



## Occurrence of winter phytoplankton bloom in the open southern Adriatic: Relationship with hydroclimatic events in the Eastern Mediterranean

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### ABSTRACT

The characteristics and intensity of winter phytoplankton blooms in the Open Southern Adriatic (OSA) were investigated from 1994 to 2012 by combining available unpublished and literature data on phytoplankton abundance, in situ chlorophyll-*a* (Chl-*a*) and satellite-derived Chl-*a* surface data. We used original data from Februaries 1994 and 1995 (phytoplankton, physico-chemical and meteorological data), the years affected by East Mediterranean Transient (EMT), and analysed them in relation to data available from literature for winters of 1997 and from 2007 to 2012. Chl-*a* satellite data from 1998 to 2012 was used to get insight into large scale bloom dynamics with fine temporal and spatial resolution. Particular attention was paid to the different circulation regimes in the Ionian Sea, namely to the anticyclonic and cyclonic phases of the Northern Ionian Gyre (NIG), both of which influence the physical and biochemical properties of the Southern Adriatic. The presented data demonstrate that winter blooms are persistent features of the OSA and they can occur during both anticyclonic and cyclonic phases of the Northern Ionian Gyre, but by different mechanisms. Moreover, intense blooms have occurred under certain hydroclimatic conditions such as the Eastern Mediterranean Transient (EMT) and extremely cold winter years. This was also confirmed by cluster analysis based on satellite Chl-*a* distribution.

### 1. Introduction

The open Southern Adriatic Sea (OSA) is oligotrophic, phytoplankton abundance and biomass typically are low and smaller sized species dominate (Viličić, 1991, 1989; Turchetto et al., 2000; Cerino et al., 2012). Nevertheless, some extraordinary peaks ( $\geq 10^5$  cells L<sup>-1</sup>) in microphytoplankton abundance for the OSA have been observed in April 1986 and 1987 (Viličić et al., 1989), March 1997 (Turchetto et al., 2000), September 2007 (Cerino et al., 2012) and March 2012 (Ljubimir et al., 2017).

The phytoplankton community in the OSA was not continuously investigated, with long gaps in time series and without any in situ data in some periods (1998–2006). Hence the timing and magnitude of phytoplankton blooms, as well as their recurrence (sporadic, under specific hydroclimatic conditions, or regular) are still unclear issues. Available data, based mainly on episodic samplings, suggest that the maximum of the total autotrophic abundances and biomass in the OSA occurred in spring (Viličić et al., 1989, 1995; Viličić, 1989; Socal et al.,

1999; Cerino et al., 2012). However, the latest investigations in the area indicated that phytoplankton blooms can occur in winter under favourable hydro-meteorological conditions (Ljubimir et al., 2017).

Satellite chlorophyll-*a* (Chl-*a*) data showed that, in general, phytoplankton blooms in the OSA are more frequent than we assumed before and that they happen with significant interannual variability (Santolero et al., 2003; D'Ortenzio and d'Alcala, 2009). This variability is dependent on the meteorological conditions that affect the open-ocean convection, which drives the mixing and uplifting of the nutrients from the rich intermediate layers into the euphotic zone (Gačić et al., 2002).

Besides meteorological conditions, incursion of different water masses into the OSA, especially during winter, modify not only thermal but also chemical properties (e.g. different nutrient load) in the area (Civitaresse and Gačić, 2001; Civitaresse et al., 2010). The Bimodal Oscillating System (BiOS) plays a role in this regard as it influences exchange between the Adriatic and Ionian Seas by driving decadal oscillations in the Northern Ionian Gyre (NIG). The anticyclonic phase implies advection of less saline Ionian water, diluted by Atlantic

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Water (AW), while the cyclonic phase, due to the absence of the AW, implies advection of salty Levantine/Cretan Intermediate Waters (LIW/CIW) into Adriatic Sea (Civitarese et al., 2010). The anticyclonic phase and AW advection presumably are accompanied by an increase of nutrients from upwelling at the periphery of the anticyclonic NIG (Civitarese et al., 2010). Conversely, cyclonic phase in the Ionian Sea depresses the nitricline along the borders of the northern Ionian, favoring inflow of nutrient-poorer but saltier waters. After entering through the Strait of Otranto, these saltier waters have the larger potential to produce dense water in the OSA by deep winter convection which injects nutrients into the euphotic zone, thereby stimulating primary production in the otherwise oligotrophic OSA (Gačić et al., 2002). The dense water formed through open-ocean deep convection in the south Adriatic Pit is the most important source of the Eastern Mediterranean Deep Water (EMDW) (Ovchinnikov et al., 1985). However, in the early 1990s, the source of EMDW originally located in the Adriatic Sea, shifted to the Aegean Sea (Roether et al., 1996). A newly formed water mass (Cretan Sea Overflow Water, CSOW) warmer and saltier than the EMDW of Adriatic origin, overflowed from the Cretan Sea and spread all over the deep eastern Mediterranean causing an abrupt change of the eastern Mediterranean circulation. This phenomenon is known as the Eastern Mediterranean Transient (EMT) (Klein et al., 1999; Malanotte-Rizzoli et al., 1999; Roether et al., 2007).

A direct consequence of this hydroclimatic change for the Adriatic Sea, was advection of nutrient-rich, oxygen-poor, less salty mid-depth water that upwelled to intermediate depths (i.e., Klein et al., 2000). As such, it flowed into the Adriatic and strengthened AW inflow (Vilibić et al., 2012). Klein et al. (1999) and Civitarese et al. (2010) suggested during the EMT period a local increase of primary production and autotroph biomass in the Southern Adriatic and Ionian Seas. However, the lack of appropriate biological and chemical observations from the EMT peak period did not allow a proper quantification of the related changes in the Mediterranean Sea. Moreover, satellite Chl-*a* observations for this period also do not exist. Therefore, this study concerns in detail phytoplankton, physico-chemical and meteorological data from February 1994 and 1995, years which were strongly affected by EMT and AW inflow into the Southern Adriatic. We try to assess the impact of this hydroclimatic change on the OSA biology. In addition, we analysed these data together with available literature data from winters of 1997 and 2007–2012 (Turchetto et al., 2000; Batistić et al., 2012; Cerino et al., 2012; Ljubimir et al., 2017) in the same area and under particular circulation regimes. The goal was to shed light to key factors in the development of OSA winter blooms. Finally, long-term satellite-derived surface Chl-*a* data from December 1997, the first available year, to March 2012, are analysed to provide insight into the frequency and timing of OSA winter blooms at decadal time scales.

The hypotheses were:

- winter phytoplankton blooms in the OSA are frequent and recurrent events over the years which account for a large fraction of OSA annual production and the inter-annual variability in phytoplankton abundance and biomass.
- the OSA is not exclusively oligotrophic, as has been concluded in earlier investigations.
- both circulation regimes of the NIG (anticyclonic and cyclonic) and accordingly the respective different water masses flowing into the Southern Adriatic shape the conditions for OSA winter blooms by enriching euphotic layer with nutrients. This happens directly, during the anticyclonic regime, by inflow of the nutrient-rich water within the euphotic layer and indirectly, during the cyclonic regime, when poorer in nutrients but saltier water preconditions the area for winter deep vertical convection which brings the nutrients from the depth to the surface. In both cases, wind induced mixing may enhance the effects.
- specific hydroclimatic events like EMT and extreme winter conditions are responsible for intensive bloom in the OSA.

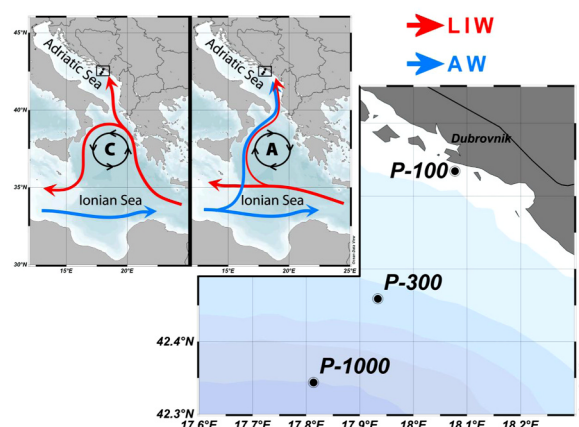


Fig. 1. Map of the Southern Adriatic Sea indicating the study area and sampling stations. Different circulation patterns in the Ionian Sea: A (anticyclonic) and C (cyclonic), after Gačić et al. (2010).

## 2. Material and methods

Field study was conducted at three stations (P-100, P-300, P-1000 indicating position over the isobate) in the Southern Adriatic (Fig. 1) with R/V “Bios” on February 27, 1994 and February 21, 1995. Number of samples collected in Februaries 1994 and 1995, and investigated parameters were presented in Table S1 in Supplementary material.

Vertical profiles of temperature (°C) and salinity (psu, practical salinity unit), averaged over 1-m intervals within the depth from 0 to 1000 m, were obtained with a multi-parametric CTD probe (Sea-Bird Electronics Inc., USA). Potential temperature and potential density anomaly (from here on referred to as potential density, in  $\text{kg}/\text{m}^3$ ) were referenced to 0 dbar. Water samples were taken with 5-L Niskin bottles at 0, 5, 10, 20, 50, 75, 100, 200, 300, 400, 600, 800, and 1000 m. Dissolved oxygen was determined by the Winkler method (Winkler, 1888), and oxygen saturation ( $\text{O}_2/\text{O}_2^*$ ) was calculated from the solubility of oxygen in seawater as a function of temperature and salinity (the equation number 2 in paper of Weiss, 1970; UNESCO, 1973).

Nutrients (orthophosphate— $\text{PO}_4$ , orthosilicate— $\text{SiO}_4$ , ammonium— $\text{NH}_4$  and nitrate— $\text{NO}_3$ ) were analysed by standard oceanographic methods (Strickland and Parsons, 1972) using a Perkin Elmer UV/VIS spectrophotometer (Lambda 15).

Phytoplankton samples were collected with 5-L Niskin bottles and preserved in 2% neutralized formaldehyde solution. Abundance was determined with an inverted microscope (Olympus IX 71) equipped with phase contrast. Depending on abundance, samples of 50–100 ml were settled in an Utermöhl chamber (Utermöhl, 1958). Microphytoplankton (MICRO, cells longer  $> 20 \mu\text{m}$ ) were counted at a magnification of 200x in 2–3 transects of the central chamber and 100x in transects along the rest of the base-plate. Nanophytoplankton (NANO, cells long 2–20  $\mu\text{m}$ ) were counted in 30 randomly selected fields along the chamber bottom at 400x. Whenever possible, taxa were identified to the level of species or genus using standard keys, monographs, and taxonomic guides.

