Nitzschia braarudii*, (**e**) *Thalassionema nitzschioides* var, *parvum*, (**f**) *Cocconeis* sp, (**g**) *Thalassiosira* sp, (**h**) *Chaetoceros* sp, (i) *D. brightwellii*, (**j**) *Coscinodiscus* sp, (**k**) *N. bicapitata*, (**l**) *Odontella* sp., (**m**) *Rhizosolenia* sp. and (**n**) *Bacteriastrum* sp. Scale bars: e, f, k = 5 μm; c, g, h, j, l, m, n = 10 μm; b = 20 μm; a, d, i = 25 μm.
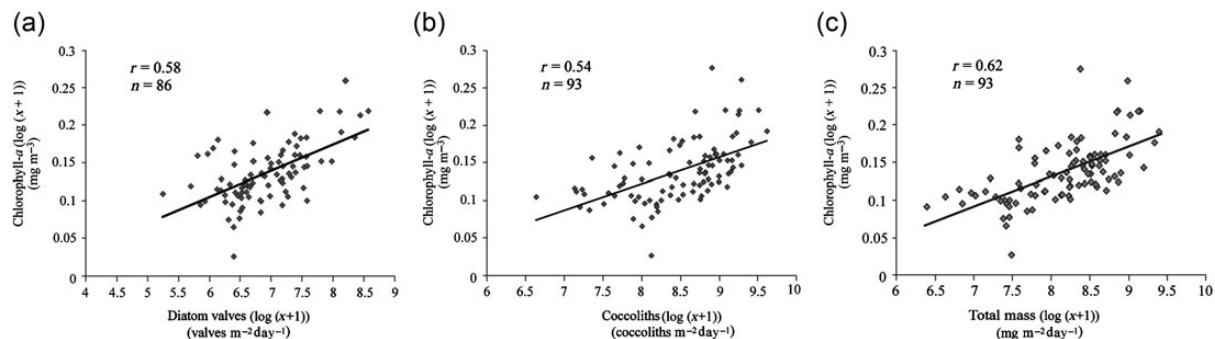
Fig. 5. Correlations between the chlorophyll-*a* (mg m^{-3}) and diatom valve flux (valves m^{-2} day^{-1}) (**a**) the chlorophyll-*a* (mg m^{-3}) and coccolith flux (coccoliths m^{-2} day^{-1}) (**b**) and the chlorophyll-*a* (mg m^{-3}) and total mass flux (mg m^{-2} day^{-1}) (**c**) for all available paired data. A log-transformation (log $(x + 1)$) was applied to all variables before analysis.

observations agree with previous studies (Lévy *et al.*, 1998; Marty *et al.*, 2002; Gutiérrez-Rodríguez *et al.*, 2010), which have described diatoms as major contributors to the winter–spring phytoplankton bloom in the NW Mediterranean. Coccolith fluxes also show maximum values during the winter–spring bloom; however, they exhibit a gradual increase starting in October, whereas diatom fluxes do not increase significantly until February when they increase sharply (Fig. 2). The affinity for weak-mixing conditions and the low nutrient-concentration requirements of coccolithophores (Brand, 1994) possibly favor them during autumn, when diatom growth is still limited. This so-called "coccolithophore autumn–winter bloom" has already been reported from the Alboran Sea (Bárcena *et al.*, 2004; Hernández-Almeida *et al.*, 2011). In contrast, during summer and the beginning of autumn the oligotrophic conditions and strong stratification of the photic zone are responsible for the annual minima of both diatom and coccolith fluxes. During this period non-siliceous phytoplankton, such as dinoflagellates, dominate the micro-phytoplankton community (Marty *et al.*, 2002; Leblanc *et al.*, 2003).

Flux patterns of diatom species

The Planier record shows rich diatom diversity (up to 80 taxa); however, only a small number of species dominate the assemblage (Table I). More precisely, only *Skeletonema* sp., *T. frauenfeldii* and the *Chaetoceros* Resting-Spore group, are responsible for 78% of the integrated 12-year diatom assemblage. The variations in the relative abundance and flux patterns of these three diatom taxa can be related to changes of the conditions of the water column during our 12-year series. The small-celled genus *Skeletonema* is by far the most abundant taxon in the record (44% of the overall, 12-year diatom assemblage). *Skeletonema* sp. exhibits a clear unimodal pattern with

maximum fluxes and relative abundance during the winter–spring bloom of the average year (Fig. 6). Along the 12-year time series, however, *Skeletonema* sp. showed a strongly fluctuating flux pattern, appearing during the winter–spring bloom of only some years (Fig. 7). When present, *Skeletonema* sp. develops massive blooms, e.g. during in 1996, 1997, 1999 and 2000, while during 1995, 1998, 2002 and 2004 it appeared to be absent from the flux (Fig. 7). Our data suggest that the water column mixing and nutrient-rich conditions of the photic zone during the winter–spring period favor the development of *Skeletonema* sp. which is reputed to react quickly to freshly upwelled waters through high rates of production and nutrient uptake (Conway and Harrison, 1977; Margalef, 1978; Smetacek, 1999; Ochoa *et al.*, 2010). In the Mediterranean Sea, *Skeletonema* sp. has often been reported as an important contributor to phytoplankton blooms (e.g. Caroppo *et al.*, 1999 in the Adriatic Sea; Castellví, 1971 in the Barcelona coastal area; Ribera D'alcalà *et al.*, 2004 in the Gulf of Naples).

