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Deep silicon maxima in the stratified oligotrophic Mediterranean Sea

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Abstract

The silicon biogeochemical cycle has been studied in the Mediterranean Sea during fall 1999 and summer 2008. The distribution of nutrients, particulate carbon and silicon, fucoxanthin (Fuco) and total chlorophyll-*a* (Tchl-*a*) were investigated along an eastward gradient of oligotrophy during two cruises (PROSOPE and BOUM) encompassing the entire Mediterranean Sea during the stratified period. At both seasons, surface waters were depleted in nutrients and the nutriclines gradually deepened towards the East, the phosphacline being the deepest in the easternmost Levantine basin. Following the nutriclines, correlated deep maxima of biogenic silica (DSM), fucoxanthin (DFM) and Tchl-*a* (DCM) were evidenced during both seasons with maximal concentrations of $0.45 \mu\text{mol L}^{-1}$ for BSi, $0.26 \mu\text{g L}^{-1}$ for Fuco, and $1.70 \mu\text{g L}^{-1}$ for Tchl-*a*, all measured during summer. Contrary to the DCM which was a persistent feature in the Mediterranean Sea, the DSM and DFMs were observed in discrete areas of the Alboran Sea, the Algero-Provencal basin, the Ionian sea and the Levantine basin, indicating that diatoms were able to grow at depth and dominate the DCM under specific conditions. Diatom assemblages were dominated by *Chaetoceros* spp., *Leptocylindrus* spp., *Pseudonitzschia* spp. and the association between large centric diatoms (*Hemiaulus hauckii* and *Rhizosolenia styliformis*) and the cyanobacterium *Richelia intracellularis* was observed at nearly all sites. The diatom's ability to grow at depth is commonly observed in other oligotrophic regions and could play a major role in ecosystem productivity and carbon export to depth. Contrary to the common view that Si and siliceous phytoplankton are not major components of the Mediterranean biogeochemistry, we suggest here that diatoms, by persisting at depth during the stratified period, could contribute to a large part to the marine productivity and biological pump, as observed in other oligotrophic areas.

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1 Introduction

Diatoms play an important role in the ocean biological pump and are responsible for an estimated 30% of the global oceanic primary production (Nelson et al., 1995; Tréguer et al., 1995). This large averaged value hides wide differences between eutrophic areas, where diatoms contribution to primary productivity reaches up to 75% and oligotrophic areas where it scales down to 10–30% (Nelson et al., 1995; Uitz et al., 2010). The lowest particulate Si biomass accumulation ever measured has been observed in open ocean oligotrophic gyres, such as in the Sargasso Sea (Nelson et al., 1995; Nelson and Brzezinski, 1997; Krause et al., 2009a). Despite low abundance and chronic Si limitation, diatoms still play a significant role by contributing close to 25% of annual primary productivity in both the Sargasso Sea and the Central North Pacific (Brzezinski and Nelson, 1995; Nelson and Brzezinski, 1997; Krause et al., 2009a; Brzezinski et al., 1998) and representing up to 30% of the annual carbon export in the Sargasso Sea (Krause et al., 2009b; Nelson and Brzezinski, 1997). Hence, the functioning of these systems shows that despite widespread N and P limitation, Si availability is also important to consider and that diatoms may play a crucial role in the biological C pump even in highly oligotrophic regions.

The Mediterranean Sea (MS) is one of the most oligotrophic oceanic systems of the World Ocean (Ryan, 1966; Dugdale, 1976) and is characterised by a longitudinal gradient of oligotrophy increasing eastwards (Azov, 1991) and a near complete P depletion in the stratified layer during summer and fall, comparable to that observed in open ocean oligotrophic gyres. During the last century, the eastern Mediterranean basin has also become increasingly oligotrophic since the construction of the Assouan dam on the river Nile, whereas the western basin remains well supplied by the Rhône and Po river inputs and entering surface Atlantic waters (Béthoux et al., 1998). This gradient of oligotrophy correlates with a gradient of biomass, with an extremely low chlorophyll content in the eastern basin. In a review of the seasonal development of the surface phytoplankton bloom using a ten year archive of SeaWifs data, D’Ortenzio and Rib-

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era d'Alcala (2009) evidenced distinct regions in the MS with different bloom phasings throughout the year. The main patterns observed over this decadal study were a clear biomass maximum in the western basin in spring with some early starts in November and December, while the eastern basin showed higher chl-*a* values during winter and experienced the lowest values during summer, from May to September. Most of the eastern basin, and parts of the western basin are characterised as “non-bloom” areas which would together cover about 60% of the MS (D'Ortenzio and Ribera d'Alcala, 2009). However, this study concerns surface chl-*a* distribution as observed by satellites and ignores the potential deep phytoplankton accumulation, which we will show in this study, could modulate this clear cut pattern.

Severe oligotrophic conditions appear with the onset of a strong thermal summer stratification in the MS and lead to the development of a Deep Chlorophyll-*a* Maximum (DCM) closely associated to the nutricline, which has been repeatedly observed across the entire basin and compared to similar structures of the oligotrophic Atlantic and Pacific Ocean (Ediger and Yilmaz, 1996). During summer, primary production rates are usually low, the autotrophic community is dominated by pico- and nanophytoplankton, and the microbial food web becomes predominant under internal nutrient recycling conditions (Thingstad and Rassoulzadegan, 1995). Several studies have documented the limitation of phytoplankton production by nitrogen and phosphorus (Agusti et al., 1998; Bethoux et al., 1992; Krom et al., 1991; Moutin et al., 2002). The MS deep waters are known to have a strong P deficit, with N:P ratios close to 28, while it is close to 16 in all other oceanic basins (Krom et al., 2004; Pujo-Pay et al., 2010). A thorough review by Thingstad and Rassoulzadegan (1995) concluded that the Mediterranean planktonic ecosystems experience a general physiological P-limitation but questions still remain on the exact mechanism responsible for the decreased availability of P vs. N. Several hypotheses have been suggested, such as increased P adsorption onto dust particles, increased N₂ fixation by both benthic and pelagic organisms or dystrophic atmospheric and riverine inputs (Krom et al., 2004, 2010) but none has yet been widely accepted as the sole responsible factor for the anomalous N:P ratios in the MS. High N₂-fixation

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rates have been measured only once in the Cyprus warm-core eddy (Rees et al., 2006) but other measurements carried out in the MS reported negligible fluxes (Garcia et al., 2006; Krom et al., 2010; Ibello et al., 2010). Diazotrophic organisms such as the filamentous cyanobacterium *Trichodesmium* and the symbiotic associations between the cyanobacterium *Richelia intracellularis* and diverse diatom species have never been reported in abundance in the MS and should play an insignificant role in nitrogen fixation according to Krom et al. (2010). However, a recent review of plankton in the MS evidences the presence of large diatom accumulations at depth during summer (Siokou-Frangou et al., 2010). Our results shed new light on this debate and seem to confirm the latter hypothesis.

While the focus has been placed on the N and P cycles, the Si cycle remains poorly investigated in the MS, and the potential contribution of diatoms to primary production and export in the open basins of the MS is similarly poorly constrained while data is mainly available for coastal and near shore areas. This paper presents a comparative study of the availability of dissolved Si and siliceous phytoplankton distribution patterns over a vast oligotrophic gradient covering the entire MS during summer and fall. The results presented in this paper originate from two cruises that were carried out almost a decade apart over very similar longitudinal gradients and sampling strategies. Vertical distributions of silicic acid, biogenic and lithogenic silica, main (chl-*a*) and accessory (fucoxanthin) pigments as well as particulate organic carbon are presented for the PROSOPE cruise (Productivity of Oceanic Pelagic Systems) and the BOUM cruise (Biogeochemistry from the Oligotrophic to the Ultra-oligotrophic Mediterranean) conducted in fall 1999 and summer 2008, respectively. The objectives of this article are to document the dissolved and particulate Si cycle and assess diatoms contribution to phytoplankton community as well as their potential role in N₂ fixation, over both the western and eastern Mediterranean basins during the stratified period. Interestingly, a deep silica maximum was recurrently observed closely associated to the well identified DCM and we will explore the potential formation mechanisms and ecological role of this “deep glass forest” in the Mediterranean Sea.

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2 Methods

2.1 Study areas and sampling strategies

Seawater samples were collected during two cruises conducted in the western and eastern basins (Fig. 1). The CNRS/INSU PROSOPE (Productivity of Oceanic Pelagic Systems) cruise was part of the JGOFS (Joint Global Ocean Flux Study) program and was carried out in 1999 during late summer-early autumn (4 September to 4 October) on board *N.O. Thalassa*. The CNRS/INSU BOUM cruise (Biogeochemistry from the Oligotrophic to the Ultra oligotrophic Mediterranean sea) was part of the SESAME (Southern Europeans Seas: Assessing and Modelling Ecosystem Changes) integrated project supported by the European Commission, and was conducted in 2008 during summer (20 June to 22 July) on board *N.O. L'Atalante*. During the PROSOPE cruise, hydrological, biological and chemical parameters were studied at 9 short-term stations and 2 long-term (5 days) process study sites (DYF and MIO located in the Ligurian and Ionian Sea, respectively). During the BOUM cruise, hydrological, biological and chemical parameters were studied at 27 short-term stations and 3 long-term (4 days) process study sites (A, B, C, respectively located in the Algero-Provencal, the Tyrrhenian, and the Levantine basins) located in the center of anticyclonic gyres, where lateral advection was expected to be minimum.

2.2 Dissolved and particulate matter analysis

Seawater samples were collected at selected depths between the surface and 200 m depth with 12 L Niskin bottles mounted on a seabird CTDO rosette sampler (model SBE 911). Nitrate (NO_3) and phosphate (PO_4) were determined with standard automated colorimetric method on a Bran&Luebbe Technicon autoanalyzer (Tréguer and Le Corre, 1975). The detection limits were, respectively 30 nM, and 20 nM for NO_3 , and PO_4 . For orthosilicic acid (H_4SiO_4), 20 ml of seawater collected on each Niskin were filtered onto 0.2 μm polycarbonate filters and analysed for H_4SiO_4 according to the colorimetric

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method of (Mullin and Riley, 1962, adapted by Strickland and Parsons, 1972), with a detection limit of 50 nM.

For particulate biogenic and lithogenic silica (BSi and LSi) analyses, 1 to 2.3 L of seawater were filtered onto 47 mm 0.6 µm pore size polycarbonate filters. Filters were folded and stored in plastic Petri dishes, oven dried (60 °C) for 24 h and stored at room temperature until processing at the laboratory. Filters were then analysed for BSi following the sequential NaOH/HF digestion technique described by Nelson et al. (1989). The detection limit was 0.011 µmol L⁻¹ for BSi and 0.008 µmol L⁻¹ for LSi.

For pigment analyses 2 L of seawater were filtered onto pre-combusted Whatman GF/F 25 mm filters and stored in liquid nitrogen until processing. Extraction was achieved in 3 mL 100% methanol, followed by a sonication and another filtration on a new GF/F filter to clarify the extracts. Pigments were then analysed by HPLC (High Performance Liquid Chromatography) following the method of Vidussi et al. (1996) (PROSOPE cruise) and Ras et al. (2008) (BOUM cruise). In this paper we only present the distributions of total chlorophyll-*a* (Tchl-*a*) and fucoxanthin (Fuco), the former including chlorophyll-*a* and divinyl-chlorophyll-*a*, the latter being a diagnostic pigment for diatoms (Vidussi et al., 2000). The limit of detection for Tchl-*a* and Fuco were 2.4 ng L⁻¹ for the PROSOPE cruise (Claustre et al., 2004) and better than 0.2 ng L⁻¹ for the BOOM cruise (see Hooker et al., 2009; for the performances of the Ras et al., 2008 method).

Particulate Organic Carbon (POC) samples were collected by gentle filtration of 1.2 L for the PROSOPE cruise and 3 L for the BOUM cruise of seawater on precombusted (450 °C for 24 h) Whatman GF/F filters (25 mm in diameter). After filtration, filters were immediately placed in 25 ml Pyrex bottles (Duran Schott) fitted with screwcap equipped with Teflon ring and dried in an oven at 50 °C and stored in a dessicator until analyses at the laboratory. POC was determined according to the wet oxydation procedure described by Raimbault et al. (1999) for the PROSOPE samples, and on an elemental CHN analyser Perkin Elmer 2400 for the BOUM samples.

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3 Results

3.1 Nutrient distributions

3.1.1 Large-scale nutrient distribution during the PROSOPE cruise (late summer-early autumn)

5 For the sake of clarity, we have presented the data acquired during PROSOPE as two different transects: a longitudinal transect 1 from station 1 to station 6 (Fig. 2) and a meridian transect 2 from station DYF to station MIO (Fig. 3), partially overlapping at stations 6 and MIO. Surface waters were Si-depleted with concentrations below 1 μM except at the northern DYF station of transect 2 where the surface concentration reached 1.31 μM (Figs. 2a and 3a). On transect 1, the Alboran Sea, characterised by the low surface salinity signature of entering Modified Atlantic Waters (MAW) (Perkins et al., 1990), exhibited low H_4SiO_4 concentrations ($<0.5 \mu\text{M}$) in the upper 50 m at station 1, and at shallower depths at stations 2 (30 m) and 3 (10 m). Surface H_4SiO_4 concentrations then increased along the longitudinal gradient reaching between 0.48–10 0.88 μM on the easternmost part of the transects (stations 5, 6, and MIO). On transect 1, station 3 and to a lesser extent stations 2 and 4 were characterised by a H_4SiO_4 minimum between 80 and 110 m. As a general pattern, the 1 μM H_4SiO_4 isopleth marked the beginning of the silicacline and deepened towards the east, from ~ 65 m (station 1) and ~ 40 m (station 9) to ~ 110 m (MIO), although undulations characteristic of the strong mesoscale dynamics of the Algerian Current were clearly visible on transect 1 (Fig. 2). The highest H_4SiO_4 concentrations (3.6 to 5.8 μM) were observed in the Ligurian and Tyrrhenian Seas (stations 8, 9, and DYF) at 150 m (Fig. 3a).

NO₃ and PO₄ distributions (Figs. 2b,c and 3b,c, respectively) followed the same general pattern of surface water depletion, and a more severe oligotrophy at the eastern stations (6 and MIO). Following the pattern seen for H_4SiO_4 , a similar disturbance of the smooth gradient of increasing concentrations with depth is observed at station 3 for NO₃ and PO₄, and is likely linked to some mesoscale or submesoscale activity of the

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Algerian current. Both the nitracline (starting around $0.5 \mu\text{M NO}_3$) and the phosphacline (starting around $0.05 \mu\text{M PO}_4$) deepened progressively towards the East but the phosphacline deepening was much steeper. The largest difference was observed at MIO station where the phosphacline was deeper (~ 200 m) than the nitracline (~ 100 m).

- 5 Contrary to what was observed for H_4SiO_4 , the highest concentrations of NO_3 and PO_4 were observed at the entrance in the Gibraltar Strait at station 1 ($7.16 \mu\text{M NO}_3$ and $0.47 \mu\text{M PO}_4$ at 150 m) while elevated although lower concentrations characterised the DYF station ($5.70 \mu\text{M NO}_3$ and $0.21 \mu\text{M PO}_4$ at 150 m).

3.1.2 Large-scale nutrient distribution during the BOUM cruise (summer)

- 10 The nutrient distribution observed during the BOUM cruise is presented in Fig. 4. The cruise track can be divided into a meridional part (between stations 27 and A) crossing the Ligurian basin and a longitudinal part (between stations A and C) successively crossing the Algero-Provencal basin, the Sicilian Strait, the Ionian basin, and finally the Levantine basin. In addition the BOUM cruise allowed us to extend the observations
- 15 to the Levantine Basin and thus obtain a complete picture of the zonal gradient of oligotrophy in summer.

- The highest H_4SiO_4 concentrations were measured in the Ligurian basin at stations 25 25 and 26 at 175 m, respectively reaching 5.86 and $5.83 \mu\text{M}$ (Fig. 4a). The general pattern of H_4SiO_4 distribution was again characterised by a general depletion in surface waters and a deepening of the silicacline marked by the $1 \mu\text{M}$ isopleth (Fig. 4a), from ~ 25 – 40 m in the Ligurian basin (stations 26 and 27) to ~ 150 m at the entrance of the Ionian basin (station 12), to finally >200 m on the easternmost side of the Levantine basin (stations 11 and C). This general pattern is disrupted in the transition zone between the Ionian and Levantine basins. We observe indeed a substantial enrichment of surface waters, from stations B to 5, with H_4SiO_4 concentrations ranging between $1 \mu\text{M}$ at the surface and $5.20 \mu\text{M}$ at 175 m (station 2).

NO_3 and PO_4 distributions paralleled that of H_4SiO_4 (Fig. 4b and c). The maximum NO_3 concentration was again observed in the Ligurian Sea at station 25 ($9.23 \mu\text{M}$ at

200 m). Contrasting with that deep maximum, severe surface oligotrophy was encountered at every station with NO_3 concentrations close to or below the detection limit. A deepening of the nitracline eastwards was again observed during the BOUM cruise, from ~ 40 m in the Ligurian basin (stations 25 to 27) to ~ 75 m in the Algero-Provençal basin. After a new deepening at the entrance of the Ionian basin, the nitracline stabilised between 100–125 m all over the eastern Mediterranean. It should also be noted that the enrichment observed for H_4SiO_4 was not found for NO_3 except a localised peak observed at stations 3 and 4 (1.51 and $2.65 \mu\text{M}$ at 75 m, respectively).

