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Open sea hydrographic forcing of nutrient and phytoplankton dynamics in a Mediterranean coastal ecosystem



Laura Arin*, Jorge Guillén, Mariona Segura-Noguera¹, Marta Estrada

Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta, 37-49, E08003 Barcelona, Spain

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ABSTRACT

The dynamics of inorganic nutrients and phytoplankton was studied along two transects located in the coastal area of Barcelona (NW Mediterranean), from March 2002 to March 2006. Similar seasonal variability patterns were observed in the four annual cycles and in general, the nutrient concentrations were highest in winter and lowest in summer. Two phytoplankton peaks, composed mainly by diatoms and nanoflagellates, were generally detected during the year with the main peak during winter-early spring, linked to different fertilization mechanisms, and a secondary peak generally found in autumn, probably related both to the new availability of nutrients due to the disruption of the thermocline and to freshwater inputs. During the rest of the year, with a stratified water column and low nutrient concentrations, phytoplankton remained at a low abundance and comprised mainly small dinoflagellates, although there was smaller scale variability conditioned by rainfall events and subsequent freshwater discharges. Despite the similarity of the seasonal patterns, there were interannual changes in origin of new nutrient inputs into the coastal zone and in the taxonomic composition of the winter-early spring phytoplankton maxima. The main source of nutrients for the winter-early spring maxima of 2003 and 2004 was river runoff, while fertilization events in the two following winters were mainly due to the intrusion, onto the Barcelona shelf, of intermediate waters in 2005, and of surface offshore waters, which also carried a different phytoplankton community, in 2006. These changes were linked to unusually cold and dry weather in the winters of 2005 and 2006, which resulted in strong vertical mixing and deep water formation events in the NW Mediterranean basin. The overall amount of nutrients provided to the coastal zone by offshore water fertilization was higher (2005) or equal (2006) than that provided by freshwater inputs in 2003 and 2004. Our findings highlight the importance of identifying the different sources of nutrients in understanding the dynamics of phytoplankton and for devising management strategies of the coastal environment.

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1. Introduction

The Mediterranean Sea is overall characterized by low primary production (Margalef, 1985), especially in its eastern basin although its oligotrophic character varies in space and time due to fertilization events which may considerably increase primary production. Coastal areas, in particular, may be much more productive than the open sea, in part because shallow depths favor vertical mixing of the water column and limit the dispersal of cells to aphotic depths, but also due to supplementary inputs of nutrients due to coastal

upwelling or freshwater discharges. The latter, in turn, may be more or less influenced by agricultural or urban wastewaters. In addition, coastal areas may be affected by oceanographic events occurring in the open sea, as in the NW Mediterranean, where one of the most important mechanisms of fertilization is provided by the strong vertical mixing in winter in the central divergence zone of the Liguro-Provençal region (Estrada, 1996; D'Ortenzio and Ribera d'Alcalá, 2009); years with intense mixing may bring more nutrients into the euphotic zone (San Feliu and Muñoz, 1971). The interplay between the intensity of this mixing and the position of the Catalan slope-shelf Front, which separates the relatively low salinity waters of the Catalan Current, which flows in anticyclonic sense, from the more saline waters of the central divergence, may control the arrival of offshore water masses and their nutrients into the coast.

In the NW Mediterranean, as typically happens in temperate and subtropical oceanic zones, the annual dynamics of phytoplankton

* Corresponding author.
E-mail address: larin@icm.csic.es (L. Arin).

¹ Present address: Department of Oceanography, Center for Microbial Oceanography: Research and Education (C-MORE), School of Ocean & Earth Science & Technology (SOEST), University of Hawaii, Honolulu, HI, USA.

present seasonal variability. A phytoplankton maximum is observed in winter-spring, after mixing processes brings nutrients from deep waters, while minimum concentrations are found in summer, when the water column is stratified and low nutrient concentrations are found in the photic layers (Estrada, 1996; D'Ortenzio and Ribera d'Alcalà, 2009). However, in coastal areas, especially when affected by urbanization, the seasonal patterns may vary (Mura et al., 1996; Vila and Masó, 2005; Guadayol et al., 2009; Llebot et al., 2011) due to the irregular supply of nutrients from land, oceanic and atmospheric origin (Cloern and Jassby, 2008).

In general, the phytoplankton community of the Mediterranean is quantitatively dominated (both in terms of abundances and biomass) by picoplanktonic cyanobacteria, mainly of the genera *Prochlorococcus* and *Synechococcus* (Siokou-Frangou et al., 2010), which present their maximum abundances mainly in summer (Agawin et al., 1998; Gutiérrez-Rodríguez et al., 2011; Estrada and Vaqué, 2013). However, the biomass of winter-spring phytoplankton bloom and other high chlorophyll-*a* (Chl-*a*) peaks tends to be dominated by diatoms and other nano and microphytoplankters (Siokou-Frangou et al., 2010). Margalef et al. (1957) and Margalef (1962, 1978) suggest the typical succession of nano- and microphytoplankton includes three main stages: 1) flagellates and fast-growing diatoms with a high surface:volume ratio which quickly react to an input of nutrients and need a high degree of turbulence in the water (winter-spring bloom conditions); 2) diatoms with a lower surface:volume ratio and moderate growth rate, adapted to suspension and able to thrive in transition situations between winter-spring and summer conditions, and 3) motile organisms with relatively low growth rates such as dinoflagellates, adapted to a high stability of the water column and low nutrient availability in the euphotic zone (summer conditions). Within this general framework, there are differences in the taxonomic composition of the different phytoplankton assemblages, which can be related to the history and characteristics of the water masses in which they develop. In particular, in coastal environments, the complexity of environmental interactions may result in a high variety of phytoplankton succession patterns.

Coastal zones are fundamental from socio-economical points of view and are subjected to a strong human pressure that results in eutrophication and other environmental problems. In the EU, the importance of healthy coastal ecosystems has been recognized by the Water Framework Directive (WFD, 2000/60/EC), which aims for a good ecological and chemical status of all European coastal waters by 2015. The phytoplankton is one of the biological indicators required by the WFD to evaluate this ecological status. Determining the different nutrient sources and fertilization pathways to better understand the dynamics of phytoplankton are important for such management purposes. With the aim of acquiring long term data to approach these questions, the Coastal Oceanographic Observatory (COO), established in coastal waters off Barcelona, has been obtaining a time series of oceanographic variables since 2002. This allows the investigation of the dynamics of nutrients and phytoplankton, in relation to both, local forcing due for example to land runoff, and the influence of hydrographic conditions in the open sea. Of particular interest, in this context, were the effects of the exceptional hydrographic conditions observed in the NW Mediterranean Sea during the winters of 2005 and 2006. During these periods, an unusual meteorological situation with air temperatures lower than the climatological average, high and persistent cold and dry winds from the north (López-Jurado et al., 2005; Font et al., 2007; Marty and Chiavérini, 2010), and a long period of low precipitation (2003–2005), increased the density of coastal surface waters and originated, during the winter of 2005 and 2006, an intense and persistent cascading of dense shelf

water that propagated along and across the continental slope (Canals et al., 2006; Font et al., 2007; Ulses et al., 2008; Palanques et al., 2012). Due to this situation, during these years, the convection process that produces the Western Mediterranean Deep Water covered not only the Gulf of Lions area, but also the Catalan and the western Ligurian sub-basins (Salat et al., 2006; Smith et al., 2008), resulting in an intense water column mixing that in 2006 reached a depth of 2000 m (Marty and Chiavérini, 2010; Palanques et al., 2012). As a consequence, unusually high nutrient concentrations were measured in open surface waters of the Ligurian Sea (DYFAMED site), with the subsequent development of high phytoplankton biomass (Marty and Chiavérini, 2010).

The anomalous hydrographic situation observed in the NW Mediterranean was also identified in the coastal waters of Barcelona (NW Mediterranean). Exceptionally high water densities (exceeding 29 kg m^{-3}) were recorded in this coastal zone during the winters of 2005 and 2006, suggesting that dense water formed in the Gulf of Lions and the Catalan shelves (Gulf of Roses) had reached, at least, the Barcelona shelf (unpubl. data). In March 2005, dense water generated from shelf-cascading was also identified along a transect between the central divergence zone of the Catalano-Balearic Sea and the Barcelona shelf by Salat et al. (2006). These authors suggested that the intensity of the cascading and convection processes had induced the rise of intermediate waters (especially Levantine Intermediate Water or LIW) to relatively shallow levels in the vicinity of the continental shelf. These phenomena, in addition to the increase of salinity in coastal waters due to the low rainfall, could have caused the weakening or disappearance of the Catalan Front. In March 2006, the characteristics of the coastal waters off Barcelona pointed also to an intrusion of offshore waters.

This work studies the dynamics of physico-chemical variables and (nano- and micro-) phytoplankton in the coastal waters off Barcelona during four annual cycles (March 2002–March 2006) monitored by the COO, with an especial emphasis in the changes related to the exceptional hydrographic situation of the winters of 2005 and 2006. We also discuss the relationship of these environmental conditions with a harmful algal event and with jellyfish outbreaks occurred during this period.