Thalassionema frauenfeldii, considered to be a tropical–subtropical to temperate species (Hasle, 2001; Simonsen, 1974), is the second most abundant species in the record, representing ca. 20% of the 12-year diatom assemblage (Table I). It dominates from November to January in the average year (Fig. 6), i.e. from the breakdown of the thermocline until just before mixing processes in the water column reach their maximum intensity. The semi-mixing of the photic zone during this period seems to be optimum for the growth of *T. frauenfeldii*. However, the relatively constant high fluxes of *T. frauenfeldii* throughout the 12-year record (Fig. 7) suggest that it can thrive well under a broad range of environmental conditions. This corroborates previous studies that have described this species as "perennial" in the NW Mediterranean (Travers, 1971; Gómez and Gorsky, 2003).

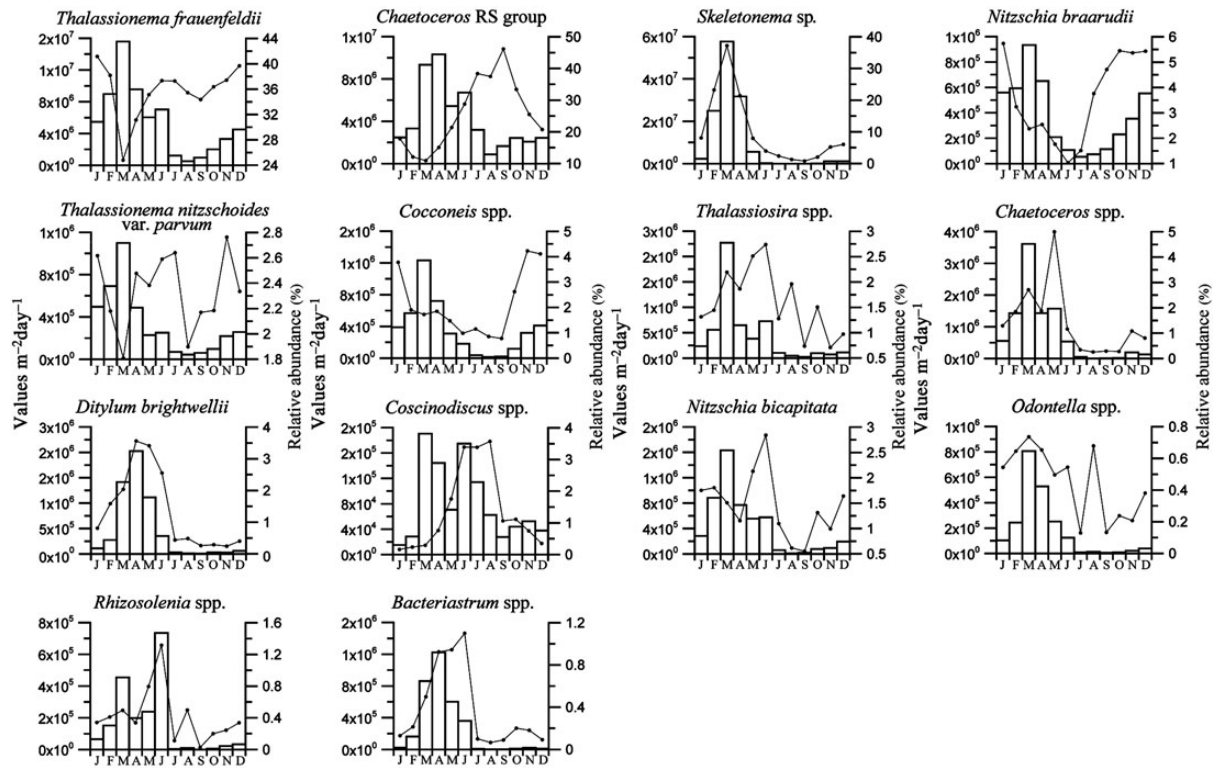The vegetative and resting stages of the genus *Chaetoceros* represent ca. 3 and 14% of the total diatom

Fig. 6. Monthly flux (bars; valves m^{-2} day^{-1}) and relative abundances (lines; %) of the most relevant diatom species of the Planier sediment trap record.
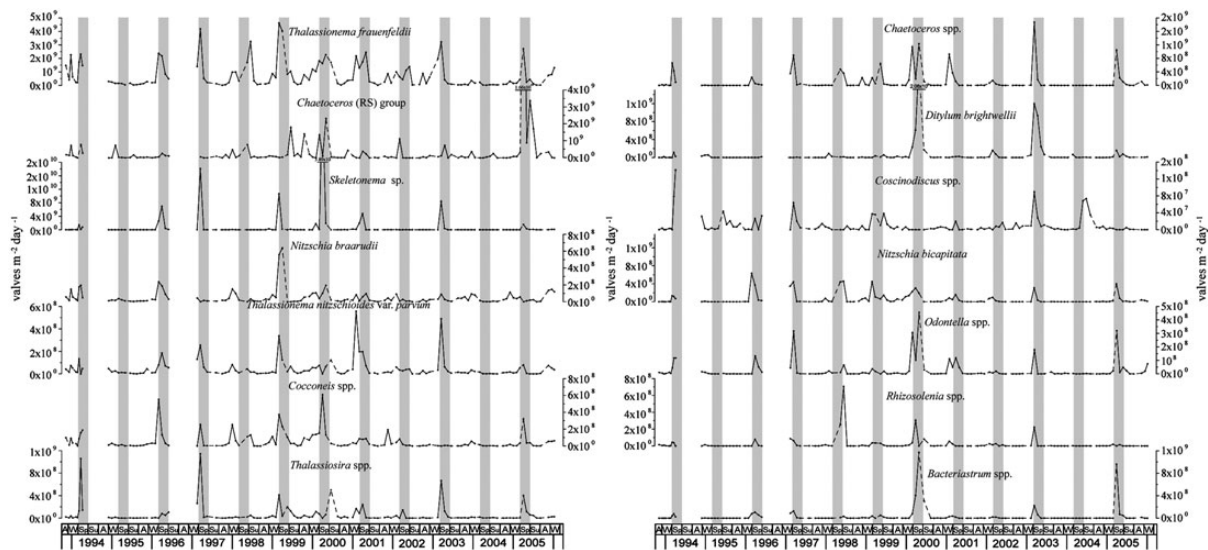