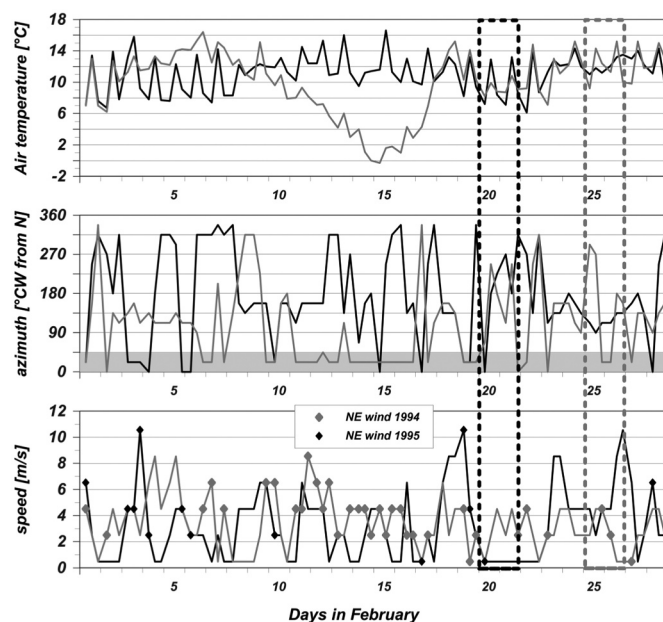
In order to present winter phytoplankton abundance and in situ Chl-*a* in the OSA over the years and during particular hydro-meteorological conditions we also used available literature data from 1997 and from 2007 to 2012 (Turchetto et al., 2000; Batistić et al., 2012; Cerino et al., 2012; Ljubimir et al., 2017). These data were presented in Table 1.

Daily satellite Chl-*a* concentrations, with a 4 km resolution, delivered by the Ocean Colour Climate Change Initiative (OC-CCI) project version 1.0 (<http://www.esa-oceancolour-cci.org/>) were used to provide insights into Southern Adriatic blooms after 1995. The OC\_CCI dataset, which covers the period September 1997 to July 2012, was created by band-shifting and bias-correcting MERIS and MODIS data to

**Table 1**  
Review of the available literature data on the highest winter abundances of the microphytoplankton (MICRO) and nanophytoplankton (NANO), maximum in situ Chl-*a* concentrations (Chl-*a*), and hydro-meteorological conditions at the deep (1000 / 1200 m) Southern Adriatic stations.

Month/Day/Year (source)	NIG circulation	salinity (AVG 200–800 m)	Weather before cruise	Vertical convection	MICRO (cells L <sup>-1</sup> )	NANO (cells L <sup>-1</sup> )	Chl- <i>a</i> (mg m <sup>-3</sup> )
March 4–17, 1997 (Turchetto et al., 2000)	R (AC/C)	From 200 m to bottom: 38.6–38.7 (Gačić et al., 2002)	Mild winter climatic condition (Civitarese and Gačić, 2001).	Almost complete absence of vertical convection (Gačić et al., 2002).	2.80 × 10 <sup>5</sup>	–	0.6
February 22, 2007 (Cerino et al., 2012)	AC	38.74	Mild, no cooling event, <i>bura</i> wind ≥ 8 m s <sup>-1</sup> * (DHMZ).	Medium-deep vertical mixing (Cardin et al., 2011).	5.66 × 10 <sup>4</sup>	2.20 × 10 <sup>6</sup>	–
February 19, 2008 (Batistić et al., 2012)	AC	38.76	Strong cooling event, <i>bura</i> wind > 10 m s <sup>-1</sup> * (DHMZ).	Deep vertical mixing (> 400 m).	1.40 × 10 <sup>4</sup>	6.80 × 10 <sup>5</sup>	–
February 23, 2009 (Ljubimir et al., 2017)	AC	38.71	Strong cooling event, <i>bura</i> wind > 10 m s <sup>-1</sup> * (DHMZ).	Deep vertical mixing (> 600 m).	4.32 × 10 <sup>3</sup>	3.74 × 10 <sup>4</sup>	0.67
February 8, 2010 (Ljubimir et al., 2017)	AC	38.73	Cooling event, <i>bura</i> wind ≥ 8 m s <sup>-1</sup> * (DHMZ).	Deep vertical mixing (February, > 600 m).	5.19 × 10 <sup>3</sup>	5.51 × 10 <sup>5</sup>	0.50
February 14, 2011 (Ljubimir et al., 2017)	R (AC/C)	38.72	Mild, no cooling event * (DHMZ).	Shallow.	7.48 × 10 <sup>3</sup>	2.18 × 10 <sup>5</sup>	0.18
February 18, 2012 (Ljubimir et al., 2017)	C/AC/C	38.69	Extremely cold winter, long-lasting strong cooling with <i>bura</i> wind in February 2012 (Mišanović et al., 2013).	Deep vertical mixing (February, > 800 m).	3.20 × 10 <sup>3</sup>	3.33 × 10 <sup>4</sup>	0.16
March 29, 2012 (Ljubimir et al., 2017)	C/AC/C	38.69	Mild, no cooling events * (DHMZ).		5.20 × 10 <sup>5</sup>	3.43 × 10 <sup>5</sup>	4.86

Abbreviations: NIG circulation: AC = anticyclonic, C = cyclonic; \*DHMZ = Croatian Meteorological and Hydrological Service. R = reversal years when NIG turned from anticyclonic to cyclonic and vice versa.



**Fig. 2.** Time series of air temperature, wind direction, and wind speed at the Dubrovnik meteorological observatory (7, 14, 21 h). Symbols in the speed plot correspond to NE wind episodes (directions between 0° and 45° azimuth, CW = clockwise from north). Thick dotted rectangles denote in situ sampling dates. Colour code: grey for February 1994, black for February 1995.

match SeaWiFS data and by merging the datasets with a simple average.

Meteorological parameters such as air temperature and wind were extracted from monthly climatological reports issued by the Croatian Meteorological and Hydrological Service (DHMZ) for the on-shore Dubrovnik meteorological station.

To track different circulation regimes of the North Ionian Gyre (NIG), we used average temperature and salinity values from 1993 to 2012 in the 200–800 m depth layer in the Southern Adriatic from the Medatlas database (MEDAR, 2002). A five-degree polynomial curve is fitted to the data in order to capture the interannual temporal changes and to associate them with the periods of the cyclonic and anticyclonic circulation in the NIG (Fig. 13), as in Civitarese et al. (2010). Number of data points per year and coefficients for the five-degree polynomial used are presented in Supplementary material (Tables S2 and S3).

Cluster analysis was used to analyze the variability in satellite Chl-*a* over seasons (December, January, February and March) and among years (Legendre and Legendre, 1983). An agglomerative, hierarchical clustering algorithm based on Bray-Curtis similarity matrix and Ward's method for determination of group linkages was used. Chl-*a* concentrations were logarithmically transformed [ $\log(x + 1)$ ] before analysis. Statistical analyses were performed using PRIMER v6 software (Clarke and Gorley, 2006).

### 3. Results

#### 3.1. Ecological conditions in Februaries 1994 and 1995 in the OSA

##### 3.1.1. Meteorological conditions

Fig. 2 shows time series of air temperature, wind direction and speed in February 1994 and 1995, respectively. The only significant cooling/mixing event in 1994 occurred on 14–16 February, two weeks before the in situ sampling. It was associated with a cold, dry NE wind – known in the region as *bura* – of gentle to moderate intensity. Even though the wind speed did not exceed 10 m s<sup>-1</sup> for the whole month, *bura* episodes were quite frequent. A year later, in February 1995, there were no significant cooling events, and only in two occasions the wind

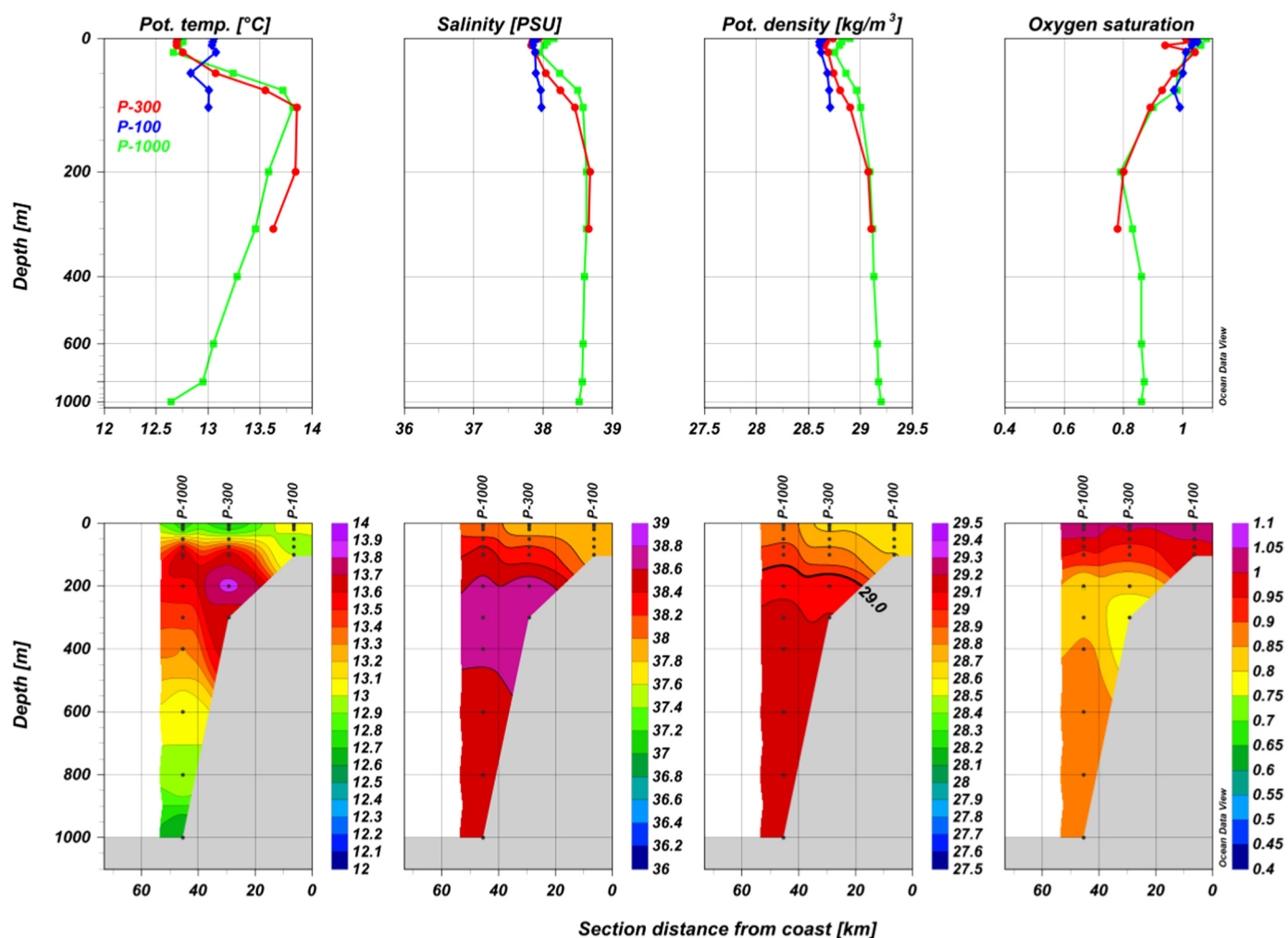


Fig. 3. Water properties in the study area in February 1994. Potential temperature ( $^{\circ}\text{C}$ ), salinity (psu), potential density ( $\text{kg}/\text{m}^3$ ), and oxygen saturation: vertical profiles at each station (upper panels, note the stretched y axis to make clear surface layers); vertical distribution along the transect connecting the three stations (lower panels). The isopycnal 29.0 is highlighted.