2. Material and methods

2.1. Sampling

The COO is located in front of the Olympic Harbor of Barcelona, and receives the influence of the Besòs River (17.7 Km length), which flows into the sea a short distance further north (Fig. 1a). This area of Barcelona has four storm sewer overflows (Fig. 1a) which discharge, at certain times, a great amount of freshwater from rainfall. The domestic and industrial waste waters from Barcelona, plus rain runoff, are processed in a treatment plant (which has a submarine outlet with the mouth located 3 km offshore, at 60 m depth), but in case of high rainfall, some overflows may discharge untreated residual water, together with rain runoff, into the sea. The Besòs River also discharges an important amount of treated waste water from neighboring urban and industrial areas. It is also likely that during strong rain storms, the river carries also some untreated water into the sea. Since March 2002, water samples have been regularly collected (usually once a month) at 8 stations (Stations 1.1 to 1.4 and 2.1 to 2.4, Fig. 1a) located in two transects perpendicular to the Barcelona coast, in water depths of 10 m (St. 1.1 and 2.1), 20 m (St. 1.2 and 2.2), 30 m (St. 1.3 and 2.3) and 40 m (St. 1.4 and 2.4; Fig. 1a). The transects were designed approximately 2.3 Km apart, in order to evaluate the spatial range of influence of the discharge of the Besòs River.

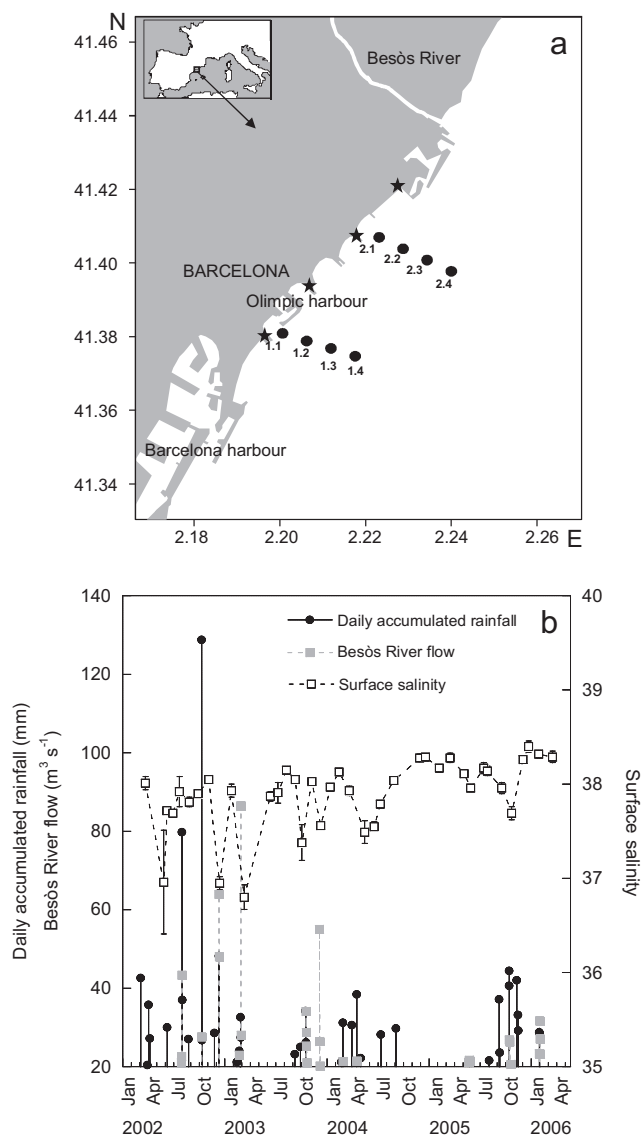


Fig. 1. a) Location of the 8 sampling stations of the Coastal Oceanographic Observatory of Barcelona (St. 1.1: 41°22.914'N, 2°11.970'E; St. 1.2: 41°22.836'N, 2°12.174'E; St. 1.3: 41°22.710'N, 2°12.504'E; St. 1.4: 41°22.542'N, 2°12.972'E; St. 2.1: 41°24.011'N, 2°13.146'E; St. 2.2: 41°23.892'N, 2°13.440'E; St. 2.3: 41°23.741'N, 2°13.782'E; 2.4: 41°23.490'N, 2°14.388'E). The stars show the location of the storm sewer overflows (Clabsa, Barcelona). b) Daily accumulated rainfall (mm), Besòs River flow (m³ s⁻¹) and median (± Median Absolute Deviation) surface salinity of each sampling day during the studied period. Note that only daily rainfall or river flow higher than 20 mm or m³ s⁻¹, respectively are shown.

At each station, CTD casts were performed and surface and bottom samples for dissolved inorganic nutrients (hereafter nutrients) and Chl-*a* determinations were collected. Salinity samples were also obtained from surface waters. Samples for phytoplankton enumeration were taken from the surface at Station 1.4 (1.9 km from the coast, Fig. 1a). Surface and bottom samples were taken with a bucket (between 0 and 0.5 m depth) and with a Niskin bottle (at 1.5 m above the bottom), respectively. This work analyzes the data of the first four annual cycles (March 2002–March 2006), but sampling at this coastal monitoring station is continuing. For simplicity, although they run from March of one year to March of the following, we will refer to the four sampling cycles as 2002/03, 2003/04, 2004/05 and 2005/06. Samples were assigned to the different seasons.

2.2. Analytical determinations and phytoplankton enumeration

Surface salinity was analyzed with an AUTOSAL salinometer and expressed using the practical salinity scale. Nutrient samples were frozen prior to their analysis. Soluble reactive phosphate, nitrate, nitrite, ammonium and silicate concentrations were analyzed with an AA3 autoanalyzer using the methods described in Grasshoff et al. (1999), with detection limits of 0.006, 0.015, 0.004, 0.020 and 0.017 μM, respectively. A method which replaces phenol with salicylate was used to measure ammonium (Bower and Holm-Hansen, 1980). An experiment performed during one of the cruises to test the effect of freezing on nutrient concentrations showed no significant differences between frozen and unfrozen samples except for nitrite, which presented significantly lower concentrations in the frozen samples (Segura-Noguera et al., 2011). For Chl-*a*, 100 ml of water were filtered through Whatman GF/F fibre filters (25 mm diameter), which were subsequently frozen until their posterior processing. For analysis, the filters were placed in 90% acetone for approximately 24 h in the dark and at 4 °C. The fluorescence of the extract was measured with a Turner-Designs fluorometer (Yentsch and Menzel, 1963). Phytoplankton samples were fixed with Lugol (first annual cycle) or formol-hexamine (the other three annual cycles) (Thronsdén, 1978), and organisms of sizes approximately >2 μm were counted using an inverted microscope (Utermöhl, 1958). Generally, one transect of the 50 ml chamber was observed at 400× to count the smaller (< 10 μm) and more frequent organisms, one transect or half of the chamber was observed at 200× to count cells of intermediate size (between 10 and 50 μm), and the whole chamber was scanned at 200× to count the large forms (>50 μm). To enumerate individual cells in *Phaeocystis* colonies, first the size of the colony was measured at 100×, then organisms from the colony were counted in one or two fields at 400× (using the micrometer to count at depth) and finally, colony cell content was calculated by extrapolating the number of *Phaeocystis* counted in the area of 400× to the entire area of the colony.

2.3. Phytoplankton biomass estimations

Phytoplankton biovolume in our samples was calculated using the volume values obtained by Arin et al. (2002a,b) for local phytoplankton samples. The volume of the *Phaeocystis* colonies was calculated according to Rousseau et al. (1990), assuming ellipsoidal colony shape. Carbon content for diatoms and dinoflagellates was estimated using equations (Segura-Noguera et al., 2012) obtained from published bulk analyses (humic oxidation and dry combustion) of cultured cells [$\log_{10}(\text{pgC}) = -0.48 + 0.78 \log_{10}(\mu\text{m}^3)$ and $\log_{10}(\text{pgC}) = -0.003 + 0.76 \log_{10}(\mu\text{m}^3)$, respectively]. Segura-Noguera et al. (2012) also propose a more accurate C conversion method based on X-ray microanalysis of single cells. However, we chose the bulk analysis equations as this was the only method available for the other phytoplankton organisms. Carbon content for coccolithophores was estimated from the conversion factor $\text{pgC cell}^{-1} = 0.109 (\mu\text{m}^3)^{0.991}$ (Montagnes et al., 1994) and for nanoflagellates from the conversion factor $\text{pgC cell}^{-1} = 0.433 (\mu\text{m}^3)^{0.863}$ (Verity et al., 1992). For free-living and colonial *Phaeocystis* cells and for mucilage carbon content, conversion factors found in Rousseau et al. (1990) were applied (10.8 pgC cell⁻¹, 14.2 pgC cell⁻¹ (Edler, 1979) and 335 ngC mm⁻³, respectively).

2.4. Statistical analyses

A non-parametric Wilcoxon-Mann-Whitney analysis was performed to test the significance of differences between variables

(KaleidaGraph 4.1 software). Statistical significance was accepted when $p \leq 0.01$.