As for NO_3 , the highest PO_4 concentrations were found in the Ligurian basin at station 26, ($0.37 \mu\text{M}$ at 200 m). PO_4 basin-scale distribution also showed a pattern similar to NO_3 with a depletion of surface waters as well as the deepening of the phosphocline eastwards, from ~ 50 to 100 m in the Ligurian basin to ~ 80 m all over the Algero-Provençal basin, a new deepening at the entrance of the Ionian basin (parallel to that of NO_3) down to >200 m and a fluctuation between 150 to >200 m in the Levantine basin (Fig. 4c). The Sicilian Strait appeared as an area of disruption, marked by the beginning of the gradual separation eastwards between the nitracline and the phosphocline, which tends to increase towards the East.

3.2 Particulate matter distribution

3.2.1 Large-scale distribution of biogenic silica and associated parameters during the PROSOPE cruise (late summer-early autumn)

In general, the Mediterranean waters had extremely low BSi contents in the surface waters, quite uniformly $<0.05 \mu\text{mol L}^{-1}$, except in the Alboran Sea where concentrations reached up to $0.38 \mu\text{mol L}^{-1}$ in a deep silica maximum (DSM) located between 60 and 95 m from station 1 to 3 (Figs. 5a and 7a). Another slight DSM was apparent at DYF station ($>0.05 \mu\text{mol L}^{-1}$ at 75 m) while a more pronounced feature was observed at MIO station (up to $0.11 \mu\text{mol L}^{-1}$ at 110 m).

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Fuco concentrations ranged from below the detection limit to $0.22 \mu\text{g L}^{-1}$ (Figs. 5b and 7b). Its distribution was very similar to that of BSi, with low values at the surface, and deep maxima at stations 1, 2, 3, MIO, and DYF coinciding with the observed DSM. The highest Fuco concentration was measured at station 2 with $0.22 \mu\text{g L}^{-1}$ at 45 m, slightly above the depth of BSi maximum. Another small deep maximum of Fuco ($0.06 \mu\text{g L}^{-1}$) was observed at station 5 at 65 m, but did not match any BSi increase. All along the two transects, a small but permanent deep Fuco maximum (DFM) was observed, deepening eastwards, from 45 m at the western end of transect 1 to 110 m at MIO station in the Ionian basin.

Tchl-*a* concentrations ranged from below the detection limit to a maximum value of $0.96 \mu\text{g L}^{-1}$ (Figs. 5c and 7c). Tchl-*a* concentrations were generally higher on transect 1 (Fig. 5c) than on transect 2 (Fig. 6c) and maximum concentrations (from 0.4 to $0.9 \mu\text{g L}^{-1}$) were found between 40 and 60 m at stations 1, 2, 3 and 5. Tchl-*a* exhibited the same pattern of distribution as BSi and Fuco, i.e., a deep Tchl-*a* maximum (DCM) present on both transects and deepening eastwards (from 40 to 60 m at the Gibraltar Strait and in the Ligurian Sea to ~ 90 m in the Ionian basin). Unlike the patchy distribution of BSi and Fuco, the DCM appeared as a more regular feature all along the two transects.

The distribution of particulate organic carbon is presented together with BSi:POC ratios in Figs. 7 and 9. POC distribution reveals a very similar pattern compared to Tchl-*a* with maximum concentrations found in the Alboran Sea at 50 m ($7 \mu\text{mol L}^{-1}$), spreading in the Algero-Provencal basin at depth, and a new increase in the Ionian basin between stations 5 and MIO, reaching $3 \mu\text{mol L}^{-1}$. POC was very low below 100 m ($<1 \mu\text{mol L}^{-1}$) except at site 1, where moderate concentrations were measured at 150 m (Fig. 7a). BSi:POC ratios were quite elevated, by comparison to the Brzezinski (1985) ratios, in the Alboran Sea (reaching 0.25 at station 2 at 90 m) and over the Sicily Strait (0.19 at 120 m; Fig. 7b). A third increase was observed at the MIO station, where BSi:POC ratio reached 0.11 at 130 m. On the second transect, POC distribution was quite monotonous (Fig. 8a), with a small subsurface maximum spreading from the DYF

station to the MIO station without much decrease in depth. Surprisingly, a subsurface maximum was observed at station 7 between 10 and 50 m (4.6 to $5.5 \mu\text{mol L}^{-1}$) which did not match any increase in chl-*a*, Fuco or BSi, which could reflect the presence of heterotrophic biomass. BSi:POC ratios were low (<0.01) over the entire 0–50 m layer, but increased at depth and in particular at two locations, at station 9 at 150 m (0.10) and at station MIO as mentioned above (Fig. 8b).

3.2.2 Large-scale distribution of biogenic silica and associated parameters during the BOUM cruise (summer)

Surface (0–50 m) BSi concentrations were low ($<0.05 \mu\text{mol L}^{-1}$) throughout the transect except at the coastal station 27 in the Gulf of Lions ($0.36 \mu\text{mol L}^{-1}$ at 5 m) (Fig. 9a). A core of slightly higher concentrations (range: 0.05 – $0.15 \mu\text{mol L}^{-1}$) was observed between 50–175 m on the continental margin and in the northern Ligurian Sea (stations 23 to 27). However, the most striking feature was the observation of three successive DSM along the transect in a patchy distribution with hot spots of BSi accumulation at depth in discrete areas. The first DSM, located between south of Sardinia (station 21) and the Sicilian Strait (station 16), largely spread from 50 to 125 m depth with concentrations ranging from $0.15 \mu\text{mol L}^{-1}$ (station 21) to $0.44 \mu\text{mol L}^{-1}$ (station 20). A second large DSM was encountered in the Ionian basin between stations 1 and 9 from 50 to 175 m, with concentrations reaching up to $0.45 \mu\text{mol L}^{-1}$ at 100 m at station 3, the highest BSi value measured on the transect. A third DSM occurred at the eastern end of the transect south of Cyprus in the Levantine basin (stations 11 and C) and was characterised by a maximum value of $0.24 \mu\text{mol L}^{-1}$ at 100 m at station C.

Fuco distribution was in good agreement with BSi since the locations of three successive DFMs closely matched those of the DSM (Fig. 9b). A small increase of Fuco was observed in the northern Ligurian Sea with concentrations reaching up to $0.06 \mu\text{g L}^{-1}$ at the surface (stations 26 and 27). From station 25, the Fuco peaks tended to deepen and were always found below 50 m at all other stations of the transect. A first accumulation area was seen between south of Sardinia and the Sicilian Strait with a maximum

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concentration of $0.20 \mu\text{g L}^{-1}$ at station 18 (75 m), the second DFM was observed in the Ionian basin with a maximum concentration of $0.26 \mu\text{g L}^{-1}$ at station 3 (100 m) and the third DFM was seen in the Levantine basin with a maximum concentration of $0.08 \mu\text{g L}^{-1}$ at station C (100 m). A small increase of Fuco concentrations ($0.05 \mu\text{g L}^{-1}$) was also observed at station 13 at 150 m depth, slightly below a small BSi peak present at 125 m.

Tchl-a followed a very similar pattern but looked like a more continuous feature, as mentioned above for the PROSOPE cruise, with a DCM present at every station (Fig. 9c), except at station 27 where *Tchl-a* showed the highest surface value ($0.37 \mu\text{g L}^{-1}$). Despite the continuous presence of the DCM deepening eastwards, several hot spots with increased concentrations of *Tchl-a* were clearly visible, which locations matched those of the DSM and DFMs. The most important DCM was located in the Ligurian Sea with the highest *Tchl-a* concentration measured ($1.70 \mu\text{g L}^{-1}$ at station 25, 50 m). Other more pronounced DCMs were detected between the Sicilian Strait and south of Sardinia ($0.87 \mu\text{g L}^{-1}$ at station 18, 75 m), in the Ionian basin ($0.68 \mu\text{g L}^{-1}$ at station 13, 100 m), and in the Levantine basin ($0.40 \mu\text{g L}^{-1}$ at station C, 100 m).

Finally, the deep structures observed during BOUM appeared more pronounced, showing higher biomass values, than those observed during PROSOPE. Station 3 of the BOUM cruise, geographically very close to MIO station of PROSOPE, is a good example of this trend: maximum BSi concentration was $0.45 \mu\text{mol L}^{-1}$ at station 3 vs. $0.12 \mu\text{mol L}^{-1}$ at station MIO; maximum Fuco concentration was $0.26 \mu\text{g L}^{-1}$ at station 3 vs. $0.02 \mu\text{g L}^{-1}$ at station MIO and *Tchl-a* highest value was $0.68 \mu\text{g L}^{-1}$ at station 3 vs. $0.18 \mu\text{g L}^{-1}$ at station MIO. Hence, the siliceous phytoplankton biomass was generally higher in summer 2008 than in fall 1999.

Particulate organic carbon follows the same trends than BSi and *chl-a* with 4 maxima ($\sim 6 \mu\text{mol L}^{-1}$) located in the northern Algero-Provencal basin near the surface, and at depth over the Sicilian strait, in the Ionian Sea and at station C (Fig. 10a). Low BSi:POC ratios (<0.01) were observed from the surface to as deep as 125 m in the Ionian and

Levantine basins, but increased between 100 and 150 m to more elevated values (0.05 to 0.09) at the three main DSM locations but with a slight offset with depth (Fig. 10b).

3.3 Large-scale distribution of lithogenic silica in summer and fall

LSi distributions observed during both cruises are presented in Fig. 11. Measurements made during the PROSOPE cruise showed moderate LSi concentrations ranging from below the detection limit to $0.14 \mu\text{mol L}^{-1}$. The highest value was located at station 2 (75 m) and coincided with a BSi maximum (Fig. 5a). LSi concentrations were highest at the Gibraltar Strait (station 1) and in the Alboran Sea (station 2) with values ranging from 0.05 to $0.14 \mu\text{mol L}^{-1}$ in the first 100 m. LSi concentrations remained low ($<0.03 \mu\text{mol L}^{-1}$) over the rest of transect 1 (Fig. 11a) but a slight increase near the surface was observed at stations 3 to 6 (reaching a maximum of $0.08 \mu\text{mol L}^{-1}$ at station 4). The eastern end of the transect was the most impoverished region and LSi remained $<0.02 \mu\text{mol L}^{-1}$ all over the water column at station MIO. Surface LSi enrichment was also observed in the upper 25 m on transect 2 (Fig. 11b) reaching up to $0.10 \mu\text{mol L}^{-1}$ at station 9. At the northern end of this transect, in the Ligurian Sea, a core of deep waters (below 50 m) enriched with LSi was separated from the surface maximum by an intermediate layer of low LSi concentrations ($<0.02 \mu\text{mol L}^{-1}$).

During the BOUM cruise, some very high LSi concentrations were measured in the Gulf of Lions and on the Tunisian plateau (Fig. 11c). Maximum concentrations of 0.54 and $2.24 \mu\text{mol L}^{-1}$ were found, respectively at the surface (5 m) and near the bottom (100 m) at station 27. Lower maxima were located in the Sicilian Strait with $0.30 \mu\text{mol L}^{-1}$ at station 17 from 125 to 175 m and at station 13 with 0.25 to $0.31 \mu\text{mol L}^{-1}$ from 75 to 85 m, reflecting a general trend of increasing values near the seabed of the continental shelf. Besides these high LSi accumulation areas, concentrations were generally low in the water column over the rest of the transect ($<0.02 \mu\text{mol L}^{-1}$) while a moderate enrichment of surface waters was observed at nearly all stations with values close to $0.04 \mu\text{mol L}^{-1}$. As a general trend, the eastern basin was generally more depleted in LSi compared to the western basin, a feature which was persistent during both cruises.

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3.4 Integrated BSi and LSi stocks

Integrated (0–150 m) silicon stocks during both cruises are presented in Figs. 12 and 14. During PROSOPE (Fig. 12a), the western basin exhibited the highest BSi stocks which ranged from 2.6 to 25.0 mmol m⁻², with the highest stocks at the three western-most stations (1 to 3). Stocks were several folds lower in the eastern basin and ranged from 2.2 to 5.8 mmol m⁻². During the BOUM cruise (Fig. 12b), integrated BSi stocks were on average higher despite a similar range of values from 1.1 to 28.2 mmol m⁻². Despite some large spatial variability due to the presence of several hot spots of BSi accumulation in both basins, the average BSi stock in the western basin (station 27 to 17) was higher (11.6 mmol m⁻²) than the average value for the eastern basin (5.8 mmol m⁻²).

LSi stocks during PROSOPE cruise ranged from 1.0 (MIO) to 8.0 (station 9) mmol m⁻² (Fig. 13a). The shallowest stations exhibited highest integrated stocks with 8.0 mmol m⁻² for station 9, 5.1 mmol m⁻² for station 1 and 5. An elevated LSi stock (7.7 mmol m⁻²) was also observed at station 2. LSi stocks were much higher during the BOUM cruise with values from 0.3 to 38.9 mmol m⁻² (Fig. 13b). Highest integrated stocks were again observed at the shallowest stations with 38.9 mmol m⁻² at station 27 and 9.9 mmol m⁻² at station 17. An elevated stock was also observed at station 13 (20.3 mmol m⁻²) despite higher depth. Similarly to BSi, LSi stocks were on average more important in the western (8.1 mmol m⁻²) than in the eastern (3.9 mmol m⁻²) basin.

4 Discussion

4.1 Oligotrophic gradient in the Mediterranean Sea

The gradient of oligotrophy is well documented in the Mediterranean Sea (McGill, 1961; Sournia, 1973; Krom et al., 1991; Moutin and Raimbault, 2002) and is a consequence

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of the anti-estuarine thermohaline circulation and the nutrient input's asymmetry between the western and the eastern basins. The degree of oligotrophy along this gradient is then determined by the balance between biological processes such as production, remineralisation and export but can be locally affected by mesoscale or submesoscale structures like hydrological fronts and eddies (Crise et al., 1999). Accordingly, we observed that surface waters of the Mediterranean Sea were nutrient depleted during both summer and fall and that all nutriclines deepened towards the East (Figs. 2 to 4). The phosphocline was generally deeper than the nitracline and silicacline in particular in the eastern basin, which induced a general P limitation in the Ionian and Levantine basins (Pujo-Pay et al., 2010). The P deficit in both surface and deep waters of the Mediterranean Sea is well established but the responsible mechanisms are still a matter of debate (Krom, 1995). Considering the canonical N:P ratio of 16 (Redfield et al., 1963), the general P limitation of the Mediterranean Sea is further emphasized by the integrated surface N:P ratios which are generally well >20 (Figs. 14a and 16a) except in a few areas such as the Alboran Sea during fall and at only three stations during summer (stations 6, 14 and C). The P deficit is more intense in the eastern basin during both seasons, with extremely high N:P ratios during summer (40–80 and sometimes >100) when P is close to the detection limit, and slightly lower ratios during fall in the Ionian sea (40–65), when N becomes more depleted. Our data are consistent with high ratios usually found in the Mediterranean Sea (around 20–30 in the deep waters and up to 100 in the surface waters) (McGill, 1969; Jacques and Tréguer, 1986; Moutin and Raimbault, 2002).

If nitrogen and phosphorus are usually considered as limiting in the Mediterranean Sea, silicon has been considered for a long time abundant in the euphotic zone (Jacques and Tréguer, 1986; Krom et al., 1993) and often ignored as a potential limiting factor in biogeochemical models (Crispi et al., 2002). Yet, we observed during summer and fall a potential Si deficit compared to N in the entire Algero-Provencal basin and as far towards the East as the Tunisian continental shelf, with integrated Si:N ratios <1 in the first 150 m (Figs. 14b and 16b). If we consider the empirical Si:N ratio ≈ 1

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for siliceous phytoplankton (Brzezinski, 1985) Si availability could be limiting for diatom growth. The Si deficiency is relieved in the Ionian and Levantine basins where Si:N ratios remain well over 1 during both seasons, but with local minima close to 1 between stations 3 and 8 during BOUM, where a large DSM was observed. Considering the Si:N:P ratios simultaneously, N and P constitute the prominent potential limiting factors in the Mediterranean Sea, but Si appears as potentially limiting to diatom growth in the western basin and over the Tunisian continental shelf. The little attention given to orthosilicic acid distribution in the MS is likely coupled to the idea that the DCM observed during stratified oligotrophic conditions is overall dominated by pico- and nanophytoplankton. We show that during both summer and fall, this is not always the case and that diatoms may locally dominate the DCM. We explore tentative explanations for the co-occurrence of the DSM with the DCM in the following paragraphs.

4.2 Occurrence of a deep silica maximum (DSM) in the Mediterranean Sea and similar features worldwide

The data obtained during the BOUM cruise confirmed the recurrence of DSM in the different Mediterranean basins during the stratified oligotrophic period, an observation that was initially made during PROSOPE. DSM were found in the Alboran, Ionian and Ligurian basins during late summer-fall 1999 (Figs. 5a and 7a) and were also observed in the Levantine basin and in the Sicilian Strait in summer 2008 (Fig. 9a). Similar characteristics of the DSM during both seasons were a patchy distribution (while the DCM was a more continuous feature across the MS) and a progressive deepening of this structure towards the East, following that of the nutriclines. Differences consisted in chl-*a* maximum values that were almost twice as high in fall compared to summer despite similar concentration ranges of both BSi and Fuco, which could indicate a lower relative contribution of diatoms to the phytoplankton community later in the season. The marked DCM observed during summer is clearly associated to diatom biomass accumulation, while the fall DCM probably corresponds to an adaptation response to increasing light limitation and complete nutrient exhaustion rather than to higher biomass.