speed was greater than  $10 \text{ m s}^{-1}$  (on 4 and 18 February), which might be responsible for enhanced mixing within the uppermost layer in the sea. The meteorological conditions during these two Februaries were unfavorable for deep convection, although sporadic wind-induced mixing was possible, influencing probably just a shallow surface layer.

### 3.1.2. Physical and chemical conditions

#### 3.1.2.1. Temperature, salinity, density, and oxygen distribution.

February 1994 featured relatively uniform temperatures ( $12.84\text{--}13.08 \text{ }^{\circ}\text{C}$ ), salinities ( $37.86\text{--}37.92 \text{ psu}$ ), and densities ( $28.60\text{--}28.69 \text{ kg}/\text{m}^3$ ) at nearshore station P-100 (Fig. 3, Table S1 in Supplementary material). Different features of these parameters were recorded in offshore stations P-300 and P-1200 (Fig. 3, Table S1 in Supplementary material). Offshore stations P-300 and P-1000 had cooler (max.  $12.76 \text{ }^{\circ}\text{C}$ ) and fresher ( $37.95 \text{ psu}$ ) water in the surface layer (0–50 m) than from 50 to 300 m: the corresponding values ranged within  $13.08\text{--}13.87 \text{ }^{\circ}\text{C}$ ,  $38.04\text{--}38.68 \text{ psu}$  at P-300 and  $13.25\text{--}13.83 \text{ }^{\circ}\text{C}$ ,  $38.24\text{--}38.63 \text{ psu}$  at P-1000 (Fig. 3). Below 300 m depth both gradually decreased. The highest densities were on the bottom:  $29.09 \text{ kg}/\text{m}^3$  (300 m) at P-300 and  $29.16 \text{ kg}/\text{m}^3$  (1000 m) at P-1000 (Fig. 3). The water column was well oxygenated at all stations (Fig. 3, Table S1 in Supplementary material). Mean oxygen saturation was 1.01 at P-100 and 0.93 at both P-300 and P-1000 (Fig. 3). However, the relative oxygen minimum was evident between 200 and 400 m.

In February 1995 (Fig. 4) we observed low surface values of

temperature ( $12.09 \text{ }^{\circ}\text{C}$ ), salinity ( $36.08 \text{ psu}$ ) and density ( $27.41 \text{ kg}/\text{m}^3$ ) at P-100. Temperature, salinity and density increased gradually with depth reaching  $13.79 \text{ }^{\circ}\text{C}$ ,  $38.13 \text{ psu}$  and  $28.65 \text{ kg}/\text{m}^3$ , respectively, near the bottom at 100 m. Range of these parameters are presented in Table S1 in Supplementary material. Temperature was relatively uniform at P-300 ( $13.71\text{--}13.87 \text{ }^{\circ}\text{C}$ ), except at 150 m where the minimum value ( $13.3 \text{ }^{\circ}\text{C}$ ) was observed (Fig. 4, Table S1 in Supplementary material). Salinity and density increased with depth spanning  $38.32\text{--}38.69 \text{ psu}$  and  $28.80\text{--}29.08 \text{ kg}/\text{m}^3$  from the surface down to the 300 m depth (Fig. 4, Table S1 in Supplementary material). Rather uniform temperature ( $13.33\text{--}13.45 \text{ }^{\circ}\text{C}$ ), are evident from the surface to 400 m at P-1000 (Fig. 4). Temperature decreased below 400 m reaching minimum of  $12.85 \text{ }^{\circ}\text{C}$  at 1000 m depth. Overall, salinity slightly decreased from the surface ( $38.61 \text{ psu}$ ) to the bottom ( $38.52 \text{ psu}$ ), while density increased from  $29.04$  to  $29.16 \text{ kg}/\text{m}^3$  (obviously, due to the temperature diminution, Fig. 4).

Oxygen saturation ranged  $0.77\text{--}1.05$ ,  $0.61\text{--}0.94$  and  $0.41\text{--}0.91$  at P-100, P300, and P-1000, respectively (Fig. 4, Table S1 in Supplementary material). Lower oxygen below 200 m and extremely low concentrations at 600 m indicate a lack of the deep ventilation at P-1000.

#### 3.1.2.2. Nutrients.

In February 1994, nitrate ( $\text{NO}_3$ ), silicate ( $\text{SiO}_4$ ) and phosphate ( $\text{PO}_4$ ) concentrations were low in the upper 75–100 m at all three stations (Fig. 5). They increased markedly below 100 m at P-300 (max.  $5.29 \text{ } \mu\text{M}$  nitrate;  $5.9 \text{ } \mu\text{M}$  silicate,  $0.19 \text{ } \mu\text{M}$  phosphate) and P-1000 (max.  $4.08 \text{ } \mu\text{M}$

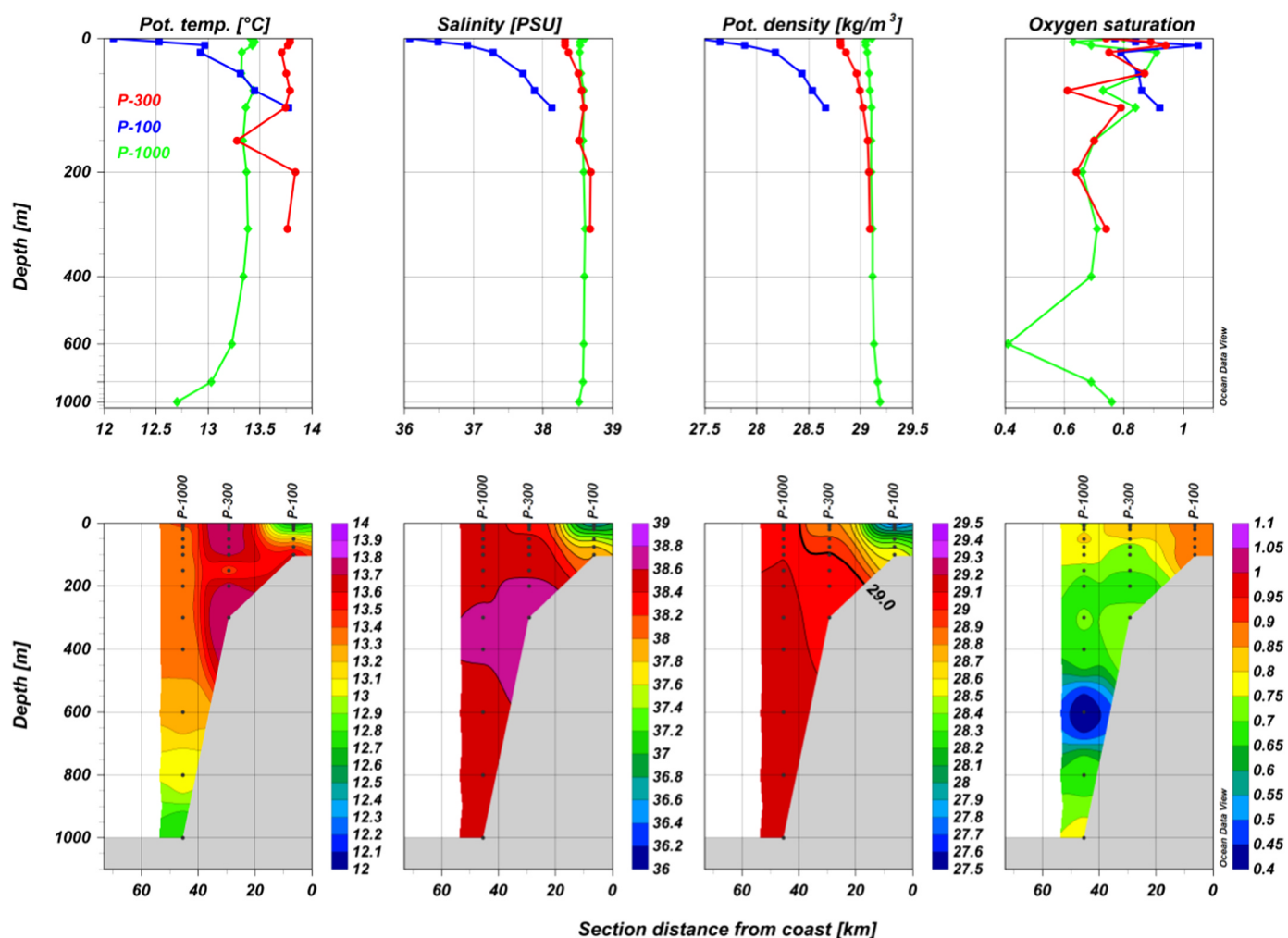


Fig. 4. Water properties in the study area in February 1995. Potential temperature ( $^{\circ}\text{C}$ ), salinity (psu), potential density ( $\text{kg}/\text{m}^3$ ), and oxygen saturation: vertical profiles at each station (upper panels, note the stretched y axis to make clear surface layers); vertical distribution along the transect connecting the three stations (lower panels). The isopycnal 29.0 is highlighted.

nitrate;  $12.46 \mu\text{M}$  silicate at the bottom,  $0.13 \mu\text{M}$  phosphate). Ammonium ( $\text{NH}_4$ ) was in general higher offshore (Fig. 5). However, its vertical distribution at the three stations was not uniform. There was a local peak at the surface and at 75 m. Moreover, two additional maxima at 200 m and 400 m concern the deepest station P-1000. In general, the upper layer is nutrient depleted and the nutricline was relatively deep, between 150 and 200 m. Ranges of nutrient concentrations are presented in Table S1 in Supplementary material.