Fig. 7. Valve fluxes (valves m^{-2} day^{-1}) of the main diatom species along the Planier record. Small gaps in the time series are represented by a dotted line. Gray shading highlights the spring season.

assemblage, respectively (Table I). The lower abundance of the vegetative stages is due to their greater susceptibility to dissolution: a larger fraction of the valves of the vegetative forms are dissolved in the euphotic zone, whereas the strongly silicified resting spores are more resistant to dissolution (Smetacek, 1985; Crosta *et al.*, 1997). *Chaetoceros* spp. grow fast in the nutrient-rich conditions of the winter–spring bloom, exhibiting their maximum

relative abundance from February to May (Fig. 6). This agrees with previous studies that have described this genus as a typical component of the Mediterranean spring bloom (c.f. Kemp *et al.*, 2000; Siokou-Frangou *et al.*, 2010). *Chaetoceros* resting spores show their highest relative abundances from June to October, coinciding with stratification of the water column (Fig. 2) and nutrient depletion (Leblanc *et al.*, 2003). The resting spores are formed within the vegetative cells of *Chaetoceros* species (subgenus *Hyalochaete*) after the bloom and represent a specialized life cycle stage for maintaining populations during unfavorable conditions (McQuoid and Hobson, 1996; Crosta *et al.*, 1997).

Apart from the abundance patterns that have been observed within the three most abundant taxa, the composition of the whole diatom assemblage revealed an annual succession that can be related to the annual cycle of the water column. The beginning of the cycle can be placed in autumn, i.e. September to November. During that period the cooling of the surface layer begins, ending the strong stratification and the oligotrophic conditions of the summer. Together with the ubiquitous *T. frauenfeldii*, *Chaetoceros* Resting Spore group, *T. nitzschiodes* var. *parvum*, *N. braarudii* and *Cocconeis* spp. show high relative abundances in the trap during this period (Fig. 6), which indicates an ecological preference of these taxa for semi-mixing conditions in the water column. Between February and March the water column mixing reaches its maximum intensity (Fig. 2) and nutrients are at their highest. Most of the diatom species exhibit their highest fluxes during this period (Fig. 6), reflecting the opportunistic behavior of this group. As previously mentioned, the diatom assemblage during the winter–spring transition is dominated by *Skeletonema* sp., which indicates the affinity of this taxon for nutrient-rich and turbulent environments. From March, the day length and solar elevation increase, while the turbulence in the water column gradually decreases. The photic zone remains rich in nutrients, but those steadily decrease due to phytoplankton uptake and build-up of biomass (Leblanc *et al.*, 2003). In April and May, other taxa show their maximum relative abundances such as *Chaetoceros* spp., *Odontella* spp., *Bacteriastrum* spp. and *D. brightwellii* (Fig. 6). The last of these species is a good representative of this group of diatoms; its weakly silicified valves and large vacuoles allow it to thrive under high light levels and low nutrient concentrations (Margalef, 1978; Smetacek, 1999). The last stage of the annual cycle is the summer, i.e. June to August, characterized by maximum solar radiation, strong thermal stratification and oligotrophic conditions in the water column. Diatom fluxes reach their annual minimum, and living diatom assemblages are probably confined to the deep chlorophyll maximum (Marty *et al.*,

2002). Diatom flux is dominated by *Chaetoceros* resting spores that are formed in response to the nutrient depletion. *Nitzschia bicapitata*, *Thalassiosira* spp., *Rhizosolenia* spp. and *Coscinodiscus* spp. also reach their annual maxima of relative abundance during this season (Fig. 6). *Rhizosolenia* and *Coscinodiscus* have been described as components of the "shade flora", and could be defined as deep dwellers that normally possess larger cells (with a greater intracellular volume) and slower growth rates than the spring bloom species (Kemp *et al.*, 2000). The "shade flora" species have characteristics that allow them to grow in stratified waters, such as symbiotic relationships with nitrogen-fixing cyanobacteria (e.g. *Rhizosolenia*) (Villareal, 1990; Villareal *et al.*, 1993), capacity to grow in low-light conditions (e.g. *Stephanopyxis* and *Coscinodiscus*) and regulation of their buoyancy (e.g. *Rhizosolenia* and *Ethmodiscus*) (Kemp *et al.*, 2000).

