Biogeosciences Discuss., 7, 7315–7358, 2010
www.biogeosciences-discuss.net/7/7315/2010/
doi:10.5194/bgd-7-7315-2010

Biogeosciences Discussions

Integrated survey of elemental stoichiometry (C, N, P) from the Western to Eastern Mediterranean Sea

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Received: 22 July 2010 – Accepted: 5 September 2010 – Published: 11 October 2010

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

This paper provides an extensive vertical and longitudinal description of the biogeochemistry in the whole Mediterranean Sea during the summer 2008. During this strong stratified period, the distribution of nutrients, particulate and dissolved organic carbon (DOC), nitrogen (DON) and phosphorus (DOP) were investigated along a 3000 km transect (BOUM cruise) crossing the Western and Eastern Mediterranean basins. The partitioning of chemical C, N and P species among all these mineral and organic pools has been analysed to produce a detailed spatial and vertical extended examination of the elemental stoichiometry. Surface Mediterranean waters were depleted in nutrients and the thickness of this depleted layer increased towards the East from about 10 m in the Gulf of Lion to more than 100 m in the Levantine basin, concomitantly to the gradual deepening of the thermocline and nutriclines. We used threshold in oxygen concentration to discriminate the water column in three layers; surface (Biogenic Layer BL), intermediate (Mineralization Layer ML), and deep layer (DL) and to propose a schematic representation of biogeochemical fluxes between the different compartments and to compare the functioning of the two basins. The stoichiometry revealed a clear longitudinal and vertical gradient in the mineral fraction with a P-depletion evidenced on both dimension. As a consequence of the severe deficiency in phosphorus, the C:N:P ratios in all pools within the BL largely exceed the Redfield ratios. Despite these gradients, the deep estimated fluxes in the mineral compartment tend towards the canonical Redfield values in both basins. A change in particulate matter composition has been evidenced by a C increase relative to N and P along the whole water column in the western basin and between BL and ML in the eastern one. More surprisingly, a decrease in N relative to P with depth was encountered in the whole Mediterranean Sea. We suggest that there was a more rapid recycling of N than P in intermediate waters (below BL) and a complete use of DOP in surface waters. DOC accumulated in surface waters according to the oligotrophic status but this was not the case for nitrogen nor phosphorus. Our data clearly showed a noticeable stability of the

BGD

7, 7315–7358, 2010

DOC:DON ratio (12–13) in the whole Mediterranean Sea, contradicting the fact that N is recycled faster than C in the DOM but in agreement with a P limitation of bacterial activity. Finally, comparisons between these elemental distributions and ratios along the West-East Mediterranean gradient of trophic status provide new insights for identifying and understanding fundamental interactions between marine biogeochemistry and ecosystems, which will help to predict the impacts of environmental climate changes on the Mediterranean marine ecosystems. Indeed, the outflowing through the various Mediterranean straits have been shown to be changing, the functioning of the BL ecosystem could be impacted, not only by changes in nutrients surface sources but also by changes in deep nutrients one.

1 Introduction

The carbon, nitrogen, phosphorus (C:N:P) elemental composition of mineral and organic matter in marine environments is a key factor for relating carbon and nutrient cycles. Stoichiometric ratios are powerful tools to model basic biogeochemical patterns of the sea. Since Redfield (1934, 1958) presented this concept of closely linked elemental ratios in the biogeochemical cycles of the ocean, it has served as one of the foundations of biogeochemical researches (Falkowski, 2000; Falkowski and Davis, 2004). Indeed, the nutrient ratios in the sea have been recurrently used as water mass tracers and as effective markers of biotic and of the biogeochemical processes taking place in the ocean interior (Redfield et al., 1963; Sterner and Elser, 2002). The canonical values proposed by Redfield (molar ratio of 105:16:15:1 in the North-Atlantic for C:N:Si:P) still hold as a reference (e.g., Takahashi et al., 1985). Measurements of C:N:P ratios and anomalies relative to the Redfield values are generally useful to describe the functioning of complex food webs and to examine the processes that regulate marine biogeochemistry. These anomalies have been successfully used to trace temporal changes occurring in the global ocean on a wide range of scales (e.g., Anderson and Sarmiento, 1994; Béthoux et al., 2002; Falkowski, 1997; Pahlow and

BGD
7, 7315–7358, 2010

Riebesell, 2000), including estimation of the global distribution of anthropogenic carbon (Gruber and Sarmiento, 1997), rate of nitrogen fixation (Deutsch et al., 2007), and denitrification (Tyrrell and Lucas, 2002), and ocean mixing (Broecker, 1974).

Although the scientific community has gained greater insights into elemental cycling by using the Redfield ratios, the processes that create the near constancy in elemental ratios continue to be examined (i.e., Klausmeier et al., 2008). It is known that the elemental composition of biotic and abiotic compartments can widely vary with environmental conditions (light, temperature, trophic status), or growth rate of living organisms (Fukuda et al., 1998; Hansell and Carlson, 2002; Anderson et al., 2005; Conan et al., 2007; Sterner et al., 2008). Spatial variability in elemental ratios has been reported with respect to remineralisation of organic matter changing with depth and with ambient oxygen levels (Li and Peng, 2002; Anderson and Pondaven, 2003; Paulmier and Ruiz-Pino, 2009). The degree to which organisms maintain a constant chemical composition relative to the variations in their environment is referred to "stoichiometric homeostasis". One of the major hypotheses in the functioning of marine pelagic ecosystems ("the light-nutrient hypothesis" related to "the bottom-up vs. top-down ecosystem control") states that the importance of the microbial food web relative to grazing impacts by zooplankton and the nature of the relationships between algae and bacteria (competition or commensalism) are affected by the balance of light and nutrients experienced by phytoplankton (Conan et al., 1999, 2007; Elser et al., 2007; Thingstad et al., 2008). The control of the food web by limiting nutrients (Elser et al., 2007) and trophic relationships (Conan et al., 1999; Thingstad et al., 2008) has deep consequences for biogeochemical processes and rates in marine ecosystems (Salihoglu et al., 2008), especially because of the continuous recycling of particulate organic matter (POM) and dissolved organic matter (DOM) to dissolved inorganic matter (DIM) and back again.

Climate change effects are predicted to play a prominent role in modifying the Mediterranean nutrient status that can result from a direct change of the total input rates and/or alteration of nutrient stoichiometry, which will affect the microbial activity and diversity and subsequently, the whole ecosystem. For example, the predicted

BGD
7, 7315–7358, 2010

increase in sea surface temperature combined with changes in thermohaline circulation will accentuate the thermal stratification of the surface layer which will in-turn reduce the supply of nutrients to the photic layer through vertical transport. This is likely to increase the severity of oligotrophic conditions and therefore, the potential role of external inputs operating on larger time-scales will become relatively more important in controlling the nutritional status of the Mediterranean Sea (for more details, see U.N.E.P.-M.A.P., 2003). The Mediterranean Sea is an elongated semi-enclosed basin with significant exchanges only at the Gilbraltar Strait. It is divided in two sub-basins, linked via the Sicily Strait, which has a shallow sill that helps to decouple the hydrodynamic and ecological conditions in the two sub-basins, the western and the eastern basins. The presence of these 2 shallow sills precludes a significant exchange of deep waters with the Atlantic Ocean as well as between the two Mediterranean basins. The general circulation transforms surface Atlantic Water (AW) into a set of cooler and saltier typical Mediterranean Waters that are formed in different areas within the sub-basins and thus have distinct hydrological characteristics. The Mediterranean Sea is generally considered as a three-layer system (Ribera d'Alcalà et al., 2003). The upper layer (from the surface down to 150–300 m, according to the basin and the season) is occupied by Modified Atlantic Water (MAW), which strongly modified its properties as it flows from west to east after entering the Strait of Gibraltar. The underlying layer (200–1000 m, but with a high variability within sub-basins; see for example Conan and Millot, 1995 in the Gulf of Lion) is occupied by Levantine Intermediate Water (LIW), which forms in the easternmost part of the basin and basically closes the open thermohaline cell with the Atlantic Ocean. Finally, in the deep layer different water masses fill the two neighboring basins, the Eastern Mediterranean Deep Water (EMDW), and the Western Mediterranean Deep Water (WMDW).

The Mediterranean Sea has long been known as a low nutrient concentration basin (Mc Gill, 1965; Krom et al., 1991) and as one of the largest nutrient-depleted area in the world (Ignatiades, 2005; Crise et al., 1999) though exhibiting increasing oligotrophy from west to east. Mediterranean coastal areas directly interact with the pelagic

BGD
7, 7315–7358, 2010

environment, since the shelves are relatively narrow. The Mediterranean response to external conditions is relatively fast compared to the other oceans (Crispi et al., 2001) and physical/ecological interactions at basin scale may have profound influence in determining the evolution of the ecosystems. Local environmental events such as wind-driven mixing, mesoscale hydrodynamical processes and river discharges have an important role on the local fertilization. The Mediterranean Sea is particularly relevant for biogeochemical studies, because literature reported anomalous values in nutrient ratios as compared to other oceanic provinces (Béthoux and Copin-Montégut, 1988; Herut et al., 1999; Kress and Herut, 2001; Ribera d'Alcalà et al., 2003; Ediger et al., 2005; Krom et al., 2005). This anomaly, though frequently explored, still represents an open issue for the understanding of the functioning of the Mediterranean Sea (see Mermex group, 2010; Krom et al., 2010). Because of the typical scales and morphology of the Mediterranean basins, nutrient ratios and the elemental partitioning in organic matter should depend on, and therefore reveal, the relevant internal processes of the sea, thus becoming a powerful tool to reconstruct its internal dynamics.