In February 1995 (Fig. 6), nitrate concentration at P-100 and P-300 was low,  $2.25 \mu\text{M}$ . At the deep station P-1000 it was also low in the upper 50 m, and then it markedly increased to a maximum of  $4.77 \mu\text{M}$ , at 600 m.

Silicate concentrations were higher at the nearshore and deep stations. The maxima were  $8.24 \mu\text{M}$  at the surface of P-100, and  $11.24 \mu\text{M}$  at 1000 m at P-1000 (Fig. 6). Values at the intermediate station P-300 were considerably lower especially in the upper layer, while the peak of  $4.83 \mu\text{M}$  was measured at 300 m.

Ammonium concentrations reached maximum value of  $0.66 \mu\text{M}$  at 150 m of station P-300 and  $0.64 \mu\text{M}$  at 600 m of P-1000 (Fig. 6). Maximum phosphate concentration of  $0.26 \mu\text{M}$  was at the surface (5 m) of station P-100. It locally increased between 300 and 600 m at the offshore stations. As a summary, the nutricline was shallower than in February 1994 and more nutrients were available in the subsurface layers. Ranges of nutrient concentrations are presented in Table S1 in

### Supplementary material.

#### 3.1.3. Nano- and microphytoplankton

NANO and MICRO abundances in February 1994 were shown in Fig. 7. NANO abundance varied between  $1.4 \times 10^4$  and  $4.1 \times 10^5$  cells  $\text{L}^{-1}$  while MICRO abundance was two orders of magnitude lower:  $1.8 \times 10^2$  to  $5.5 \times 10^3$  cells  $\text{L}^{-1}$  (Table S1 in Supplementary material). NANO abundance was higher in the surface (upper 20 m) at the two stations (P-100 and P-300) where the values were roughly between 2 and  $4 \times 10^5$  cells  $\text{L}^{-1}$ . MICRO had similar vertical distributions at P-100 and P-300 with maximum values near surface. At the deep station (P-1000) abundances were low in the surface, while high and low abundances were alternating with depth. Local peaks were at 20, 75, and 200 m (this last depth had  $3.3 \times 10^3$  cells  $\text{L}^{-1}$ ).

Seventy-one taxa within 44 genera of MICRO were identified. These were mainly diatoms (44 taxa), followed by dinoflagellates (19), coccolithophorids (5), two silicoflagellates, and one prymnesiophyte (Table S4 in Supplementary material). Unidentified flagellates (2–10  $\mu\text{m}$  long cells) were the major fraction (> 99%) of NANO abundance.

Composition of the MICRO abundance in February 1994 were shown in Fig. 8. Diatoms dominated almost everywhere with 19–100% (average 71%), dinoflagellates contributed 1–55% (average 21%) and generally increased locally in the subsurface layers. Dinoflagellates

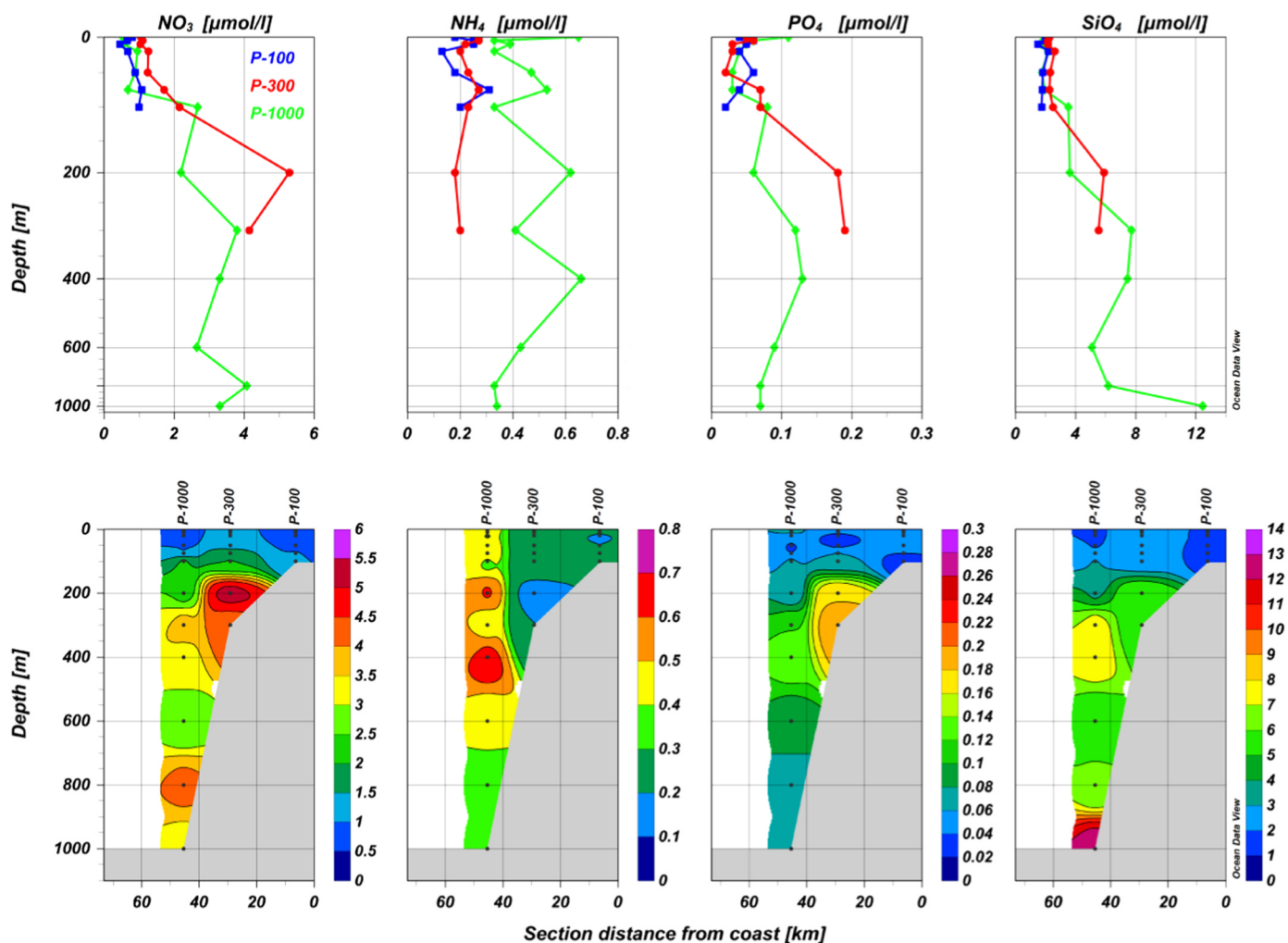


Fig. 5. Nutrient concentrations in February 1994: vertical profiles at each station (upper panels, note the stretched y axis to make clear surface layers); vertical distribution along the transect connecting the three stations (lower panels).

were most abundant ( $10^3$  cells  $L^{-1}$ , or 55% of the total) at 20 m at P-1000 owing to *Gymnodinium simplex*. Other groups (silicoflagellates and coccolithophorids) made up less than 22% of MICRO abundance.

The most abundant diatom (exceeding  $10^3$  cells  $L^{-1}$ ) was *Pseudo-nitzschia* spp. The more frequent (in at least 65% of samples and with abundance  $< 10^3$  cells  $L^{-1}$ ) were: *Coscinodiscus* sp., *Nitzschia longissima* and *Thalassionema nitzschioides*.

NANO and MICRO abundances in February 1995 were plotted in Fig. 9, while ranges of both parameters were presented in Table S1 in Supplementary material. MICRO abundance was unusually high ( $2.02 \times 10^5$  to  $4.04 \times 10^5$  cells  $L^{-1}$ ) in the upper 50 m of P-1000. This exceeded or nearly equaled that of NANO in the upper 5 m. NANO at P-1000 varied from  $6.2 \times 10^4$  to  $5.9 \times 10^5$  cells  $L^{-1}$ . Toward the coast, MICRO was by two orders of magnitude lower in the upper 50 m with minimum of  $1.17 \times 10^3$  cells  $L^{-1}$  at P-100. MICRO abundance at P-300 increased with depth; and the maximum,  $1.13 \times 10^5$  cells  $L^{-1}$ , was reached at 150 m.

Eighty-five MICRO species were identified within 50 genera. These were mainly diatoms (57 taxa), dinoflagellates (17), coccolithophorids (7), two silicoflagellates, and one of each, prymnesiophyte and chrysophyte (Table S4 in Supplementary material). Among NANO, Unidentified phytoflagellates with 2–10  $\mu m$  cell size contributed more than 79% in terms of NANO abundance.

The coccolithophorid *Emiliania huxleyi* was particularly abundant in the 0–20 m layer ( $1.8 \times 10^4$ – $3.2 \times 10^4$  cells  $L^{-1}$ ) at P-300, contributing

from 7% to 21% of abundance.

Composition of the MICRO abundance in February 1995 was shown in Fig. 10.

Diatoms dominated MICRO (57–100%), Fig. 10. The most abundant diatoms ( $> 2.0 \times 10^4$  cells  $L^{-1}$ ) were: *Asterionellopsis glacialis*, *Chaetoceros affinis*, *Ch. curvisetus*, *Ch. decipiens*, *Detonula pumila*, *Lauderia annulata* and *Lioloma pacificum*. The most abundant dinoflagellate ( $5.2 \times 10^3$  cells  $L^{-1}$  or 42% at 50 m of P-300) was *Prorocentrum micans*.

### 3.2. Ocean colour observations (December 1997 to March 2012)

Time and space distribution of the chlorophyll-*a* concentrations (Chl-*a*) along the Southern Adriatic transect is depicted in Fig. 11 (Figs. S1 and S2 in Supplementary material). Yearly variability (left panel) is expanded only for the winter months of each year, when the Chl-*a* were the highest (right panel). One winter period ranges from December (year n-1) to March (year n). In winter 1998, satellite Chl-*a* data display high concentrations in December 1997 along the Southern Adriatic transect. In addition, the highest values were also observed in the winters of 1999, 2000, 2002 and 2012 (right panel). Lowest winter Chl-*a* concentrations were observed in 2001, 2007 and 2011 (right panel).