3. Results

3.1. Meteorology and hydrology

The daily accumulated rainfall, the Besòs River flow and the median surface salinity during the study are shown in Fig. 1b. Seasonal median ($\pm$ Median Absolute Deviation – MAD) salinity values ranged from 37.81 ± 0.22 to 38.10 ± 0.18 at the surface and from 37.88 ± 0.28 to 38.20 ± 0.09 at the bottom (Table 1). The median annual surface salinity in the four annual cycles increased from 37.58 (2002/03) to 38.13 (2005/06), the result of a reduction in precipitation and Besòs River discharges. During the first two annual cycles (2002/03 and 2003/04) there were 23 days with a daily accumulated rainfall of more than 20 mm, while in the last two annual cycles (2004/05 y 2005/06) only 14 days reached this amount (data from a local meteorological station, Fig. 1b). Two major rain events (>50 mm of rainfall per day) were observed in July and October 2002. There were some discrepancies between the flow records of the Besòs River ($>20 \text{ m}^3 \text{ s}^{-1}$) and the amount of

rainfall in Barcelona, as the river discharge is also affected by precipitation in the upper part of the Besòs basin, but the relationship between both variables was evident (Fig. 1b). Strong precipitation events and high river flow were associated with marked decreases in surface salinity (Fig. 1b). The wettest seasons were autumn (seasonal accumulated rainfall >200 mm) in 2003, 2005 and 2006, and spring (195 mm) in 2004.

The temperature, salinity and density (sigma-theta) distributions during the four annual cycles at Station 1.4 show a marked seasonality, with maximum vertical homogeneity in the winter months (mainly January–February) and increasing stratification throughout spring and summer (Fig. 2a). The median water surface temperature (from the 8 sampling stations) in the summer seasons was 23.62 ± 1.08 °C ($\pm$ MAD), with a maximum of 28 °C observed during a heat wave in August 2003 (Table 1). At the bottom, the median summer temperature was approximately 4 °C lower than at the surface (19.90 ± 2.22 °C). In winter, the median ($\pm$ MAD) temperatures at surface and bottom were, respectively, 13.04 ± 0.54 °C and 12.62 ± 0.30 °C (Table 1). A marked seasonality, mainly driven by temperature changes, was also observed in water density (Fig. 2c). At the shallower stations (depth <10 m, data not shown), the annual cycle of water density followed similar patterns,

Table 1

Seasonal median ($\pm$ Median Absolute Deviation – MAD) and mean ($\pm$ Standard Deviation – SD) from the 8 sampling stations and value ranges of physicochemical variables and Chlorophyll-*a* (Chl-*a*) for the four annual cycles studied (March 2002–March 2006). Temperature (°C), Nutrients (μM), Chl-*a* ($\mu\text{g L}^{-1}$); DIN = Dissolved Inorganic Nitrogen; b.d. = below detection.

	Median $\pm$ MAD		Mean $\pm$ SD		Min		Max	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Spring								
Temperature	18.47 ± 2.02	14.96 ± 1.44	18.05 ± 2.47	15.71 ± 2.47	14.14	12.91	21.90	20.67
Salinity	37.81 ± 0.22	37.88 ± 0.28	37.73 ± 0.36	37.94 ± 0.27	36.42	37.41	38.15	38.29
Phosphate	0.18 ± 0.07	0.10 ± 0.02	0.27 ± 0.28	0.12 ± 0.07	0.04	0.03	1.41	0.35
Ammonium	4.78 ± 3.28	1.77 ± 1.05	7.32 ± 11.92	2.51 ± 2.62	b.d.	b.d.	65.95	10.08
Nitrite	0.43 ± 0.25	0.26 ± 0.12	0.59 ± 0.49	0.42 ± 0.40	0.04	0.04	2.43	1.63
Nitrate	0.56 ± 0.45	0.13 ± 0.13	0.97 ± 1.21	0.34 ± 0.51	b.d.	b.d.	6.35	2.39
DIN	5.72 ± 3.97	2.32 ± 1.06	8.88 ± 12.65	3.26 ± 3.01	0.06	0.05	68.76	11.51
Silicate	0.57 ± 0.40	0.44 ± 0.22	1.08 ± 1.39	0.64 ± 0.62	b.d.	b.d.	8.34	2.67
Chl- <i>a</i>	1.14 ± 0.47	1.42 ± 0.56	1.53 ± 0.98	1.81 ± 1.38	0.33	0.30	3.86	7.70
Summer								
Temperature	23.62 ± 1.08	19.90 ± 2.22	24.00 ± 1.61	19.58 ± 3.00	21.40	13.77	28.00	25.43
Salinity	38.03 ± 0.13	37.98 ± 0.11	38.00 ± 0.20	38.00 ± 0.14	37.59	37.72	38.60	38.63
Phosphate	0.08 ± 0.03	0.08 ± 0.03	0.10 ± 0.09	0.10 ± 0.08	0.01	b.d.	0.53	0.42
Ammonium	1.31 ± 1.04	1.73 ± 1.21	2.07 ± 2.55	2.10 ± 2.09	b.d.	b.d.	13.72	8.87
Nitrite	0.14 ± 0.07	0.13 ± 0.07	0.34 ± 0.40	0.17 ± 0.14	0.01	b.d.	1.79	0.77
Nitrate	0.27 ± 0.20	0.05 ± 0.05	0.36 ± 0.45	0.12 ± 0.16	b.d.	b.d.	2.71	0.68
DIN	1.81 ± 1.33	1.99 ± 1.23	2.77 ± 2.99	2.38 ± 2.17	0.04	b.d.	15.01	9.26
Silicate	0.64 ± 0.25	0.88 ± 0.26	0.68 ± 0.41	0.93 ± 0.41	b.d.	0.21	2.02	2.53
Chl- <i>a</i>	0.64 ± 0.29	0.64 ± 0.25	0.77 ± 0.51	0.88 ± 0.66	0.10	0.23	3.38	3.59
Autumn								
Temperature	16.00 ± 1.90	15.74 ± 1.36	17.28 ± 3.34	16.37 ± 2.33	13.60	13.50	23.50	22.18
Salinity	38.01 ± 0.28	38.09 ± 0.20	37.88 ± 0.46	38.02 ± 0.30	36.51	37.18	38.53	38.40
Phosphate	0.13 ± 0.06	0.10 ± 0.03	0.19 ± 0.17	0.14 ± 0.14	b.d.	0.02	0.90	0.84
Ammonium	1.50 ± 1.19	0.94 ± 0.65	2.18 ± 2.37	1.15 ± 1.13	b.d.	b.d.	12.41	5.70
Nitrite	0.34 ± 0.10	0.26 ± 0.11	0.38 ± 0.23	0.29 ± 0.20	b.d.	0.01	1.44	1.06
Nitrate	0.97 ± 0.52	0.44 ± 0.28	1.06 ± 0.88	0.57 ± 0.42	0.02	0.05	4.81	1.64
DIN	2.98 ± 0.79	1.80 ± 0.65	3.62 ± 2.81	2.01 ± 1.19	0.06	0.21	16.53	7.27
Silicate	1.40 ± 0.37	1.35 ± 0.28	1.54 ± 0.72	1.37 ± 0.43	0.12	0.50	3.78	2.65
Chl- <i>a</i>	0.87 ± 0.30	0.65 ± 0.24	0.95 ± 0.38	0.75 ± 0.40	0.26	0.17	1.78	2.27
Winter								
Temperature	13.04 ± 0.54	12.62 ± 0.30	13.04 ± 0.72	12.60 ± 0.44	11.73	11.59	14.90	12.94
Salinity	38.10 ± 0.18	38.20 ± 0.09	37.92 ± 0.57	38.16 ± 0.20	35.01	37.42	38.41	38.43
Phosphate	0.17 ± 0.06	0.15 ± 0.04	0.29 ± 0.38	0.15 ± 0.06	0.06	0.03	2.09	0.37
Ammonium	2.67 ± 1.70	1.00 ± 0.77	6.17 ± 9.81	2.21 ± 2.45	b.d.	b.d.	57.92	11.88
Nitrite	0.37 ± 0.13	0.31 ± 0.12	0.62 ± 0.45	0.52 ± 0.44	0.16	0.11	1.72	1.46
Nitrate	1.81 ± 0.78	1.52 ± 0.68	2.90 ± 3.23	2.08 ± 1.71	b.d.	b.d.	21.91	6.86
DIN	5.56 ± 2.34	3.50 ± 1.40	9.69 ± 12.26	4.81 ± 3.66	0.86	0.62	65.89	18.56
Silicate	1.69 ± 0.64	1.68 ± 0.62	2.25 ± 2.08	1.71 ± 0.94	0.16	0.16	12.47	4.37
Chl- <i>a</i>	1.91 ± 0.83	1.75 ± 0.98	2.22 ± 1.30	2.36 ± 1.74	0.60	0.48	5.08	7.97