There is a strong need to get a mechanistic understanding of the biogeochemical processes in order to predict changes in the Mediterranean Sea, as they strongly influence biodiversity, fisheries, invasive species ultimately, will likely modify carbon sequestration via the alteration of the biological pump. Our investigation during the BOUM cruise (July 2008) has allowed a description of the present inorganic and organic matter distributions along a longitudinal transect extending from the Levantine Sea (eastern basin) to the Gulf of Lion (North Western Mediterranean). Here, we report nutrient, dissolved and particulate organic matter concentration from surface to deep waters and their C, N and P stoichiometry. We then focus our analysis on the elemental partitioning and on the potential relationships between the various compartments. The potential similarities and differences between the western and the eastern basins of the Mediterranean Sea provide new insights such as in the biogeochemical cycling of the Mediterranean Sea.

BGD
7, 7315–7358, 2010

2 Materials and methods

2.1 Study area and sampling

During the "BOUM" cruise (Biogeochemistry from the Oligotrophic to the Ultra oligotrophic Mediterranean Sea) that took place during the summer 2008 on the Research Vessel l'Atalante, a transect of 30 stations from the Levantine basin to the North Western Mediterranean Sea has been investigated and a description of the relevant biogeochemical parameters from surface to bottom across the Mediterranean Sea (Fig. 1) has been performed. More informations (e.g. date, Geographical coordinates) concerning all the stations are given in Moutin et al. (2010). The east-west cruise track crossed the main areas of the Mediterranean Sea, the Levantine basin, the Cretan passage region, the Ionian basin, and the Sicily strait before entering the western basin. In the western basin, there was a south-north transect from a central station (A) toward the mouth of the Rhone River in the Gulf of Lion (Fig. 1). Profiles of temperature, conductivity, oxygen and fluorescence were performed with a SBE 911 PLUS Conductivity-Temperature Depth (CTD) system manufactured by Sea-Bird Electronics Inc. Water samples for the determination of the whole set of biogeochemical parameters were collected from CTD casts at the 30 stations with a carousel equipped with 24 Niskin Bottles of 12 l volume. Water was sampled at 12–17 depths, from few meters above the sea bottom up to the surface (0–5 m), the number of samples depending on the parameter and on the station's water depth.

2.2 Analysis of nutrient and particulate and dissolved organic matter

Nutrients

Samples for nitrate (NO_3), nitrite (NO_2) and phosphate (PO_4) were directly collected from the Niskin bottles in 20 ml acid washed polyethylene vials. They were immediately analysed on board according to classical methods using the automated colorimetric

BGD
7, 7315–7358, 2010

technique (Tréguer and Le Corre, 1975; Wood et al., 1967) on a segmented flow Bran Luebbe autoanalyser II. Accuracy of measurements was 0.02 µM, 0.005 µM and 0.005 µM for NO_3, NO_2, and PO_4 respectively and detection limits for the procedures were 0.02 µM, 0.01 µM and 0.01 µM for NO_3, NO_2, and PO_4 respectively. Nutrient standardisation and data quality were assured through successfull and continuous participation in international intercalibration exercices. During the cruise, measurements were further verified with the use of OSIL (Ocean Scientific International Ltd) marine nutrient standards (ISO 9001 accredited). Samples for ammonia (NH_4) were collected in ultra cleaned glass bottles with care to avoid contamination. NH_4 determinations were performed on board by fluorimetry according to Holmes et al. (1999) on a fluorimeter Jasco FP-2020. Accuracy of measurements was 2 nM and detection limit for the procedure was 3 nM.

Total inorganic carbon

Samples for total inorganic carbon (DIC) were collected from the Niskin bottles in borosilicate glass bottles. They were poisoned with a saturated $HgCl_2$ solution then sealed and stored. At the end of the cruise, they were shipped to the laboratory for analysis. The measurements were performed by potentiometry using a closed cell, according to the DOE handbook of methods for Analysis of the Various Parameters of the Carbon Dioxide System in Seawater (DOE, 1994). Typical analytical accuracy was less than ±2 µmol kg^{-1}. The accuracy was verified using regular measurements of reference material (CRM) bought from Dr. A. Dickson's laboratory (Scripps, USA).

Dissolved organic matter

Samples for dissolved organic matter (DOM) were collected from the Niskin bottles in combusted glass bottles. Samples where then immediately filtered through 2 precombusted (24 h, 450 °C) glass fiber filters (Whatman GF/F, 25 mm). Samples for dissolved organic carbon (DOC), collected into precombusted glass tubes and acidified

BGD
7, 7315–7358, 2010

with Orthophosphoric acid (H_3PO_4), were immediately analyzed on board by high temperature catalytic oxidation (HTCO) (Sugimura and Suzuki, 1988; Cauwet, 1994, 1999) on a Shimadzu TOCV analyzer. Typical analytical precision is ±0.1–0.5 (SD) or 0.2–1% (CV). Standardisation and data quality were assured through the successfull and continuous participation in laboratory international intercalibrations exercices. Furthermore, consensus reference materials (http://www.rsmas.miami.edu/groups/biogeochem/CRM.html) was injected every 12 to 17 samples to insure stable operating conditions. Samples for Dissolved organic nitrogen (DON) and phosphorus (DOP), collected in Teflon vials, were immediately analyzed by Persulfate wet-oxidation according to Pujo-Pay and Raimbault (1994) and Pujo-Pay et al. (1997).

Particulate matter

Particulate nitrogen (PN) and phosphorus (PP) were collected onto precombusted (24 h, 450 °C) glass fiber filters (Whatman GF/F, 25 mm), that were immediately oxidized after filtration into Teflon vial and simultaneously analyzed on board according to the wet oxidation procedure of Pujo-Pay and Raimbault (1994). Particulate organic carbon (POC) was collected on precombusted (24 h, 450 °C) glass fiber filters (Whatman GF/F, 25 mm). Filters were dried in an oven at 50 °C and stored, in ashed glass vial and in a dessicator until analyses when return from the cruise, on a CHN Perkin Elmer 2400.

3 Results

3.1 Hydrological characteristics

The Mediterranean Sea is divided in two main basins, the western (stations 18 to 27, and A) and eastern (stations 17 to 1, B and C) basins which are separated by the channel of Sicily (Fig. 1). The overall circulation and the physical and hydrologic characteristics (e.g. T-S properties) of the different water masses in the Mediterranean Sea

BGD
7, 7315–7358, 2010

has been previously well described, likewise full details for the BOUM cruise can be found in Moutin et al. (2010). The present study is not discriminating for different areas or precise water masses but considers the observations at a basin scale, in order to enlighten similarities and/or differences between the Western and Eastern Mediterranean basins. This approach is relevant when considering the potential evolution of basin exchanges and their impact on the ecosystems. During the summer BOUM cruise, surface temperatures ranged from 24 °C in the western basin (at station A) to 27.5 °C in the central eastern part (at station B). Chlorophyll concentration (as in situ fluorescence unit) showed a well defined Deep Chlorophyll Maximum (DCM), more pronounced in the western basin, and deepening from west (~40 to 80 m) to east (from 80 to >100 m) (for details, see Crombet et al., 2010).

3.2 Evolution of biogeochemical parameters

Dissolved inorganic nutrients

In surface waters (above the top of the thermocline), concentrations of nitrate+nitrite (NO_{3+2}), NO_2 and PO_4 are low and close or below the detection limit of conventional micromolar technology (Fig. 2a). Concentrations of NH_4 are also low (0–10 nM) with a patchiness pattern and maxima in subsurface, similarly to NO_2 distribution with a peak (maximal values about 0.2 µM) at the base of the DCM (Fig. 2b). Below this depleted nutrient layer, concentrations rise through the nutriclines and reach maximal values of about 9.8, 0.09, 0.055 and 0.44 µM in the western basin and of about 6.3, 0.22, 0.056 and 0.25 µM in the eastern basin for NO_{3+2}, NO_2, NH_4 and PO_4 respectively. Below these maxima (500–1000 m layer), concentrations of NO_{3+2} and PO_4 slightly decrease to reach homogeneous values (9.1 and 0.39 µM in the western basin and 5.1 and 0.17 µM in the eastern basin) in deep waters (Fig. 2c). Significantly higher values are found in the western basin compared to the eastern one. In the Sicily Strait, the shape of the various isolines changes at station 18 and a nutrient anomaly is encountered near 1000 m, where concentrations are ≤ 0.3 µM of PO_4 and ≤ 5.5 µM of

BGD
7, 7315–7358, 2010

NO_{3+2} as compared to average western values at the same depth (~0.40–0.45 µM of PO_4 and 9.0–9.5 µM of NO_{3+2}). This characterizes the flow of subsurface eastern waters to the western basin.

The thicknesses of the nutrient depleted layer changes along the west-east transect from 10–20 m in the Gulf of Lion to more than 100 m in the Levantine basin (Fig. 3). Taking into account the bias introduced by discrete sampling, the upper limit of the nitracline is close to the base of the thermocline. The top of the phosphacline is generally located deeper than the top of the nitracline, above the base of the thermocline in the western basin but below it in the eastern one. The discrepancy between the two nutriclines increases eastward as the phosphacline deepens more rapidly than the nitracline and the thermocline. It is important to note that we have considered a threshold in the gradient to define the top of the nutriclines. When the nitracline and the phosphacline are separated with depth, weak PO_4 concentrations are generally measured in the gap (concentration < 0.08 µM) but the vertical gradient is then insufficient to meet the criteria.

Dissolved and particulate organic matter, and elemental partitioning

In surface waters, DOP, DOC and DON show different distribution patterns (Fig. 4a). Indeed, DOC concentration roughly follows an inverse distribution compared to nutrients, with maxima in surface waters and an increase from west (69.4 µM) to east (72.4 µM). For both DON and DOP, maximal concentrations are also measured in the surface waters, but highest values are encountered in the central part of the transect (at station B in the eastern basin). The two basins have similar mean surface DON concentration (4.7 ± 0.5 µM) whereas the western basin is slightly richer in DOP (0.06 ± 0.02 µM) than the eastern one (0.04 ± 0.02 µM). Below this surface layer, a steep gradient is encountered for DOM and fairly homogeneous concentrations follow in deep waters (Fig. 4b). The whole water column is not shown for DOP because there is no detectable concentration below 300–500 m. Contrary to nutrients, DOM distribution in deep waters does not reveal significant gradient between the western and eastern basins (Fig. 4b).