Cluster analysis distinguished two main groups and year of 1998 which was differentiated from others (Fig. 12). The first group consists of years of 1999, 2000, 2002 when cyclonic circulation characterized the NIG (Fig. 13) and high Chl-*a* during the winter months occurred. The

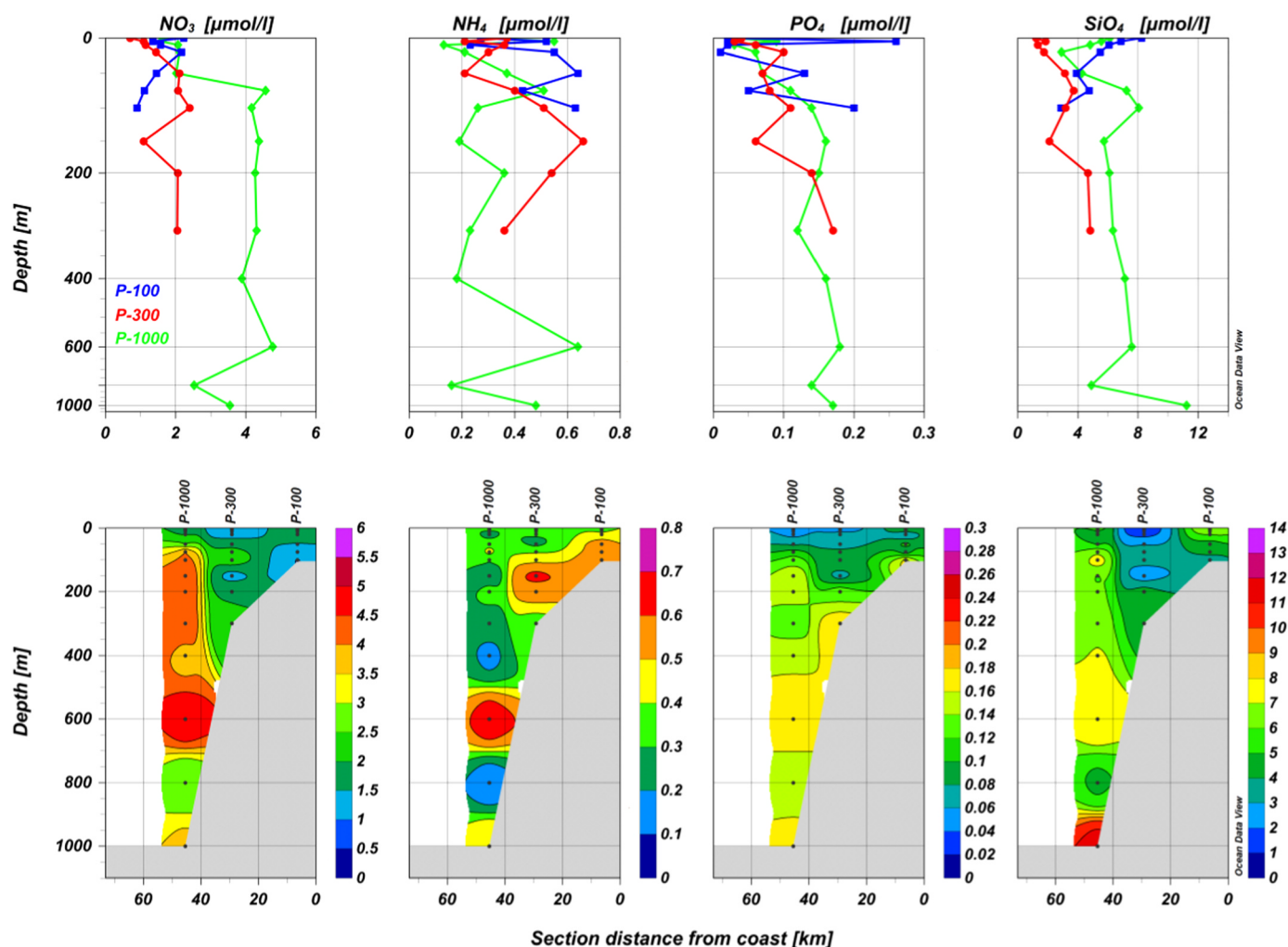


Fig. 6. Nutrient concentrations in February 1995: vertical profiles at each station (upper panels, note the stretched y axis to make clear surface layers); vertical distribution along the transect connecting the three stations (lower panels).

second group is divided into two subgroups with similar Chl-*a* distribution where both type of circulation took place (Fig. 13). Overall, clusters confirmed high similarity between years.

#### 4. Discussion

##### 4.1. Phytoplankton in the OSA during the EMT years (Februarys 1994 and 1995)

Winter sampling in both 1994 and 1995 coincided with a large-scale change in thermohaline circulation known as the Eastern Mediterranean Transient (EMT) that drove nutrient-rich, oxygen depleted and less saline “old” Eastern Mediterranean Deep Water (EMDW) in intermediate and deep layers of the southern Adriatic, in addition to pure LIW (Klein et al., 1999, 2000; Manca et al., 2003; Lipizer et al., 2014). This was accompanied by a massive intrusion of nutrient enriched Atlantic Water (AW) into Adriatic Sea upper layers (50–200 m) during the anticyclonic phase (Fig. 13) of the Bimodal Adriatic-Ionian Oscillation (BiOS) which has been uniquely strengthened by the EMT (Vilibić et al., 2012). Overall, the result was a rapid change in the physical (Cardin et al., 2011), biogeochemical (Civitaresse and Gačić, 2001; Civitaresse et al., 2010), and biological properties (Batistić et al., 2014) of the southern Adriatic.

Open sea bloom in February 1995, with a microphytoplankton (MICRO) maximum of  $4.04 \times 10^5$  cells  $L^{-1}$ , seems to be a consequence of these processes. Nanophytoplankton (NANO) abundance was of the

same order as MICRO in the upper 50 m. This is not common for these oligotrophic waters dominated by small-size phytoplankton (Vilibić et al., 1989; Cerino et al., 2012). The intensity of the February 1995 open sea bloom is more typical for the coastal spring bloom in considerably eutrophicated ecosystems along the eastern Adriatic coast (Vilibić, 1989). However, in this case, coastal MICRO was two orders of magnitude lower than at the deep open sea station.

The high nutrient concentrations supported a marked increase of phytoplankton in the OSA in February 1995. Nutrients were reduced in the upper 50 m (likely owing to the uptake) but were still high ( $NO_3 \geq 4.0 \mu M$ ) below 50 m. The changes in the vertical distribution of water masses in the Eastern Mediterranean due to the EMT were associated with a significant upward nutrient transport which caused a nutrient-rich water to come closer to the euphotic zone than previously (Klein et al., 1999). This phenomenon peaked in 1995 when, compared with other EMT years, the largest concentration of nutrients was observed together with very shallow nutricline depths. In the eastern Ionian Sea as well as in the Southern Adriatic nutricline depth was about at 100 m (Klein et al., 1999, 2000). Year of 1995 was mild and under influence of the low-salinity inflow that accompanies the anticyclonic circulation in the NIG which was responsible for greater vertical stability of the water column in the OSA (Gačić et al., 2009). Under such conditions, when the intensity of winter vertical mixing is weak or even absent, nutrients from deeper layers are not available to phytoplankton. But, because of the relatively shallow depth of nutrient-rich water in February 1995, a very shallow vertical mixing would have been sufficient to supply

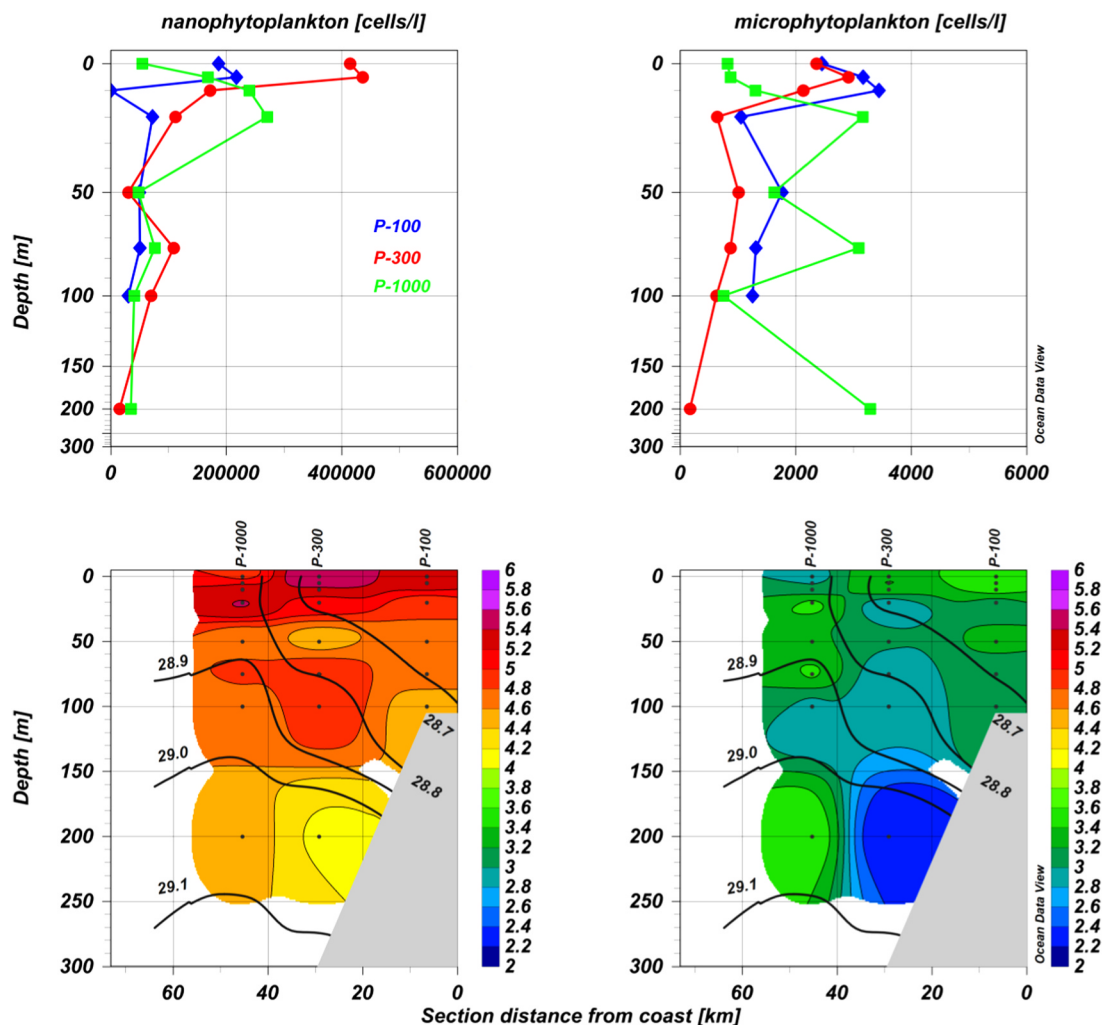


Fig. 7. Distribution of the nano- and microphytoplankton abundances in February 1994. Upper panels: vertical profiles at each station (note the stretched y axis to make clear surface layers). Lower panels: vertical distribution of abundances along the transect. Note the log scale applied to the contouring of the vertical distribution. Isopycnals 28.7, 28.8, 28.9, 29.0 and 29.1 (extracted from the potential density distribution in Fig. 4) overlay the abundances colour shading.

