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Abiotic control of phytoplankton blooms in temperate coastal marine ecosystems: A case study in the South Atlantic Ocean

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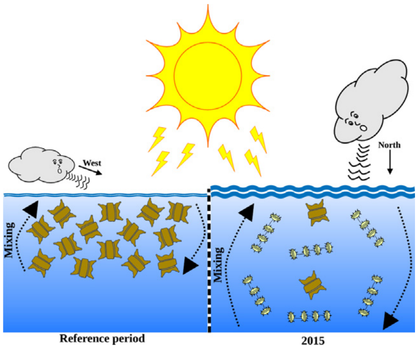
HIGHLIGHTS

- The high productivity of coastal SAO is maintained by winter phytoplankton blooms.
- These blooms peaked during June and were dominated by microplanktonic diatoms.
- In 2015 the bloom occurred in August and had a higher proportion of nanoplankton.
- Changes in wind patterns caused the shifts in the 2015 phytoplankton bloom.

GRAPHICAL ABSTRACT



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ABSTRACT

Coastal waters of the South Atlantic Ocean (SAO) sustain one of the highest levels of production of the World's ocean, maintained by dense phytoplankton winter blooms that are dominated by large diatoms. These blooms have been associated to calm weather conditions that allow the formation of a shallow and well illuminated upper mixed layer. In Bahía Engaño, a coastal site in Patagonia, Argentina (chosen as a model coastal ecosystem) winter blooms recurrently peaked on June and they were dominated almost entirely by the microplanktonic diatom *Odontella aurita*. However, during the year 2015, a new wind pattern was observed - with many days of northerly high-speed winds, deviating from the calm winter days observed during a reference period (2001–2014) used for comparison. We determined that this new wind pattern was the most important factor that affected the phytoplankton dynamics, precluding the initiation of a June bloom during 2015 that instead occurred during late winter (August). Furthermore, the 2015 bloom had a higher proportion of nanoplanktonic cells (as compared to the reference period) and it was co-dominated by *O. aurita* and *Thalassiossira* spp. Other variables such as nutrient supply and incident solar radiation did not have an important role in limiting and/or initiating the June 2015 bloom, but temperature might have benefited the growth of small cells during August 2015. If these changes in the timing and/or the taxonomic composition of the bloom persist, they may have important consequences for the secondary production and economic services of the coastal SAO.

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1. Introduction

Coastal ecosystems worldwide are characterized by their high biodiversity and strong gradients in solar radiation, temperature and nutrients (among others) making them sites of special ecological interest (Cloern et al., 2014). Coastal areas represent a small fraction of the total oceanic area i.e., ~5%, however, they are one of the most productive ecosystems on the Earth (Uitz et al., 2010; Rousseaux and Gregg, 2014), providing also highly valuable services (UNEP, 2006). Among these services, food (in the form of fisheries catch) is one of the most important, accounting for ~80 million tons yr^{-1} over the globe, with a big share of captures in temperate coastal areas (FAO, 2012). In particular, the coastal waters of the South Atlantic Ocean (SAO) sustain one of the highest production levels of the World's ocean (Longhurst, 1998; Skewgar et al., 2007). They are also important for nursery and recruitment of several species of commercial interest (e.g., hake, Argentine red and Patagonian shrimp; Boschi, 1997), and breeding of several flagship species (e.g., the austral right whale, orca and the Magellan penguin; IWC, 2013).