Interannual fluctuations of diatom and coccolith fluxes

Superimposed on the seasonal fluctuations of the phytoplankton flux registered at the Planier site, a significant interannual variability was observed (Fig. 3). The winter–spring diatom bloom is a recurrent feature along the 12-year time series, but its intensity varies from year to year and seems to be related to the intensity of the winter northwesterly winds. Winds affecting winter mixing and coastal upwelling are considered to be one of the main physical factors responsible for the build-up of phytoplankton biomass in the Mediterranean Sea (Siokou-Frangou *et al.*, 2010). In winter, cold and dry northwesterly winds prevail over the Gulf of Lions, inducing strong cooling and evaporation of the coastal and off-shelf waters (Millot, 1990). The intensity of the winter mixing shows a strong interannual variation (Durrieu De Madron *et al.*, 2005) that depends on the wind intensity and air temperatures during winter (Herrmann *et al.*, 2008). Winter mixing replenishes nutrients in the photic zone and triggers development of a pronounced phytoplankton bloom in late winter–early spring (Vidussi *et al.*, 2000; Marty *et al.*, 2002; Rigual-Hernández *et al.*, 2010). In the Planier record, the highest diatom flux pulses occur during the winter–spring blooms of years with intense wind stress during winter, i.e. 1997, 1999, 2000, 2001, 2003 and 2005 (Fig. 3). In contrast, years with low wind stress and consequent weakening of the winter mixing are liable to be less productive for diatoms, as seen from the low diatom valve fluxes registered during 1998, 2002 and 2004 (Fig. 3). The well-mixed and nutrient-rich photic zone during years of intense winter winds provides optimum conditions for the development of large diatom blooms. Owing to their faster growth and

greater nutrient uptake (Fogg, 1991) diatoms can outcompete other phytoplankton in relatively turbulent, nutrient-rich environments, and that could explain the high diatom pulses during years with intense winter northwesterly winds. This agrees with previous observations on the continental shelf of the Gulf of Lions, where large pulses of fresh pelagic diatoms during late winter have been linked to strong NW wind events (Leblanc *et al.*, 2005).

Coccolith fluxes exhibited a more stable annual pattern than diatom fluxes (Fig. 3). During 2 of the 3 years with the highest coccolith flux pulses, 1995 and 2004, no diatom bloom was recorded. We speculate that coccolithophores either gained an advantage in those years, preventing diatom proliferation, or that the inhibition of diatom growth by other factors, such as mild water column mixing enhanced coccolithophore development due to the absence of nutrient competition. The variability of the diatom and coccolith fluxes in relation to the intensity of the mixing of the water column agrees with previous observations in the NW Mediterranean, such as by Estrada *et al*. (Estrada *et al.*, 1999) who reported an increase in the diatom cell numbers related to decreasing vertical stratification, while coccolithophores exhibited an opposite pattern.

Additionally, major climatological phenomena affecting the NW Mediterranean were considered as possible sources of the interannual variability of the microplankton fluxes. In their review based on historical data, Gómez and Gorsky (Gómez and Gorsky, 2003) suggested that the variability of the NAO could have a direct effect on the magnitude of the diatom spring bloom in the Northern Basin. The variability of the flow through the Corsica Channel, which feeds the NC (Fig. 1), is correlated with the winter state of the NAO (Vignudelli *et al.*, 1999). Low or negative values of the winter NAO index are associated with an intensification of that transport and with strong spring diatom blooms, whereas positive values are coupled with less water transport in the Corsica channel and weaker diatom blooms (Gómez and Gorsky, 2003). In our time series, only the years with the most extreme NAO winter values (Fig. 3) reflected the hypothesis advanced by Gómez and Gorsky (Gómez and Gorsky, 2003): during 1996 the NAO index showed the most negative values of the record and high diatom valve fluxes were recorded, whereas during 1995 the NAO winter index exhibited its highest values and no winter–spring diatom bloom was observed (Fig. 3). However, for the rest of the years this relationship was not so obvious. Despite the observations of Gómez and Gorsky (Gómez and Gorsky, 2003), our time series showed no consistent relationship between the winter state of the NAO and the magnitude of the winter–spring diatom bloom.

In addition, extreme ENSO events can influence the Mediterranean climate (Brönnimann *et al.*, 2007), and, therefore, have been considered as a possible source of variability in phytoplankton flux. Our time series encompasses the period 1997–1998, when the strongest El Niño event of the past century occurred (Wolter and Timlin, 1998; McPhaden, 1999a,b). During that period, major climatic anomalies were registered around the world and linked to this tropical phenomenon (McPhaden, 1999b). In the Alboran Sea Garcia-Gorriz and Carr (Garcia-Gorriz and Carr, 2001) described abnormally high SSTs and a weakening of the winds during the summer and autumn of 1997. The strong ENSO resulted in a weaker winter bloom and changes in the microplankton communities (Mercado *et al.*, 2005, 2007). Moreover, significant changes in the microplankton fluxes and assemblages were observed during winter 1997–1998 in both Alboran Gyres (Bárcena *et al.*, 2004; Hernández-Almeida *et al.*, 2011). In the Gulf of Lions anomalous hydrographic and atmospheric conditions were also observed during this period: (i) high SSTs during autumn 1997 ($\sim$1.6°C higher than the 12-year average), (ii) highest winter SSTs on record during winter 1997–1998 ($\sim$0.7°C higher than the 12-year winter average), and (iii) remarkably low wind intensity during autumn and winter of 1997–1998 (Fig. 3). We surmise that these mild conditions possibly led to weak winter mixing and consequently low diatom productivity during the 1998 winter–spring bloom (Fig. 3). Furthermore, the highest pulse of *Rhizosolenia* spp. in the record registered during May and June of 1998 (Fig. 7), likely linked to the stronger thermal stratification of the water column in that year. In addition, remarkably low fluxes of other microplankton groups and a pulse of warm-water foraminifera species have been reported at the Planier site during this period and linked to the 1997–1998 ENSO event (Rigual-Hernández *et al.*, 2010, 2012).