nutrients to the euphotic zone. There were no cooling events, but two episodes of a strong *bura* (greater than  $10 \text{ m s}^{-1}$ ) might have been responsible for shallow wind-induced mixing. In addition, a sharp frontal zone (large density gradient between station closes to the coast and open sea stations) was evident. Turbulent mixing at shelf-break frontal zones between less dense coastal water and denser open sea water, or velocity shear along the eastern coast and/or eddy instability are other mechanisms that can drive upper-layer mixing favourable for primary production (Mann and Lazier, 2006). Thus, there was a possibility for more than one bloom to develop in winter 1995, with similar intensity as such as we recorded on February, 21. Unfortunately, remotely sensed Chl-*a* data for this year are not available to confirm this assumption.

MICRO abundance maximum was also found at 150 m at station P-300 in February 1995. Similar accumulations (the order of  $10^5 \text{ cells L}^{-1}$ ) and of similar species composition were observed in surface layer (0–50 m) at P-1000. This peculiar characteristic is possibly a consequence of the strong horizontal density gradient between P-1000 and P-300 as evidenced by the isopycnal outcropping. The isopycnal slope in the upper layer suggests the possibility that water sliding along isopycnals conveyed phytoplankton from the upper 50 m at P-1000 to 150 m at P-300. This deep phytoplankton accumulation could contribute to the enrichment of the water column with organic matter in winter. In addition, with sufficient vertical mixing, any viable phytoplankton from these deep layers might be raised to the more favourable

surface light environment to develop a new bloom.

Phytoplankton abundance in February 1994 was 2–3 orders of magnitude lower than in February 1995. The water column was stratified and nutrients were very low in the upper 100 m, possibly owing to an earlier phytoplankton bloom. Nutrients could not be replenished from deeper layers because of the lack of vertical mixing. In the period from 1989 to 1999, 1994 was the warmest year recorded in the Southern Adriatic (Cardin and Gačić, 2003). According to the meteorological data, there was one *bura*-related cooling event (mid-February) with gentle winds of about  $4 \text{ m s}^{-1}$ . This apparently was not sufficient to reduce the buoyancy of the upper 300 m, hence there was no vertical convection and enrichment of the euphotic layer. Neither was there evidence of a frontal zone between the station closes to the coast and offshore stations, as in February 1995. More precisely, all three stations feel influence of the fresh water originating from the coast in February 1994. Zooplankton abundance, especially of copepods, however, was high ( $480 \text{ ind. m}^{-3}$ , Batistić et al., 2003). Grazing is important in regulating diatom abundance (Calbet, 2001, and references therein), so this might be an additional indication of a bloom that had matured earlier in winter and since then had been cropped substantially by zooplankton prior to our sampling. Moreover, in support to this assumption we cite phytoplankton abundance maximum of  $1.3 \times 10^5 \text{ cells L}^{-1}$  registered earlier in February 1994 in the eastern side of the Otranto Strait (Socal et al., 1999). It was directly influenced by the



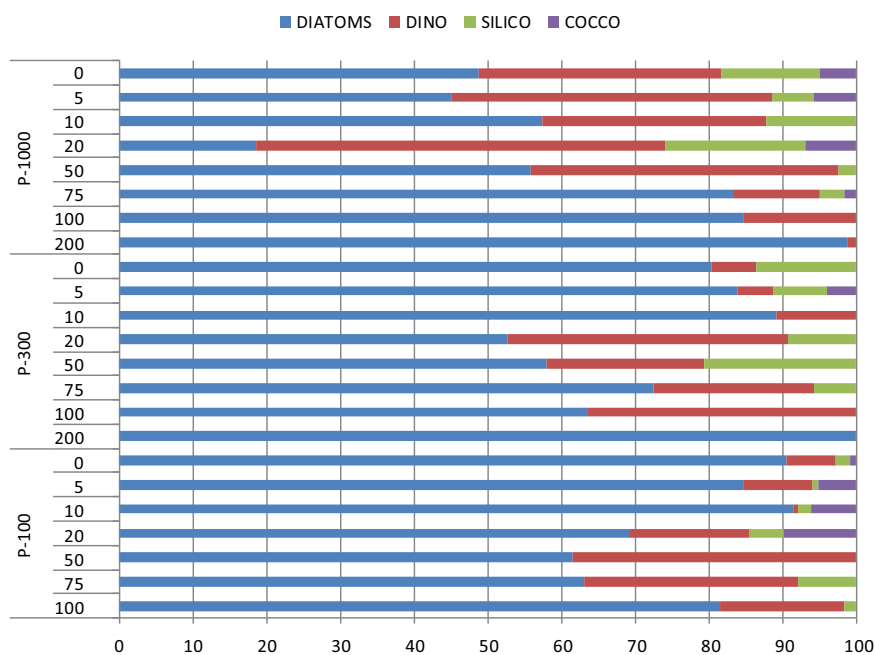


Fig. 8. Percentage contribution (% , x-axis) of different taxonomic groups (diatoms, DINO = dinoflagellates, SILICO = silicoflagellates and COCCO = coccolithophorids) to microphytoplankton abundance along the transect in February 1994 (y-axis labels: stations and sampling depths).

surface water from the Ionian Sea, actually by AW enriched in nutrients due to upwelling at the periphery of the anticyclonic NIG (Civitarese et al., 2010).

Data presented herein support model results (Stratford and Haines, 2002; Mattia et al., 2013) that predict increased production in the Eastern Mediterranean owing to circulation changes consistent with those associated with the EMT. According to Stratford and Haines (2002), the level of biological production in the eastern basin shows a rising trend (20–30%) until 1995, consistent with more widespread significant lifting of the nutricline caused by EMT. Similar results were found by Mattia et al. (2013).

On the other hand, Sea WiFS satellite Chl-*a* data imaging (D'Ortenzio et al., 2003) does not reveal strong relationship between the EMT and the productivity in the Eastern Mediterranean. Those data, however, are available from 1998 on, when the EMT was already in a waning phase (Borzelli et al., 2009).

The phytoplankton community also showed some peculiarities in February 1995 at the open-sea station (P-1000). As usual, during winter in the OSA, diatoms dominated the MICRO fraction (Cerino et al., 2012; Batistić et al., 2012) with high contribution of *Chaetoceros* taxa. The *Chaetoceros*–*Rhizosolenia* association is characteristic of the Eastern Mediterranean (Kimor, 1983; Kimor et al., 1987) and has been observed over the whole year in the Strait of Otranto (Viličić et al., 1995). *Chaetoceros* dominated in winter 2008 (Batistić et al., 2012), and alongside with *Pseudo-nitzschia* and *Thalassionema nitzschioides* in winter of 2009, 2010 and 2011 (Ljubimir et al., 2017).

Unusual for the OSA, the winter diatom bloom in 1995 was also consisted by *Asterionellopsis glacialis*, *Detonula pumila*, *Lauderia annulata* and *Lioloma pacificum*, each of which exceeded  $10^4$  cells  $L^{-1}$ . All of these are associated with high nutrients and most thrive in upwelling and mixing environments (Odebrecht et al., 1995; Cabeçadas et al., 1999; Rörig and Garcia, 2003; Pannard et al., 2008; Zúñiga et al., 2011; Ospina-Alvarez et al., 2014). *Lauderia annulata*, in particular, grows fast under light-limitation (Sommer, 1994; Reigman et al., 1996). Viličić et al. (1989) found high abundances of *Asterionellopsis glacialis* ( $> 10^4$  cells  $L^{-1}$ ) in the Southern Adriatic spring bloom in 1987, but only at the western coast (near the city of Bari, Italy).

These species are common and some of them make a bloom in the more eutrophicated waters of the Northern Adriatic (Fonda Umani,

Beran, 2003; Bosak et al., 2009; Godrijan et al., 2013). The diatom *A. glacialis* and coccolithophorid *Emiliania huxleyi* provide their regular blooms, while *L. annulata* occurs sporadically (Bernardi Aubri et al., 2004; Viličić et al., 2009). In the period from November 1994 to February 1995, *A. glacialis* and especially *L. annulata* had low abundances in the western part of the Northern Adriatic while *D. pumila* and *L. pacificum* have not been recorded (R. Kraus, personal communication). This fact reduces a possibility that mentioned species were transported from the Northern to the Southern Adriatic (SA) by West Adriatic Current. On the other hand, the Atlantic Water (AW) strongly influenced the Southern Adriatic in 1995 (Civitarese et al., 2010; Vilibić et al., 2012; Mihanović et al., 2015) and could have been responsible for transporting certain phytoplankton species. Indeed, in February 1995, some zooplankton species (for example calycopteran *Muggiaea atlantica*), common in the Atlantic Ocean and Western Mediterranean, have been also recorded in the Adriatic Sea and some of them for the first time (Batistić et al., 2014).

Regarding AW's broader influence over the Mediterranean Basin in 1995, the early winter diatom bloom in the Bay of Tunis (SW Mediterranean Sea), with salinity  $< 36.8$ , was dominated by *A. glacialis* and *L. annulata* (Daly Yahia-Kéfi et al., 2005) with abundances greater than  $10^4$  cells  $L^{-1}$ . The diatoms *A. glacialis* and *L. annulata*, and the coccolithophorid *E. huxleyi* were among the most abundant species in the upwelling zone of the Alboran Sea (SW Mediterranean Sea), an area strongly influenced by the Atlantic current (Mercado et al., 2005).