BGD
7, 7315–7358, 2010

Average DOC and DON concentrations in deep waters are 39.9 ± 1.1 µM, 3.3±0.4 µM for the western basin and 44 ± 4.3 µM, 3.5 ± 0.6 µM for the eastern basin.

For both basins, in surface waters DIC represents more than 97% of the total carbon pool, whereas DOC and POC represent about 2.5 and 0.1%, respectively (Table 1). For the N and P pools, differences are encountered between western and eastern basins: In the western surface waters, nitrogen pool is composed of ~25, 70 and 5% of dissolved inorganic nitrogen (DIN), DON and PN respectively, and phosphorus pool by 40, 40 and 20% of dissolved inorganic phosphorus (DIP), DOP and PP, respectively. In the eastern surface waters, nitrogen pool is composed by 10, 85 and 5% of DIN, DON and PN and phosphorus pool by 15, 60 and 25% of DIP, DOP and PP. The west-east oligotrophic gradient is characterized by a decrease in the proportion of mineral to organic forms (Table 1). This is confirmed by the surface vertical section of POM along the transect (Fig. 5). The highest concentrations for C, N and P are measured in the western basin above 100 m. The Gulf of Lion is the richest area but high concentrations are also measured close to the Sicily Strait and in the central part of the Ionian Sea. As compared to the hydrological structure, the particulate organic matter (POM) distribution is not characterized by west-east deepening of isolines. Below 100 m, the importance of POM as a reservoir of C, N and P declined with depth, concomitantly to the rise of the contribution of the dissolved inorganic reservoir. Indeed, in the deep waters, in terms of C and P, this inorganic reservoir represents 98% as the organic reservoir (particulate and dissolved) represents 2% whereas the proportion for N is 70% in DIN and 30% in DON in the western basin, and 60% in DIN and 40% in DON in the eastern basin due to a lesser content in DIN (Table 1).

To compare the evolution of the different parameters from the western and eastern basins, and especially their global water column content in the different pools, we compared the integrated quantities over the 0–2500 m water column at each deep station (Fig. 6). The parameters can then be divided into 2 sets; the first one showing significant differences between the western and the eastern basins (Pot.T, Sal, Iσ, ICO_2, INO_3, IPO_4, IDOC) and the second one with no significant difference (IO_2, INH_4, INO_2,

BGD
7, 7315–7358, 2010

IDON, IDOP, IPOC, IPN, IPP). In the first set, a well identified linear positive west-east gradient exists for Pot.T and IDOC (particularly in the east part), and with a lesser extent for Sal. On the opposite, ICO_2, INO_3, and IPO_4, are characterized by a negative west-east gradient due to higher quantities in the western basin.

3.3 Evolution of elemental stoichiometry

To study elemental stoichiometry, we differentiated three successive vertical layers in both basins. (i) An upper layer named hereafter the "Biogenic Layer (BL)", between 0 and about 100–270 m, which roughly corresponds to the surface (above the top of the thermocline) and the euphotic layers where major primary production processes take place; (ii) an intermediate layer, hereafter "Mineralization Layer (ML)", below the BL to ~1000–2000 m, which includes the Oxygen Minimum Zone (OMZ) and highest nutrient concentrations when present; and (iii) a deep layer, hereafter "Deep Layer (DL)", below the ML to the sea floor. Yet, the principle of a fixed depth to define the top and the bottom of each layer is obviously not appropriate in considering the vertical and latitudinal variability and evolution of the parameters described above. Indeed, the vertical limits of these 3 layers should be spatially variable along the west-east transect. In the objective of studying the potential relationships between the mineral, dissolved and particulate organic compartments, one considered that the best indicator of the existence of biogeochemical fluxes between these pools is certainly the oxygen which is produced, consumed and/or exchange during the various physical and biological processes. Therefore, we defined the upper and lower limits of each layer by a threshold in O_2 concentration. Consequently, the thickness of the three layers varies from station to station along the west-east transect (Fig. 7). The upper limit of the BL is the surface, whereas its lower limit (i.e. the upper limit of the ML) is fixed by an O_2 concentration of 195 $\mu mol\,kg^{-1}$ following a relative maximum. The lower limit of the ML (i.e. the upper limit of the DL) is then fixed by an O_2 concentration of 180 $\mu mol\,kg^{-1}$ following a relative minimum. The result of applied this criterion along the transect is shown on Fig. 7.

BGD
7, 7315–7358, 2010

By pooling the stations for western and eastern basins in addition to the previous criterion, we could calculate average values for all the parameters to physically and chemically characterized each layer (Table 2). This clearly illustrates that eastern waters are warmer, saltier, denser, and poorer in PO_4 and NO_3 than western waters, whereas relative homogeneous concentrations in NO_2, NH_4, DON, and DOP are encountered in both basins in the three layers. The eastern waters are slightly richer in DOC, but poorer in POC.

There are two approaches to study the elemental stoichiometry a selected pool. We can consider (i) the concentration ratios of two elements and then, average these ratios over depth and/or distance, or (ii) the equation of the linear relationship between these two elements in an element-element plot. It is worth mentioning that the interpretation for both approaches is different (Ribera d'Alcalà et al., 2003) but complementary and can bring important information for interpretation of the various processes involved in the relationship. Note that Redfield (1934, 1958) in his original approach used both possibilities. As already pointed out by Kress and Herut (2001) in most studies, the N:P ratios are studied as the proper ratio, while in others they are obtained from the slope of the linear regression of N:P. In fact, both ratios coincide if the regression line passes through the origin, in what is referred to a non-fractionated or "ideal" nutrient covariation by Fanning (1992). In that case, the ratio of the net reaction rates involving N and P in each one is equal to its concentration ratio and organisms are in balance with the ratio in which the nutrients are present. However, we often observe linear N:P regressions with non-zero intercepts (positive or negative), which could even become quite large if the surface water layer (above the thermocline), where N or P are likely to be small, is considered. Thus, the reaction rate ratio of N to P does not equal the N:P proper ratio. The term b in the linear regression equation ($y=ax+b$) indicates an excess nitrate present after phosphate utilization (or removal) for a positive intercept or reversely for a negative intercept.

We used these two concepts to model our ecosystem for the previously defined successive layers. Thus, the mean C:N:P ratio in a given compartment will be

BGD
7, 7315–7358, 2010

representative of the present stock at the sampled time, whereas the slope of the linear regression will be treated as a first order approximation to the reaction rate ratio, i.e. a net budget of the various exchange fluxes corresponding to production/consumption processes. The slope of the regressions in the order of ~16 for N:P, ~106 for C:P, and 6.6 for C:N matches the canonical "Redfield" model. The b value of the equation provides information regarding the lacking/exceeding element. A first illustration of this approach is proposed in Fig. 8 for the NO_{3+2}-PO_4 relationship. The average ratio strongly increases from the western (24.5; Fig. 8a) to eastern (37.8; Fig. 8b) basin, in relation with the well-known Mediterranean phosphorus deficiency compared to the Redfield requirement. The average ratio for the pooled data is 32.4 (Fig. 8c). This is in agreement with the equations of the linear regressions but the phosphorus deficiency and the west-east gradient are lower with the slope of the element-element plot (22.9 and 27.9, respectively; Fig. 8a and b), corresponding to a pooled slope of 23.3. The intercepts indicate a concentration of 0.3 µM of nitrate when phosphate is exhausted for both basins (0.6 for pooled data, Fig. 8c.).

It is particularly evident that the coefficients of the regressions vary in the different layers (Fig. 8). For example, when excluding the concentrations in BL, the average ratio is still high (27.7), the excess of nitrate sharply increase (2.1 µM), but the slope of the regression fall down to a value of ~17 surprisingly close to the Redfield ratio, and similar for the two basins.

In applying this concept to C, N, and P for mineral, organic dissolved and particulate matter, we obtain a broad picture of the stocks and the fluxes inside the two basins or in the Mediterranean Sea (Table 3). In the mineral pool, the excess of carbon and the increase from west to east compared to N and P is shown by high ratios, but when compared the slopes and intercepts, values are close between west and east, especially for pooled data (~8 for DIC:NO_{3+2} and ~169 for DIC:PO_4). In the DOM, high and similar C:N:P average ratios are observed in the western and eastern basins. However, the slopes of the regressions are similar to those observed in the mineral compartment in the western basin, whereas they are lower and close to the Redfield

BGD
7, 7315–7358, 2010

values in the eastern basin (Table 3). In POM, it is quite different as the relationships tend towards an ideal elemental covariation, with an intercept equal to 0, at least for PN:PP and for west. Then the average ratios and regression slopes are similar. When considering the whole water column, the highest ratios are encountered in the western basin, which indicates a POM enriched in C compared to N and P, and in N compared to P.

4 Discussion and conclusion

This study provides an extensive examination of element distributions and stoichiometry across the nearly entire open Mediterranean Sea. The examination of chemical pools in marine environments rarely consider the three components, particulate and dissolved organic, and inorganic simultaneously along the whole water column. As a consequence, our knowledge on the partitioning of matter between these pools is still poor, particularly in the Mediterranean Sea. It is generally assumed that a reliable account of the stoichiometry of nutrient elements in the ocean should incorporate the dissolved organic pool (Jackson and Williams, 1985), because this is a major reservoir of both organic carbon and nutrients in the biogenic layer, especially in oligotrophic waters (Eppley et al., 1977; Butler et al., 1979; Orret and Karl, 1987; Vidal et al., 1999). Our study contributes to bridging this gap by examining the distribution of C, N, and P in their particulate and dissolved organic, and inorganic forms in three distinct layers in the Western and Eastern Mediterranean basins. The examination of the ratios between C, N, P is used to draw inferences on the recycling of nutrients and their possible role as limiting factor for primary production and mineralization but also to reveal a similar comportment of biological compartment along the longitudinal Mediterranean trophic gradient.