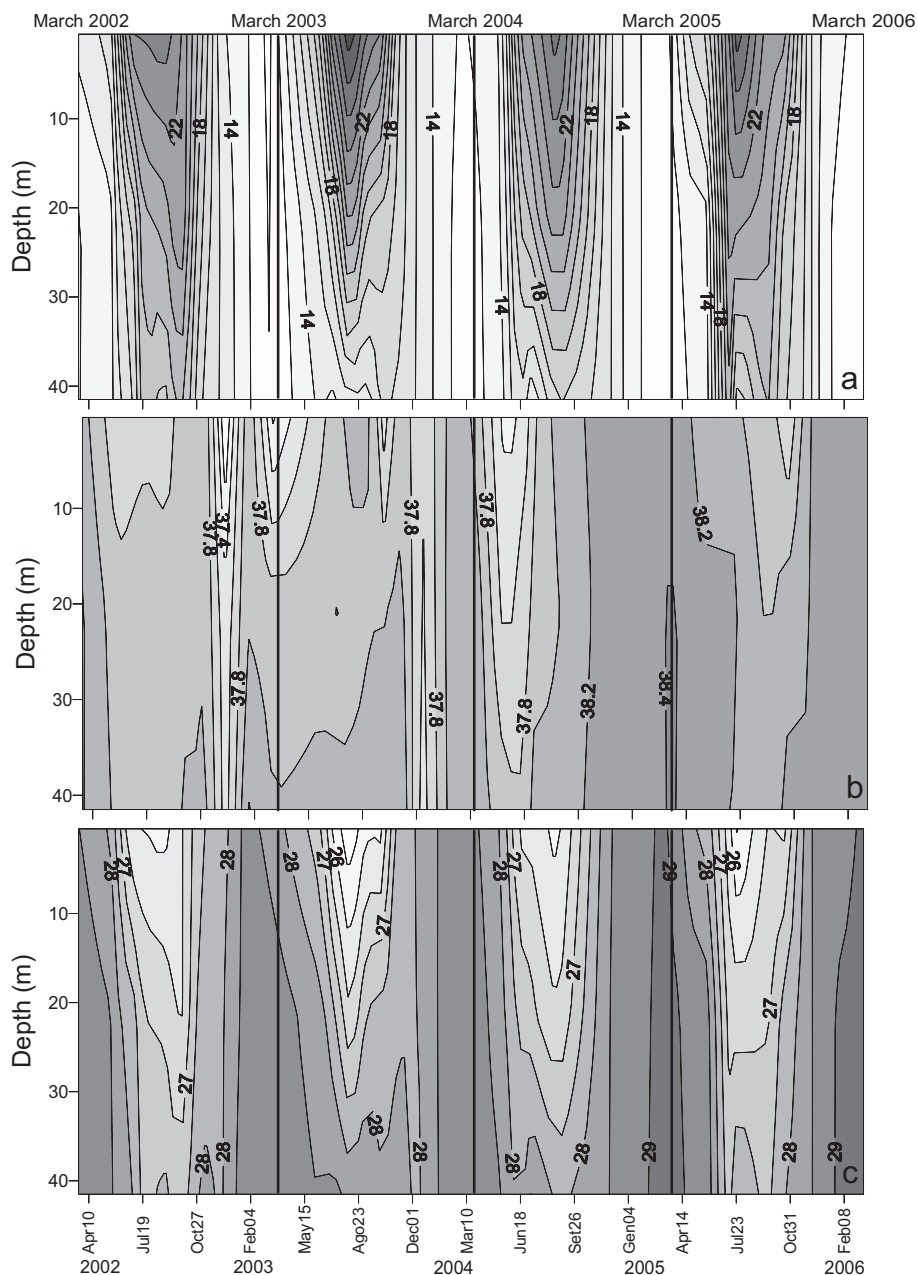


Fig. 2. a) Temperature ($^{\circ}\text{C}$), b) Salinity and c) Sigma-theta (kg m^{-3}) during the 4 annual cycles studied (March 2002–March 2006) at Station 1.4.

but the water column was generally well mixed. In the winters of 2005 and 2006, density anomalies exceeded 29 kg m^{-3} (Fig. 2c).

Temperature, salinity and density values along Transect 1 on March 10, 2003 and March 15, 2005 show that in March 2003, the freshwater discharges from de Besòs River (Fig. 1b) influenced the whole region, inducing a marked stratification in the upper layers of the water column (Fig. 3a–c). The low precipitation during winter 2005 (Fig. 1b) was reflected in an almost vertically homogeneous water column (Fig. 3d–f).

3.2. Nutrient and Chl-*a* distributions

Minimum and maximum median (and mean) values of phosphate, nitrate, nitrite and silicate were generally observed in summer and winter, respectively; the exception was the bottom median concentration of silicate, which presented a minimum in spring

(Table 1, Fig. 4b–d). Ammonium did not show any seasonal trend, with median values in general lower than $8 \mu\text{M}$ at surface and lower than $5 \mu\text{M}$ at the bottom in most of the samplings, except in two cases in which very high median concentration of ammonium (more than $18 \mu\text{M}$) were found at surface (27/05/02 and 15/03/05; Fig. 4e).

Throughout the first two annual cycles (2002/03 and 2003/04), high phosphate, nitrate and silicate concentrations at surface were associated with low salinity values, as indicated by the highly significant negative correlations between nutrients and salinity at the surface; at the bottom, there were significant negative correlations between salinity and phosphate ($p < 0.01$; 2002/03) and between salinity and silicate ($p > 0.05$; 2003/04, Table 2). In contrast, in the last two annual cycles (2004/05 and 2005/06), there was no correlation between nutrients and salinity at the surface and a significant positive correlation between salinity and nitrate and between salinity and silicate at the bottom (Table 2).

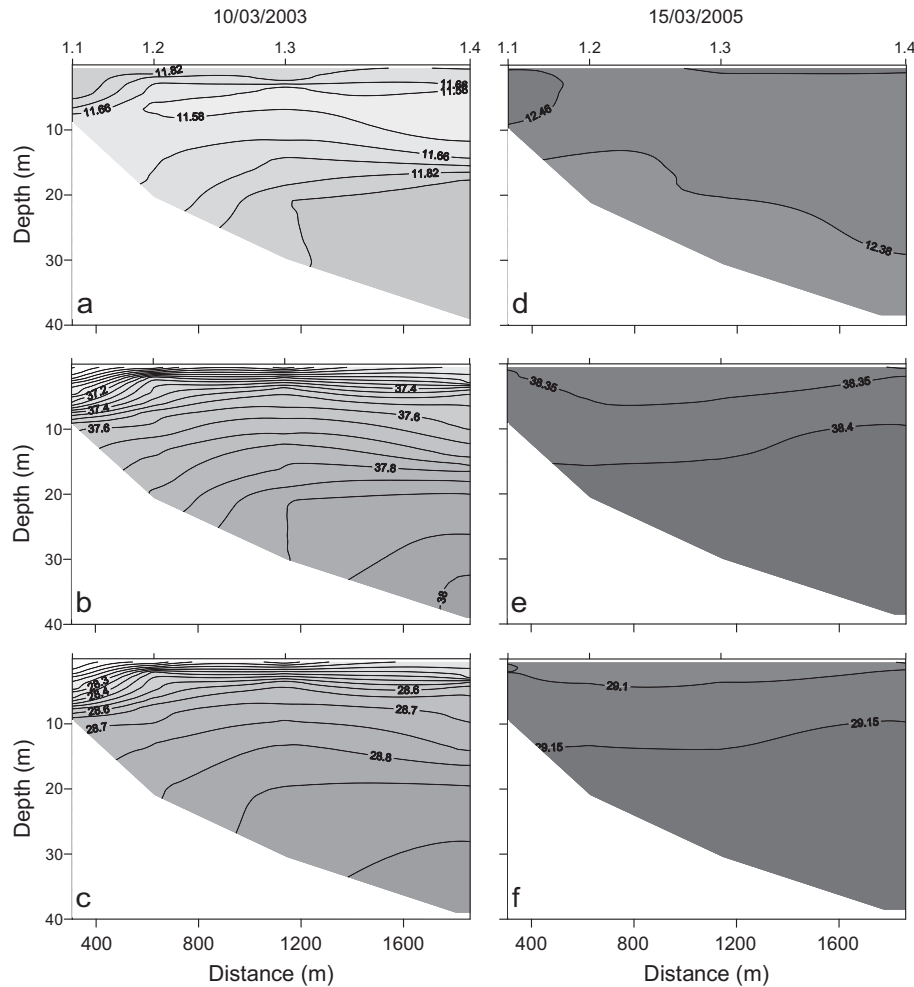


Fig. 3. Temperature ($^{\circ}\text{C}$), Salinity and Sigma-theta (kg m^{-3}) along Transect 1 (see Fig. 1a) for days 10/03/2003 (figures a, b and c, respectively) and 15/03/2005 (figures d, e and f, respectively).