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The occurrence of DSM has been punctually observed in Mediterranean waters before (Price et al., 1999b), but it has never been reported to be a recurrent feature of the stratified open Mediterranean Sea. The first reference in the MS goes back two decades ago in a coastal system off the coasts of Egypt close to the Nile River mouth, where Abdel-Moati (1990) evidenced the presence of a DSM, closely coupled to the DCM at 100 m depth, with elevated BSi concentrations ($1.35 \pm 0.49 \mu\text{mol L}^{-1}$); while in the Algerian current, Gould and Wiesenburg (1990) observed a narrow band of chl-*a* at 54 m largely dominated at 98% by *Thalassiosira parthenia*. Smaller DSM ($\text{BSi} < 0.1 \mu\text{mol L}^{-1}$) were later observed in the Cretan Sea in spring and fall by Price et al. (1999a). Finally, Leblanc et al. (2004) reported a moderate DSM ($\text{BSi} < 0.2 \mu\text{mol L}^{-1}$) during winter in the Almeria-Oran Front inside an anti-cyclonic gyre but which was mainly attributed to lateral advection of a frontal bloom and cross-frontal exchanges of biomass along the isopycnal slopes.

Nonetheless, the DSM is a feature that has been observed in several other oceanic systems worldwide in recent years. In the oligotrophic environment of the Sargasso Sea in the Atlantic Ocean, Brzezinski and Kosman (1996) observed the development of a small DSM near Bermuda well associated to the DCM and the nutricline. A 15-year study of the Si cycle in the same area evidenced the recurrent presence of this DSM at the BATS site, with the average peak BSi concentrations found between 80 and 100 m (Krause et al., 2009a), despite very low concentrations ($< 0.03 \mu\text{mol L}^{-1}$) due to strong Si limitation of diatom growth (Brzezinski and Nelson, 1996). Studies of the oligotrophic gyres of the Equatorial and Central North Pacific revealed the occurrence of moderate DSM ($< 0.25 \mu\text{mol L}^{-1}$) associated to the DCM and the nitracline (Blain et al., 1997; Brzezinski et al., 1998; Scharek et al., 1999) and a long term survey of the ALOHA site evidenced the recurrence of diatom summer blooms at depth (Dore et al., 2008, and references there in). This feature has also been recurrently observed in the Polar Front Zone (PFZ) and Permanently Open Ocean Zone (POOZ) of the Southern Ocean in all sectors (Atlantic, Pacific and Indian) but with often much higher biogenic silica concentrations (Quéguiner, 2001; Leblanc et al., 2002; Quéguiner and Brzezinski,

2002; Beucher et al., 2004; Mosseri et al., 2008), up to a record $21.3 \mu\text{mol L}^{-1}$ in the PFZ (Quéguiner et al., 1997). The persistence of the DSM coupled to a DCM in the PFZ was recognized by Parslow et al. (2001). However, tentative explanations for the formation of DSM in the Southern Ocean are likely to vary along the latitudinal gradient and over the productive season.

4.3 Deep chlorophyll-*a* maximum (DCM) and potential formation mechanisms

The DCM is a well known structure in the ocean, ubiquitous in stratified oligotrophic areas such as the Pacific (Cullen and Eppley, 1981; Cullen, 1982; Takahashi et al., 1985), the Atlantic (Herbland and Voituriez, 1979) and the entire Mediterranean Sea (Berman et al., 1984; Estrada, 1985; Estrada et al., 1993; Ediger and Yilmaz, 1996; Abdel-Moati, 1990; Tselepides et al., 2000; Herut et al., 2000). To explain DCM formation, several mechanisms have been invoked. Physical mechanisms occurring in frontal regions can produce chl-*a* maxima at the density barrier at the pycnocline, as observed for instance in the English Channel (Pingree, 1978); microscale accumulation of chl-*a* can also develop with temperature gradients (Derenbach et al., 1979). Physiological adaptation to light limitation can also create DCM in stratified systems, decreasing irradiance and increasing nutrient supply at depth stimulate increases in chlorophyll relative to phytoplankton carbon (Steele, 1964; Cullen, 1982) and rather corresponds to low-light photoadaptation than a true local growth of algae. Phytoplankton growth at depth can induce formation of DCM as described by Herbland and Voituriez (1979) in the Typical Tropical Structure (TTS) in the Atlantic Ocean. They described the mechanism by which phytoplankton grows at maximum photosynthetic activity at the base of a nutrient depleted surface layer near the nitracline, where the balance between sufficient light and nutrient supply is optimal. Eventually, behavioural aggregation of phytoplankton can lead to formation of DCM, by controlling their vertical position, phytoplanktonic organisms can accumulate at the nutricline depth, notably diatoms which are able to control their buoyancy and thus aggregate around the nitracline (Steele and

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Yentsch, 1960). This has been observed in the Pacific Ocean with the occurrence of migrating *Rhizosolenia* mats (Villareal, 1988). Rather than one of these mechanisms alone, the coupling between all the processes described above and abiotic parameters such as nutrient availability based on diffusive flux towards the pycnocline, light penetration, and grazing will allow formation and maintenance of deep maxima of phytoplankton biomass. If the DCM is sustained for several weeks or months it implies that gain terms (local growth or accumulation from passive sinking at the pycnocline) must balance out with loss terms (grazing and sinking out of the euphotic layer) as described in detail by Parslow et al. (2001) for the Southern Ocean. During the BOUM study, the vertical distribution of small copepods and nauplii closely matched the DCM along the entire transect (Nowaczyk et al., 2010), implying some degree of grazing upon the algae forming the DCM, which in turn strongly indicates that local growth was occurring to compensate for this loss term and maintain this feature throughout summer. However DCM formation mechanisms in the MS are somewhat different than in the tropics where this feature is generally permanent throughout the year and sustained on regenerative processes, while it is mainly seasonal in the MS and the result of a transitory state between post vernal mixing and summer stratification.

4.4 Correlations between DCM, DSM and DFM in the Mediterranean Sea

The DSM was not systematically correlated to the DCM, which is a widespread feature of the MS (Estrada et al., 1993), but the presence of a DSM was observed at a large majority of stations (83%) during summer and at just about half of the stations (45%) during fall. However, the more intense DSM were observed over more restricted areas along the cruise tracks.

During late summer/fall 1999, three main DSM were observed at stations 1–2; MIO and DYF. The most important DSM was observed in the Alboran Sea at the entrance of the MS at stations 1 and 2, where a large BSi peak spread from below 40 m to the base of the euphotic layer. The deep maxima were not strictly correlated, at stations 1 and 2, DCM and DFM were both located at 50 m whereas the DSM was located 30–40 m

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below. In the Ionian Sea (station MIO), the DSM, DCM and DFM were well correlated between 110 and 150 m while the deep maxima in the Ligurian Sea (station DYF) showed a 25 m offset between DSM/DFM (75 m) and the DCM (50 m). Cell counts revealed that the DSM in the Alboran Sea at station 2 (30 m) was dominated by *Guinardia delicatula* (5300 cells L⁻¹), *Dactyliosolen fragilissimus* (2780 cells L⁻¹), *Leptocylinndrus minimus* (3530 cells L⁻¹) and *L. danicus* (2840 cells L⁻¹). *L. danicus* (590 cells L⁻¹) and *Pseudo-nitzschia* spp. (300 cells L⁻¹) dominated at station MIO, whereas *Thalassionema frauenfeldii* and *Thalassionema nitzschioides* showed the highest abundance at station DYF. However, silicoflagellates (*Dictyocha speculum* and *Dictyocha octonaria*) were more abundant than diatoms at all other depths from 25 to 110 m at DYF, and probably contributed to a large part to the DSM, which was also the case at stations 8 and 9, despite very low abundances. Diatoms constituting those deep maxima did not seem to be actively photosynthesizing as suggested by the negligible primary production rates measured at these depths (*data not shown*). The detrital aspect of diatoms was further emphasized by the BSi:POC ratio in the Alboran and Ligurian Sea (Figs. 7 and 9). At site MIO, BSi:POC ratios ranged from 0.09–0.11 between 110 and 150 m (Fig. 7) which could indicate potentially healthy diatoms (Brzezinski, 1985); however primary production remained low.

During summer 2008, we encountered three main DSM spreading widely at depth over several stations (Fig. 9). At this season, the DSM, DFM and DCM were always correlated and located at the same depths, at 75 m in the Algero-Provencal basin and at 100 m in the Ionian and Levantine basins. Cell counts revealed an important number of diatoms at all DSM but with a diminishing trend going eastwards. Total diatom abundance reached 51 700 cells L⁻¹ at station 20 (75 m), 36 000 and 28 300 cells L⁻¹, respectively at station 3 and 5 (100 m) and finally 15 500 cells L⁻¹ at station C (100 m) (F. Gomez, personal communication). This surprisingly high numbers of diatoms (between 10 000 and 40 000 cells L⁻¹) have already been reported before in oligotrophic areas (Riley, 1957; Hulburt, 1990) and during the summer blooms at station ALOHA in the Central North Pacific (Dore et al., 2008). The main feature here was an overall

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dominance at all DSM by the centric diatom genus *Chaetoceros*. The DSM located in the western basin showed a much higher species diversity than the other two DSM, with a large contribution of pennates such as *Pseudo-nitzschia* spp. (up to 14 000 cells L⁻¹ at 75 m at station 20) but also many other genera such as *Bacteriastrum*, *Leptocylindrus* or *Rhizosolenia*. This dominant diatom assemblage is quite similar to the one described in previous syntheses presented by Estrada et al. (1993) and Béthoux et al. (2002b) for the MS. On the other hand, the DSM observed in the eastern basin were much less diverse, and exhibited very few pennate diatoms while *Chaetoceros* spp. again dominated among the centric species. Silicification, and hence active growth occurred in all the DSM as evidenced by the measured increased uptake of the fluorescent probe PDMPO, which is a proxy for Si production, and a clear indentation in the silicic acid vertical profiles showing the inverse mirror image of the BSi peaks (Leblanc et al., 2010).

Another moderate DSM was observed on the Tunisian continental slope at stations 12 and 13 as deep as 175 m, which was not associated to a DCM, but to a slight increase of Fuco. Cell counts indicated an increase in diatom abundance at 100 and 125 m at station 13 in particular, but samples were not taken for microphytoplankton abundance at the DSM depth thus preventing any comparison with the DCM community. However, available data suggest that this DSM likely corresponded to living or senescent diatoms with low pigment content, probably sinking out of the euphotic layer rather than to an episode of sediment resuspension above the Tunisian continental slope.

An intriguing difference between the two cruises were the similar amounts of BSi in the DSM (maximum concentrations around 0.2–0.35 μmol L⁻¹ for both cruises), while diatom cell counts was an order of magnitude higher during BOUM (up to 51 700 cells L⁻¹) than during PROSOPE (up to 5300 cells L⁻¹). This difference is most likely due to the presence of different diatom species during summer and fall, with smaller species (*Chaetoceros*, *Bacteriastrum*) dominating during BOUM, while larger species (*Guinardia*, *Leptocylindrus*, *Pseudo-nitzschia*, *Thalassionema*) were observed

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during PROSOPE. Alternatively, diatoms could be less silicified in summer than later in the season. If diatoms in summer were in a better physiological state and exhibited higher division rates this could lead to lower Si content per cell, while senescent diatoms tend to be more heavily silicified (Martin-Jézéquel, et al., 2000).

5 As the season progresses to the highest oligotrophic degree in late summer/fall, diatoms forming the DSM seem to maintain themselves deeper following the descent of nutriclines, still at the DCM depth but probably at reduced growth rate and under a more or less senescent state as suggested by the pigment decrease observed at site MIO and DYF, and the higher BSi:POC ratios encountered at the DSM during fall.

10 Despite being prominent in our study, the occurrence of coupled DSM and DFM is not a global feature of the Mediterranean Sea during summer, suggesting that DSM formation is controlled by complex biotic interactions and results from a temporary competitive advantage of diatoms over other phytoplankton groups such as nano- and picoplankton as well as by hydrological features and nutricline depth oscillations. To explain the nutrients supply mechanisms into the euphotic zone, several authors demonstrated that formation of cyclonic and mode-water eddies and interactions between such mesoscale features could induce such sporadic injections into the euphotic zone, directly assimilated by phytoplankton (Falkowski et al., 1991; McGillicuddy and Robinson, 1997; McNeil et al., 1999). These mesoscale events led to great siliceous biomass enhancement at depth as it has been observed in numerous areas, for instance in the Pacific (Benitez-Nelson et al., 2007) or in the Atlantic (McNeil et al., 1999; Steinberg et al., 2001; Conte et al., 2003; McGillicuddy et al., 2007) with the greatest BSi concentrations at BATS related to mesoscale events (Krause et al., 2009a). This has also been reported for the MS by Theodorou et al. (1997) who observed higher BSi contents (~0.36 $\mu\text{mol L}^{-1}$) associated to the passage of two cyclonic eddies in the Cretan Sea. Enhanced biological production and chlorophyll accumulation were observed in cyclonic eddies generated by the Algerian current (Moran et al., 2001), while the impact of anticyclonic eddies on biological activity was investigated in the same area during the ELISA program (Taupier-Letage et al., 2003). If chlorophyll biomass was generally

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lower at the center of anticyclonic eddies, the relationship between chl-*a*, nutrients and eddy structure was found to be highly variable with the season, age of the eddy, location and internal dynamics (Taupier-Letage et al., 2003). In the Eastern basin, warm core eddies, and notably the Cyprus anticyclonic eddy (which would correspond to station C in this study), were found to harbour local enhancement of chl-*a*, attributed to very deep winter mixing within the eddy (Zohary et al., 1998). This is confirmed by the Argo drifting float immersed during BOUM which stayed in the eddy during the following winter and revealed a winter mixing depth down to 400 m (Moutin et al., 2010). It is hence likely that the local intense deep diatom blooms are linked to mesoscale features and to eddy formation, but there is insufficient data still to properly explore the different mechanisms at play within cyclonic or anticyclonic eddies and to relate them to the DCM/DSM formation during our study. If the DSM are closely linked to hydrological features, their heterogeneous nature probably led to systematic under sampling as also suggested by Siokou-Frangou et al. (2010) and might explain why they have rarely been reported in the MS.

4.5 Ecological and biogeochemical implications of the presence of DSM in stratified oligotrophic systems

During PROSOPE and BOUM cruises, the diatom community was dominated by *Chaetoceros* spp., *Leptocylindrus* spp. and *Pseudonitzschia* spp., which are commonly observed in the Mediterranean DCM (Estrada, 1985; Kimor et al., 1987) but also in other oligotrophic mid-ocean gyres (Blain et al., 1997; Brzezinski et al., 1998; McGillicuddy et al., 2007). Interestingly, the potentially symbiotic association between the centric diatoms *Hemiaulus hauckii* and *Rhizosolenia styliformis* and the N₂ fixing cyanobacterium *Richelia intracellularis* were also observed during both cruises but in low abundance. During the BOUM cruise, phytoplankton net hauls revealed that they were present at all stations sampled across the entire basin. On two occasions, *Hemiaulus hauckii* together with *Richelia intracellularis* were even the most abundant species observed in the net hauls (station 7 and 19). Cell counts done at discrete depths gave a higher abundance of *Hemiaulus* at 100 m at station 19 and at 50 m at

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station 7, showing that it did not systematically contribute to the DSM but could also be located above it. This association was commonly observed in the world oligotrophic ocean and the MS (Guillard and Kilham, 1978; Ignatiades, 1969) and has already been observed as an important component of the diatom community in the DCMs of the North Pacific oligotrophic gyres (Dore et al., 2008 and references there in). The presence of a heterocyst in the cyanobacterium *R. Intracellularis* allows N₂ fixation and probably constitutes an ecological advantage for the associated diatom by providing a nitrogen source under N-depleted conditions (Villareal, 1991; Villareal et al., 1999). In the tropical Atlantic, Carpenter et al. (1999) encountered an extensive bloom of *Hemiaulus hauckii* and evaluated that in addition to *Trichodesmium* sp., they could supply up to 25% of the total N demand through the water column. In the NPSG (North Pacific Subtropical Gyre) at station ALOHA, Dore et al. (2008) estimated that the highest integrated N₂ fixation rates occurred during summer while either *Trichodesmium* or diatom blooms (mainly constituted by *Rhizosolenia* sp. or *Hemiaulus* sp. with *Richelia*) were observed.

Intense nitrogen fixation by *Posidonia* mats and planktonic organisms such as *Trichodesmium* and the diatom-cyanobacteria association have been invoked as one of the reasons that could explain the higher N:P ratios in Mediterranean deep waters (Sachs and Repeta, 1999) but this assertion remains to be substantiated (Béthoux et al., 2002a) and has been discarded recently by Krom et al. (2010). N₂ fixation was measured during the BOUM cruise and revealed only negligible fluxes (Bonnet et al., 2010). But the presence of both *Hemiaulus* and *Rhizosolenia* hosting *Richelia* in the entire basin during both summer and fall as well as the presence of sporadic *Trichodesmium* filaments could indicate that these species may play a larger role in N₂ fixation at other periods of the year or maybe that the sampling strategy for N₂ fixation measurements did not allow us to perform adequate measurements. But the functioning of these deep diatom summer blooms show a lot of similarities to those observed in the NPSG (Dore et al., 2008), and a potential explanation to low N₂ fixation rates could reside in an extreme P-limitation.