This study documented the spatial succession of the oligotrophic to ultra-oligotrophic regime in the Mediterranean Sea encountered during summer stratified condition.

BGD
7, 7315–7358, 2010

A strong thermocline was ubiquitous in the Mediterranean Sea and a deepening DCM was associated with the increasing trend in oligotrophy toward east. The distribution of nutrients reached classical concentrations already observed in the Mediterranean Sea. The presence of the prominent nitrite maximum (PNM) at the base of the DCM has been ascribed by some authors to an incomplete assimilatory reduction of nitrate by phytoplankton (phytoplankton excretion), with chemoautotrophic oxidation of ammonium by nitrifying bacteria playing only a supporting role (Lomas and Lipschultz, 2006). Biological and physical interactions are likely to be also important in controlling PNM formation and maintenance. The presence of low but measurable ammonia in the photic zone suggests that grazing was a non negligible process since ammonia is the first product of microbial grazing, which is then rapidly recycled through bacterial and phytoplankton production (Thingstad et al., 2005).

As frequently observed during Mediterranean summer stratification (Pujo-Pay et al., 1995), the phosphacline was located deeper than the nitracline. The resulting unusually high DIN:DIP ratios suggest incomplete nitrate utilization by phytoplankton due to the lack of phosphate at the bottom of the photic layer (discussed in Diaz and Raimbault, 2000). It is generally accepted that in such systems, biological consumption and subsequent export and remineralisation of nutrients in the upper ocean determine their vertical distribution (Anderson and Sarmiento, 1994). The consumption of nutrient to support planktonic production exhausts the surface sea layer and leads to oligotrophic conditions. This demand also generates the vertical concentration gradient driving an upward flux of dissolved inorganic nutrients regenerated in deeper waters. We can assume that the upward diffusive supply of nutrients to the Surface waters was correlated to the concentration gradient across the thermocline and inversely related to the stability of the water column. The position of the thermocline is usually a major determinant of the position and sharpness of nutrient gradients (Conan et al., 1999). The increasing discrepancy between the two nutriclines toward east encountered during our study is coherent with the oligotrophic gradient but clearly identifies the Levantine basin where the gap between phosphacline and nitracline/thermocline increased drastically

BGD
7, 7315–7358, 2010

(∼130 m). The literature has previously reported such differences between nutriclines in the Eastern Mediterranean Sea, like 300–400 m in the South-Eastern Ionian Sea (Klein et al., 1999) or 600 m in the Levantine Basin (Ediger and Yilmaz, 1996). Krom et al. (2005) debated that the discrepancy between the phosphacline and nitracline in the Levantine basin could be due to the use of conventional micromolar methodology for nutrient determinations, as when phosphate is measured using nanomolar technology, small but detectable concentrations can be present. In their study, only one station in the Cyprus eddy is concerned by nanomolar measurements in both N and P, for the other stations nitrate was not determined in the same time by nanomolar technology (so nitrate can also be present above their NO_3 exhausted measured area), so it could be interesting to investigate more intensively and on a the whole eastern basin, this point during future studies. Crispi et al. (2001) clearly showed that the sole hydrodynamic regime (inverse estuarine circulation) was not sufficient to explain the oligotrophic status and that the trophic gradient between the Western and the Eastern Mediterranean was maintained in the long run by the biological pump. We can assume that the patterns observed during our study were the result of an unbalance and disequilibrium of the loads emitted in the basins, with greater inputs into the Western Mediterranean Sea. Riverine and atmospheric inputs all have N:P ratios that significantly exceed the Redfield ratio in both basins (Chap. 4.4 in Mermex group, 2010), and atmospheric deposition is the major external source of bioavailable N to the eastern basin (Krom et al., 2010). The downward fluxes of organic matter played then a role in sustaining and stabilizing the oligotrophy.

In the present study, POC and PON represented a minor percentage of total organic C and N throughout the water column and most (> 80%) of the organic matter was present as DOC and DON as previously observed for other oligotrophic waters (Béthoux and Copin-Montégut, 1988; Vidal et al., 1999). There was a systematic decrease in POM concentration with depth which reflects the progressive decomposition of labile organic matter by bacterial consumption and respiration. In oligotrophic areas, particle flux is generally low, but strongly reacts to localized and

BGD
7, 7315–7358, 2010

episodic mesoscale phenomena and is not always coupled with respect to surface ocean primary production (Lutz et al., 2002). Nevertheless, the estimations of fast sinking rates (Patara et al., 2009) is evidence of the biological pump efficiency in sequestering organic matter from the surface layer of the Eastern Mediterranean basin, which could be extended to the western basin. Aerobic decomposition of the sinking organic matter is supposed to produce a build-up of C relative to N and P, and N relative to P. Our measurements reinforce this view by showing an increase of C relative to N and P in POM for the western basin and in the ML for the eastern basin, but surprisingly, a decrease in N relative to P with depth in the whole Mediterranean Sea. It seems that N was recycled more rapidly than P below the BL during our sampling period. Krom et al. (2005) obtained similar results in the eastern basin. A possible explanation is a rapid recycling of P occurring within the BL while N was recycled less rapidly in the ML and DL. This clearly emphases the role of DOM in the export and mineralisation processes (discussed below). Indeed, the labile and semi-labile DOM fraction can be major sources of N and P for planktonic food webs via bacterial assimilation (Thingstad and Rassoulzadegan, 1995). The downward fluxes of DOM may comprise an important fraction of the deep matter export in C and N (e.g., Vidal et al., 1999; Pujo-Pay and Conan, 2003), rendering dissolved organic matter an important link between the BL, ML and DL layers.

At very low nutrient concentration, DOM could accumulate in the Surface waters suggesting that recycling processes were limited by nutrient availability (Pujo-Pay and Conan, 2003), particularly that of P in the case of Mediterranean Sea (Van Wambeke et al., 2002; Lucea et al., 2003). Bacteria require external nutrient sources to recycle DOM. Our present results confirm that DOC accumulated in surface in relation to the oligotrophic status, especially in the eastern basin. This accumulation was less important and not related to the oligotrophic gradient for DON and not-detectabled for DOP. Vertical trends in DOC and DON have been interpreted elsewhere as a result of nutrient limited phytoplankton production, continuing to fix carbon after running out of N and/or P. Krom et al. (2005) pointed out DOC and DON content in the surface of

BGD
7, 7315–7358, 2010

eastern Mediterranean waters as high as for other oceanic areas, despite the fact that primary productivity levels are much lower in the Mediterranean Sea. Our measurements extend this trend to the study of phosphorus element as well as for the whole Mediterranean, with concentrations ranging between 38–72, 3–6.5, and 0–0.1 µM for DOC, DON and DOP, respectively. These values are in the range of average oceanic values given in Hansell and Carlson (2002), i.e. 35–90, 1.5–7.5, 0–0.4 µM for DOC, DON and DOP.

Despite a high surface variability encountered especially for nutrient concentrations (Schroeder et al., 2010) and the relative homogeneity in deep waters, our investigation along the Mediterranean Sea transect allowed for clear differentiation between western and eastern basins. Our results show that both basins display different patterns, yet have some "biological" similarities. In contrast to the relative continuity observed in the surface layer, the deep nutrient distributions showed a net transition occurring at the Sicily Strait, between a "richer" western basin and a "poorer" eastern basin. The shape of the various isolines in the Sicily Strait illustrates the westward passage of the Eastern Overflow Water (EOW), cascading down to the strait in western deep waters (Millot et al., 2006). Its chemical signature was clearly nutrient deprived. These exchanges (west-east in surface and east-west deeper) are of great importance in the Mediterranean-Atlantic nutrient flux exchanges because EOW comprises a fraction of waters which flow into the Atlantic, across the Gibraltar strait. Moreover, Millot et al. (2006) demonstrated that outflows through the various Mediterranean straits have been continuously changing during the last two decades. The functioning of the western basin could be impacted not only by changes in nutrients surface sources but also by changes in deep nutrient source, a major source for open sea. In theory, the elemental ratios in the deep ocean can only change on timescales comparable to residence times of the major nutrients ($\sim 10^4$ years for NO_3 and PO_4, Falkowski and Davis, 2004) but the Mediterranean Sea is characterized by very short ventilation and residence times (~70 years) when compared to the other oceans (500–1000 years). Krom et al. (2010) have recently discussed the build-up of high N:P ratios in eastern deep

BGD
7, 7315–7358, 2010

waters, prior to export via the Straits of Sicily. Such tendancies suggest that alteration of the deep Mediterranean characteristics could rapidly impact the surface layers.

In our study, the C:N:P ratios in DIM, POM and DOM pools within the BL largely exceed the Redfield ratios, as a consequence of the severe deficiency in phosphorus under summer conditions due to biological uptake. This deviance from Redfield was effectively observed in both western and eastern BL, where nutrients are depleted, but when nutrient concentrations increase (i.e. in the ML and DL) the slopes of the linear regression plots tended toward the Redfield values, whatever the P-deficiency in the mineral pool. While nutrient supply sets an upper limit to the biological production, the planktonic organisms exert a tight control on the elemental distribution, affecting the chemical composition of both DOM and POM (Redfield et al., 1963). Considerable knowledge can be gained based on the investigation of the C:N:P stoichiometry like particle formation, settling and mineralization. The Redfield stoichiometry reflects the interaction of multiple processes, including the acquisition of the elements by plankton, the mineralization by bacteria, as well as various losses of nutrients (burial in the sediments, outgassing to the atmosphere...). It is achieved during maximum cell growth rate in nutrient-sufficient conditions (Geider and La Roche, 2002) but when nutrient limitation is imposed on microbial populations, an offset in the C:N:P ratios is observed (Conan et al., 2007). Under limiting conditions in N and/or P, some photoautotrophic organisms can store C as lipid or carbohydrate (Karl et al., 2001), thereby increasing their C:N and C:P ratios. Also, stoichiometry could be impacted by the predicted increase of DIC in seawater. For example, heterotrophic bacteria would be indirectly affected by rising DIC, which is likely to lead to successive changes in the quality of organic matter. In green algae this increase can lead to higher protein content and increases cellular N quotas whereas in diatoms, it increases the C:P and N:P ratios and decreases the C:N ratios.