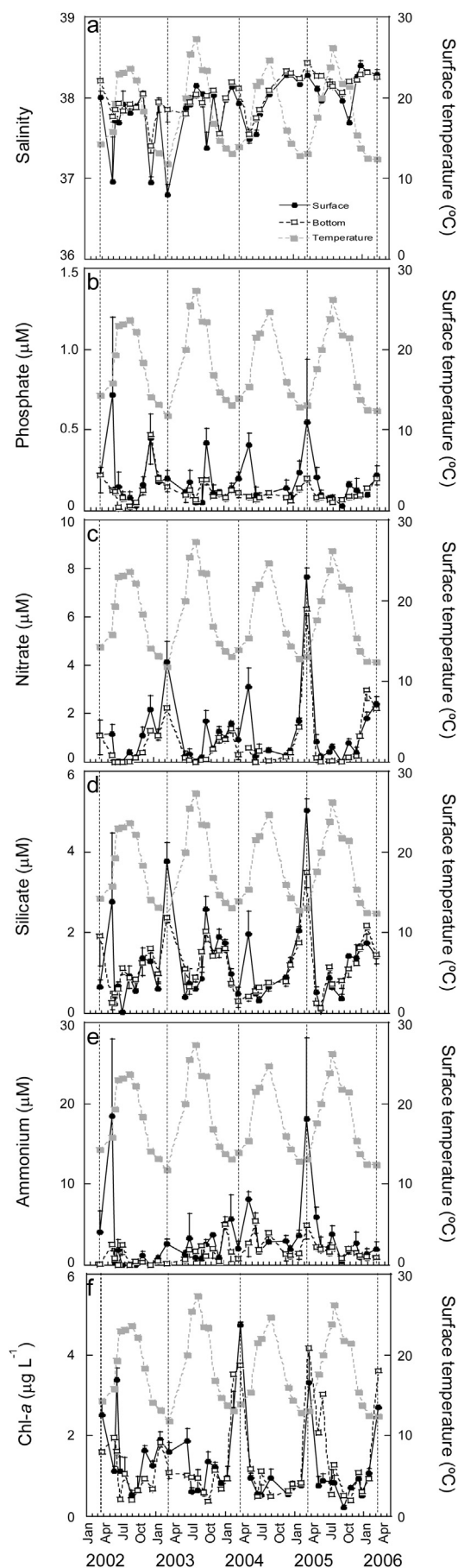
Salinity and nutrient (phosphate, nitrate, silicate and ammonium) concentrations corresponding to the nutrient maxima showed different dynamics in the winters of 2003 (10/03/2003), when nutrients were negatively correlated with salinity at surface, and of 2005 (15/03/2005), when nitrate and silicate were positively correlated with salinity at the bottom (Fig. 5). In 2003, an intrusion of nutrients associated to an important decrease in salinity in the surface waters, which could be attributed to freshwater runoff from the Besòs River, was evident in the offshore stations of transect 2 (Fig. 5 a–e). In contrast, in 2005, the relatively high surface and bottom concentrations of nitrate and silicate (with median values around $7 \mu\text{M}$ and $4 \mu\text{M}$, respectively) found along the two transects were not associated to freshwater inputs, as indicated by the corresponding salinity values, which ranged between 37.62 at surface and 38.43 at depth. In contrast, the high concentrations of phosphate and ammonium mainly at Stations 2.1 and 2.2 of 2005, associated with a slight decrease in salinity (Fig. 5f, j), were probably due to overflow from a storm sewer carrying a proportion of urban waste waters (characterized by high phosphate and ammonium concentrations).

The highest Chl-*a* concentrations were found in the winter-early spring period, usually in March (Fig. 4f, Table 1). The maximum Chl-*a* values reached during this period were around $5 \mu\text{g L}^{-1}$ and $8 \mu\text{g L}^{-1}$ for the surface and the bottom samples, respectively. A

lower Chl-*a* peak (lower than $2.0 \mu\text{g L}^{-1}$) was generally observed in autumn (Figs. 4f and 7a). In summer, the median Chl-*a* concentration was $0.64 \mu\text{g L}^{-1}$ both at surface and at the bottom (mean values were $0.77 \mu\text{g L}^{-1}$ and $0.88 \mu\text{g L}^{-1}$ for the surface and the bottom, respectively; Table 1). The minimum surface value, $0.10 \mu\text{g L}^{-1}$, was observed in August 2003. In general, at the end of spring-beginning of summer, the deepest stations presented higher Chl-*a* concentrations at the bottom than at surface (up to 10 times), with some values reaching almost $8 \mu\text{g L}^{-1}$ (Table 1).

The DIN:P ratio (DIN = ammonium + nitrite + nitrate) seasonal medians (for the surface and bottom samples of all stations in each annual cycle) varied between 5.9 and 64.7 in all sampled seasons with no particular seasonal trend (data not shown). However, when considering the relationship Nitrate:N:P (hereafter N:P) seasonal differences were observed, with seasonal median ratios <5.3 in spring and summer, 3.3–6.3 in autumn and 9.3–18.6 in winter. Silicate concentration (Si) always exceed nitrate concentrations in summer and autumn (seasonal medians of the Si:N ratio between 1.3 and 15.4). In winter the seasonal medians of the Si:N ratio were ≤ 1 (except in 2004 when the ratio was 1.20) and in spring were between 1.4 and 6.7 in 2002 and 2003, around 0.75 in 2004 and around 0.65 in 2005.

There were interannual differences in the median seasonal concentration of nutrients and Chl-*a* (Fig. 6). In winter, the highest median values of phosphate, nitrate and silicate were observed in

**Table 2**

Correlations between nutrient concentrations (phosphate, nitrate and silicate, μM) and salinity for the four annual cycles studied (March 2002–March 2006) for surface and bottom (r = Pearson correlation coefficient, P = significance level, n = number of samples; n.s. = non-significant).

Nutrient	Annual cycle	Surface			Bottom		
		r	P	n	r	P	n
Phosphate	2002/03	−0.73	<0.01	87	−0.42	<0.01	80
	2003/04	−0.62	<0.01	80	0.04	n.s.	70
	2004/05	−0.20	n.s.	64	0.18	n.s.	63
	2005/06	−0.20	n.s.	80	0.04	n.s.	80
Nitrate	2002/03	−0.72	<0.01	87	−0.18	n.s.	80
	2003/04	−0.62	<0.01	80	0.003	n.s.	70
	2004/05	−0.07	n.s.	64	0.47	<0.01	63
	2005/06	0.10	n.s.	80	0.30	<0.05	80
Silicate	2002/03	−0.83	<0.01	87	−0.11	n.s.	80
	2003/04	−0.72	<0.01	80	−0.26	<0.05	70
	2004/05	0.11	n.s.	64	0.63	<0.01	63
	2005/06	0.07	n.s.	80	0.22	<0.05	80

2005. Nitrate and phosphate concentrations in 2006 were also relatively high and not statistically different from those in 2005. Nitrate, phosphate and silicate concentrations in 2004 were significantly lower than in 2005 and 2006, while nitrate was significantly lower in 2003 than in 2005. Winter Chl-*a* concentrations were not statistically different throughout the period although the lowest median value was observed in 2005 (Fig. 6). In summer, nitrate concentrations were significantly higher in 2004 and 2005 than in 2002 and 2003, while in spring the highest median nitrate value was observed in 2004 (although the difference was only statistically significant between 2004 and 2003). There were no clear trends for the other variables. Nutrient concentrations and Chl-*a* in autumn were slightly higher in 2002 and 2003 than in 2004 and 2005; the differences were significant for all parameters between 2003 and 2004, for Chl-*a*, phosphate and silicate between 2003 and 2005 and for Chl-*a* between 2002 and 2004.

3.3. Phytoplankton biomass and composition

Diatoms and dinoflagellates presented a marked seasonal pattern; the maximum abundance of diatoms was observed in winter-early spring, while the highest dinoflagellate abundances were found mainly during the late spring-early summer months (Fig. 7a, b). Nanoflagellates (Fig. 7c) and coccolithophores (data not shown) did not show any seasonal trend.

Diatoms and nanoflagellates were the most abundant organisms in the autumn and winter-early spring Chl-*a* peaks. *Chaetoceros* spp. and *Pseudo-nitzschia* spp. were the most abundant diatom taxa in the winter-early spring peaks of 2002, 2003, 2004 and 2005. However, in 2006, the typical diatom community of previous years was partially replaced by high abundances of *Bacteriastrium delicatulum* and *Rhizosolenia* cf. *imbricata* (Fig. 8a). In this year, the phytoplankton community was clearly dominated by a bloom of *Phaeocystis* sp. (93% of the total abundance). Based on colony morphology, this *Phaeocystis* species was initially classified as *Phaeocystis globosa* (Arin et al., 2006), but later cell observations rejected this identification. Unlike previous years, when the

Fig. 4. Surface and bottom median values (± Median Absolute Deviation) from the 8 sampling stations for the four annual cycles (March 2002–March 2006): a) salinity, b) phosphate (μM), c) nitrate (μM), d) silicate (μM), e) ammonium (μM) and f) Chl-*a* (μg L⁻¹). Surface temperature (°C) is represented in all the graphics in order to indicate the annual cycle. The vertical discontinuous line indicates the sampling date of March.