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Concerning primary production and as mentioned earlier in this paper, diatom growth in oligotrophic system is of major importance. Goldman (1988) first suggested that diatoms might be important for new production and export of particulate carbon in oligotrophic ocean gyres. They hypothesized that episodic injections of new nutrients near the base of the euphotic zone would lead to rapid diatom growth and a coupled enhanced export flux. However a more recent study evidenced that there was no need of episodic injections to maintain a balanced system in the permanently oligotrophic and stratified ocean (Riser and Johnson, 2008). In the oligotrophic Sargasso Sea, diatom contribution to primary production was as high as 26–48% and they contributed to 30% of the carbon export through the year (Brzezinski and Nelson, 1995; Nelson and Brzezinski, 1997). Other investigations carried out in the Central-North Pacific revealed that the siliceous phytoplankton can account for up to 25% of the primary productivity (Brzezinski et al., 1998). Diatom contribution to primary production is disproportionate compared to their relatively low contribution to Tchl-*a* biomass, which was for instance <5% at BATS (Goericke, 1998; Steinberg et al., 2001). A similar situation was observed in the HNLC area of the Equatorial Pacific (Blain et al., 1997), where diatoms contribution to primary production was estimated to represent up to 34% despite a low contribution to C biomass (<6%). Given these previous observations, we suggest that diatoms in the MS during the oligotrophic period may play a similar important role in the ecosystem productivity and contribute to a large part of new production and carbon export, despite their relatively low contribution to biomass during stratified conditions. This latter assumption can also be revised in the light of our present data on the recurrence of non negligible DSM in both the western and eastern basins, as far as in the ultra-oligotrophic Levantine basin. Furthermore, the concentrations of BSi found in these DSM were much higher than those found in the Sargasso Sea, the Equatorial or Central North Pacific in the studies cited above, which could also result in an even higher contribution of diatoms to C export. However, the mere fact that the DSM/DCM is a persistent feature in the MS implies that export rates remain low while this structure is present, or are otherwise compensated by higher productivity within the DCM.

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In this case, the contribution to export would be restrained to the onset of winter mixing and disruption of the stratified layer, which would then lead to an increased particulate matter flux at depth. However, if intense grazing upon the DCM is confirmed, potential higher C export from faecal pellets could already occur during late summer. Long-term immersion of sediment traps, as well as the deployment of biogeochemical and bio-optical Argo-like floats in open waters of the MS would be necessary to confirm this hypothesis.

4.6 Review of the Si cycle data in the Mediterranean Sea

Adding our new findings, the silicon biogeochemistry still remains poorly documented in the MS. In this paragraph, we present a short review of the Si data available in the MS, from Si stocks (dissolved and particulate) to Si fluxes (production and export) (Tables 1 and 2). Characteristics of this dataset are that sampling occurred mainly in coastal regions and that very few data is available for the open MS, with the eastern basin being much less covered than the western basin.

Orthosilicic acid stocks in the Mediterranean Sea appear severely depleted in surface waters and could reach values lower than the detection limit in both basins at all seasons, even during winter. However, as a general trend the western basin seemed generally more prone to Si depletion than the eastern basin. The H_4SiO_4 concentrations extracted from the DYFAMED database covering 15 years worth of data (from 1991 to 2006) show that despite punctual high concentrations in the 0–100 m layer (up to $8 \mu M$), a calculation of Si:N ratios between 0 and 100 m yield 74% of the data with values <1 ($n=1095$). The general Si deficit of the MS has been evidenced by Béthoux et al. (2002a) through global deep water budgets and the authors evidenced an increasing Si deficit over the last decades due to damming of the Assouan river, and reduced outputs from the Black Sea related to damming of the Danube. Hence, despite a widespread N and P limitation of phytoplankton growth, a better assessment of silicic acid stocks is of importance as Si may be limiting diatom growth in the MS.

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Particulate silica stocks (biogenic and lithogenic) are very scarce for the MS and lithogenic silica data are only available for the western basin. As a general pattern, LSi concentrations are quite low in the open MS (from the LD to $\sim 0.04 \mu\text{mol L}^{-1}$) in the surface layer but could probably reach much higher values following episodic wet or dry Saharan dust deposition events. Higher values (up to $2.13 \mu\text{mol L}^{-1}$) are found on continental margins due to sediment resuspension or near river mouths due to the high input of mineral particles (e.g., values measured at the SOFi site at the entrance of the Gulf of Lions). Vertically integrated LSi stocks ($J\text{LSi}$) in the western basin range from 4.8 to 93.3 mmol m^{-2} and are higher than in the eastern basin (2.7 to 4.2 mmol m^{-2}).

Biogenic silica concentrations have been reported in few locations of the western MS, mainly close to the coasts of France and Spain. In the eastern basins, reports exist for the Adriatic and Otranto strait, the Cretan Sea, and the coasts of Egypt and Israel. As a general trend, despite a high heterogeneity, BSi concentrations seem to be on average higher in the western basin, with maximum values of $1.6 \mu\text{mol L}^{-1}$ off Catalonia, but can also reach high values at the Nile River mouth in the East (up to $1.35 \mu\text{mol L}^{-1}$). The eastwards decrease of diatom biomass is more visible on vertically integrated stock data ($J\text{BSi}$), which range from 1.0 to 50 mmol m^{-2} in the western basin and from 3.87 to 6.37 mmol m^{-2} in the eastern basin. The BSi stocks measured in the western MS were comparable to those observed in the Sargasso Sea (7.6 to 56.3 mmol m^{-2}) by Brzezinski and Nelson (1995), while stocks measured in the eastern basin were closer to those measured in the Central North Pacific (average 7.1 mmol m^{-2}) (Brzezinski et al., 1998).

Silicon fluxes can be obtained through quantification of Si uptake rates (through the use of stable- ^{30}Si , or radioactive- ^{32}Si isotopes) and Si export fluxes were obtained from sediment traps (Table 2). Si uptake data were only measured on two occasions in the western MS, once during a monthly survey in the Gulf of Lions (Leblanc et al., 2003) and once during the Almofront program in the Alboran Sea (Leblanc et al., 2004). Integrated production rates ($J\rho\text{BSi}$) ranged from 0.45 to $1.14 \text{ mmol Si m}^{-2} \text{ d}^{-1}$, which is in the similar range than data obtained in the Sargasso Sea (0.2 to $1.5 \text{ mmol Si m}^{-2} \text{ d}^{-1}$)

by Brzezinski and Nelson (1989, 1996) and in the Central North Pacific (0.47 to 2.9 mmol Si m⁻² d⁻¹) by Brzezinski et al. (1998), and corresponds to average values found in open oligotrophic oceanic zones (Leblanc, 1999).

Concerning BSi export fluxes, more data are available coming from several yearly sediment trap time series which have been conducted in the Gulf of Lions and in the Alboran Sea for the western basin, and in the Adriatic, Cretan, Aegean and Ionian Sea for the eastern basin (Table 2). The highest export fluxes were observed in the Alboran Sea (up to 514 mmol Si m⁻² y⁻¹ at 1000 m), which is a highly productive area thanks to the Almeria-Oran front (Priour and Sournia, 1994), in the Southern Adriatic (up to 420 mmol Si m⁻² y⁻¹ at 1050 m), which is the place of intense deep winter convection which supplies nutrients to the surface layer (Boldrin et al., 2002) and finally in the Gulf of Lions (up to 204 mmol Si m⁻² y⁻¹ at 900 m), which is enriched by the Rhone river nutrient supply (Moutin et al., 1998). These high values are characteristic of mesotrophic systems, while oligotrophic regions are characterized by Si fluxes <30 mmol Si m⁻² y⁻¹ (Ragueneau et al., 2000). The data obtained in the Aegean, Cretan and Ionian Sea are hence characteristic of oligotrophic systems with fluxes ranging between 3 and 32 mmol Si m⁻² y⁻¹. In comparison to open ocean gyres, reported fluxes for the western oligotrophic Atlantic were 10 mmol Si m⁻² y⁻¹ (at 670 m) and 70 mmol Si m⁻² y⁻¹ (at 1600 m) for the oligotrophic region of the Pacific, bracketing the values reported for the oligotrophic regions of the Mediterranean Sea (Ragueneau et al., 2000). Fluxes obtained during our study originate from drifting sediment traps, usually immersed for 1 to 5 days at the long term study sites (MIO, DYF, A, B and C). These fluxes can therefore not be extrapolated to yearly budgets, but the very low fluxes measured during summer qualify as characteristic of ultra-oligotrophic regions (0.002 to 0.009 mmol Si m⁻² d⁻¹ at 400 m). The Si export fluxes measured at the MIO station during fall were on the other hand several orders of magnitude higher (1.80 mmol Si m⁻² d⁻¹ at 250 m) than the ones measured during summer in the same region, and comfort the hypothesis of a potential high contribution of diatoms to export later in the season.

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The Mediterranean ecosystem during summer and fall constitutes a large oligotrophic system characterized by a longitudinal gradient of stratification and nutrient depletion increasing towards the East. In this system, N and P appear to be the prominent limiting factors although Si could limit the growth of diatoms at some stations. In this ecosystem, the phytoplankton biomass is constrained within a deep chlorophyll maximum where organisms take benefit from the nutrient diffusive fluxes through the nutricline and sufficient light at the base of the euphotic layer. Considering the definition of phytoplankton bloom defined by Wilson (2003) as sustained chl-*a* values $>0.15 \mu\text{g L}^{-1}$, it would be adequate to characterise the MS as hosting a deep summer bloom that is not visible by satellite imagery and that would lead to modulate the characterization of the Eastern basin as a “non bloom” region as suggested by D’Ortenzio and Ribera d’Alcala (2009). Although usually thought to be dominated by pico- and nanophytoplankton, we show that this DCM can host an abundant diatom community as suggested by the locally associated deep silica and fucoxanthin maxima and diatom counts. The dominant genera *Chaetoceros*, *Pseudo-nitzschia*, *Thalassiosira*, *Hemiaulus*, and *Rhizosolenia* as well as the N_2 -fixing symbionts *Richelia intracellularis* can take advantage of increasing nutrient fluxes probably modulated by mesoscale eddies controlling the successive deepening/shoaling of nutriclines. Under some circumstances, diatom growth in those oligotrophic systems and their ability to locally dominate the DCM community over nano- and picoplankton could profoundly affect the ecosystem, notably by increasing new production and carbon export.

Thanks to the PROSOPE and BOUM cruises, large-scale data on the silicon cycle covering the whole Mediterranean Sea during the stratified period were obtained for the first time. There is now evidence that diatoms can actively develop in one of the most oligotrophic systems of the World Ocean, following the intense vernal mixing characteristic of temperate systems. As the seasons progress and surface nutrients become depleted, diatoms are sustained by exploiting the nutrients diffusive fluxes at the base

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of the pycnocline forming a “deep glass forest” in the MS during summer and fall. We suggest that these DSM are recurrent seasonal features, similar to those observed in the NPSG, though not permanent throughout the year and that the contribution of diatoms harbouring cyanobacteria to N₂ fixation needs to be further evaluated as these DSM have most likely been under sampled. Future studies are needed to investigate the contribution of this structure to the global MS productivity and to carbon export at depth as well as the role of physical processes such as mesoscale or submesoscale features on the formation and persistence of the DCM/DSM throughout the summer/fall thermal stratification.

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References

- Abdel-Moati, A. R.: Particulate organic matter in the subsurface chlorophyll maximum layer of the Southeastern Mediterranean, *Oceanol. Acta*, 13, 307–315, 1990.
- Agusti, S., Satta, M. P., Mura, M. P., and Benavent, E.: Dissolved esterase activity as a tracer of phytoplankton lysis: Evidence of high phytoplankton lysis rates in the Northwestern Mediterranean, *Limnol. Oceanogr.*, 43, 1836–1849, 1998.

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- Azov, Y.: Eastern Mediterranean – a marine desert? *Mar. Pollut. Bull.*, 23, 225–232, 1991.
- Benitez-Nelson, C. R., Bidigare, R. R., Dickey, T. D., Landry, M. R., Leonard, C. L., Brown, S. L., Nencioli, F., Rii, Y. M., Maiti, K., Becker, J. W., Bibby, T. S., Black, W., Cai, W.-J., Carlson, C. A., Chen, F., Kuwahara, V. S., Mahaffey, C., McAndrew, P. M., Quay, P. D., Rappe, M. S., Selph, K. E., Simmons, M. P., and Yang, E. J.: Mesoscale eddies drive increased silica export in the subtropical Pacific Ocean, *Science*, 316, 1017–1021, 10.1126/science.1136221, 2007.
- Berman, T., Townsend, D. W., El Sayed, S. Z., Trees, C. C., and Azov, Y.: Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli coast, *Oceanol. Acta*, 7, 367–372, 1984.
- Bethoux, J. P., Morin, P., Madec, C., and Gentili, B.: Phosphorus and nitrogen behaviour in the Mediterranean Sea, *Deep Sea Res. Pt. 1*, 39, 1641–1654, 1992.
- Béthoux, J. P., Morin, P., Chaumery, C., Connan, O., Gentili, B., and Ruiz-Pino, D.: Nutrients in the Mediterranean Sea, mass balance and statistical analysis of concentrations with respect to environmental change, *Mar. Chem.*, 63, 155–169, 1998.
- Béthoux, J. P., Durieu de Madron, X., Nyffeler, F., and Tailliez, D.: Deep water in the Western Mediterranean: Peculiar 1999 and 2000 characteristics, shelf formation hypothesis, variability since 1970 and geochemical inferences, *J. Marine Syst.*, 33–34, 117–131, 2002a.
- Béthoux, J. P., Morin, P., and Ruiz-Pino, D. P.: Temporal trends in nutrient ratios: Chemical evidence of Mediterranean ecosystem changes driven by human activity, *Deep-Sea Res. Pt. 2*, 49, 2007–2016, 2002b.
- Beucher, C., Tréguer, P., Hapette, A.-M., Corvaisier, R., Metzl, N., and Pichon, J.-J.: Intense summer si-recycling in the surface Southern Ocean, *Geophys. Res. Lett.*, 31, L09305, doi:10.1029/2003GL018998, 2004.
- Blain, S., Leynaert, A., Tréguer, P., Chretiennot-Dinet, M.-J., and Rodier, M.: Biomass, growth rates and limitation of equatorial pacific diatoms, *Deep-Sea Res. Pt. 1*, 44, 1255–1275, 1997.
- Boldrin, A., Miserocchi, S., Rabitti, S., Turchetto, M. M., Balboni, V., and Socal, G.: Particulate matter in the Southern Adriatic and Ionian Sea: characterisation and downward fluxes, *J. Marine Syst.*, 33–34, 389–410, 2002.
- Brzezinski, M. A.: The Si:C:N ratios of marine diatoms: interspecific variability and the effect of some environmental variables, *J. Phycol.*, 21, 345–357, 1985.
- Brzezinski, M. A. and Nelson, D. M.: Seasonal changes in the silicon cycle within a gulf stream warm-core ring, *Deep-Sea Res. A*, 36, 1009–1030, 1989.

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- Brzezinski, M. A. and Nelson, D. M.: The annual silica cycle in the Sargasso Sea near Bermuda, *Deep-Sea Res. Pt. 1*, 42, 1215–1237, 1995.
- Brzezinski, M. A. and Kosman, C. A.: Silica production in the Sargasso Sea during spring 1989, *Mar. Ecol. Prog. Ser.*, 142, 39–45, 1996.
- 5 Brzezinski, M. A. and Nelson, D. M.: Chronic substrate limitation of silicic acid uptake rates in the Western Sargasso Sea, *Deep-Sea Res. Pt. 2*, 43, 437–453, 1996.
- Brzezinski, M. A., Villareal, T. A., and Lipschultz, F.: Silica production and the contribution of diatoms to new and primary production in the Central North Pacific, *Mar. Ecol. Prog. Ser.*, 167, 89–104, 1998.
- 10 Carpenter, E. J., Montoya, J. P., Burns, J., Mulholland, M. R., Subramaniam, A., and Capone, D. G.: Extensive bloom of a N_2 -fixing diatom/cyanobacterial association in the tropical atlantic ocean, *Mar. Ecol. Prog. Ser.*, 185, 273–283, doi:10.3354/meps185273, 1999.
- Claustre, H., Hooker, S. B., Van Heukelem, L., Berthon, J.-F., Barlow, R., Ras, J., Sessions, H., Targa, C., Thomas, C. S., van der Linde, D., and Marty, J.-C.: An intercomparison of hplc
15 phytoplankton pigment methods using in situ samples: Application to remote sensing and database activities, *Mar. Chem.*, 85, 41–61, 2004.
- Conte, M. H., Dickey, T. D., Weber, J. C., Johnson, R. J., and Knap, A. H.: Transient physical forcing of pulsed export of bioreactive material to the deep Sargasso Sea, *Deep-Sea Res. Pt. 1*, 50, 1157–1187, 2003.
- 20 Copin-Montégut, C.: Eléments majeurs des particules en suspension de la méditerranée occidentale, *Oceanol. Acta*, N° sp, 9, 95–102, 1988.
- Crise, A., Allen, J. I., Baretta, J., Crispi, G., Mosetti, R., and Solidoro, C.: The Mediterranean pelagic ecosystem response to physical forcing., *Prog. Oceanogr.*, 44, 219–243, 1999.
- Crispi, G., Crise, A., and Solidoro, C.: Coupled Mediterranean ecomodel of the phosphorus and nitrogen cycles., *J. Marine Syst.*, 33–34, 497–521, 2002.
- 25 Cullen, J. J. and Eppley, R. W.: Chlorophyll maximum layers in the Southern California bight and possible mechanisms of their formation, *Oceanol. Acta*, 4, 23–32, 1981.
- Cullen, J. J.: The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll-*a*, *Can. J. Fish. Aquat. Sci.*, 39, 791–803, 1982.
- 30 D’Ortenzio, F. and Ribera d’Alcalà, M.: On the trophic regimes of the Mediterranean Sea: a satellite analysis, *Biogeosciences*, 6, 139–148, doi:10.5194/bg-6-139-2009, 2009.
- Derenbach, J. B., Astheimer, H., Hansen, H. P., and Leach, H.: Vertical microscale distribution of phytoplankton in relation to the thermocline, *Mar. Ecol. Prog. Ser.*, 1, 187–193, 1979.