To summarize our observations and produce a final budget for the Mediterranean Sea, we propose a novel representation of the system (Fig. 9), separating the western from the eastern basin which considers the three previously defined layers as BL, ML

BGD
7, 7315–7358, 2010

and DL. We assumed that the average ratio of two elements represents a stock, and that the slope of the linear regression plots represents a net flux (see results section). Then, we hypothesize that in the BL, the dominant fluxes were from mineral to POM by biological consumption (i.e. the slope of mineral plots), then from POM to DOM by excretion, lyses or grazing (i.e. the slope of POM plots), and from DOM to nutrients by mineralization processes (i.e. the slope of DOM plots). In the ML and DL layers, we reverse the flux from POM to nutrients because nutrient uptake was supposed to be weak and because the main source of nutrients is the biological material sinking from the upper layers, and remineralized in deep layers. The link between the three layers is symbolized by the POM downward flux, the nutrients upward flux and DOM exchanges. We then compared the functioning of the two basins and the transfer along the water column, in considering the Redfield ratios as a reference.

The stoichiometry observed in the mineral compartment revealed a clear longitudinal gradient (Fig. 9). On the vertical dimension, the relative P-depletion increased by a factor 3 from BL to ML in the western basin (84 to 250 for N:P) and only by a factor 2 in the eastern basin (120 to 250 for N:P). In the western basin, this depletion also increased deeper (i.e. 250 to 400 for N:P) whereas it was quite constant (250–300 for N:P) in the eastern basin. As previously discussed, a vertical evolution was dominant for the POM pool and its composition changed through the water column. The POM stoichiometry in the BL was relatively homogeneous in the both basins (C:N~10), but slightly poorer in P in east compared to west. This was due to similar net composition of influx, but outflux richer in C and N for west (C:P = 160–95 for west-east). In the western basin, POM progressively becomes enriched in C relative to N and P with depth, whereas this modification was limited between BL and ML in the eastern basin. In the DL, POM reached similar stoichiometry in both basins, not far from the Redfield canonical values for N and P. The P deficiency becomes more evident when the highly P-depleted dissolved organic pool (C:N:P ratios higher than 1000:80:1 everywhere) is considered. DOM stoichiometry in the BL of the eastern basin showed a stronger P-deficit than the western basin one (C:P = 1050–1560 and N:P = 84–120 for west-east

BGD
7, 7315–7358, 2010

for similar C:N of 12–13), to reach surprisingly similar stoichiometry in the ML. Then, DOM continues to be depleted, in P in the western basin compared to the eastern one (Fig. 9).

Finally, during our study, despite a clear difference in N:P ratios between both basins, the input of nutrients in the BL allowed for synthesis of POM and DOM, slightly depleted in P compared to C and N but finally rather identical in their composition between both basins. Then this organic matter sinks and is mineralized by heterotrophic activity. The DOM accumulation in a system usually provides evidence for the refractory nature of DOM pool. In our case, organic phosphorus was consumed in the ML of the eastern basin, imposing a threshold of ~300:20:1 and ~3000:250:1 for POM and DOM, respectively. In the western basin, this threshold for DOM is higher and maximal in the DL (5000:400:1) (Fig. 9). The P-depletion of DOM is a general feature derived from a rapid recycling of the P-rich molecules within DOM (Thingstad and Rassoulzadegan, 1995; Thingstad et al., 2008). As a consequence, and as shown in our study, the C:N:P ratios increased drastically during regeneration processes. It is generally assumed that the same observation could be applied to the C:N ratio, as N is supposed to be recycled more rapidly than C. Yet, our data clearly show a noticeable stability of the DOC:DON ratio (12–13) in the whole Mediterranean Sea, surprisingly contradicting the fact that N is recycled faster than C in the DOM. We can hypothesize that this constancy indicates such a severe P-deficiency, that bacteria could not meet their needs in P required to use more DON than DOC. The west-east trophic gradient is then revealed by an increase in P-demand, in agreement with the deepening of the phosphacline compared to the nitracline observed along our transect, and by regeneration processes active all along the water column and intense in the ML for the western basin, but limited to the BL in the eastern basin. This conclusion partly explains why there is no clear deep nutrient maxima in the ML of the eastern basin contrary to the western one. In that case, OMZ could be formed in the ML of the western basin and then diffuse towards east. If we consider that the continental slope could also be a zone of OMZ formation, the pattern distribution of oxygen concentration supports this hypothesis (Fig. 7).

BGD
7, 7315–7358, 2010

As a consequence of the unique nature of the Mediterranean Sea, climate change effects are predicted to play a prominent role in modifying its nutrient status. The stoichiometric ratios (C:N:P) are powerful tools to model basic biogeochemical patterns of the Sea, to describe the functioning of complex food webs and to examine the processes that regulate marine biogeochemistry. Any change in nutrient stoichiometry is expected to affect rapidly microbial activity and diversity and subsequently, the whole ecosystem. Measurements of the C:N:P ratios and their anomalies in this extensive study as well as the general biogeochemical picture that has been drawn for the Mediterranean Sea will help future work and model approaches to identify and understand fundamental interactions between marine biogeochemistry and ecosystems and to examine the response of the environment to perturbations. For example, this study will help to validate/build multi-element biogeochemical models (like nutrient and biological production concepts that affect the calculations of the biotically effected CO_2 uptake by the ocean) and finally lead to a mechanistic understanding of the biogeochemical processes allowing to predict impact of environmental climate changes on the Mediterranean marine ecosystems.

Acknowledgements. This work is a contribution to the BOUM (Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean) project financed by the French national LEFE-CYBER program and the European commission SESAME IP. The authors thank the captain and the crews of the RV L'Atalante for outstanding shipboard operations. We really want to thank A. Murray for her helpful comments and corrections in the English language in the manuscript.

The publication of this article is financed by CNRS-INSU.

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BGD

7, 7315–7358, 2010

Table 1. Proportion (%) in C, N, P in the various compartments, inorganic, dissolved organic and particulate for the upper mixed layer (UML) and below 1000 m, in the western and eastern basins. ns means weak contribution of POM in deep waters.

	Western basin		Eastern basin	
	Surface	>1000 m	Surface	>1000 m
DIC	97.3±0.2	98.4±0.1	97.3±0.2	98.3±0.1
DOC	2.5±0.2	1.6±0.1	2.6±0.1	1.7±0.1
POC	0.2±0.1	ns	0.1±0.1	ns
DIN	24±8	73±2	9±4	62±4
DON	69±7	27±2	86±5	38±4
PN	7±2	ns	6±1	ns
DIP	37±9	98±2	16±9	98±4
DOP	46±7	2±2	59±7	2±4
PP	17±4	ns	25±4	ns

BGD
7, 7315–7358, 2010

Table 2. Mean physical characteristics and chemical content of the "Biogenic Layer (BL)", "Mineralization Layer (ML)" and "Deep Layer (DL)" for the western and eastern basins of the Mediterranean Sea during the BOUM cruise. The standard deviations, as well as minimal and maximal values, are indicated for each variable.

		Western basin			Eastern basin		
		mean	sigma	[min–max]	**mean**	sigma	[min–max]
BL							
Depth	m	**56**	43	[0–150]	**85**	56	[0–250]
Potential T	°C	**17.20**	4.15	[13.12–25.12]	**17.91**	2.99	[15.03–26.77]
Salinity		**38.05**	0.29	[37.30–38.44]	**38.61**	0.53	[37.29–39.44]
Sigma	$kg\,m^{-3}$	**27.74**	1.19	[25.05–29.03]	**28.03**	0.93	[14.79–29.10]
O_2	µM	**227**	18	[200–261]	**224**	13	[200–247]
CO_2	µM	**2315**	47	[2228–2391]	**2334**	42	[2221–2395]
PO_4	µM	**0.05**	0.06	[0–0.17]	**0.01**	0.02	[0–0.11]
NO_{3+2}	µM	**1.56**	2.19	[0–5.84]	**0.56**	0.88	[0–3.45]
NO_2	µM	**0.020**	0.025	[0–0.088]	**0.023**	0.033	[0–0.215]
NH_4	µM	**0.007**	0.012	[0–0.055]	**0.008**	0.008	[0–0.056]
DOC	µM	**58.7**	7.4	[45.3–69.4]	**61.5**	5.9	[49.4–72.4]
DON	µM	**4.7**	0.4	[4.1–5.5]	**4.7**	0.6	[3.5–6.3]
DOP	µM	**0.06**	0.02	[0.02–0.09]	**0.04**	0.02	[0.01–0.10]
POC	µM	**4.31**	1.73	[1.45–8.70]	**3.08**	0.90	[0.80–5.41]
PN	µM	**0.45**	0.17	[0.14–0.87]	**0.30**	0.11	[0.08–0.66]
PP	µM	**0.022**	0.009	[0.010–0.045]	**0.014**	0.005	[0.004–0.030]
ML							
Depth	m	**420**	352	[75–1250]	**500**	309	[150–1250]
Potential T	°C	**13.43**	0.32	[12.91–14.06]	**14.17**	0.54	[13.54–15.16]
Salinity		**38.50**	0.12	[38.11–38.70]	**38.83**	0.08	[38.67–39.01]
Sigma	$kg\,m^{-3}$	**29.02**	0.12	[28.58–29.11]	**29.11**	0.09	[28.79–29.19]
O_2	µM	**181**	8	[167–195]	**186**	9	[174–195]
CO_2	µM	**2395**	10	[2361–2412]	**2388**	16	[2319–2405]
PO_4	µM	**0.33**	0.07	[0.15–0.44]	**0.17**	0.05	[0.04–0.25]
NO_{3+2}	µM	**8.03**	1.42	[4.64–9.81]	**5.16**	1.00	[2.82–6.30]
NO_2	µM	**0.010**	0.005	[0–0.024]	**0.010**	0.008	[0–0.032]
NH_4	µM	**0.001**	0.002	[0–0.007]	**0.002**	0.004	[0–0.023]
DOC	µM	**42.9**	3.8	[37.6–53.3]	**44.0**	4.3	[37.5–54.1]
DON	µM	**3.5**	0.4	[2.5–4.1]	**3.5**	0.6	[2.1–5.4]
DOP	µM	**0.01**	0.02	[0–0.06]	**0.01**	0.02	[0–0.07]
POC	µM	**1.35**	0.28	[0.82–1.83]	**1.27**	0.28	[0.70–1.96]
PN	µM	**0.12**	0.04	[0.03–0.22]	**0.08**	0.04	[0.01–0.21]
PP	µM	**0.009**	0.005	[0.001–0.020]	**0.006**	0.003	[0.001–0.013]

BGD
7, 7315–7358, 2010

Table 2. Continued.