The high production, richness and biodiversity of species in the SAO is maintained by dense phytoplankton blooms occurring all over the continental shelf (Villafañe et al., 2004; Romero et al., 2006; Guinder et al., 2015) or at the shelf break (Saraceno et al., 2005; Painter et al., 2010; Balch et al., 2014). These blooms may be directly or indirectly affected by diverse drivers (e.g., vertical mixing, solar radiation, temperature and nutrients; Behrenfeld and Boss, 2014), including those of anthropogenic origin. In particular, there is much concern about the impact of excessive inputs of organic and inorganic nutrients via rivers (which in turn is associated to human activities; Cloern et al., 2014) or in the form of atmospheric dust (Jickells and Moore, 2015). These inputs may result in an increase in the biomass and shifts in the phytoplankton structure towards taxa that may be of low nutritional quality, inedible or even toxic for consumers (Smith et al., 1999; Fauchot et al., 2005; Carstensen et al., 2007). All these drivers can affect, in different degree, the dynamics of coastal ecosystems, as well as the functioning and timing of the annual phytoplankton succession, and particularly of the blooms. Since the early work of Sverdrup (1953) on the potential causes that trigger blooms, great efforts have been put to develop a general theory; however, as today, there are many uncertainties respect to: 1) the specific requirements that trigger these massive growth events, 2) when and how are they triggered and, 3) what factors (biotic or abiotic) influence their duration and intensity.

It is already known that blooms usually respond to changes in physical forcing originating in the coastal ocean (e.g., tides), the atmosphere (wind), or on the land surface (precipitation and river runoff) (Paerl et al., 1996; Carstensen et al., 2015). Some abiotic factors are known to directly affect the initiation and the development of phytoplankton blooms, such as light, nutrients (as essential requirements for photosynthesis) and temperature (as catalyst of several enzymatic reactions involved in the CO_2 uptake reactions; Toseland et al., 2013). Wind (speed and direction) may also influence the strength and duration of phytoplankton blooms, as it conditions the stratification and the depth of the upper mixed layer (UML) that in turn, will control the light availability for photosynthesis (Yin et al., 2004; Fitch and Moore, 2007). For the particular case of coastal areas of the SAO it was proposed (Villafañe et al., 2004) that the phytoplankton blooms are triggered by the calm weather conditions characteristic of the winter time. On the other hand, during spring and summer, strong winds predominate, keeping the cells circulating within a relatively deep and poor-illuminated layer and thus the growth of phytoplankton is low (i.e., pre- and post-bloom conditions; Villafañe et al., 2004; Helbling et al., 2005).

During the year 2015 we determined a change in the wind pattern (as compared to previous years) for the area of Bahía Engaño – a coastal site in the Chubut Province (Patagonia, Argentina). This change gave us the opportunity to study the influence of this new wind pattern on the onset and development of the phytoplankton bloom, using Bahía Engaño as a model coastal ecosystem for coastal SAO. To this purpose, we compared not only the patterns of wind but also of other abiotic variables (solar radiation, temperature, nutrients, etc.) for the year 2015 against a reference period (2001–2014) to evaluate their impact on the local phytoplankton dynamics. Our work has an evident usefulness, as the understanding of the link between changes in abiotic factors and the dynamics of phytoplankton blooms will allow for a prediction of future impacts on the secondary production and, ultimately, on the regional economy.

2. Materials and methods

2.1. Study area

Bahía Engaño is located at the mouth of the Chubut River (Patagonia, Argentina) (Fig. 1). The flow of the Chubut River is regulated by the Florentino Ameghino Dam, 150 km upstream of the river's mouth (Fig. 1). The largest cities of the area (Trelew, Rawson, Gaiman, Dolavon, ~150.000 inhabitants in total, www.indec.gov.ar) are located in the fertile Chubut River valley - between the dam and the river's mouth. In this valley the river is diverted into several irrigation channels that supply water for agricultural and animal breeding activities. About 80% of the horticultural production of the Chubut Province is found along the margin of the Chubut River, in the last 100 km before it reaches the sea. In the past decade, the land use for agricultural activities has doubled and therefore, the use of fertilizers (mainly organochlorine and organophosphate compounds) - without adequate control - had increased (Antolini, 2012; Kopprio et al., 2015). Fishing industries also release their wastes near the mouth of the river reaching, ultimately, Bahía Engaño (Chiarandini Fiore et al., 2013). Thus the study area, as a whole, can be considered as highly impacted by anthropogenic activities.