Dore, J. E., Letelier, R. M., Church, M. J., Lukas, R., and Karl, D. M.: Summer phytoplankton blooms in the oligotrophic North Pacific Subtropical Gyre: historical perspective and recent observations, *Prog. Oceanogr.*, 76, 2–38, 2008.

Dugdale, R. C.: Nutrient cycles, in: *The Ecology of the Sea*, edited by: Cushing, D. H., Blackwell, 1976.

Ediger, D. and Yilmaz, A.: Characteristics of deep chlorophyll maximum in the Northeastern Mediterranean with respect to environmental conditions, *J. Marine Syst.*, 9, 291–303, 1996.

Estrada, M.: Primary production at the deep chlorophyll maximum in the Western Mediterranean, 19th European Marine Biology Symposium (EMBS), 1985, 109–121,

Estrada, M., Marrasé, C., Latasa, M., Berdalet, E., Delgado, M., and Riera, T.: Variability of deep chlorophyll maximum characteristics in the Northwestern Mediterranean, *MEPS*, 92, 289–300, 1993.

Fabres, J., Calafat, A., Sanchez-Vidal, A., Canals, M., and Heussner, S.: Composition and spatio-temporal variability of particle fluxes in the western alboran gyre, *Mediterranean Sea, J. Marine Syst.*, 33–34, 431–456, 2002.

Falkowski, P. G., Ziemann, D., Kolber, Z., and Bienfang, P. K.: Role of eddy pumping in enhancing primary production in the ocean, *Nature*, 352, 55–58, 1991.

Garcia, N., Raimbault, P., Gouze, E., and Sandroni, V.: Fixation de diazote et production primaire en méditerranée occidentale, *C. R. Biol.*, 329, 742–750, 2006.

Goericke, R.: Response of phytoplankton community structure and taxon specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda, *Limnol. Oceanogr.*, 43, 921–935, 1998.

Goldman, J. C.: Spatial and temporal discontinuities of biological processes in pelagic surface waters, in: *Toward a Theory on Biological-Physical Interactions in the World Ocean*, edited by: Rothschild, B. J., Kluwer Academic, Dordrecht, 1988.

Gould, R. W. and Wiesenburg, D. A.: Single-species dominance in a subsurface phytoplankton concentration at a Mediterranean Sea front, *Limnol. Oceanogr.*, 35, 211–220, 1990.

Guillard, R. R. L. and Kilham, P.: The ecology of marine planktonic diatoms. in: *The Biology of Diatoms*, edited by: Werner, D., University of California Press, Berkeley, 1978.

Herbland, A. and Voituriez, B.: Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean, *J. Marine Res.*, 37, 87–101, 1979.

Herut, B., Almogi-Labin, A., Jannink, N., and Gertman, I.: The seasonal dynamics of nutrient and chlorophyll-*a* concentrations on the SE Mediterranean shelf-slope, *Oceanol. Acta*, 23,

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771–782, 2000.

Hooker, S. B., Van Heukelem, L., Thomas, C. S., Claustre, H., Ras, J., Schülter, L., Clementson, L., Van der Linde, D., Eker-Develi, E., Berthon, J.-F., Barlow, R., Sessions, H., Ismail, H., and Perl, J.: The third seawifs hplc analysis round-robin experiment (seaharre-3), NASA Technical Memorandum, 2009-215849, 2009.

Hulburt, E. M.: Description of phytoplankton and nutrient in spring in the Western North Atlantic ocean, *J. Plankton Res.*, 12, 1–28, doi:10.1093/plankt/12.1.1, 1990.

Ibello, V., Cantoni, C., Cozzi, S., and Civitarese, G.: First basin-wide experimental results on n₂ fixation in the open Mediterranean Sea, *Geophys. Res. Lett.*, 37, L03608, doi:10.1029/2009gl041635, 2010.

Ignatiades, L.: Annual cycle, species diversity and succession of phytoplankton in lower saronicos bay, Aegean Sea, *Mar. Biol.*, 3, 196–200, 1969.

Jacques, G. and Tréguer, P.: Les écosystèmes pélagiques marins iii. L'océan antarctique, la méditerranée occidentale, Masson, ed., Paris, 255, 1986.

Kerhervé, P., Heussner, S., Charrière, B., Stavrakakis, S., Ferrand, J. L., Monaco, A., and Delsaut, N.: Biogeochemistry and dynamics of settling particle fluxes at the Antikythra Strait (Eastern Mediterranean), *Prog. Oceanogr.*, 44, 651–675, 1999.

Kimor, B., Berman, T., and Schneller, A.: Phytoplankton assemblages in the deep chlorophyll maximum layers off the Mediterranean coast of Israel, *J. Plankton Res.*, 9, 433–443, doi:10.1093/plankt/9.3.433, 1987.

Krause, J. W., Lomas, M. W., and Nelson, D. M.: Biogenic silica at the Bermuda atlantic time-series study site in the Sargasso Sea: temporal changes and their inferred controls based on a 15-year record, *Global Biogeochem. Cy.*, 23, GB3004, 10.1029/2008GB003236 2009a.

Krause, J. W., Nelson, D. M., and Lomas, M. W.: Biogeochemical responses to late-winter storms in the Sargasso Sea, ii: Increased rates of biogenic silica production and export, *Deep-Sea Res. Pt. 1*, 56, 861–874, 2009b.

Krom, M.: The oceanography of the eastern Mediterranean Sea, *Ocean Challenge*, 5, 22–28, 1995.

Krom, M. D., Kress, N., and Brenner, S.: Phosphorus limitation of primary productivity in the eastern Mediterranean Sea, *Limnol. Oceanogr.*, 36, 424–432, 1991.

Krom, M. D., Brenner, S., Kress, N., Neori, A., and Gordon, L. I.: Nutrient distributions during an annual cycle across a warmcore eddy from the E. Mediterranean Sea, *Deep-Sea Res. Pt. 1*, 40, 805–825, 1993.

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- Krom, M. D., Herut, B., and Mantoura, R. F. C.: Nutrient budget for the Eastern Mediterranean: Implications for phosphorus limitation, *Limnol. Oceanogr.*, 49, 1582–1592, 2004.
- Krom, M. D., Woodward, E. M. S., Herut, B., Kress, N., Carbo, P., Mantoura, R. F. C., Spyres, G., Thingstad, T. F., Wassmann, P., Wexels-Riser, C., Kitidis, V., Law, C. S., and Zodiatis, G.: Nutrient cycling in the south east levantine basin of the Eastern Mediterranean: Results from a phosphorus starved system, *Deep-Sea Res. Pt. 2*, 52, 2879–2896, 2005.
- Krom, M. D., Emeis, K. C., and Van Cappellen, P.: Why is the Eastern Mediterranean phosphorus limited?, *Prog. Oceanogr.*, 85, 236–244, 2010.
- Leblanc, K.: Variabilité spatiale et temporelle du cycle du silicium dans divers milieux oligotrophes et mésotrophes, PhD, Université de la Méditerranée – Aix-Marseille II, Marseille, 287 pp., 1999.
- Leblanc, K., Quéguiner, B., Fiala, M., Blain, S., Morvan, J., and Corvaisier, R.: Particulate biogenic silica and carbon production rates and particulate matter distribution in the indian sector of the Subantarctic Ocean, *Deep-Sea Res. Pt. 2*, 49, 3189–3206, 2002.
- Leblanc, K., Quéguiner, B., Garcia, N., Rimmelin, P., and Raimbault, P.: Silicon cycle in the NW Mediterranean Sea: seasonal study of a coastal oligotrophic site, *Oceanol. Acta*, 26, 339–355, 2003.
- Leblanc, K., Quéguiner, B., Prieur, L., Claustre, H., Oubelkheir, K., and Bruyant, F.: Siliceous phytoplankton production and export related to trans-frontal dynamics of the almeria-oran frontal system (Western Mediterranean Sea) during winter, *J. Geophys. Res.-Oceans*, 109, C07010, doi:10.1029/2003JC001878, 2004.
- Leblanc, K., Quéguiner, B., Raimbault, P., and Garcia, N.: Efficiency of the silicate pump at a coastal oligotrophic site in the Mediterranean Sea, *Biogeosciences*, 2, 219–229, doi:10.5194/bg-2-219-2005, 2005.
- Lucea, A., Duarte, C. M., Agustí, S., and Søndergaard, M.: Nutrient (N, P and Si) and carbon partitioning in the stratified NW Mediterranean, *J. Sea Res.*, 49, 157–170, 2003.
- Martin-Jézéquel, V., Hildebrand, M., and Brzezinski, M.: Silicon metabolism in diatoms: Implications for growth, *J. Phycol.*, 36, 821–840, 2000.
- McGill, D. A.: A preliminary study of the oxygen and phosphate distribution in the Mediterranean Sea, *Deep-Sea Res.*, 8, 259–268, doi:10.1016/0146-6313(61)90027-2, 1961.
- McGill, D. A.: A budget for dissolved salts in the Mediterranean Sea, *Cah. Oceanogr.*, 21, 543–554, 1969.
- McGillicuddy, D. J. and Robinson, A. R.: Eddy-induced nutrient supply and new production in

Deep silicon maxima in the stratified oligotrophic Mediterranean Sea

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the Sargasso Sea, *Deep-Sea Res. Pt. 1*, 44, 1427–1450, 1997.

McGillicuddy, D. J., Jr., Anderson, L. A., Bates, N. R., Bibby, T., Buesseler, K. O., Carlson, C. A., Davis, C. S., Ewart, C., Falkowski, P. G., Goldthwait, S. A., Hansell, D. A., Jenkins, W. J., Johnson, R., Kosnyrev, V. K., Ledwell, J. R., Li, Q. P., Siegel, D. A., and Steinberg, D. K.:
5 Eddy/wind interactions stimulate extraordinary mid-ocean plankton blooms, *Science*, 316, 1021–1026, doi:10.1126/science.1136256, 2007.

McNeil, J. D., Jannasch, H. W., Dickey, T., McGillicuddy, D., Brzezinski, M., and Sakamoto, C. M.: New chemical, bio-optical and physical observations of upper ocean response to the passage of a mesoscale eddy off Bermuda, *J. Geophys. Res.*, 104, 15537–
10 15548, 1999.

Miserocchi, S., Faganeli, J., Balboni, V., Heussner, S., Monaco, A., and Kerherve, P.: Characteristics and sources of the settling particulate organic matter in the South Adriatic Basin, *Org. Geochem.*, 30, 411–421, 1999.

Monaco, A., Durrieu de MAadron, X., Radakovitch, O., Heussner, S., and Carbonne, J.: Origin and variability of downward biogeochemical fluxes on the rhone continental margin (NW
15 Mediterranean), *Deep-Sea Res. Pt. 1*, 46, 1483–1511, 1999.

Moran, X. A. G., Taupier-Letage, I., Vázquez-Domínguez, E., Ruiz, S., Arin, L., Raimbault, P., and Estrada, M.: Physical-biological coupling in the Algerian Basin (SW Mediterranean): influence of mesoscale instabilities on the biomass and production of phytoplankton and
20 bacterioplankton, *Deep-Sea Res. Pt. 1*, 48, 405–437, 2001.

Mosseri, J., Quéguiner, B., Armand, L., and Cornet-Barthaux, V.: Impact of iron on silicon utilization by diatoms in the Southern Ocean: a case study of Si/N cycle decoupling in a naturally iron-enriched area, *Deep-Sea Res. Pt. 2*, 55, 801–819, 2008.

Moutin, T., Raimbault, P., Golterman, H. L., and Coste, B.: The input of nutrients by the Rhône River into the Mediterranean Sea: recent observations and comparison with earlier data, *Hydrobiologia*, 373/374, 237–246, 1998.

Moutin, T. and Raimbault, P.: Primary production, carbon export and nutrients availability in western and Eastern Mediterranean Sea in early summer 1996 (minos cruise), *J. Marine Syst.*, 33–34, 273–288, 2002.

Moutin, T., Thingstad, T. F., Van Wambeke, F., Marie, D., Slawyk, G., Raimbault, P., and Clairet, H.: Does competition for nanomolar phosphate supply explain the predominance of the cyanobacterium *Synechococcus*?, *Limnol. Oceanogr.*, 47, 1562–1567, 2002.

Mullin, J. B. and Riley, J. P.: A modified single solution method for determination of phosphate
30

Deep silicon maxima in the stratified oligotrophic Mediterranean Sea

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in natural waters, *Anal. Chim. Acta*, 27, 31–36, 1962.

Nelson, D. M., Smith, W. O., Muench, R. D., Gordon, L. I., Sullivan, C. W., and Husby, D. M.: Particulate matter and nutrient distributions in the ice-edge zone of the weddell sea: relationship to hydrography during late summer, *Deep-Sea Res. A*, 36, 191–209, 1989.

5 Nelson, D. M., Tréguer, M. A., Brzezinski, M. A., Leynaert, A., and Quéguiner, B.: Production and dissolution of biogenic silica in the ocean : Revised global estimates, comparison with regional data and relationship to biogenic sedimentation, *Global Biogeochem. Cy.*, 9, 359–372, 1995.

10 Nelson, D. M., and Brzezinski, M. A.: Diatom growth and productivity in an oligotrophic mid-ocean gyre: a 3-yr record from the Sargasso Sea near Bermuda, *Limnol. Oceanogr.*, 42, 473–486, 1997.

Parslow, J. S., Boyd, P. W., Rintoul, S. R., and Griffiths, F. B.: A persistent subsurface chlorophyll maximum in the inter-polar frontal zone south of Australia: Seasonal progression and implications for phytoplankton-light-nutrient interactions, *J. Geophys. Res.*, 106, 31543–31557, 2001.

15 Peinert, R., and Miquel, J. C.: The significance of frontal processes for vertical particle fluxes: a case study in the Alboran Sea (SW Mediterranean Sea), *J. Marine Syst.*, 5, 377–389, 1994.

20 Perkins, H., Kinder, T., and Violette, P. L.: The atlantic inflow in the Western Alboran Sea, *J. Phys. Oceanogr.*, 20, 242–263, doi:10.1175/1520-0485(1990)020<0242:TAITW>2.0.CO;2, 1990.

Pingree, R. D.: Mixing and stabilization of phytoplankton distributions on the Northwest European Continental Shelf, in: *Spatial Patterns in Plankton Communities*, edited by: Steele, J. H., Plenum Press, New York, 1978.

25 Price, N. B., Brand, T., Pates, J. M., Mowbray, S., Theocharis, A., Civitarese, G., Miserocchi, S., Heussner, S., and Lindsay, F.: Horizontal distributions of biogenic and lithogenic elements of suspended particulate matter in the Mediterranean Sea, *Prog. Oceanogr.*, 44, 191–218, 1999a.

30 Price, N. B., Lindsay, F. S., and Pates, J. M.: The biogeochemistry of major elements of the suspended particulate matter of the Cretan Sea, *Prog. Oceanogr.*, 44, 677–699, 1999b.

Prieur, L. and Sournia, A.: “Almofront-1” (April-May 1991): An interdisciplinary study of the almeria-oran geostrophic front, SW Mediterranean Sea, *J. Marine Syst.*, 5, 187–203, 1994.

Quéguiner, B., Tréguer, P., Peeken, I., and Scharek, R.: Biogeochemical dynamics and the

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silicon cycle in the atlantic sector of the Southern Ocean during austral spring 1992, *Deep-Sea Res. Pt. 2*, 44, 69–89, 1997.

Quéguiner, B.: Biogenic silica production in the Australian sector of the subantarctic zone of the Southern Ocean in late summer 1998, *J. Geophys. Res.*, 106, 31627–31636, 2001.

5 Quéguiner, B. and Brzezinski, M. A.: Biogenic silica production rates and particulate organic matter distribution in the atlantic sector of the Southern Ocean during austral spring 1992, *Deep-Sea Res. Pt. 2*, 49, 1765–1786, 2002.

Ragueneau, O., Tréguer, P., Leynaert, A., Anderson, R. F., Brzezinski, M. A., DeMaster, D. J., Dugdale, R. C., Dymond, J., Fisher, G., François, R., Heinze, C., Maier-Reimer, E., Martin-Jézéquel, V., Nelson, D. M., and Quéguiner, B.: 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, 2000.