		Western basin			Eastern basin		
		mean	sigma	[min–max]	**mean**	sigma	[min–max]
DL							
Depth	m	**1875**	553	[1000–2900]	**2000**	528	[1000–3000]
Potential T	°C	**12.89**	0.03	[12.86–12.98]	**13.54**	0.07	[13.40–13.64]
Salinity		**38.48**	0.01	[38.46–38.49]	**38.76**	0.02	[38.72–38.79]
Sigma	$kg\,m^{-3}$	**29.11**	0.00	[29.11–29.12]	**29.19**	0.01	[29.18–29.2]
O_2	µM	**190**	4	[182–195]	**188**	3	[183–193]
CO_2	µM	**2394**	7	[2377–2404]	**2387**	4	[2378–2395]
PO_4	µM	**0.39**	0.02	[0.37–0.42]	**0.17**	0.01	[0.14–0.20]
NO_{3+2}	µM	**9.05**	0.22	[8.60–9.44]	**5.14**	0.19	[4.80–5.64]
NO_2	µM	**0.007**	0.003	[0–0.013]	**0.008**	0.011	[0–0.047]
NH_4	µM	**nd**	nd	nd	**nd**	nd	nd
DOC	µM	**39.9**	1.1	[37.9–41.9]	**41.1**	1.4	[38.4–43.9]
DON	µM	**3.3**	0.4	[2.9–4.3]	**3.1**	0.5	[2.1–4.0]
DOP	µM	**0.01**	0.01	[0–0.03]	**0.02**	0.02	[0–0.07]
POC	µM	**1.21**	0.37	[0.74–1.80]	**1.12**	0.33	[0.80–2.03]
PN	µM	**0.06**	0.03	[0.01–0.13]	**0.07**	0.03	[0.01–0.13]
PP	µM	**0.004**	0.003	[0.001–0.010]	**0.005**	0.002	[0.001–0.008]

BGD
7, 7315–7358, 2010

Table 3. C:N:P stoichiometry expressed as the slope and the intercept (b value) of the element-element regression line and the average ratio of measured concentrations in the western and eastern basins of the Mediterranean Sea and for pooled data during the BOUM cruise. To avoid infinitive ratios, we excluded data with concentration below the detection limit.

	Western basin			Eastern basin			Pooled data		
	Slope	b value	concentration ratio	Slope	b value	concentration ratio	Slope	b value	concentration ratio
NO_{3+2}:PO_4	22.9	0.3	25.5	27.9	0.3	38.1	23.3	0.6	33.25
DIC:PO_4	230	2315	27 036	232	2344	89 237	169	2344	65 432
DIC:NO_{3+2}	9.6	2315	4982	9.9	2335	4901	7.9	2337	4931
DON:DOP	20.9	3.5	162.7	15.2	3.8	160.8	17.3	3.7	161.4
DOC:DOP	284	41	1941	132	50	2055	189	47	2019
DOC:DON	8.9	12.4	12.1	8.1	18.8	13.0	8.4	16.6	12.7
PN:PP	20.7	0	19.8	18.8	0	18.8	19.6	0	19.2
POC:PP	163	0.4	256	116	1.0	235	137	0.8	243
POC:PN	8.1	0.6	13.3	5.4	1.1	14.0	7.3	0.7	13.8

BGD
7, 7315–7358, 2010

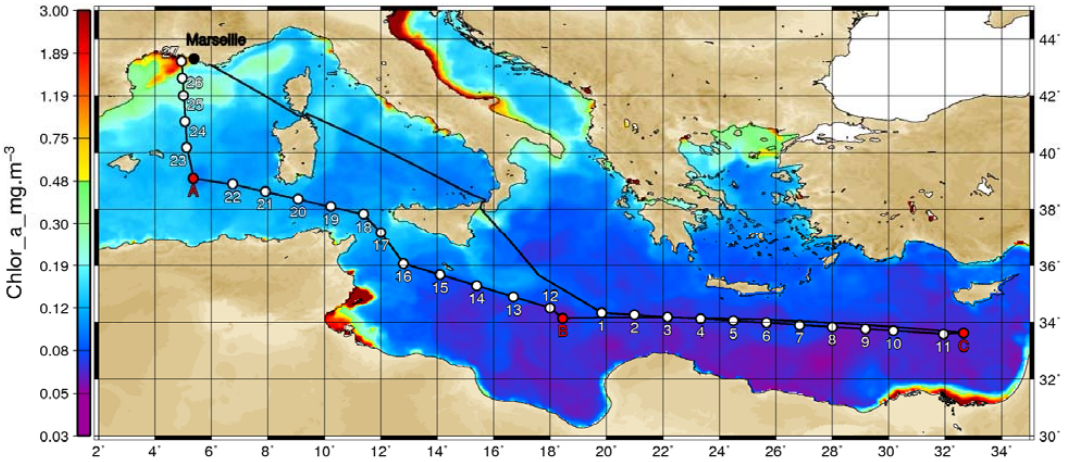

Fig. 1. Map of the BOUM cruise transect (16 June–20 July 2008) in the Mediterranean Sea superimposed on a SeaWiFS composite image of the sea surface chlorophyll a concentration (courtesy to E. Bosc). "Short duration" stations are regularly distributed and numbered from 1 to 27. The 3 "long duration (4 days)" stations A, B, and C in the western, Ionian and Levantine basins respectively are located near the centre of an anticyclonic eddy.

BGD
7, 7315–7358, 2010

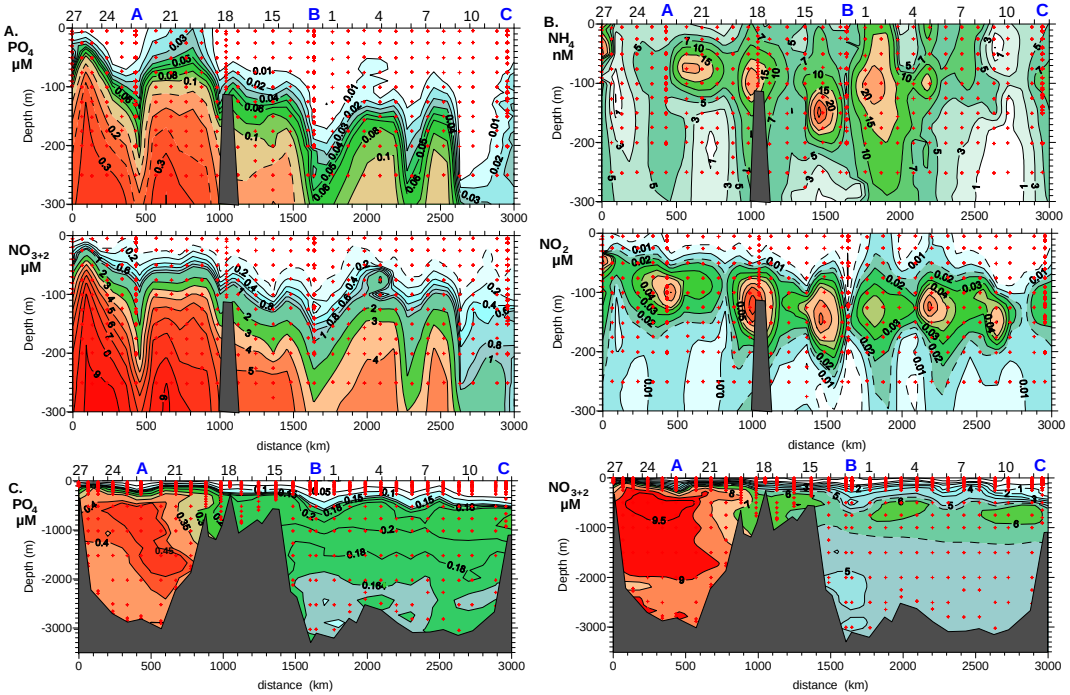

Fig. 2. Surface (0–300 m) vertical sections of **(A)** phosphate (PO_4), nitrate + nitrite (NO_{3+2}), and **(B)** ammonia (NH_4) and nitrite (NO_2) along the BOUM transect. **(C)** as in (A) for the whole water column. On the top X-axis, the station positions are indicated.