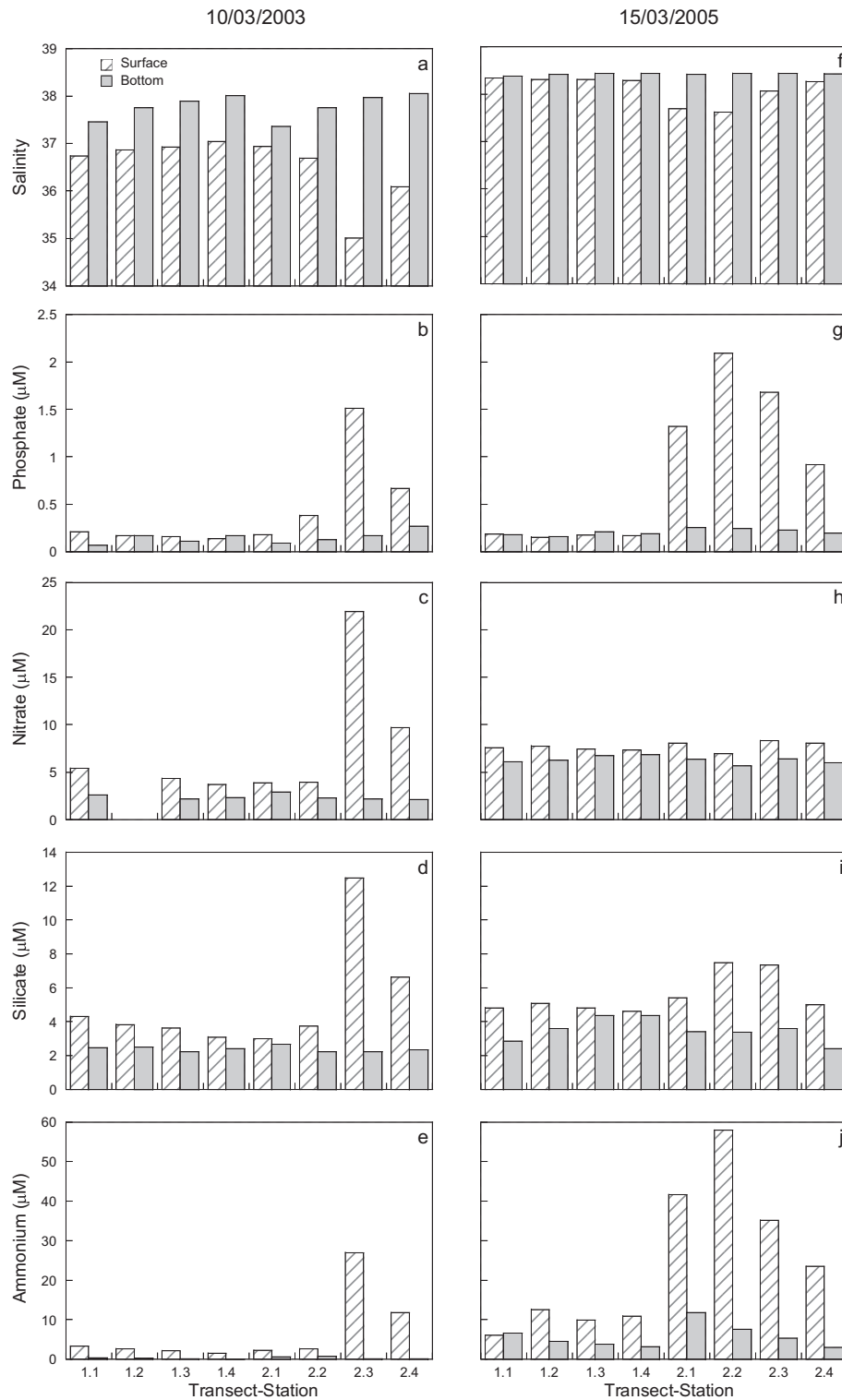


Fig. 5. Surface and bottom salinity and nutrient concentrations (phosphate, nitrate, silicate and ammonium, μM) for each sampling station for days 10/03/2003 (figures a, b, c, d and e, respectively) and 15/03/2005 (figures f, g, h, i and j, respectively).

biomass in terms of carbon was dominated by diatoms (more than 45% of total carbon), the nanoflagellate carbon contribution in 2006 (mainly due to *Phaeocystis*) was higher than that for diatoms when *Phaeocystis* mucilage is considered (approx. $32 \mu\text{g C L}^{-1}$; Table 3). *Asterionellopsis glacialis*, *Chaetoceros* spp. and *Pseudo-nitzschia* spp. were the most abundant diatom taxa in the autumn Chl-*a* peak

(Fig. 8a). The main contributors to the late spring-early summer maximum of dinoflagellates were *Scropsiella*-like spp. and small dinoflagellates (Fig. 8b). High abundances of nanoflagellates and dinoflagellates (mainly *Scropsiella*-like spp.) were responsible for the marked peak of Chl-*a* (more than $4 \mu\text{g L}^{-1}$) observed in June 2002 (07/06/2002; Fig. 7b, c and 8b).

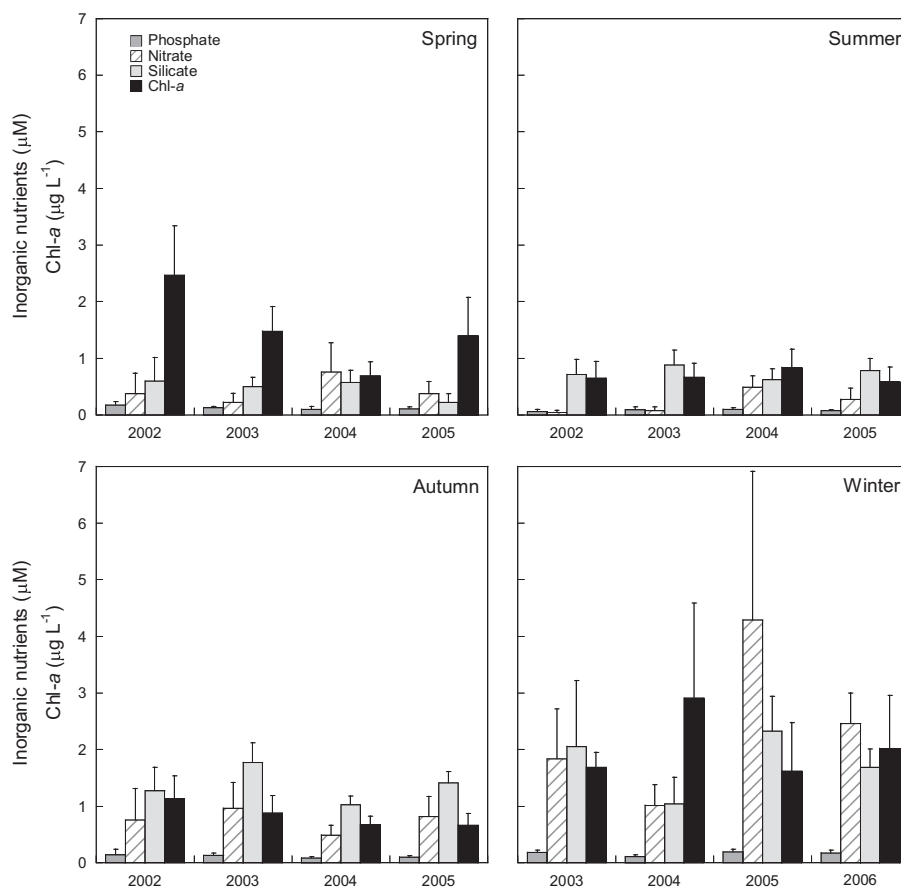


Fig. 6. Median ($\pm$ Median Absolute Deviation) of surface and bottom values for all stations sampled in each season of phosphate, nitrate and silicate (μM) and Chl-*a* ($\mu\text{g L}^{-1}$) in spring, summer, autumn and winter of each sampled year.

4. Discussion

4.1. Seasonal dynamics

In general, the observed seasonal patterns of nutrient and phytoplankton dynamics were similar to those reported for the Catalan Sea (Segura-Noguera et al., 2011) and other Mediterranean Sea areas (Siokou-Frangou et al., 2010). The highest nutrient concentrations (except ammonium) were found in winter, while minimum values were generally observed in summer (Fig. 4, Table 1). The main Chl-*a* peak, composed mostly by diatoms and nanoflagellates, was observed in the winter-early spring period, generally in March. A winter-spring phytoplankton bloom, as found in other temperate marine areas, is typical of the open waters of the NW Mediterranean Sea (D'Ortenzio and Ribera d'Alcalà, 2009) and has been associated with increasing daily irradiances and stabilization of the surface layer after winter mixing brings nutrients to the surface. However, in our study area, different fertilization mechanisms interacted to modulate the winter-spring bloom (see below). Chl-*a* generally remained at low values in summer, when the water column was stratified, and phytoplankton was mainly composed of small dinoflagellates (Figs. 4f, 7b and 8b). However, at the end of spring/beginning of summer, a layer with high values of Chl-*a* was generally observed near the bottom of the deepest stations. The origin of these high Chl-*a* layers (composed principally by diatoms) is the accumulation of nutrients (in part due to resuspension of sediment) and cells, which become trapped by the thermocline in layers close to the sediment, under sufficient solar irradiation (Guallar, 2013). The secondary Chl-*a* peak, generally

observed in autumn and also mainly composed by diatoms and nanoflagellates, probably originated from the enhanced availability of nutrients provided by the disruption of the thermocline and by the general increase of rainfall in autumn and the subsequent increment of freshwater discharges. This response of phytoplankton community to nutrient introduction linked to freshwater runoff has been observed in other coastal areas of the Mediterranean (Mozetić et al., 1998; Guadayaol et al., 2009) and other regions (Malone et al., 1988; Zhou et al., 2008). Rainfall events may also enhance phytoplankton growth by wet atmospheric deposition of nutrients (Paerl et al., 1990; Markaki et al., 2010). Superimposed on this seasonal pattern there was a smaller scale variability conditioned mainly by episodic strong rainfall events and subsequent freshwater discharges, which could include also storm sewer overflows, as presumably happened with the Chl-*a* and flagellate peaks observed on June 2002 (07/06/2002); this could be associated to the phosphate and ammonium inputs observed in the previous sampling (27/05/2002; Fig. 4b, e). The effect of freshwater runoff depends on the spatio-temporal scale considered. In the short term (hours to a few days), freshwater discharges may produce a dilution effect on the phytoplankton community, while later on the nutrients provided by the freshwater may enhance phytoplankton growth; the sampling frequency of our survey does not allow a more precise description of these processes.