10 Raimbault, P., Diaz, F., Pouvesle, W., and Boudjellal, B.: Simultaneous determination of particulate organic carbon, nitrogen and phosphorus collected on filters, using a semi-automatic wet-oxidation method, *Mar. Ecol. Prog. Ser.*, 180, 289–295, doi:10.3354/meps180289, 1999.

Ras, J., Claustre, H., and Uitz, J.: Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: comparison between in situ and predicted data, *Biogeosciences*, 5, 353–369, doi:10.5194/bg-5-353-2008, 2008.

20 Redfield, A. C., Ketchum, B. H., and Richards, F. A.: The influence of organisms on the composition of sea water, in: *The Sea, Ideas and Observations on Progress in the Study of the Seas*, edited by: Hill, M. N., Interscience Publ., New York, 1963.

Rees, A. P., Law, C. S., and Woodward, E. M. S.: High rates of nitrogen fixation during an in-situ phosphate release experiment in the Eastern Mediterranean Sea, *Geophys. Res. Lett.*, 33, doi:10.129/2006GL025791, 2006.

Riley, G. A.: Phytoplankton of the North Central Sargasso Sea, 1950–52, *Limnol. Oceanogr.*, 2, 252–270, 1957.

Riser, S. C. and Johnson, K. S.: Net production of oxygen in the subtropical ocean, *Nature*, 451, 323–325, 2008.

30 Ryan, W. B. F.: Mediterranean sea: physical oceanography, in: *The Encyclopedia of Oceanography*, edited by: Fairbridge, R. W., Van Nostrand and Reinhold, 1966.

Sachs, J. P. and Repeta, D. J.: Oligotrophy and nitrogen fixation during Eastern Mediterranean sapropel events, *Science*, 286, 2485–2488, doi:10.1126/science.286.5449.2485, 1999.

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- Scharek, R., Latasa, M., Karl, D. M., and Bidigare, R. R.: Temporal variations in diatom abundance and downward vertical flux in the oligotrophic north pacific gyre, *Deep-Sea Res. Pt. 1*, 46, 1051–1075, 1999.
- 5 Siokou-Frangou, I., Christaki, U., Mazzocchi, M. G., Montresor, M., Ribera d'Alcalá, M., Vaqué, D., and Zingone, A.: Plankton in the open Mediterranean Sea: a review, *Biogeosciences*, 7, 1543–1586, doi:10.5194/bg-7-1543-2010, 2010.
- Socal, G., Boldrin, A., Bianchi, F., Civitarese, G., De Lazzari, A., Rabitti, S., Totti, C., and Turchetto, M. M.: Nutrient, particulate matter and phytoplankton variability in the photic layer of the otranto strait, *J. Marine Syst.*, 20, 381–398, 1999.
- 10 Sournia, A.: La production primaire planctonique en méditerranée, *Newsl. Coop. Invest. Mediterr. Spec.*, 5, 1973.
- Stavrakakis, S., Chronis, G., Tselepidis, A., Heussner, S., Monaco, A., and Abassi, A.: Downward fluxes of settling particles in the deep Cretan Sea (NE Mediterranean), *Prog. Oceanogr.*, 46, 217–240, 2000.
- 15 Steele, J. H. and Yentsch, C. S.: The vertical distribution of chlorophyll, *J. Mar. Biol. Assoc. UK*, 39, 217–226, 1960.
- Steele, J. H.: A study of production in the gulf of mexico, *J. Marine Res.*, 22, 211–222, 1964.
- Steinberg, D. K., Carlson, C. A., Bates, N. R., Johnson, R. J., Michaels, A. F., and Knap, A. H.: Overview of the us jgofs Bermuda atlantic time-series study (bats): a decade-scale look at ocean biology and biogeochemistry, *Deep-Sea Res. Pt. 2*, 48, 1405–1447, 2001.
- 20 Strickland, J. D. H. and Parsons, T. R.: A practical handbook of seawater analysis, *Fish. Res. Board Can. Bull.*, 167, 310, 1972.
- Takahashi, M., Nakai, T., Ishimaru, T., Hasumoto, H., and Fujita, Y.: Distribution of the subsurface chlorophyll maximum and its nutrient-light environment in and around the euroshio off japan, *J. Oceanogr.*, 41, 73–80, 1985.
- 25 Taupier-Letage, I., Puillat, I., Millot, C., and Raimbault, P.: Biological response to mesoscale eddies in the algerian basin, *J. Geophys. Res.*, 108, 3245, doi:10.1029/1999jc000117, 2003.
- Theodorou, A., Theocharis, A., and Balopoulos, E.: Circulation in the Cretan Sea and adjacent regions in late winter 1994, *Oceanol. Acta*, 20, 585–596 1997.
- 30 Thingstad, T. F. and Rassoulzadegan, F.: Nutrient limitations, microbial food webs, and biological c-pump : Suggested interactions in a P-limited Mediterranean, *Mar. Ecol. Prog. Ser.*, 117, 299–306, 1995.
- Tréguer, P. and Le Corre, P.: Manuel d'analyses des sels nutritifs dans l'eau de mer. Utilisation

Deep silicon maxima in the stratified oligotrophic Mediterranean Sea

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de l'auto analyzer ii technicon., Laboratoire d'Océanographie Chimique, U. B. O., Brest, 1975.

Tréguer, P., Nelson, D. M., Van Bennekom, A. J., D. J., D., Leynaert, A., and Quéguiner, B.: The silica balance in the World Ocean: a reestimate, *Science*, 268, 375–379, 1995.

5 Tselepidis, A., Zervakis, V., Polychronaki, T., Danovaro, R., and Chronis, G.: Distribution of nutrients and particulate organic matter in relation to the prevailing hydrographic features of the Cretan Sea (NE Mediterranean), *Prog. Oceanogr.*, 46, 113–142, 2000.

Uitz, J., Claustre, H., Gentili, B., and Stramski, D.: Phytoplankton class-specific primary production in the world's oceans: Seasonal and interannual variability from satellite observations, *Global Biogeochem. Cy.*, 24, GB3016, doi:10.1029/2009GB003680, 2010.

10 Vidussi, F., Claustre, H., Bustillos-Guzman, J., Cailliau, C., and Marty, J.-C.: Determination of chlorophylls and carotenoids of marine phytoplankton: Separation of chlorophyll-*a* from divinylchlorophyll-*a* and zeaxanthin from lutein, *J. Plankton Res.*, 18, 2377–2382, doi:10.1093/plankt/18.12.2377, 1996.

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

Villareal, T. A.: Positive buoyancy in the oceanic diatom *Rhizosolenia debyana* h. Peragallo, *Deep-Sea Res. A*, 35, 1037–1045, 1988.

20 Villareal, T. A.: Nitrogen-fixation by the cyanobacterial symbiont of the diatom genus *Hemiaulus*, *Mar. Ecol. Prog. Ser.*, 76, 201–204, 1991.

Villareal, T. A., Pilskalns, C., Brzezinski, M., Lipschultz, F., Dennett, M., and Gardner, G. B.: Upward transport of oceanic nitrate by migrating diatoms mats., *Nature*, 397, 423–425, 1999.

25 Wilson, C.: Late summer chlorophyll blooms in the oligotrophic North Pacific Subtropical Gyre, *Geophys. Res. Lett.*, 30(18), 1942, doi:10.1029/2003GL017770, 2003.

Zohary, T., Brenner, S., Krom, M. D., Angel, D. L., Kress, N., Li, W. K. W., Neori, A., and Yacobi, Y. Z.: Buildup of microbial biomass during deep winter mixing in a Mediterranean warm-core eddy, *Mar. Ecol. Prog. Ser.*, 167, 47–57, doi:10.3354/meps167047, 1998.

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Table 1. Review of literature data for the dissolved and particulate Si stocks in the Mediterranean Sea in the surface layer: orthosilicic acid concentrations (H_4SiO_4 in μM), biogenic silica (BSi in $\mu\text{mol L}^{-1}$) concentrations and integrated stocks ($\int\text{BSi}$ mmol m^{-2}), lithogenic silica concentrations (LSi in $\mu\text{mol L}^{-1}$) and integrated stocks ($\int\text{LSi}$ mmol m^{-2}).

Region	Season	H_4SiO_4 (μM)	BSi ($\mu\text{mol L}^{-1}$)	$\int\text{BSi}$ (mmol m^{-2})	LSi ($\mu\text{mol L}^{-1}$)	$\int\text{LSi}^*$ (mmol m^{-2})	References
Western basin							
Gulf of Lions (SOFi site)	Winter	2.84	<LD	2.2-12.8	0.4-0.6	17.0-71.1	1
	Spring	LD-0.12	LD-0.99	18.1-35.1	LD-0.2	5.4-23.9	1
	Summer	LD-0.14	0.95	3.7-36.9	LD-0.2	10.9-20.0	1
Alboran Sea – Almeria Oran Front	Fall	LD-0.16	LD	1.0-5.1	LD-2.13	30.3-93.3	1
	Winter	0.8-2	0.02-0.06	8-35		9-74	2
	Spring			6-50			3
Catalonia	Fall	0.25-5.5	LD-1.6				4
Liguro-provençal (offshore)	Spring		LD-0.6				5
	Summer		LD-0.3				5
Liguro-provençal (coast)	Summer		LD-0.1				5
Liguro-provençal (DYFAMED)	Yearly	LD-8					6
Gulf of Lions (station 27)	Summer	0.41-2.55	0.06-0.36	13.7	0.05-2.2	39.0	<i>This study</i>
Western basin	Summer	0.41-5.86	0.01-0.44	10.9	LD-0.30	4.8	<i>This study</i>
	Fall	LD-5.84	0.01-0.38	8.6	LD-0.14	5.2	<i>This study</i>
Eastern basin							
Adriatic/Otranto	Winter	1.4-5.1					7
	Summer	0.5-8.8					7
	Summer		LD-0.06				8
	Fall		LD-0.08				8
Cretan Sea	Spring		LD-0.17				8
	Yearly	LD-2					9
Off Israel	Summer		LD-1.35				10
Off Egypt	Spring	1-1.5					11
Levantine basin (Cyprus eddy)	Spring	1-1.5					11
Eastern basin	Summer	0.29-5.49	0.01-0.45	6.37	LD-1.30	4.19	<i>This study</i>
	Fall	0.7-4.0	0.01-0.11	3.87	LD-0.10	2.70	<i>This study</i>

[‡] Values between 0 and 200 m.

* Integrated over 200 m.

1 Leblanc et al., 2003; 2 Leblanc et al., 2004; 3 Peinert and Miquel, 1994; 4 Lucea et al., 2003; 5 Copin-Montégut, 1988; 6 <http://www.obs-vlfr.fr/dyfBase/>;
7 Socal et al., 1999; 8 Price et al., 1999b; 9 Herut et al., 2000; 10 Abdel-Moati, 1990; 11 Krom et al., 2005.

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Table 2. Review of the literature data for Si production ($\int \rho \text{Si}$ in $\text{mmol m}^{-2} \text{d}^{-1}$) and export fluxes (in $\text{mmol m}^{-2} \text{d}^{-1}$ or in $\text{mmol m}^{-2} \text{y}^{-1}$ depending on the type of sediment traps deployed) in the Mediterranean Sea.

Region	Season	$\int \rho \text{Si}^\ddagger$ ($\text{mmol m}^{-2} \text{d}^{-1}$)	BSi export ($\text{mmol m}^{-2} \text{d}^{-1}$)	BSi export ($\text{mmol m}^{-2} \text{y}^{-1}$)	References
Western basin					
Gulf of Lions (SOFi site)	Winter	0.45			1
	Spring	0.47			1
Gulf of Lions (Lacaze-Duthier Canyon)	Summer	0.58			1
	Yearly			86.8 140 m	2
	Yearly			32 100 m	3
	Yearly			103 300 m	3
Gulf of Lions (Grand-Rhone Canyon)	Yearly			163 600 m	3
	Yearly			147 80 m	3
	Yearly			207 200 m	3
Gulf of Lions (open slope)	Yearly			204 900 m	3
Alboran Sea – Western Alboran Gyre	Yearly			386 400 m	4
	Yearly			408 470 m	4
	Yearly			514 975 m	4
	Yearly			377 1300 m	4
Alboran Sea – Almeria Oran Front	Winter	0.69-1.14	0.01-0.12	100 m	5
	Winter		0.05-0.66	300 m	5
	Spring		0.03-0.70	100 m	6
	Spring		0.03-0.23	300 m	6
Liguro-provençal (coastal)	Spring		4.83	200 m	7
Liguro-provençal (offshore)	Spring		1.78	200 m	7
Liguro-provençal (DYFAMED)	Fall		2.84	100 m	<i>This study</i>
	Fall		1.80	200 m	<i>This study</i>
Site A	Summer		0.003	200 m	<i>This study</i>
	Summer		0.004	400 m	<i>This study</i>
Eastern basin					
Adriatic Basin	Yearly			211 500 m	8
	Yearly			327 1000 m	8
	Yearly			302 150 m	9
	Yearly			420 1050 m	9
Cretan Sea	Yearly			3 200 m	10
	Yearly			8 1515 m	10
Aegean Sea	Yearly			23 965 m	11
Ionian Sea	Yearly			17 880 m	11
	Yearly			32 1345 m	11
Site B	Summer		0.003	200 m	<i>This study</i>
	Summer		0.002	400 m	<i>This study</i>
Site C	Summer		0.005	200 m	<i>This study</i>
	Summer		0.009	400 m	<i>This study</i>
Site MIO	Fall		0.23	50 m	<i>This study</i>
	Fall		1.80	250 m	<i>This study</i>

‡ Integrated fluxes over 100 m. The depths in parenthesis indicate the depth of the sediment traps for BSi export fluxes.

1 Leblanc et al., 2003; 2 Leblanc et al., 2005; 3 Monaco et al., 1999; 4 Fabres et al., 2002; 5 Leblanc et al., 2004; 6 Peinert and Miquel, 1994; 7 Copin-Montégut, 1988; 8 Miserocchi et al., 1999; 9 Boldrin et al., 2002; 10 Stavrakakis et al., 2000; 11 Kerhervé et al., 1999.

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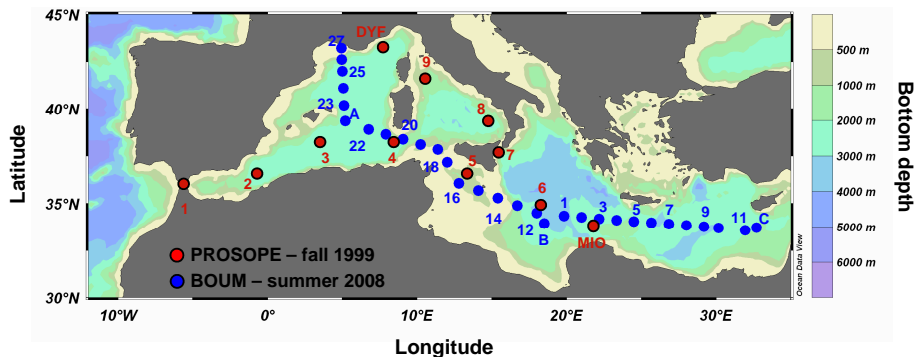


Fig. 1. Cruise tracks and sampling sites during the PROSOPE cruise in late summer/fall 1999 (red dots) and during the BOUM cruises in summer 2008 (blue dots).

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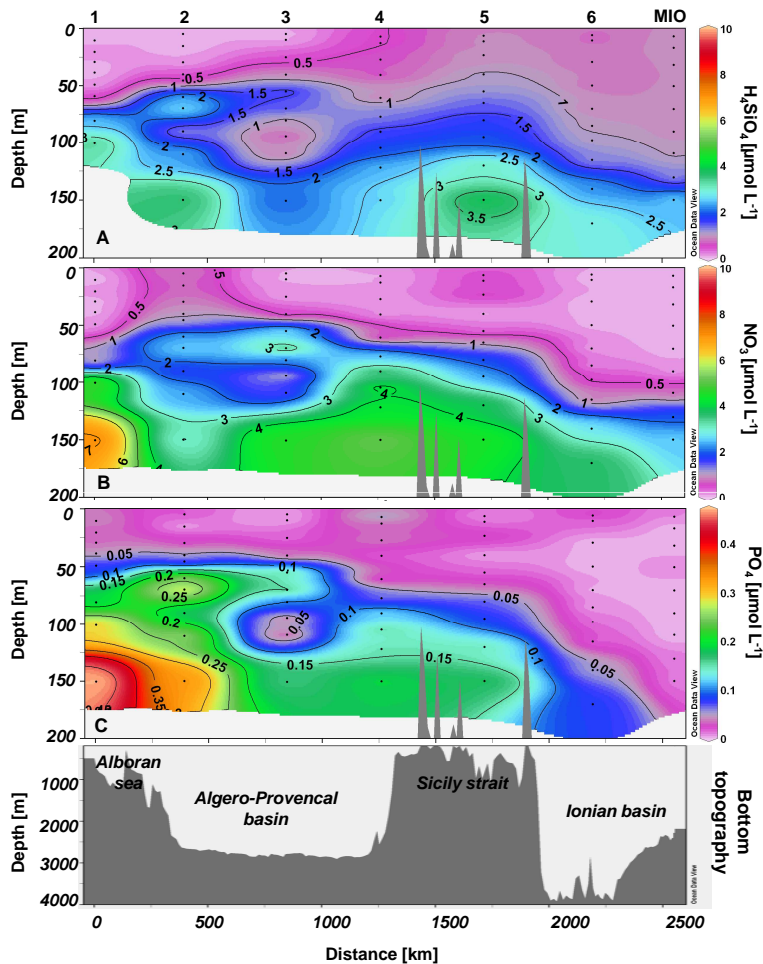


Fig. 2. Nutrient distributions (μM) along the transect 1 during PROSOPE the cruise (summer/fall 1999).