Comparison of sediment trap and surface sediment diatom assemblages

A previous study on planktonic foraminifera fluxes in the Gulf of Lions (Rigual-Hernández *et al.*, 2012) showed that the assemblage registered in the Planier trap was similar to that of the surficial sediments below the trap, indicating that the continental slope sediments integrate the seasonal flux patterns of the foraminifera living in the upper water column. Therefore, a similar behavior might be expected for diatoms. However, notable differences between the sediment trap and the surficial-sediment diatom assemblages were found, as reflected in the high dissimilarity value. The most remarkable difference is the absence in the surficial sediment sample of some of the

most abundant diatom species in the trap: the weakly silicified *Skeletonema* sp., *Chaetoceros* spp. and some species of *Thalassiosira* (Table I). On the contrary, robust diatoms such as the thick-walled *Chaetoceros* resting spores or *T. frauenfeldii* were well preserved in the surficial sediments, and their relative abundance was twice as high as in the sediment trap (Table I).

The waters of the NC in the Gulf of Lions are under saturated in silica, especially during the onset of the spring bloom when it is severely depleted from the photic zone due to phytoplankton uptake and build-up of biomass (Leblanc *et al.*, 2003). Therefore, the differences between the sediment trap and surficial sediment assemblages are most likely caused by opal dissolution that results in the selective preservation of diatom species. The lightly silicified valves are recycled before reaching the sea bed or in the sediment–water interface (Ragueneau *et al.*, 2000). Heavily silicified frustules are more resistant to dissolution and are better preserved in the sediment (Smetacek, 1985). It is noteworthy that the absence of *Skeletonema* sp. in the Planier site sedimentary record contrasts with other studies in continental margin and deep-sea settings (e.g. Brodie and Kemp, 1994; Bull and Kemp, 1995; Kemp *et al.*, 2000). Those authors reported better preservation of bloom-forming diatoms, attributing this to their capacity for post-bloom aggregation and mass sinking (Smetacek, 1985; Alldredge and Gotschalk, 1990). The silicate depletion over the entire water column during spring could be the cause of the absence in the surface sediments of some of the indicators of relative bloom productivity like *Skeletonema* sp. or *Chaetoceros* spp.

The stark difference between the sediment trap and surficial sediment diatom assemblages shows that the sedimentary record of the continental slope of the Gulf of Lions does not integrate the diatom production and assemblage or its export from the water column, but rather represents selective preservation of the most robust species.

CONCLUSIONS

The main objectives of our work were (i) to document the seasonal and interannual variability of diatom flux, diatom species composition and total coccolith flux in the NW Mediterranean and (ii) to compare the sediment trap and surficial sediment diatom assemblages in order to evaluate the validity of diatoms as indicators of paleo-conditions in the Gulf of Lions. To examine these issues we analyzed a 12-year-long sediment trap record and one box-core sediment sample from a northeastern site

in the Gulf of Lions. Our main observations are summarized as follows:

(i) Diatom and coccolith fluxes on the continental slope of the Gulf of Lions are high (3×10^7 valves m^2 day^{-1} and 6.1×10^8 coccoliths m^2 day^{-1}, respectively) and comparable in magnitude with other areas of high productivity in the Western Mediterranean.

(ii) Diatoms are the main contributors to opal production and export in the Gulf of Lions, while the main suppliers of biogenic carbonate are coccoliths and planktonic foraminifera.

(iii) Fluxes of diatom valves and coccoliths exhibited strong seasonal cyclicity that reflects the changes in the upper water column and atmosphere dynamics off the Gulf of Lions. The highest chlorophyll-*a* concentration and diatom and coccolith fluxes always occurred during the winter–spring transition when the mixing of the water column enriches the photic zone with nutrients. Annual minima were always registered during summer in response to the nutrient-depleted and stratified surface waters.

(iv) Diatom assemblages showed a seasonal succession related to the annual cycle of the water column. The three most abundant taxa occurred under different conditions in the water column: *T. frauenfeldii* was ubiquitous in the 12-year record and exhibited its maximum relative abundance during periods of moderate-to-strong water mixing; *Chaetoceros* resting spores dominated the diatom assemblages during periods of strong stratification of the water column and nutrient depletion, i.e. summer and the beginning of autumn; and *Skeletonema* sp. was responsible for some of the greatest pulses of diatom flux in the record, occurring during the winter–spring bloom associated with freshly upwelled waters.

(v) Diatom flux exhibited high interannual variability, whereas coccolith flux showed a more stable annual pattern. Highest diatom flux pulses occur during the winter–spring bloom of those years with stronger water mixing caused by intense wind stress during winter.

(vi) Diatom flux did not show a straightforward relationship with the winter state of NAO.

(vii) We hypothesize that the anomalous conditions registered during the 1997–1998 ENSO event could have caused the low diatom flux during the 1998 winter–spring bloom and the pulse of *Rhizosolenia* spp. during May and June of that year.