Further evidence of AW's influence in the OSA is the appearance of *D. pumila* at P-300 and P-1000, typical of the Atlantic current (Lecal, 1957). *Emiliania huxleyi* also reached relatively high abundance ( $> 10^4$  cells  $L^{-1}$ ) in the winter 1995. This species was considered as an indicator of AW in the Ionian Sea (Rabitti et al., 1994).

#### 4.2. Overview of available literature data on the phytoplankton abundance and Chl-*a* in the winter in OSA

Alongside February 1995, the winter increase in MICRO abundance and/or in situ Chl-*a* in the OSA was also evident in February 1997 and 2007, 2008, 2009, 2010 and 2012 (Table 1). During the 1997, a year associated with the relaxation of the EMT, anticyclonic circulation in the NIG started to reverse to the cyclonic one (Fig. 13). However, in

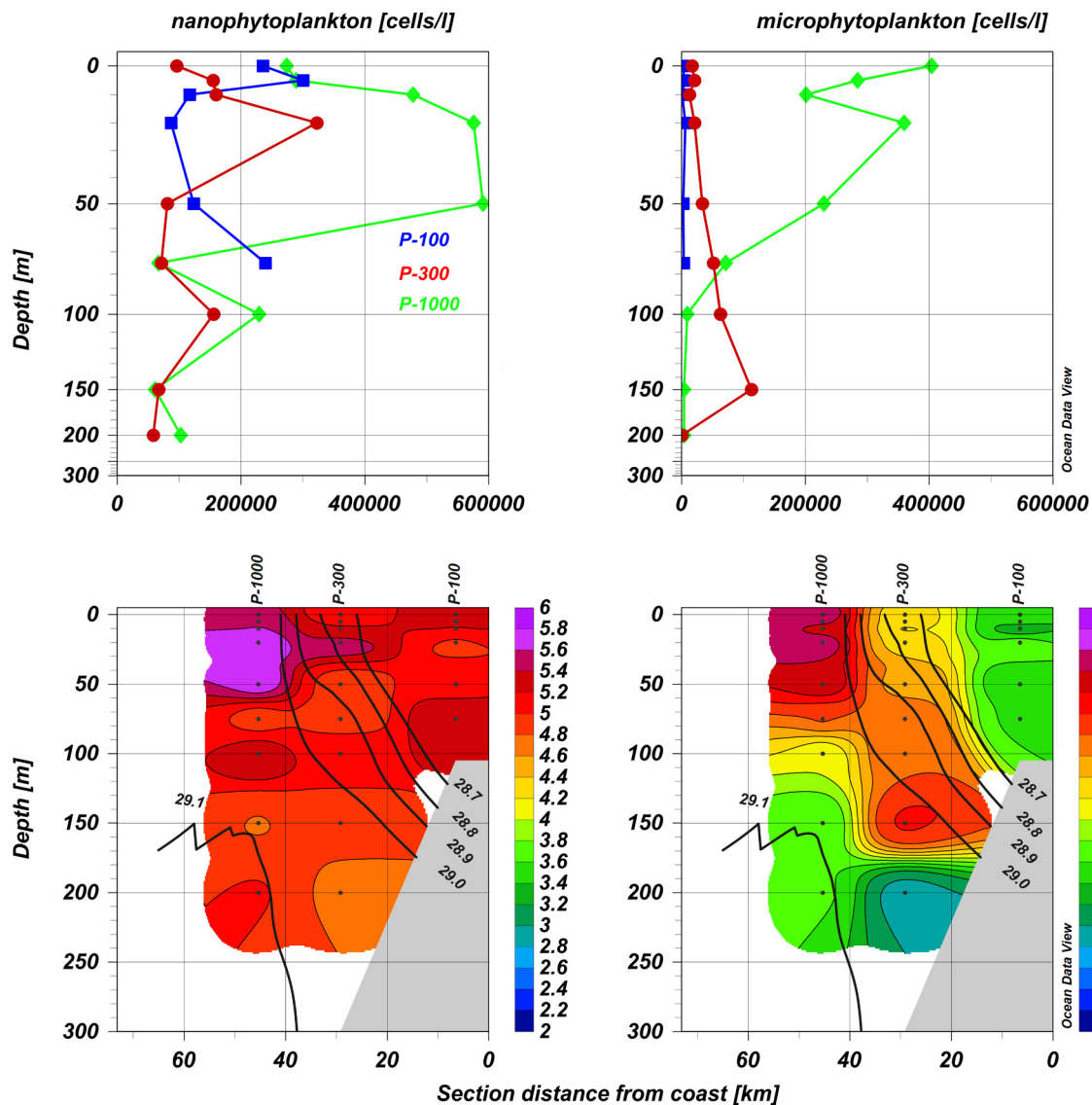


Fig. 9. Distribution of the nano- and microphytoplankton abundances in February 1995. Upper panels: vertical profiles at each station (note the stretched y axis to make clear surface layers). Lower panels: vertical distribution of abundances along the transect. Note: the log scale applied to the contouring of the vertical distribution. Isopycnals 28.7, 28.8, 28.9, 29.0 and 29.1 (extracted from the potential density distribution in Fig. 5) overlay the abundances colour shading.

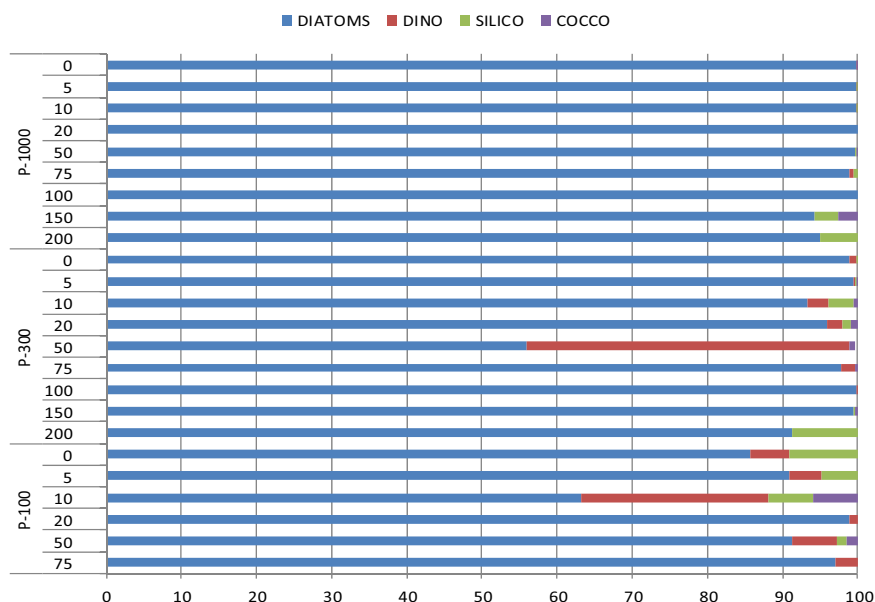
March 1997, according to the salinity values (Fig. 13), the reversal still did not completely change the Southern Adriatic water mass properties, so the influence of the nutrient-enriched AW still persisted in the OSA, with average nitrate concentration of  $5.5 \mu\text{M}$  (Civitaresse and Gačić, 2001) and supported a marked increase of phytoplankton abundance. Due to a mild winter no vertical convection took place so mode for enrichment by nutrients of upper euphotic layers was by the advection of AW waters (Table 1).

From 2007–2010 anticyclonic circulation characterized the NIG (Fig. 13) and the influence of nutrient rich AW was complemented by a high salinity intermediate water which enhanced deep vertical mixing and additionally enriched the upper layers with nutrients responsible for phytoplankton growth (Table 1). It is important to note that OSA salinity in those years was higher than in the EMT anticyclonic years of 1994 and 1995 (Fig. 13, Table 1). According to Mihanović et al. (2015) between 2006 and 2008 the BiOS reversal from cyclonic to anticyclonic was slow (lasting 2–3 years, Fig. 13) indicating that the reversal did not completely change the southern Adriatic water mass properties. On the contrary, during the exceptional conditions of BiOS regime shift in the

1990s the freshening due to the inflow of low-salinity water masses in the Adriatic happened rapidly (in less than a year).

In February 2011, low phytoplankton abundance and Chl-*a* were evident (Table 1). During the 2011, the anticyclonic mode started turning into a cyclonic one (Gačić et al., 2014, Fig. 13). Due to mild winter conditions very shallow vertical mixing occurred (Table 1) which was not enough to lift nutrients from the deep layers (Ljubimir et al., 2017).

The year of 2012 was specific with extraordinary cold winter conditions in which both circulation modes in the Ionian took place more than once: first part of the year characterized cyclonic mode which reversed to anticyclonic (May) and again to the cyclonic pattern toward the end of the year (Gačić et al., 2014, Fig. 13). Extremely cold winter of 2012 led to a formation of very dense water, which enhanced deep vertical convection in February (Table 1). This resulted in a bloom marked by an increase in OSA phytoplankton abundance (MICRO order of magnitude  $10^5 \text{ cells L}^{-1}$ ) and biomass (Chl-*a* up to  $4.86 \text{ mg m}^{-3}$ ) at the end of March 2012 (Table 1).



**Fig. 10.** Percentage contribution (% , x-axis) of different taxonomic groups (diatoms, DINO = dinoflagellates, SILICO = silicoflagellates and COCCO = coccolithophorids) to microphytoplankton abundance along the transect in February 1995 (y-axis labels: stations and sampling depths).

#### 4.3. Surface satellite Chl-*a* concentrations (1997–2012)

Direct measurements of phytoplankton abundance and biomass in the OSA during winter period are limited especially for period from 1998 to 2006, but Chl-*a* derived from satellite images (December 1997–2012) provide useful information about long-term variations. Hovmueller diagram (H-diagram) also showed high winter Chl-*a* in cyclonic years especially from 1998 to 2000 and 2002. In those years deep vertical convection occurred (Gačić et al., 2002, 2006; Santoleri et al., 2003; Manca et al., 2003). Chl-*a* concentrations derived from satellite images in February 2007 and 2008 were low which is not in accordance with phytoplankton abundance (Table 1). In the case of deep mixing and dispersal of cells throughout the water column, satellite imagery may underestimate Chl-*a*, as documented in February 2008 (Batistić et al., 2012). High winter Chl-*a* values are evident from H-diagrams for the 2012, a specific hydrometeorological year, which is in accordance with phytoplankton abundance and in situ Chl-*a* (Table 1). Cluster analysis suggests that in both circulation regimes similar Chl-*a* distribution occurred.