2.2. Data

2.2.1. Meteorological data

Data for the reference period (2001–2014) and for the year 2015 for the different meteorological variables (Table 1) were obtained as follows: Temperature, humidity, wind speed, and direction were continuously obtained (one datum per minute) with a meteorological station (Tecmes, model TS, Argentina) permanently installed (since 2001) on the roof of the Estación de Fotobiología Playa Unión (EFPU; Fig. 1). Precipitation data were obtained from the database SIPAS (Sistema de Información Patagonia Sur, www.sipas.inta.gob.ar) of the Instituto Nacional de Tecnología Agropecuaria (INTA, Trelew; ~15 km upstream from the Rawson Bridge, Fig. 1).

Incident solar radiation is continuously measured (since 1999) using an European Light Dosimeter Network (ELDONET, Real Time Computers, Germany) broadband filter radiometer that measures photosynthetically active radiation (PAR, 400–700 nm), ultraviolet A radiation (UV-A, 315–400 nm) and ultraviolet B radiation (UV-B, 280–315 nm) every second, with the data being averaged and stored every minute. The instrument is permanently located on the roof of the EFPU and is routinely calibrated (once a year) using a solar calibration procedure (Ruggaber et al., 1994; Björn and Murphy, 1985). In this work we only used data corresponding to the reference period (2001–2014) and for the year 2015.

Area-averaged daily aerosol indexes (AI) for the Bahía Engaño area were downloaded from the Earth's database of the National Aeronautics and Space Administration (NASA) (Acker and Leptoukh, 2007). The data were obtained by the Total Ozone Mapping Spectrometer – Earth Probe (TOMS-EP; 2001–2004) with a global grid resolution of 1 × 1.25 degrees, and by the Ozone Monitoring Instrument (OMI; 2005–2015) with a global grid resolution of 1 × 1 degrees. We only considered the positive values of AI as they represent absorbing aerosols (i.e., atmospheric dust).

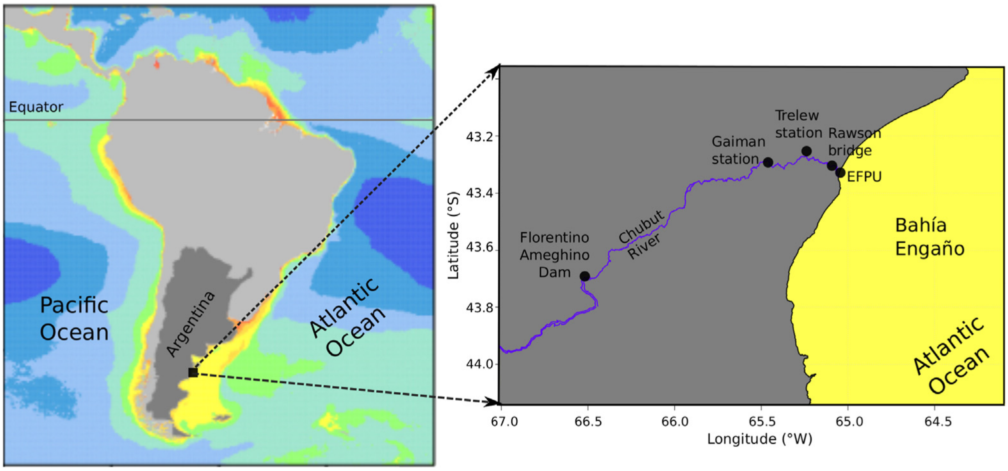

Fig. 1. Map of the study area showing the different sites in which data were obtained.