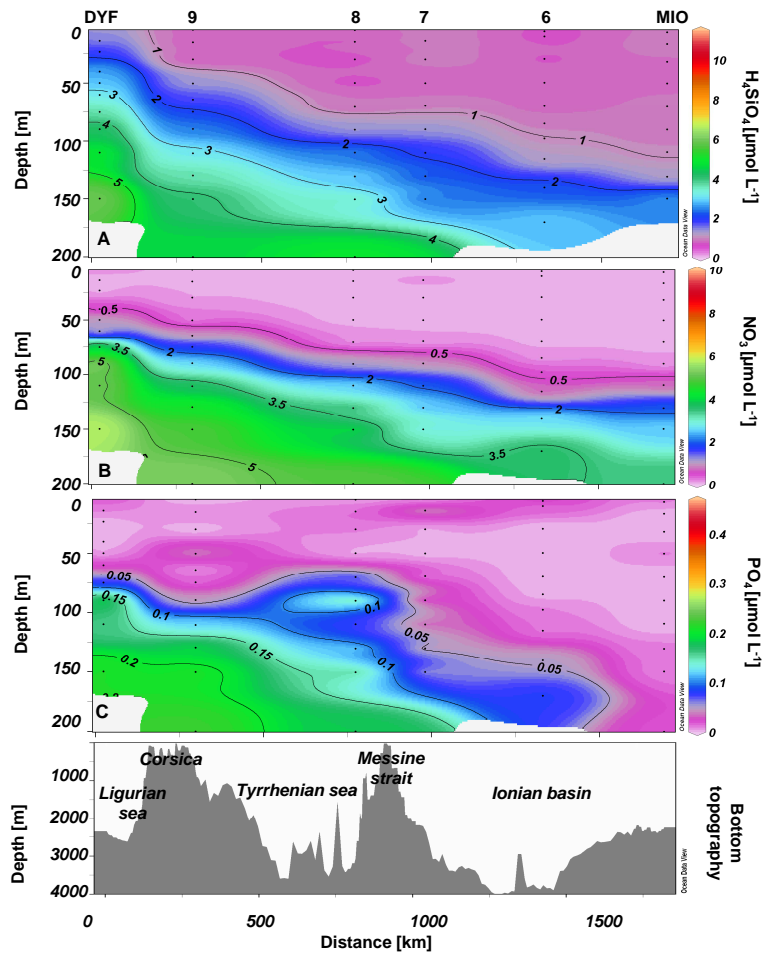


Fig. 3. Nutrient distributions (μM) along the transect 2 during PROSOPE the cruise (summer/fall 1999).

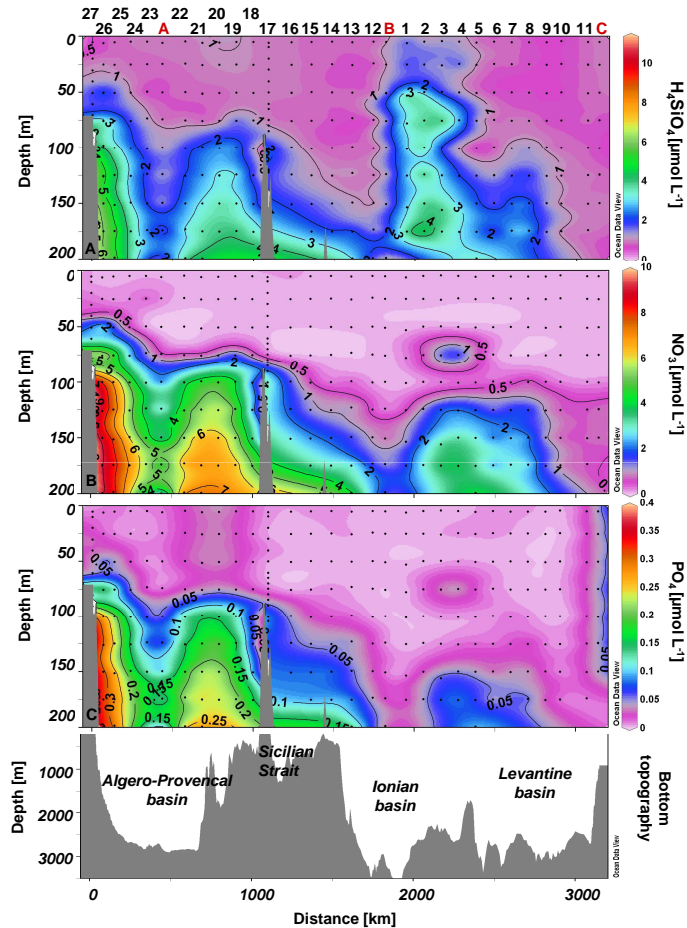


Fig. 4. Nutrient distributions (μM) during the BOUM cruise (late summer 2008).

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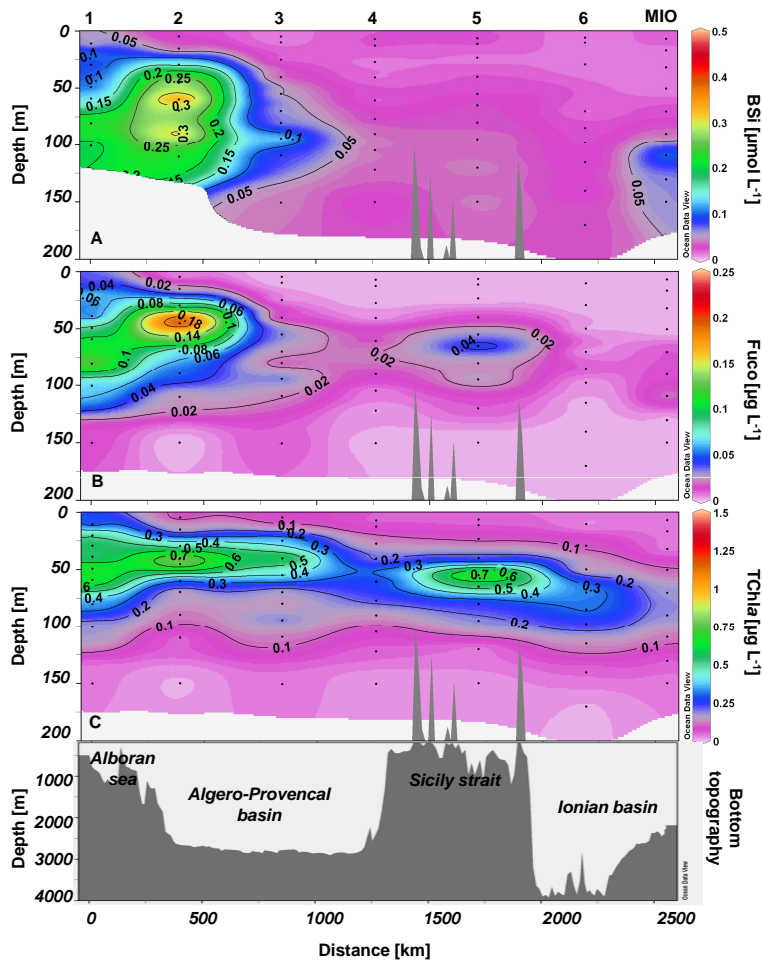


Fig. 5. Distribution of biogenic Silica (BSi) ($\mu\text{mol L}^{-1}$), fucoxanthin (Fuco) ($\mu\text{g L}^{-1}$) and total chlorophyll a (*TChl a*) ($\mu\text{g L}^{-1}$) along transect 1 during the PROSOPE cruise (summer/fall 1999).

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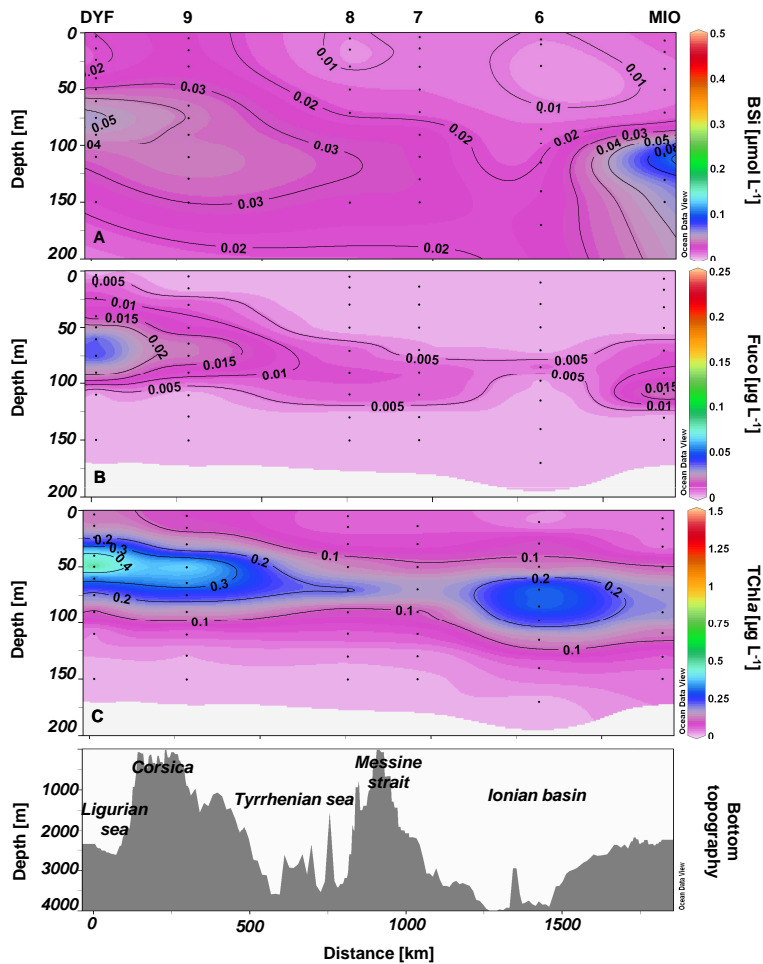


Fig. 6. Distribution of biogenic silica (BSi) ($\mu\text{mol L}^{-1}$), fucoxanthin (Fuco) ($\mu\text{g L}^{-1}$) and total chlorophyll *a* (TChl *a*) ($\mu\text{g L}^{-1}$) along transect 2 during the PROSOPE cruise (summer/fall 1999). 6837

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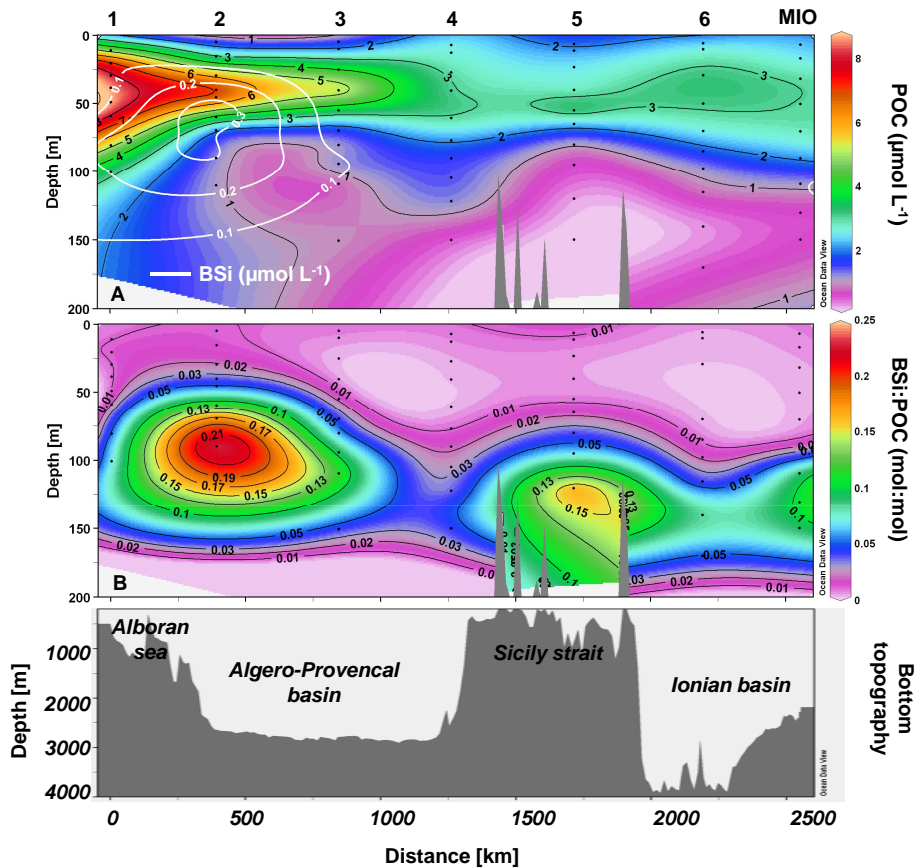


Fig. 7. (A) Distribution of particulate organic carbon (POC) ($\mu\text{mol L}^{-1}$), with BSi concentrations ($\mu\text{mol L}^{-1}$) isopleths as overlays in white and **(B)** BSi:POC ratios (mol:mol) along transect 1 during the PROSOPE cruise (summer/fall 1999).

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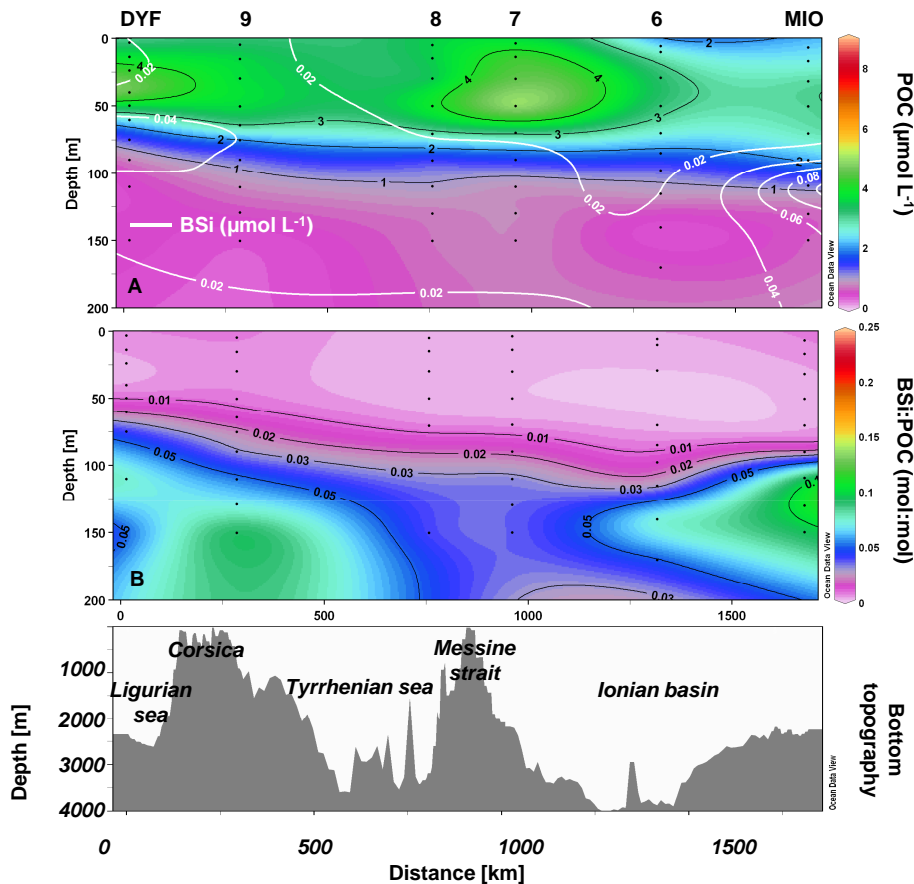


Fig. 8. (A) Distribution of particulate organic carbon (POC) ($\mu\text{mol L}^{-1}$), with BSi concentrations ($\mu\text{mol L}^{-1}$) isopleths as overlays in white and (B) BSi:POC ratios (mol:mol) along transect 2 during the PROSOPE cruise (summer/fall 1999).