4.2. Nutrient sources and phytoplankton dynamics

Although the four studied annual cycles presented generally similar seasonal patterns, the hydrographic changes that took place

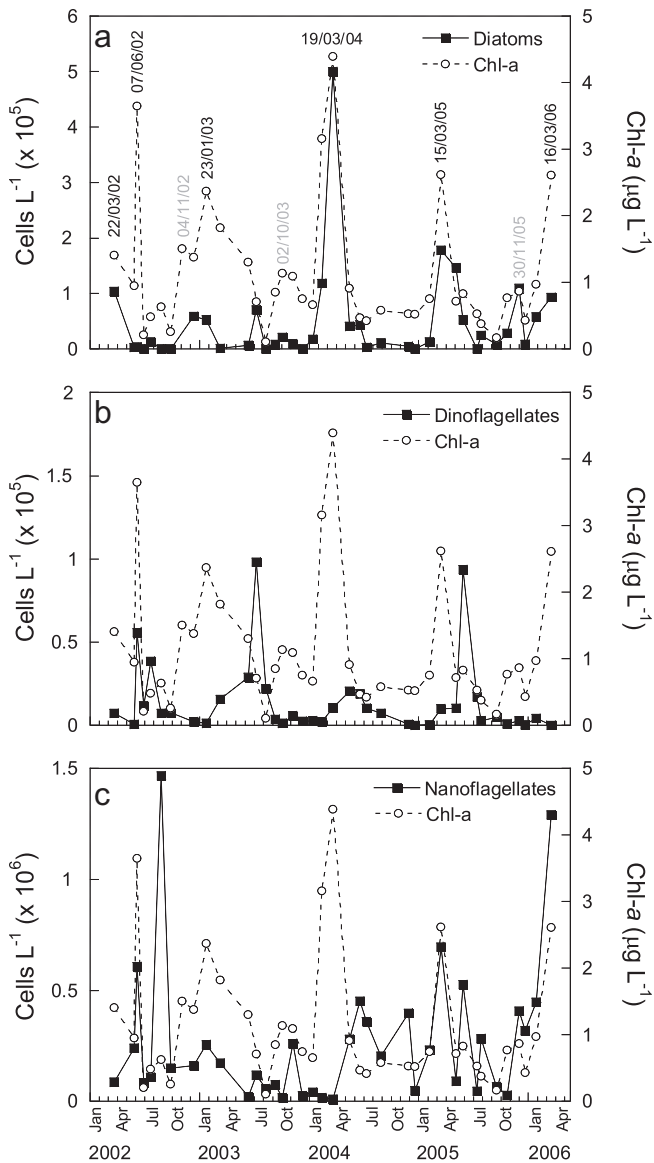


Fig. 7. a) Diatom, b) dinoflagellate and c) nanoflagellate abundances (Cells L^{-1}) for the four annual cycles (March 2002–March 2006) at Station 1.4. Chl-*a* ($\mu\text{g L}^{-1}$) values are represented in all graphics. The dates of the June 2002 peak, the annual winter-early spring Chl-*a* maxima (in black) and the autumn peak (in grey) are indicated on top of the corresponding peaks.

in the open Catalano-Balearic Sea during the winters of 2005 and 2006 induced marked differences in the nutrient and the phytoplankton composition of the Barcelona coastal ecosystem. Freshwater discharges from the Besòs River appeared to be the main nutrient source during the first two cycles (2002/03 and 2003/04), as indicated by the high significant negative correlations between major nutrients and salinity at surface (Table 2) and the observation that the higher nutrient concentrations mainly occurred in the upper layers, in association with lower salinities than those found at depth (Figs. 4 and 5a–e). In contrast, the non-significant correlations between nutrients and salinity at the surface, and the positive correlation of nitrate and silicate with salinity at the bottom during 2004/05 and 2005/06 suggest that a different process was responsible for the nutrient inputs. There was a substantial salinity increase from 2002 to 2006 (Figs. 2b and 4a), which could be linked to the reduction in rainfall and freshwater runoff observed in the last two years (Fig. 1b). In addition, there were only slight differences

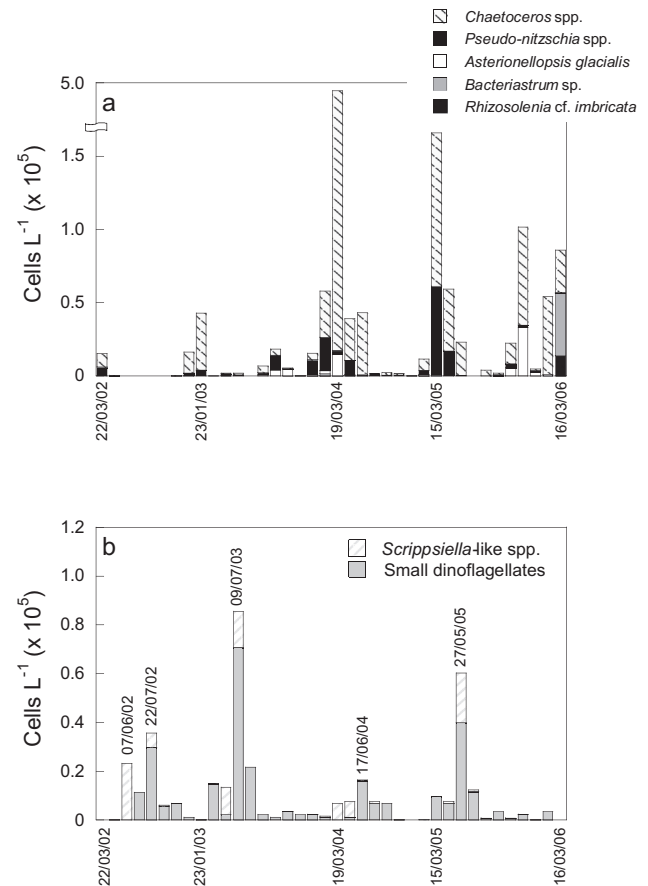


Fig. 8. Main diatoms (a) and dinoflagellates (b) (taxa that represent the 45% or more of the phytoplankton abundance in at least one of the observed samples, Cells L^{-1}) in the phytoplankton assemblages of the four annual cycles (March 2002–March 2006) at Station 1.4. The x-axis shows the dates when Chl-*a* presented its annual winter-early spring maximum (see Fig. 7a). The dates of the late spring-early summer maximum of dinoflagellates are indicated on top of the corresponding peaks in (b).

between the surface and bottom values of the nutrient peaks (especially of nitrate and silicate) observed in March 2005 and March 2006, suggesting that the input of nutrients was not limited to the superficial layers (Fig. 4c, d).

In March 2005, the observation that the high nitrate and silicate concentrations at the bottom were associated to salinities higher than 38.4 supports the idea that the lower half of the water column at the COO (Barcelona site; Fig. 5f,h,i) was affected by a particularly intense upwelling of dense and nutrient-rich intermediate waters (mainly LIW) as suggested by Salat et al. (2006). In turn, according to these authors, the strong LIW compensatory upwelling of winter 2005 was associated with an unusual situation of low precipitation and high persistency of northerlies over the NW Mediterranean, which caused an intensification of the convection processes and Deep Water formation in the central part of the basin.

The mean phosphate, nitrate and silicate concentrations obtained from the bottom values shown in Fig. 5 (0.21 μM , 6.30 μM and 3.50 μM , respectively) were lower than the mean values obtained by Segura-Noguera (2007) for the LIW (0.38 μM of phosphate, 8.32 μM of nitrate and 6.76 μM of silicate) for a data set of 28 cruises performed in the Catalan Sea. However, the mean Chl-*a* concentration at the COO was considerably higher than the average value obtained for the LIW by Segura-Noguera (3.90 $\mu\text{g L}^{-1}$ vs 0.04 $\mu\text{g L}^{-1}$), suggesting that phytoplankton growth had consumed part of the original nutrients after the arrival of the LIW to the photic layer.

Table 3
Abundance (10^4 cells L^{-1}), biovolume ($10^6 \mu m^3 L^{-1}$) and carbon biomass ($\mu g C L^{-1}$) of diatoms, dinoflagellates, coccolithophores and nanoflagellates for the winter-early spring phytoplankton maximum in surface waters of St. 1.4.* In brackets: biovolume and carbon values taking into account *Phaeocystis* mucilage.