2.2.2. Hydrology and water chemistry data

River flow data (for the reference period and for the year 2015, Table 1) were obtained from the Base de Datos Hidrológica Integrada (www.bdhi.hidricosargentina.gov.ar) of the Secretaría de Recursos Hídricos (Argentina) at the Gaiman station (~40 km upstream from the Rawson Bridge, Fig. 1). Physical (i.e., water temperature) and chemical data (i.e., nutrients) from the reference period were obtained from different published sources as well as from unpublished data collected by our research group (Table 1). During 2015, surface water samples (~0.5 m depth) were collected every 10–15 days at two sites: 1) the outer regime (Bahía Engaño, at the mouth of the Chubut River and during high tide, salinities > 33), and 2) the inner regime of the estuary (Rawson Bridge, salinities < 1; Fig. 1) to determine physical (temperature and conductivity) and chemical characteristics (nutrients) of both water bodies. Temperature and conductivity were measured in situ using a multiparameter probe (Yellow Spring Instruments, model XLM 600, USA). The samples for chemical characterization of macronutrients ($NO_3^- + NO_2^-$, PO_4^{3-}, SiO_3^{2-}; in triplicates) were immediately taken to the EFPU (10 min away from both sampling sites), put in 100-mL High-Density Polyethylene (HDPE) bottles and frozen (−20 °C) until analyses. These samples were analyzed using spectrophotometric techniques (Strickland and Parsons, 1972).

2.2.3. Phytoplankton data

Due to the scarcity of biological data for the area, we used and extended the reference period (from 1986 to 2014), including all available data for chlorophyll-*a* (Chl-*a*) concentration, taxonomic composition and abundance of phytoplankton cells. These data were obtained from different published sources as well as from unpublished data collected by our research group (Table 1). During 2015, Chl-*a* concentration and phytoplankton taxonomic composition and abundance data were obtained as follows: Surface water samples (triplicates) were collected at the aforementioned sites (i.e., inner and outer regime of the estuary) with an acid-cleaned bucket (1 N HCl), pre-screened (200 μm-mesh) to eliminate large zooplankton and put in acid-cleaned (1 N HCl) polycarbonate bottles (5 L) for further analyses/determinations. To determine the concentration of Chl-*a*, aliquots of 100–250 mL were filtered onto Munktell GF/F filters (25 mm diameter) that were placed in 15 mL centrifuge tubes. Five mL of absolute methanol (Holm-Hansen and Riemann, 1978) were added to the tubes that were then placed in a sonicator for 20 min at 20 °C, and the extraction was completed after 40 min more in darkness. After the extraction period, the samples were centrifuged at 2000 rpm for 20 min and the supernatant scanned from 250 to 750 nm, using a spectrophotometer (Hewlett Packard model HP 8453E, USA). The Chl-*a* concentration was calculated using the equation of Porra (2002).

Samples for identification and enumeration of phytoplankton were put in 250-mL brown glass bottles, and fixed with buffered formaldehyde (final concentration 0.4% in the sample) or acid Lugol solution (1% vol vol^{-1}) for sea and river samples, respectively. Sub-samples of 10–25 mL were allowed to settle for 24 h in Utermöhl chambers and, in the case of marine samples, a drop of Rose Bengal was added to better distinguish organic material from detritus. Species were identified and enumerated using and inverted microscope (Leica, model DM IL, Germany) following the technique described in Villafañe and Reid (1995). The biovolumes of the phytoplankton cells were calculated according to Hillebrand et al. (1999). Biovolumes were then converted

Table 1
Sources of data used in this study for the reference (2001–2014) and for 2015 periods, of solar radiation doses (ultraviolet A and B [UV-A and UV-B] and photosynthetically active radiation [PAR]), temperature (air, seawater and river), wind (speed and direction), precipitation, river flow, Chl-*a* and phytoplankton abundance and composition, and nutrients.

Variable/period	Frequency of data/number of observations	Sources
Solar radiation (UV-A, UV-B, PAR) (2001–2015)	Every minute	EFPU database (www.efpu.org.ar)
Air temperature (2001–2015)	Every minute	EFPU database (www.efpu.org.ar)
Wind speed/direction (2001–2015)	Every minute	EFPU database (www.efpu.org.ar)
Precipitation (2001–2015)	Monthly	SIPAS database (www.sipas.inta.gob.ar)
River flow (2001–2015)	Daily	BDHI database (www.bdhi.hidricosargentina.gov.ar)
Water temperature (1986–2015) (sea/river)	Sea: $n = 162$ River: $n = 105$	Helbling (1989); Villafañe et al. (2004); Helbling et al. (2005, 2010); Spinelli et al. (2016); Cabrerizo et al. (2017); EFPU (unpubl.)
Nutrients (1986–2015) (sea/river)	Sea: $n = 94$ River: $n = 76$	Helbling (1989); Helbling et al. (2005); EFPU (unpubl.)
Chl- *a* (1986–2015)	$n = 194$	Helbling (1989); Barbieri et al. (2002); Helbling et al. (2005, 2010); Villafañe et al. (2004, 2008); Spinelli et al. (2016); Cabrerizo et al. (2017); EFPU (unpubl.)
Phytoplankton abundance/composition/C biomass	$n = 90$	Sastre et al. (1994); Villafañe et al. (2004, 2008); Spinelli et al. (2016); EFPU (unpubl.)