(viii) Significant discrepancies between the sediment trap and surficial sediment diatom assemblages

were found. The sedimentary record was markedly enriched in heavily silicified species, such as *Chaetoceros* resting spores, indicators of the low-productivity season, while the dominant representative of the most productive periods, *Skeletonema* sp., was absent in the surficial sediments. These differences were caused by opal dissolution in the water column and in the sediment–water interface.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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REFERENCES

Acker, J. G. and Leptoukh, G. (2007) Online analysis enhances use of NASA earth science data. *Eos, Transactions. AGU*, **88**, 14–17.

Alldredge, A. L. and Gotschalk, C. C. (1990) The relative contribution of marine snow of different origins to biological processes in coastal waters. *Cont. Shelf Res.*, **10**, 41–58.

Antoine, D., Morel, A. and André, J. (1995) Algal pigment distribution and primary production in the eastern Mediterranean as derived from Coastal Zone Color Scanner observations. *J. Geophys. Res.*, **100**, 16193–16209.

Bárcena, M. A. and Abrantes, F. (1998) Evidence of a high-productivity area off the coast of Málaga from studies of diatoms in surface sediments. *Mar. Micropaleontol.*, **35**, 91–103.

Bárcena, M. A., Flores, J. A., Sierro, F. J. *et al.* (2004) Planktonic response to main oceanographic changes in the Alboran Sea (Western Mediterranean) as documented in sediment traps and surface sediments. *Mar. Micropaleontol.*, **53**, 375–398.

Beaufort, L. and Dollfus, D. (2004) Automatic recognition of coccoliths by dynamical neural networks. *Mar. Micropaleontol.*, **51**, 57–73.

Brand, L. E. (1994) Physiological ecology of marine coccolithophores. In Winter, A. and Siesser, W. G. (eds), *Coccolithophores*. Univ. Press, Cambridge, pp. 39–49.

Brodie, I. and Kemp, A. E. S. (1994) Variation in biogenic and detrital fluxes and formation of laminae in late Quaternary sediments from the Peruvian coastal upwelling zone. *Mar. Geol.*, **116**, 385–398.

Brönnimann, S., Xoplaki, E., Casty, C. *et al.* (2007) ENSO influence on Europe during the last centuries. *Clim. Dynam.*, **28**, 181–193.

Bull, D. and Kemp, A. E. S. (1995) Composition and origins of laminae in late Quaternary and Holocene sediments from the Santa Barbara Basin. In Kennett, J. P., Baldauf, J. G. and Lyle, M. (eds), *ODP, Scientific Results*. Vol. 146. Ocean Drilling Program, College Station, TX, pp. 77–87.

Caroppo, C., Fiocca, A., Sammarco, P. *et al.* (1999) Seasonal variations of nutrients and phytoplankton in the coastal SW Adriatic Sea (1995–1997). *Bot. Mar.*, **42**, 389–400.

Castellví, J. (1971) Contribución a la biología de *Skeletonema costatum* (Grev.) Cleve. *Investigación. Pesquera.*, **35**, 365–520.

Conway, H. L. and Harrison, P. J. (1977) Marine diatoms grown in chemostats under silicate or ammonium limitation. IV. Transient response of *Chaetoceros debilis*, *Skeletonema costatum*, and *Thalassiosira gravida* to a single addition of the limiting nutrient. *Mar. Biol.*, **43**, 33–43.

Crombet, Y., Leblanc, K., Quéguiner, B. *et al.* (2011) Deep silicon maxima in the stratified oligotrophic Mediterranean Sea. *Biogeosciences*, **8**, 459–475.

Crosta, X., Pichon, J. J. and Labracherie, M. (1997) Distribution of *Chaetoceros* resting spores in modern peri-Antarctic sediments. *Mar. Micropaleontol.*, **29**, 283–299.

D'Ortenzio, F. and Ribera D'alcalá, M. (2009) On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosciences*, **6**, 139–148.

Deuser, W. G., Brewer, P. G., Jickells, T. D. *et al.* (1983) Biological Control of the Removal of Abiogenic Particles from the Surface Ocean. *Science*, **219**, 388–391.

Durrieu De Madron, X., Zervakis, V., Theocharis, A. *et al.* (2005) Comments to "Cascades of dense water around the world ocean. *Progr. Oceanogr.*, **64**, 83–90.

Estournel, C., Kondrachoff, V., Marsaleix, P. *et al.* (1997) The plume of the Rhône: numerical simulation and remote sensing. *Cont. Shelf Res.*, **17**, 899–924.

Estrada, M. (1996) Primary production in the northwestern Mediterranean. *Sci. Mar.*, **60**, 55–64.

Estrada, M., Varela, R. A., Salat, J. *et al.* (1999) Spatio-temporal variability of the winter phytoplankton distribution across the Catalan and North Balearic fronts (NW Mediterranean). *J. Plankton Res.*, **21**, 1–20.

Fogg, G. E. (1991) Tansley Review No. 30. The Phytoplanktonic Ways of Life. *New Phytol.*, **118**, 191–232.

García-Gorriz, E. and Carr, M. E. (2001) Physical control of phytoplankton distributions in the Alboran Sea: a numerical and satellite approach. *J. Geophys. Res.*, **106**, 16795–16805.