By combining diverse sources (in situ data and ocean colour observations), a clear evidence of relatively high winter phytoplankton abundance and biomass over almost two decades was obtained.

## 5. Conclusion

Winter bloom in the OSA is a recurrent event over the years and can be sufficiently intense to account for a significant fraction of the region's annual production. From this perspective, the OSA is not exclusively oligotrophic.

The present data demonstrate that blooms can occur during both anticyclonic and cyclonic phases of the NIG, but by different mechanisms. During anticyclonic years, the nutricline along the borders of the Ionian Sea is shallower. This favours inflow of nutrient-rich water to the Adriatic in the 50–200 m layer, depths at which shallow vertical mixing is sufficient to raise these essential nutrients to the euphotic zone.

The nutricline along the borders of the Ionian Sea becomes deeper during cyclonic years and inflow to the Adriatic from the Ionian Sea is poorer in nutrients. Therefore a deeper mixing is necessary to enrich the euphotic zone.

Thus, there are local (originating in the southern Adriatic) and

remote (originating out of the southern Adriatic) factors influencing the phytoplankton blooms. While the local factors reflect the consequences of the convection intensity in the OSA, the remote factors act through the horizontal advection of the water masses of different thermohaline properties and nutrient load. Intense blooms occur under specific hydroclimatic events, like during years influenced by the EMT or when winter conditions are particularly extreme. The substantial winter bloom of 1995 coincided with the EMT effects. In particular, there was a strong inflow of AW into the Adriatic, which advected surface and intermediate waters richer in nutrients than usually, because of the shallower position of nutricline and upwelling of nutrients from subsurface layers. This caused shift from NANO to MICRO phytoplankton fraction, consisted mainly of diatoms, which are frequent in the more eutrophic ecosystems. The dominant bloom of MICRO taxa is not common in the OSA and likely was introduced under the strong influence of AW that year. Favourable hydrographic conditions have contributed to their unusual intensive development.

Winter bloom intensity thus depends on different water masses that enter the southern Adriatic connected with BIOS mechanism, in synergy with regional meteorological conditions and important mixing processes that affect these water masses. This also implicates the spring bloom phenology which is a topic for future investigations.

This work highlights the importance of a winter season as an active phytoplankton period and concludes that it must be considered explicitly in discussions of the OSA's biological and ecological systems. Due to the lack of high-frequency samplings (day to week), fine scale variability of phytoplankton blooms could not be detected. This variability can be significant in short time periods, which are important scales for the meteorological mechanisms that drive the dynamic processes in the water column (wind induced mixing, mesoscale vortices, filaments, meanders along the frontal zones, etc.). The occurrence of these meteorological events might reflect on the nutrient availability and consequent blooms and cell dispersions. To overcome these shortcomings we used large scale satellite analysis which confirmed results obtained by field samplings.

One of the crucial spatial and temporal driving mechanisms, which will certainly influence the timing, intensity and composition of the blooms, is the climate change (through air and sea temperatures, precipitation, wind regimes). Hence, the continuing surveying of the coastal and open sea areas is needed.

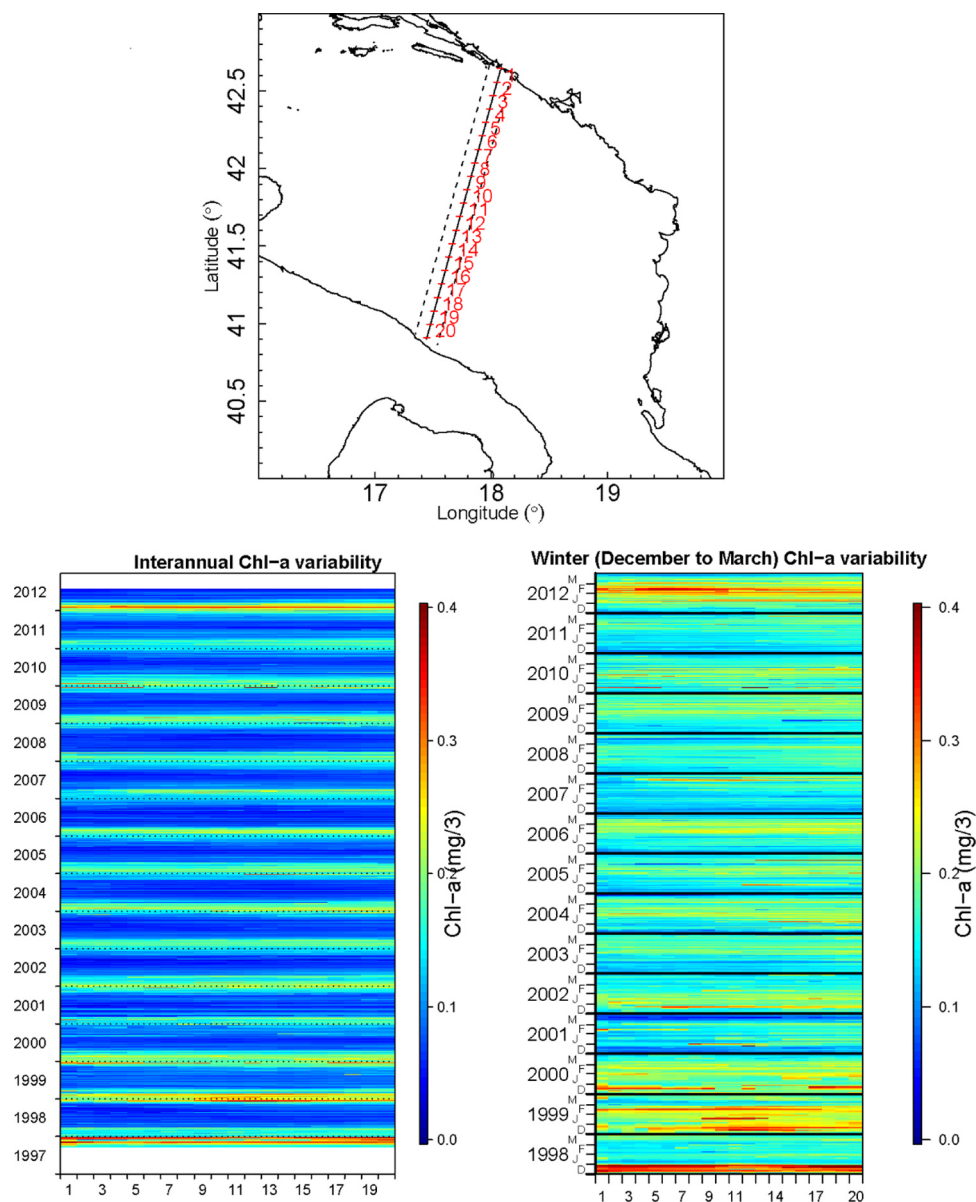


Fig. 11. Hoevmoeller diagram of satellite Chl-a daily averages for the southern Adriatic transect: numbers 1–20 indicate different positions along the transect (upper panel); the full year diagram is to the left (lower panels) whereas only winter months (D – December, J – January, F – February, M – March) are to the right.

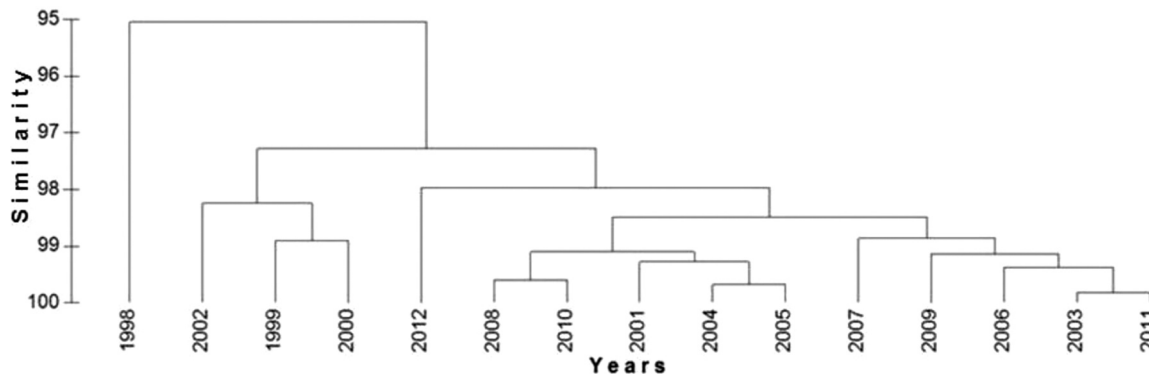
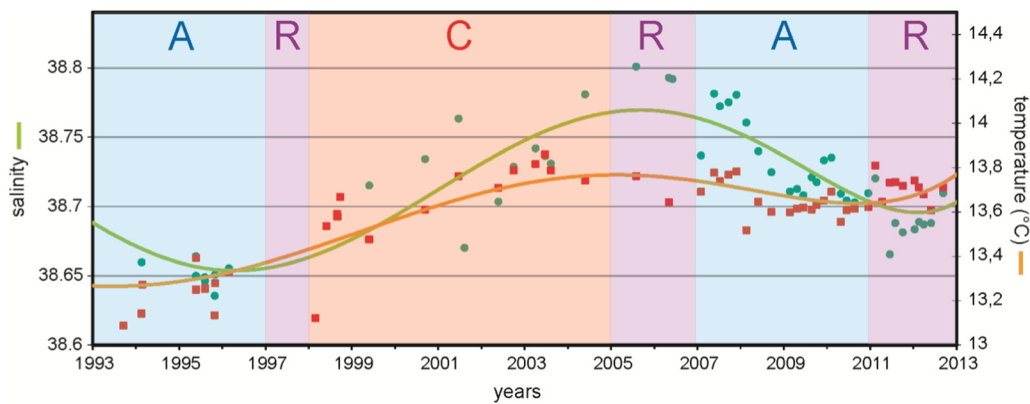


Fig. 12. Cluster dendrogram based on satellite Chl-a concentrations over seasons (December, January, February and March) and among years.



**Fig. 13.** Interannual variability of average temperature and salinity (psu) in the 200–800 m depth layer in the Southern Adriatic from 1993 to 2013 indicating different circulation regimes of the Northern Ionian gyre (NIG): anticyclonic (A) – blue, cyclonic (C) – red. Reversal years (R) are in purple indicating periods when NIG turned from anticyclonic to cyclonic and vice versa. The trend was obtained by fitting a five-degree polynomial curve (after Civitarese et al., 2010).

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.csr.2018.12.011](https://doi.org/10.1016/j.csr.2018.12.011).

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