BGD
7, 7315–7358, 2010

Integrated survey of elemental stoichiometry (C, N, P)

M. Pujo-Pay et al.

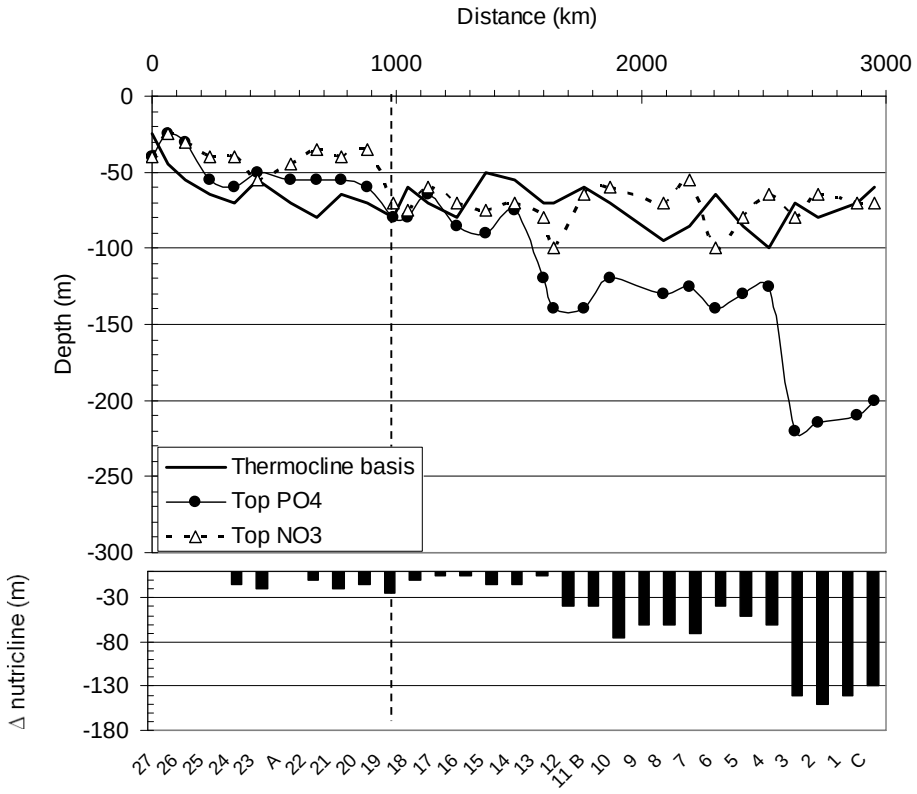

Fig. 3. Evolution of the depth of the thermocline basis, and the top of the nitracline and phosphacline along the BOUM transect. The vertical dashed line separates the western and the eastern basins. On the X-axis, the station positions are indicated. The limits are defined at the depth where the difference in concentration or temperature between two successive depths exceeds a threshold of 0.05 and 0.02 for NO_3 and PO_4 respectively, or fall under a threshold of 0.4 for temperature. The histogram shows the difference between the depths of the nitracline and phosphacline along the transect.

BGD
7, 7315–7358, 2010

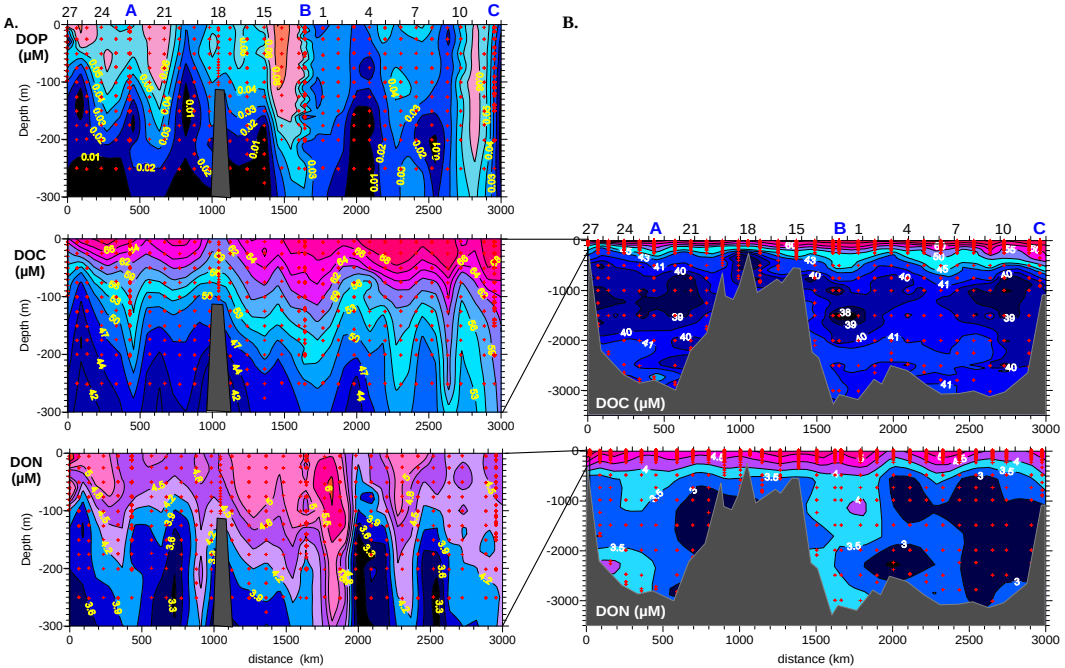

Fig. 4. Surface (0–300 m) vertical sections of **(A)** dissolved organic phosphorus (DOP), carbon (DOC), and nitrogen (DON) along the BOUM transect. **(B)** as in (A) for the whole water column, except for DOP which is undetectable in deep water. On the top X-axis, the station positions are indicated.

BGD
7, 7315–7358, 2010

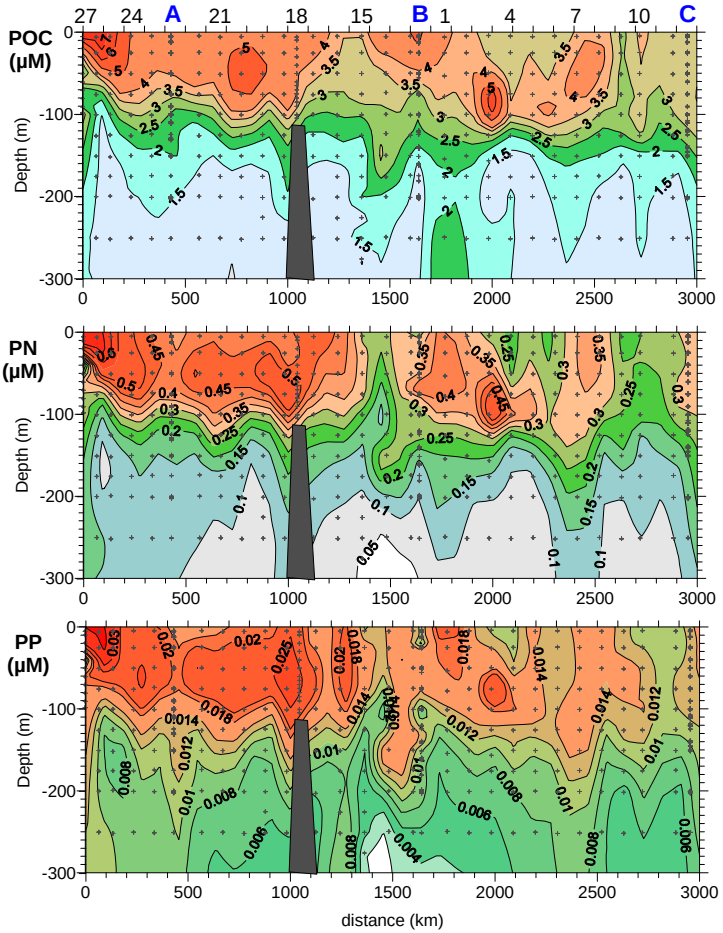

Fig. 5. Surface (0–300 m) vertical sections of Particulate Organic Carbon (POC), Nitrogen (PN) and Phosphorus (PP) along the BOUM transect (Deep sections not shown). On the top X-axis, the station positions are indicated.

BGD
7, 7315–7358, 2010

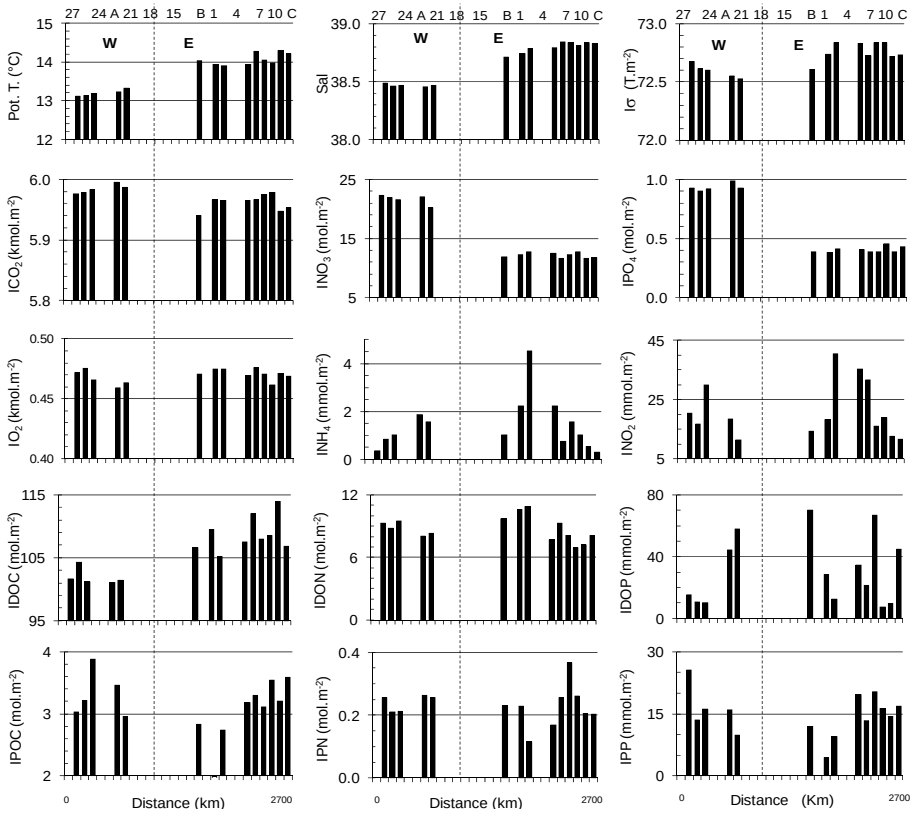

Fig. 6. Average potential temperature (Tpot) and salinity (Sal) in the 0–2500 m water column, and integrated quantities (for deep stations 0–2500 m) for density (Iσ), Dissolved Inorganic Carbon (ICO_2), nutrients (INO_3, IPO_4, INH_4, INO_2), oxygen (IO_2), Dissolved Organic Matter (IDOC, IDON, IDOP), and Particulate Organic Matter (IPOC, IPN, IPP) along the BOUM transect. The vertical dashed lines separate the western (left) and eastern (right) basins. On the top X-axis, the station positions are indicated.