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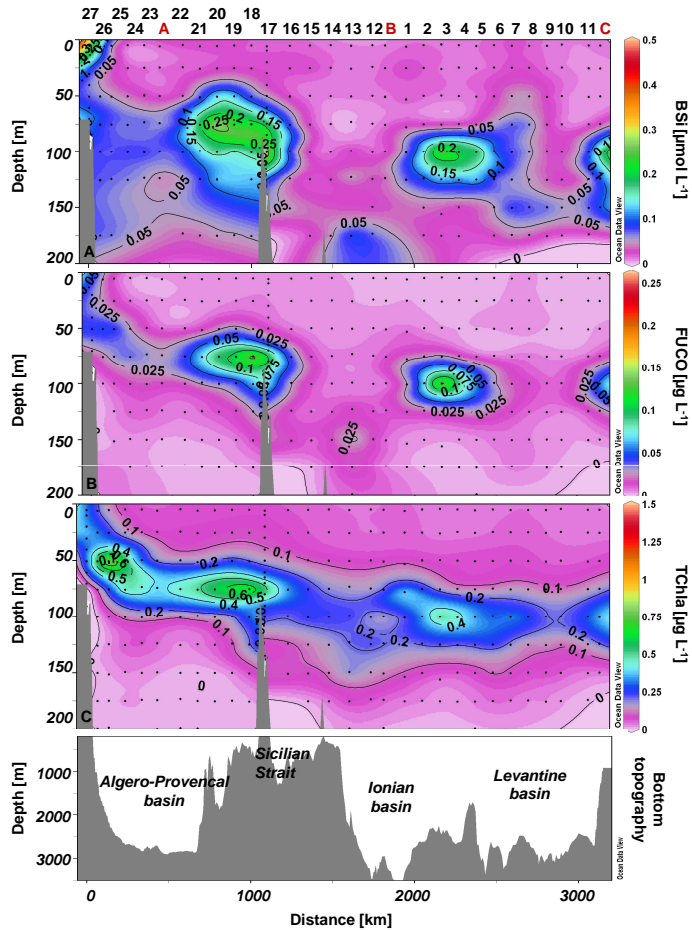


Fig. 9. (A) Distribution of biogenic silica (BSi) ($\mu\text{mol L}^{-1}$), (B) fucoxanthin (Fuco) ($\mu\text{g L}^{-1}$) and (C) total chlorophyll *a* (TChl *a*) ($\mu\text{g L}^{-1}$) during the BOUM cruise (summer 2008).

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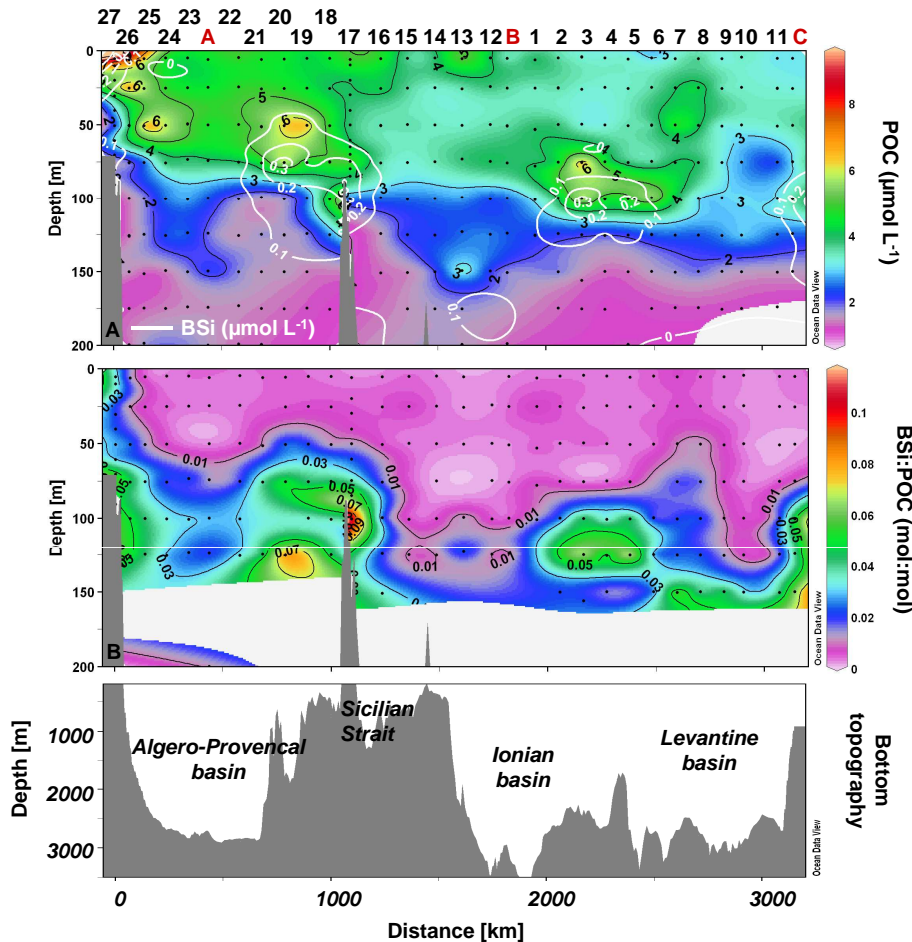


Fig. 10. (A) Distribution of particulate organic carbon (POC) ($\mu\text{mol L}^{-1}$), with BSi concentrations ($\mu\text{mol L}^{-1}$) isopleths as overlays in white and (B) BSi:POC ratios (mol:mol) along the BOUM cruise (summer 2008).

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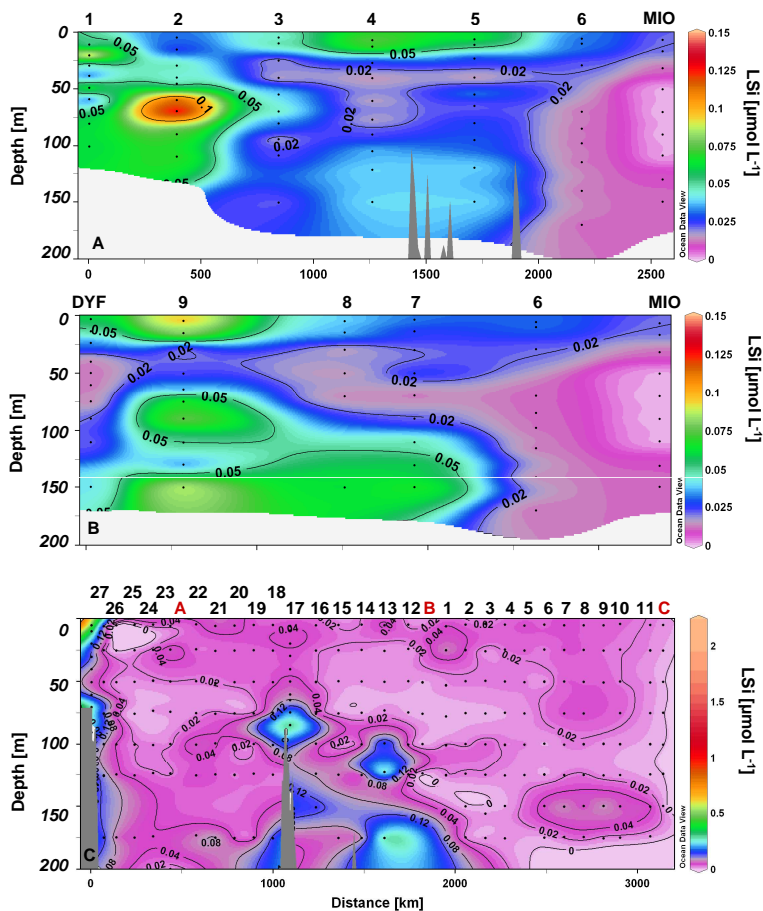


Fig. 11. Distribution of lithogenic silica (LSi) ($\mu\text{mol L}^{-1}$) along the transect 1 (A) and 2 (B) during the PROSOPE and the BOUM cruise (C).

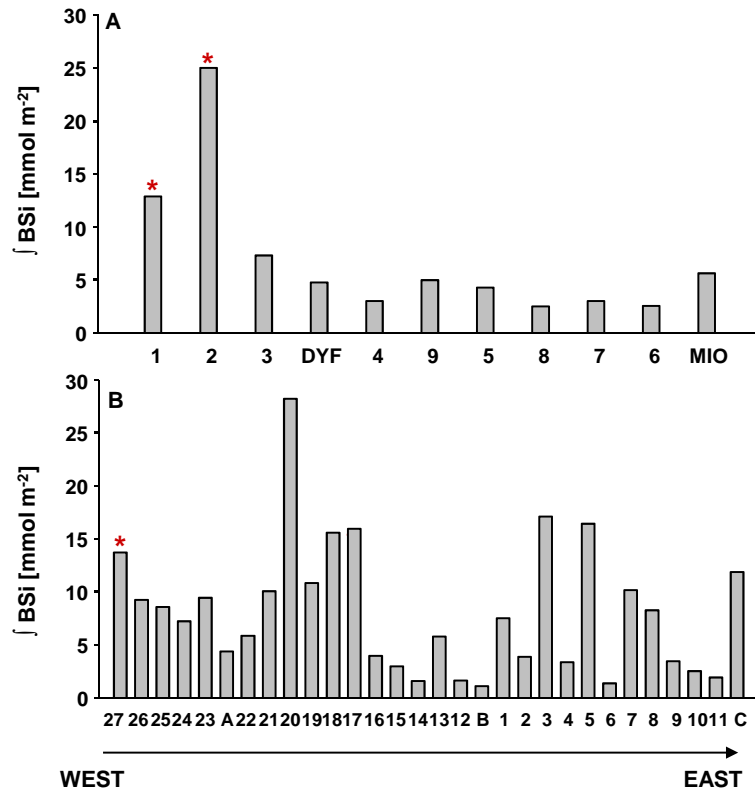


Fig. 12. Integrated biogenic silica stocks (mmol m^{-2}) over 0–150 m (with exceptions indicated by a red star) for the PROSOPE cruise **(A)** and the BOUM cruise **(B)** along a westeast gradient. Integration depths at PROSOPE stations 1 and 2 were 100 and 110 m respectively and are signified by a red star. Integration depths at BOUM stations 17 and 27 were 118 and 100 m respectively.

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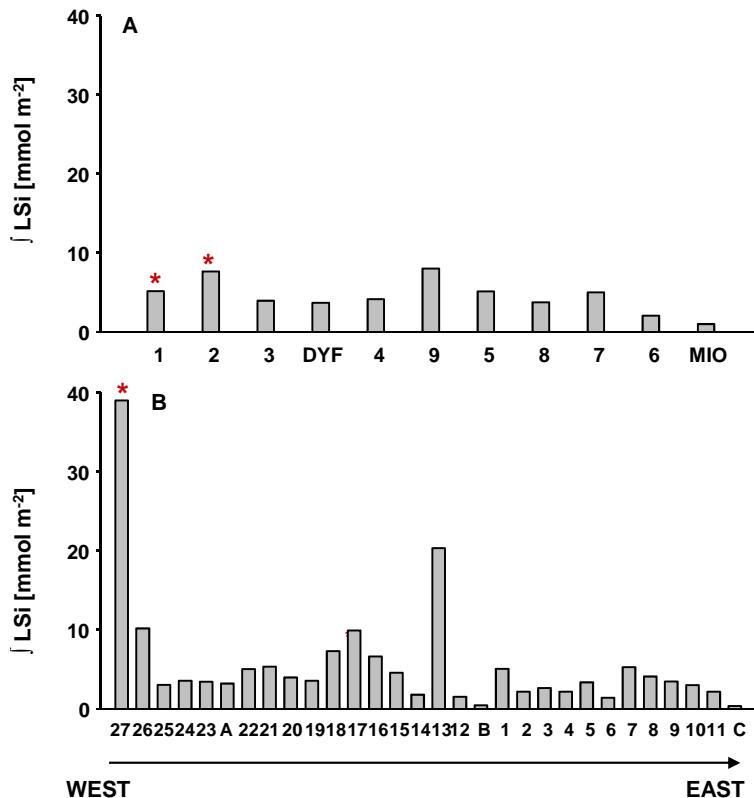


Fig. 13. Integrated lithogenic silica stocks (mmol m^{-2}) 0–150 m (with exceptions indicated by a red star) for the PROSOPE cruise **(A)** and the BOUM cruise **(B)** along a west-east gradient. Integration depths at PROSOPE stations 1 and 2 were 100 and 110 m respectively and are signified by a red star. Integration depths at BOUM stations 17 and 27 were 118 and 100 m respectively.

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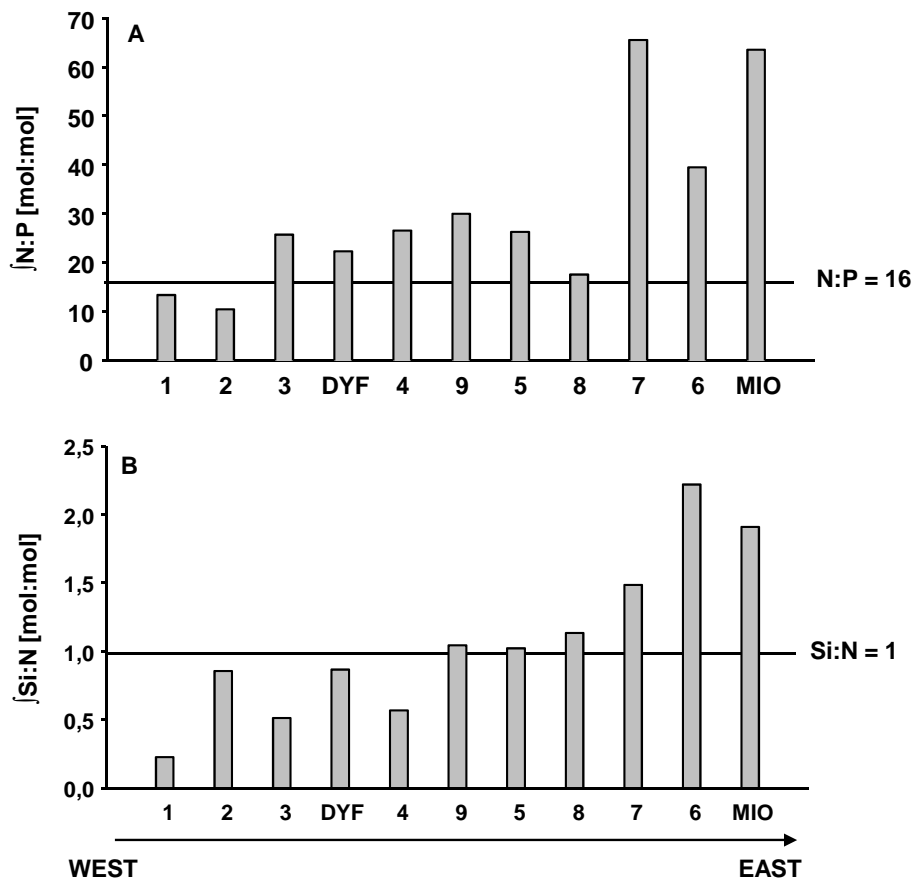


Fig. 14. Integrated N:P (**A**) and Si:N (**B**) ratios (mol:mol) over 0–150 m for the PROSOPE cruise along a west-east gradient. Integration made under 150 m is signified by the red star. Integration at stations 1 and 2 was made on 100 and 110 m respectively.

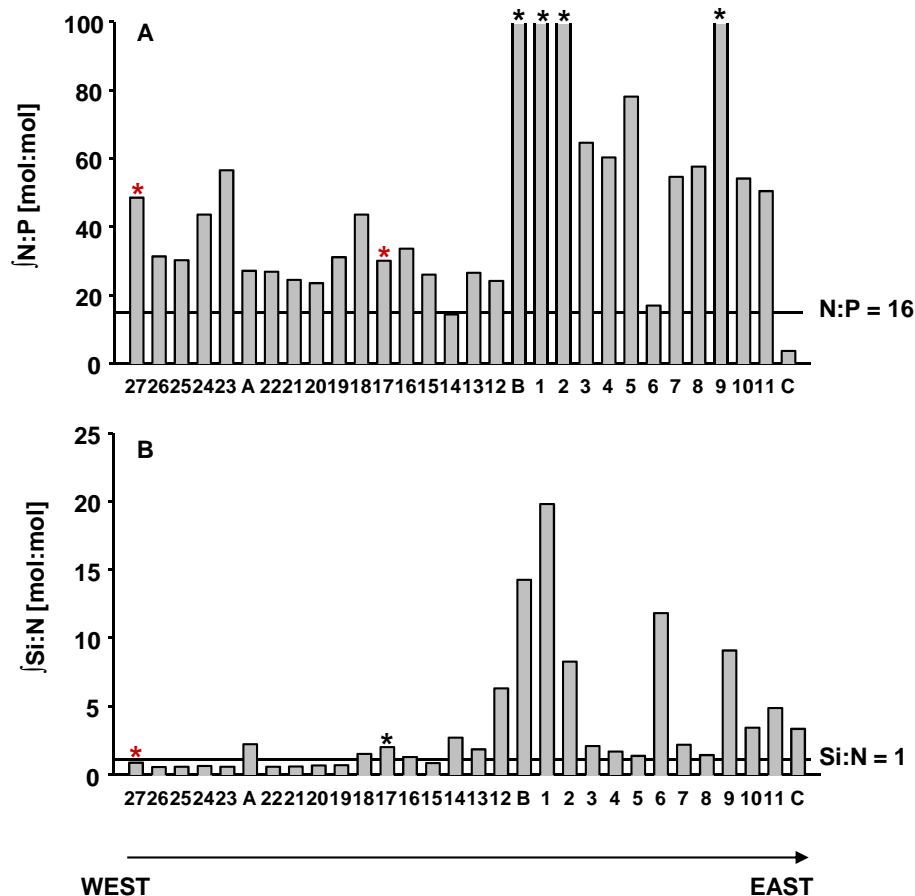


Fig. 15. Integrated N:P (**A**) and Si:N (**B**) ratios (mol:mol) over 0–150 m for the BOUM cruise along a west-east gradient. Integration made under 150 m is signified by the red star. Integration was made on 118 m for station 17 and 100 m for station 27.