into carbon content (i.e., biomass) using the equations of Strathmann (1967), considering the abundance of cells in the samples. The percentage microplankton was obtained as the number of microplankton cells relative to the total of cells (*100), or by the biomass (as carbon) in the microplacktonic fraction as compared to the total carbon biomass. There was a good agreement between both methods of calculation and thus the data presented is based on cell counts.

2.3. Data treatment

The biological data (i.e., Chl-*a*, carbon biomass, cell abundances and percentage of microplankton and diatoms) are presented as box-plots therefore medians, first and third quartiles, together with 1.5 of the interquartile range (IQR) and outliers are shown. In the case of air, river and seawater temperature data, the mean monthly values, and standard deviations (SD) were calculated for the reference period as well as for the year 2015. Mean monthly values and SD were also calculated for the river flow, precipitation data, and aerosol index. In the case of wind data, the mean numbers of days per year (i.e., frequency) having the same maximum wind speed, with a resolution of 1 km h^{-1} interval, were calculated for the bloom period (i.e., winter) for both, the reference period and for the year 2015.

Normality and homoscedasticity of the data sets were tested using the Shapiro-Wilks and Barlett tests, respectively (Zar, 1999). As the data did not follow a normal distribution, statistical differences between the year 2015 and the reference period data sets were established using the non-parametric Mann Whitney *U* test.

3. Results and discussion

One of the most important characteristics of the South Atlantic Ocean (SAO) is that it is exposed to intense winds almost all year around (Gaiero et al., 2003; Gassó and Stein, 2007) and thus the upper water column over the continental shelf is in general well mixed and with a deep upper mixed layer, UML (Neale et al., 2003). Nevertheless, there is a temporal heterogeneity in the wind patterns, being more intense during spring and summer, and less so and variable during winter (Villafañe et al., 2004; Helbling et al., 2005). We used the wind data over our reference period to calculate the numbers of days per year (i.e., frequency) with a certain wind speed, and a clear bi-modal curve was observed during winter (Fig. 2a). The first peak of the curve involves calm days, with low wind speeds (<15 km h^{-1}) occurring during winter and with a predominant west direction (Fig. 2a,c); during this period there were up to 11 days with a maximum speed ca. 10 km h^{-1}. The second peak of the curve corresponds to high wind speeds (up to 5 days with wind speeds ca. 40–45 km h^{-1}) occurring mostly during spring and summer, as previously determined by Villafañe et al. (2004) and Helbling et al. (2005). During 2015, however, a unimodal curve was determined (Fig. 2b) with up to 10 days with wind speeds ca. 30–35 km h^{-1}. Thus the characteristic calm days observed during winter, for the reference period (Fig. 2a) completely disappeared and instead, during winter 2015 the maximum wind speed was always >15 km h^{-1} and predominantly from the north (Fig. 2d).

Wind is an essential factor controlling phytoplankton dynamics, as determined not only in the early work of Sverdrup (1953) but also in other studies that proposed that strong winds could delay the initiation of blooms, while calmer winds could promote their formation (e.g., Arrigo et al., 1998; Collins et al., 2009; Ferreira et al., 2015). Previous reports (Fitch and Moore, 2007) indicate that phytoplankton biomass and blooms in the Southern Ocean peaked at low wind speeds (<18 km h^{-1}) whereas over this threshold their initiation was precluded (Weise et al., 2002). Thus, the changes in the wind pattern observed during 2015 (Fig. 2) gave us a unique opportunity to analyze the impact that it might have on the winter phytoplankton bloom in our study area.