Gómez, F. and Gorsky, G. (2003) Annual microplankton cycles in Villefranche Bay, Ligurian Sea, NW Mediterranean. *J. Plankton Res.*, **25**, 323–339.

Gutiérrez-Rodríguez, A., Latasa, M., Estrada, M. *et al.* (2010) Carbon fluxes through major phytoplankton groups during the spring bloom and post-bloom in the Northwestern Mediterranean Sea. *Deep-Sea Res. (1 Oceanogr. Res. Pap.)*, **57**, 486–500.

Hasle, G. R. (2001) The marine, planktonic diatom Family Thalassionemataceae: morphology, taxonomy and distribution. *Diatom. Res.*, **16**, 1–82.

Hedges, J. I. and Keil, R. G. (1995) Sedimentary organic matter preservation: an assessment and speculative synthesis. *Mar. Chem.*, **49**, 81–115.

Hernández-Almeida, I., Bárcena, M. A., Flores, J. A. *et al.* (2011) Microplankton response to environmental conditions in the Alboran Sea (Western Mediterranean): One year sediment trap record. *Mar. Micropaleontol.*, **78**, 14–24.

Herrmann, M., Estournel, C., Déqué, M. *et al.* (2008) Dense water formation in the Gulf of Lions shelf: Impact of atmospheric interannual variability and climate change. *Cont. Shelf Res.*, **28**, 2092–2112.

Heussner, S., Durrieu De Madron, X., Calafat, A. *et al.* (2006) Spatial and temporal variability of downward particle fluxes on a continental slope : Lessons from an 8-yr experiment in the Gulf of Lions (NW Mediterranean). *Mar. Geol.*, **234**, 63–92.

Heussner, S., Ratti, C. and Carbonne, J. (1990) The PPS 3 time series sediment traps and the trap sample processing techniques used during the ECOMARGE experiment. *Cont. Shelf Res.*, **10**, 943–958.

Jickells, T. D., Newton, P. P., King, P. *et al.* (1996) A comparison of sediment trap records of particle fluxes from 19 to 48°N in the northeast Atlantic and their relation to surface water productivity. *Deep-Sea Res.(1 Oceanogr. Res. Pap.)*, **43**, 971–986.

Kemp, A. E. S., Pike, J., Pearce, R. B. *et al.* (2000) The "Fall dump"—a new perspective on the role of a "shade flora" in the annual cycle of diatom production and export flux. *Deep-Sea Res. (2 Top. Stud. Oceanogr.)*, **47**, 2129–2154.

Leblanc, K., Quéguiner, B., García, N. *et al.* (2003) Silicon cycle in the NW Mediterranean Sea: seasonal study of a coastal oligotrophic site. *Oceanol. Acta*, **26**, 339–355.

Leblanc, K., Quéguiner, B., Raimbault, P. *et al.* (2005) Efficiency of the silicate pump at a coastal oligotrophic site in the Mediterranean Sea. *Biogeosciences*, **2**, 219–229.

Lévy, M., Mémery, L. and André, J.-M. (1998) Simulation of primary production and export fluxes in the Northwestern Mediterranean Sea. *J. Mar. Res.*, **56**, 197–238.

Locarnini, R. A., Mishonov, A. V. and Antonov, J. I. (2010) *World Ocean Atlas 2009, Volume 1: Temperature*. Vol. 1, U.S. Government Printing Office, Washington, D.C.

Loncaric, N., Van Iperen, J., Kroon, D. *et al.* (2007) Seasonal export and sediment preservation of diatomaceous, foraminiferal and organic matter mass fluxes in a trophic gradient across the SE Atlantic. *Progr. Oceanogr.*, **73**, 27–59.

Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanolog. Acta*, **1**, 493–509.

Marty, J. C., Chiavérini, J., Pizay, M. D. *et al.* (2002) Seasonal and interannual dynamics of nutrients and phytoplankton pigments in the western Mediterranean Sea at the DYFAMED time-series station (1991–1999). *Deep-Sea Res. (2 Top. Stud. Oceanogr.)*, **49**, 1965–1985.

Maynou, F. (2008) Influence of the North Atlantic Oscillation on Mediterranean deep-sea shrimp landings. *Climate Res.*, **36**, 253–257.

McPhaden, M. J. (1999a) El Niño: The child prodigy of 1997–98. *Nature*, **398**, 559–562.

McPhaden, M. J. (1999b) Genesis and evolution of the 1997–98 El Niño. *Science*, **283**, 950–954.

McQuoid, M. R. and Hobson, L. A. (1996) Diatom resting stages. *J. Phycol.*, **32**, 889–902.

Meier, S., Beaufort, L., Heussner, S. *et al.* Submitted. The role of ocean acidification in Emiliania huxleyi coccolith thinning in the Mediterranean Sea. *PLoS One*, submitted.

Mercado, J., Cortés, D., Garcia, A. *et al.* (2007) Seasonal and interannual changes in the planktonic communities of the northwest Alboran Sea (Mediterranean Sea). *Progr. Oceanogr.*, **74**, 273–293.

Mercado, J., Ramírez, T., Cortés, D. *et al.* (2005) Temporal changes of the phytoplankton communities in an upwelling area of the Alboran Sea. *Sci. Mar.*, **69**, 451–465.

Millot, C. (1990) The Gulf of Lions' hydrodynamics. *Cont. Shelf Res.*, **10**, 885–894.