BGD
7, 7315–7358, 2010

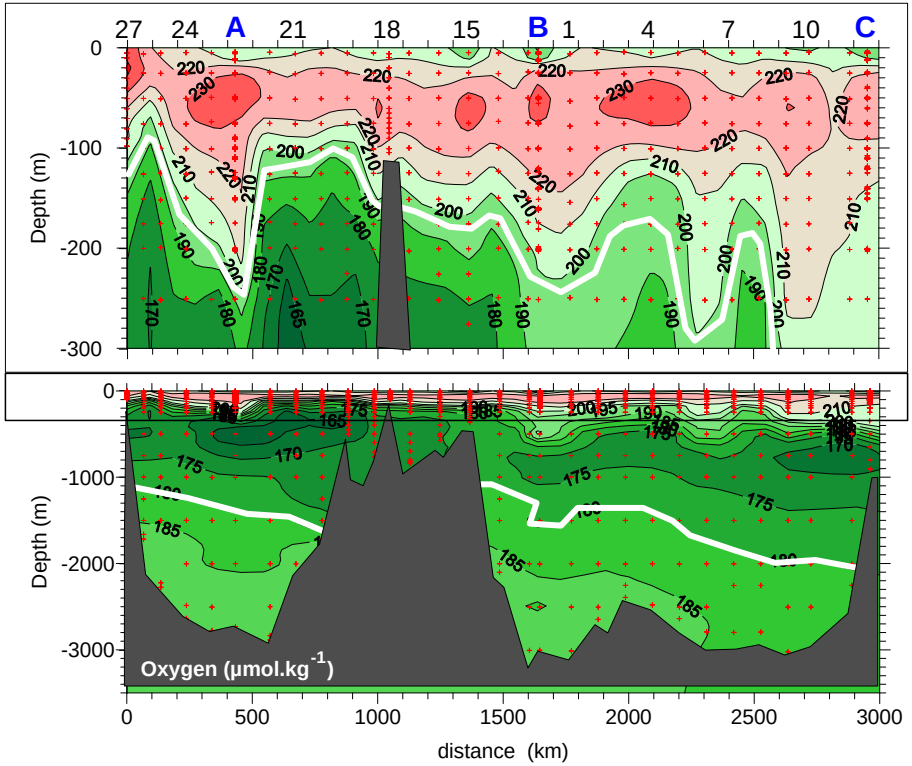

Fig. 7. Surface (up) and total water column (down) vertical sections of oxygen concentration along the BOUM transect. The white line in surface section illustrates the limit between the Biogenic Layer (BL) and the Mineralization Layer (ML) for a concentration of 195 µmol kg^{-1} following a relative maximum. The white line in the deep section illustrates the limit between the ML and the Deep Layer (DL) for a concentration of 180 µmol kg^{-1} following a relative minimum. On the top X-axis, the station positions are indicated. See text for further explanation.

BGD
7, 7315–7358, 2010

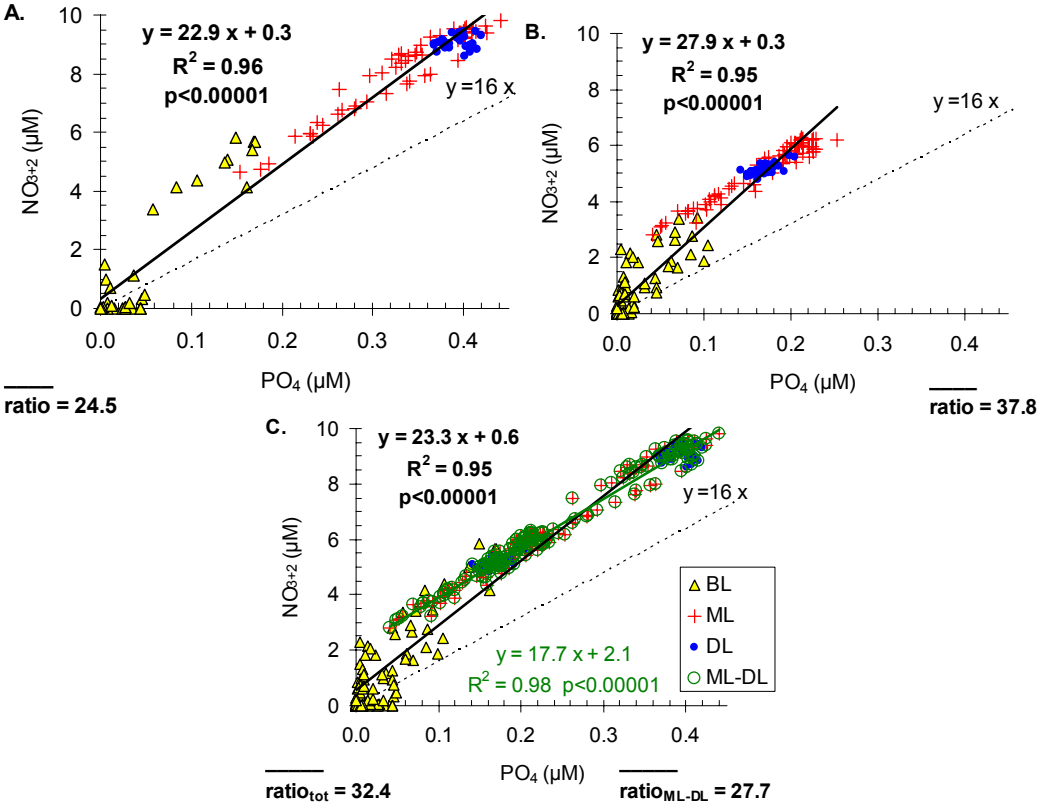

Fig. 8. Plots, linear relationships and probabilities for the slope between NO_{3+2} and PO_4 in **(A)** the western basin, **(B)** the eastern basin, and **(C)** the whole Mediterranean Sea, during the BOUM Cruise. Data are separated for the three layers defined in the text, BL, ML and DL. The Redfield value ($y=16x$) is indicated by the dashed line. For (C), data for BL have been excluded (ML-DL) to give rise to the second linear equation ($y=17.7\times+2.1$). The average ratio for data is given at the bottom of each graph.

BGD
7, 7315–7358, 2010

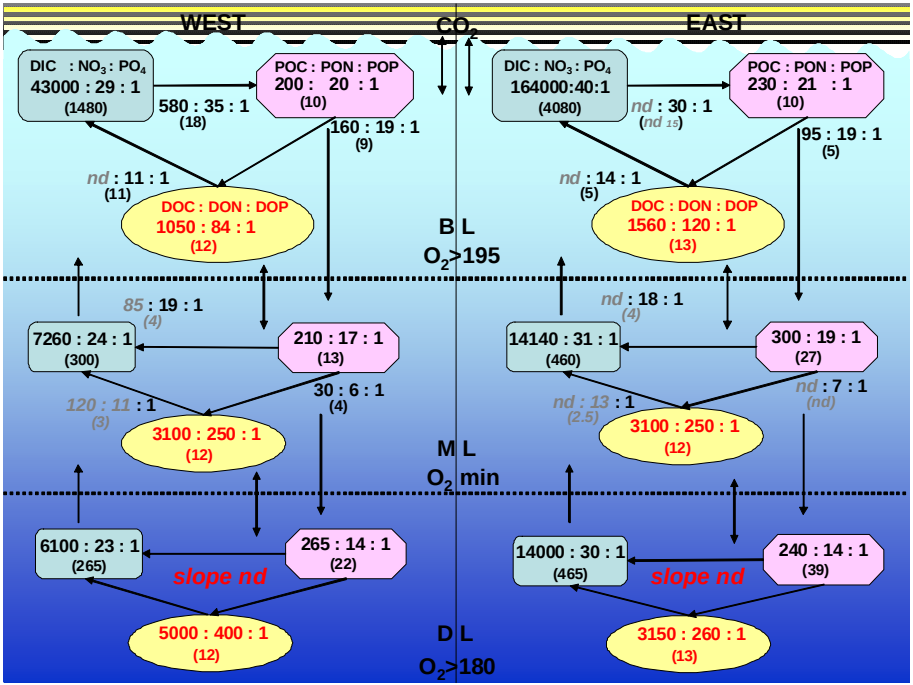

Fig. 9. Representation of the elemental C:N:P stoichiometry in terms of stocks and fluxes for the western (left) and eastern (right) basins of the Mediterranean Sea. The water column is divided in BL, ML and DL as justified in Fig. 7. The blue rectangular boxes with smooth corners symbolize the mineral compartment, the pink rectangular boxes with sharp corners symbolize the POM, whereas the yellow circles symbolize the DOM. In each box, the indicated ratios correspond to the average concentration ratios over the layer for C:P, and N:P. The values in brackets correspond to the average C:N ratio. On arrows, indicated ratios correspond to the slope of the linear regression equations between C:P, and N:P, respectively. The values in brackets correspond to the slope of the C:N plot regression. (nd) is for non significant linear relationship ($\alpha = 0.05$).

BGD
7, 7315–7358, 2010