		Diatoms	Dinoflagellates	Coccolithophores	Nanoflagellates
22/03/2002	Abundance	10.4	0.7	0.6	8.8
	Biovolume	98.8	66.2	1.4	5.8
	Carbon	6.94	6.89	0.1	1.4
23/01/2003	Abundance	5.2	0.1	0.2	25.4
	Biovolume	82.7	39.2	0.5	9.4
	Carbon	5.35	2.9	0.04	2.5
19/03/2004	Abundance	50.0	1.1	2.0	0.9
	Biovolume	797.2	108.9	5.0	0.9
	Carbon	51.92	10.34	0.5	0.2
15/03/2005	Abundance	17.8	1.0	3.2	69.6
	Biovolume	290.3	8.7	6.8	54.2
	Carbon	17.94	1.30	0.7	12.4
16/03/2006	Abundance	9.3	0.01	0.5	129.1
	Biovolume	259.3	13.0	1.1	43.2 (58461.6)*
	Carbon	14.53	0.80	0.1	13.2 (32.8)*

In March 2006, the water mass properties were similar to those observed in March 2005, although with slightly lower mean temperature, salinity and density values, suggesting also an intrusion of an offshore water mass into the Barcelona coastal zone in that year. The nutrient concentrations associated with this offshore water appeared to be lower than those provided by the upwelling of intermediate waters in 2005, but they were accompanied by greater phytoplankton carbon biomass (due to the bloom of *Phaeocystis* colonies) than in 2005 (Table 3), indicating a relatively higher level of consumption of the original nutrients than that found the previous year. In addition, the composition of the winter-early spring phytoplankton peak of March 2006 differed from that of the corresponding maxima of the previous years, in which the dominant taxa (in terms of carbon biomass) were diatoms from the genera *Chaetoceros* and *Pseudo-nitzschia* (Table 3, Fig. 8a). In the March 2006 peak, the phytoplankton was dominated by a bloom of *Phaeocystis* sp. and the typical diatom community was partially replaced by *Bacteriastrum delicatulum* and *Rhizosolenia* cf. *imbricata* (Figs. 7c and 8a). Due to the large amount of mucilage from *Phaeocystis* colonies, the carbon contribution by this organism in 2006 (when mucilage is considered) was higher than that provided by diatoms (Table 3). This phytoplankton assemblage appeared also, at the same time, in samples from several beaches (Cabrera, Mataró, St. Andreu de Llanvaneres and Cavaíó) along all the central coast of Catalonia (Sampedro et al., 2008). A similar phytoplankton composition, with the diatoms *Rhizosolenia* and *Bacteriastrum*, accompanied by nanoplankton (which could have included *Phaeocystis* spp., although no taxonomic details were reported for this group) was observed previously (Margalef et al., 1957, 1959; Margalef and Herrera, 1963) in a phytoplankton maximum that typically occurred during March–April in the Castellón coastal waters (NE Spain). This maximum (called the “second spring maximum”) appeared after the main late winter phytoplankton peak (observed in February–March, related to local fertilization by coastal upwelling and dominated by *Chaetoceros* spp.) and was associated with the presence of Atlantic offshore waters which invaded the coastal zone of Castellón, carrying also other oceanic plankton components such as *Vellela* and salps (Margalef et al., 1957; Margalef and Herrera, 1963). *Phaeocystis* is an important component of the winter-spring phytoplankton community in offshore waters of the NW Mediterranean, outside of the diatom-dominated patches that develop after deep convection in the Liguro-Provençal region (Siokou-Frangou et al., 2010; Estrada and Vaque, 2013). Small flagellates, with a large proportion of *Phaeocystis*, were dominant offshore of the Catalan Front in March 1985 (Estrada, 1991). A haptophyte-dominated phytoplankton community (including *Phaeocystis*) was also found in offshore

waters between Barcelona and the Balearic Islands, in February–March 1999, within a marked anticyclonic eddy of recent Atlantic Water (Estrada et al., 2003). In both cases, the flagellate-dominated community found offshore was clearly different to the coastal phytoplankton community, dominated by diatoms (Estrada, 1991; Estrada et al., 2003). These observations suggest that the phytoplankton composition of the March 2006 peak found off Barcelona and the central Catalan Coast, with a bloom of *Phaeocystis* and high abundances of *Rhizosolenia* and *Bacteriastrum*, resulted from an intrusion of offshore waters which had already been exposed to sufficient light to create a well-developed phytoplankton community. The water mass of March 2006 was colder and denser (mean temperature, salinity and density of 12.40 °C, 38.21 and 29.10, respectively), than the typical surface aged Atlantic Water found offshore of the Catalan Front, which separates this water mass from continental coastal waters (Salat et al., 2006). This discrepancy can be related to the intense offshore convection events observed at different sites of the NW Mediterranean, including the Catalan sub-basin (Font et al., 2007; Smith et al., 2008; Palanques et al., 2012), during winter 2005 and 2006, which produced an important mixing of the water column and changed the water mass properties of the offshore surface waters. In the Ligurian sub-basin (DYFAMED site), intense mixing during February 2006 produced an almost complete homogenization of the water column (0–2000 m), with surface water mass properties very similar to the deep water mass. As a result, the winter-spring density maximum of the surface waters (range 0–200 m) increased gradually from 28.92 in 2002 to 29.10 in 2006 (Marty and Chiavérini, 2010), thus explaining the high density of the March 2006 intrusion. Both the input of intermediate waters of March 2005 and the intrusion of offshore surface waters of March 2006 into the COO seem to have been favored by a weakening or disappearance of the Catalan Front (Salat et al., 2006).

Mechanisms relating stronger winter convection in the open Ligurian Sea to enhanced phytoplankton biomass and production over the region may include both the spreading of deep waters over a larger area and a higher degree of nutrient enrichment of the surface waters (San Feliu and Muñoz, 1971; Estrada, 1996). The expansion of dense intermediate waters reported by Salat et al. (2006) provides an example of the first mechanism, while Marty and Chiavérini (2010) document a positive relationship between stronger vertical mixing and higher nutrient concentration and phytoplankton biomass in surface waters of the Ligurian Sea DYFAMED station. At a regional scale, Volpe et al. (2012), based on remote sensing data, showed that the variability of the second Empirical Orthogonal Function (EOF) modes of sea surface temperature (SST) and log-transformed Chl-*a* values (LHCL) reflected a

link between phytoplankton blooms in the NW Mediterranean and some other areas like the southern Adriatic Gyres, and deep convection events. The spatial pattern of the LHCL EOF showed high positive values covering most of the NW Mediterranean north of 40° N (Volpe et al., 2012), indicating that the Chl-*a* enhancement effect of deep mixing covered our study area. Volpe et al. (2012) found exceptionally high values of LHCL EOF amplitude during 2005 and 2006, which could be attributed to the unusually strong winter convection (López-Jurado et al., 2005; Salat et al., 2006; Font et al., 2007) that took place during these years. Deep water formation during the winters of 2005 and 2006 was more intense than average not only in magnitude (Font et al., 2007), but also in spatial extent, since it occurred in atypical locations, such as the eastern Catalan sub-basin and the western Ligurian sub-basin (Smith et al., 2008).

During the studied period, the highest seasonal accumulated rainfall occurred in autumn (except in 2004, when the maximum accumulated rainfall was in spring). Therefore, the largest freshwater discharges from the Besòs River were generally observed in this season. The decrease in the Besòs River flow observed over the study period (Fig. 1b) probably caused the concentration of major nutrients in autumn to be slightly lower in the last two years than in the first two ones (Fig. 6). The interannual variability in the winter concentrations of phosphate, nitrate and silicate (Fig. 6) was probably linked to the relative influence of the different nutrient sources (mainly freshwater runoff in 2003 and 2004, and offshore intrusions in 2005 and 2006). Comparison of the nutrient concentrations in the two first and two later annual cycles indicates that, under circumstances as those observed in the winters of 2005 and 2006, the fertilization of the coastal zone due to oceanic waters can be as important as that originated from continental freshwater inputs.

4.2.1. Consequences of the exceptional winters 2005 and 2006 on the coastal ecosystem: harmful algal and jellyfish events

During July and August 2005, there was a very large invasion of the jellyfish *Pelagia noctiluca* on several beaches of Catalonia (Verónica Fuentes, personal communication) and other locations along the eastern Spanish coast (López, 2012). *Pelagia noctiluca* is an oceanic species that can reach the littoral when favored by certain wind and current patterns. The invasion of Catalan coastal waters by this oceanic jellyfish could have been facilitated by the weakening or absence of the Catalan Front which, when well developed, hinders the interchange between the water bodies inshore and offshore. In addition, the strong mixing processes observed in the NW Mediterranean basin during the winter of 2005, which resulted in large nutrient inputs to the euphotic zone and the posterior development of high phytoplankton biomass (Marty and Chiavérini, 2010), may have provided a strong primary production base for a trophic cascade effect and the build-up of a large biomass of oceanic jellyfish than was then transported to the coast. As *P. noctiluca* is a holoplanktonic epi-pelagic species, the effect on its population of an increase in the availability of planktonic food may be more direct than in the case of species with a benthonic phase. However, this would only be one of the reasons behind the very high proliferation of *P. noctiluca*, since other factors such as overfishing or an increased temperature of the water have also been suggested as possible causes of blooms of this and other jellyfish (Licandro et al., 2010; Brotz and Pauly, 2012). At present, due to the lack of long term data, any explanations for the variability of jellyfish abundance in the Catalan Coast remain highly speculative.

The very large invasion of jellyfish onto the coast during summer of 2005 caused problems to beach users. More than 8000 people turned to the Red Cross services in Catalonia due to jellyfish stings and many beaches had bathing restrictions. The *Phaeocystis*

bloom of March 2006 also caused a notable deterioration of the water quality of the coastal region along the central part of Catalonia, due to the accumulation of visible amounts of foam (this study, Sampedro et al., 2008). The foam is presumably originated from the deposition and degradation of ungrazed *Phaeocystis* colonies, simultaneously with windy meteorological conditions (Lancelot and Mathot, 1987), and may cause problems for local fishing (because of clogging of fishing nets) and the tourist industry. Both the jellyfish and *Phaeocystis* foam events illustrate how the hydrological changes produced by the exceptional weather conditions observed during winters 2005 and 2006 in open waters of the NW Mediterranean could cause adverse environmental and socioeconomic effects in the coastal zone.

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