Millot, C. (1999) Circulation in the Western Mediterranean Sea. *J. Mar. Syst.*, **20**, 423–442.

Miquel, J. C., Fowler, S. W., La Rosa, J. *et al.* (1994) Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean Sea. *Deep-Sea Res. (1 Oceanogr. Res. Pap.)*, **41**, 243–261.

Nelson, D. M., Tréguer, P., Brzezinski, M. A. *et al.* (1995) Production and dissolution of biogenic silica in the ocean: Revised global estimates, comparison with regional data and relationship to biogenic sedimentation. *Global Biogeochem. Cycles*, **9**, 359–372.

Ochoa, N., Taylor, M. H., Purca, S. *et al.* (2010) Intra- and interannual variability of nearshore phytoplankton biovolume and community changes in the northern Humboldt Current system. *J. Plankton Res.*, **32**, 843–855.

Ortiz, J. D. and Mix, A. C. (1997) Comparison of Imbrie-Kipp transfer function and modern analog temperature estimates using sediment trap and core top foraminiferal faunas. *Paleoceanography*, **12**, 175–190.

Ragueneau, O., Tréguer, P., Leynaert, A. *et al.* (2000) A review of the Si cycle in the modern ocean: recent progress and missing gaps in the application of biogenic opal as a paleoproductivity proxy. *Global Planet. Change*, **26**, 317–365.

Reynolds, R. W., Rayner, N. A., Smith, T. M. *et al.* (2002) An improved in situ and satellite SST analysis for climate. *J. Climate*, **15**, 1609–1625.

Ribera D'alcalà, M., Conversano, F., Corato, F. *et al.* (2004) Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrence and trends. *Sci. Mar.*, **68**, 65–83.

Rigual-Hernández, A. S., Bárcena, M. A., Sierro, F. J. *et al.* (2010) Seasonal to interannual variability and geographic distribution of the silicoflagellate fluxes in the Western Mediterranean. *Mar. Micropaleontol.*, **77**, 46–57.

Rigual-Hernández, A. S., Sierro, F. J., Bárcena, M. A. *et al.* (2012) Seasonal and interannual changes of planktic foraminiferal fluxes in the Gulf of Lions (NW Mediterranean) and their implications for paleoceanographic studies: Two 12-year sediment trap records. *Deep-Sea Res. (1 Oceanogr. Res. Pap.)*, **66**, 26–40.

Schrader, H. J. and Gersonde, R. (1978) Diatoms and silicoflagellates. In: Zachariasse, W. J., Riedel, W. R., Sanfilippo, A. *et al.* (eds), *Micropaleontological Counting Methods and Techniques—An Exercise on an Eight Metres Section of the Lower Pliocene of Capo Rossello*, Utrecht Micropaleontological Bulletins, Sicily, vol. 17, pp. 129–176.

Simonsen, R. (1974) The diatom plankton of the Indian Ocean Expedition of RV Meteor 1964–1965. *Meteor. Forschung-Ergebnisse. Reihe D Biol.*, **19**, 1–66.

Siokou-Frangou, I., Christaki, U., Mazzocchi, M. G. *et al.* (2010) Plankton in the open Mediterranean Sea: a review. *Biogeosciences*, **7**, 1543–1586.

Smetacek, V. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, **84**, 239–251.

Smetacek, V. (1999) Diatoms and the ocean carbon cycle. *Protist*, **150**, 25–32.

Travers, M. (1971) Diversité du microplancton du Golfe de Marseille en 1964. *Mar. Biol.*, **8**, 308–343.

Ulses, C., Estournel, C., Puig, P. *et al.* (2008) Dense shelf water cascading in the northwestern Mediterranean during the cold winter 2005: Quantification of the export through the Gulf of Lion and the Catalan margin. *Geophys. Res. Lett.*, **35**, L07610.

Vidussi, F., Marty, J. C. and Chiavérini, J. (2000) Phytoplankton pigment variations during the transition from spring bloom to oligotrophy in the Northwestern Mediterranean Sea. *Deep-Sea Res. (1 Oceanogr. Res. Pap.)*, **47**, 423–445.

Vignudelli, S., Gasparini, G. P., Astraldi, M. *et al.* (1999) A possible influence of the North Atlantic Oscillation on the circulation of the Western Mediterranean Sea. *Geophys. Res. Lett.*, **26**, 623–626.

Villareal, T. A. (1990) Laboratory culture and preliminary characterization of the Nitrogen-fixing *Rhizosolenia-Richelia* symbiosis. *Mar. Ecol.*, **11**, 117–132.

Villareal, T. A., Altabet, M. A. and Culver-Rymsza, K. (1993) Nitrogen transport by vertically migrating diatom mats in the North Pacific Ocean. *Nature*, **363**, 709–712.

Waniek, J. J., Schulz-Bull, D. E., Kuss, J. *et al.* (2005) Long time series of deep water particle flux in three biogeochemical provinces of the northeast Atlantic. *J. Mar. Syst.*, **56**, 391–415.

Wolter, K. and Timlin, M. S. (1998) Measuring the strength of ENSO events: how does 1997–98 rank? *Weather*, **53**, 315–325.

Ziveri, P., Rutten, A., De Lange, G. J. *et al.* (2000) Present-day coccolith fluxes recorded in central eastern Mediterranean sediment traps and surface sediments. *Palaeogeogr., Palaeoclimateol., Palaeoecol.*, **158**, 175–195.