The Chl-*a* concentration (Fig. 3a), phytoplankton carbon biomass (Fig. 3b) and abundance of cells (Fig. 3c) show a clear pattern, with a

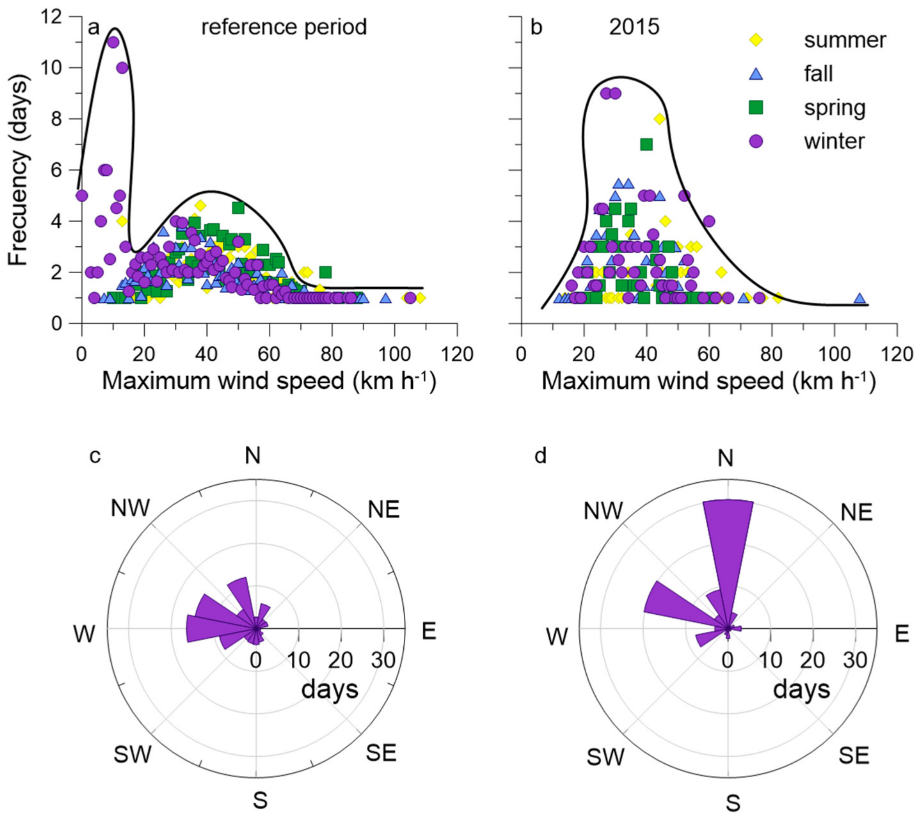

Fig. 2. Wind speed and direction for the reference period (2001–2014) and for the year 2015. a, b) Mean frequency (number of days) of maximum wind speed (km h^{-1}) for summer, fall, spring and winter. c, d) Mean frequency (number of days) for each wind direction during the winter of the reference and 2015 periods, respectively.

winter phytoplankton bloom during the reference period peaking at the month of June, and with pre- and post-bloom periods during fall, and spring - summer, respectively. The median Chl-*a*, phytoplankton carbon biomass, and cell abundances during the peak of the bloom were ca. ~30 μg Chl-*a* L^{-1}, ~450 μg C L^{-1} and 3×10^3 cells mL^{-1}, respectively, but values > 100 μg Chl-*a* L^{-1} and >5×10^3 cells mL^{-1} were previously reported for two particular years (2000–2001; Helbling et al., 2005). Outside of the winter bloom period, the Chl-*a* concentration, biomass, and phytoplankton abundance remained relatively low i.e., <10 μg Chl-*a* L^{-1}, <50 μg C L^{-1} and 2×10^3 cells mL^{-1} (Fig. 3a–c) although some months had slightly higher values (e.g., early spring). These patterns in phytoplankton abundance were in turn associated with the cell size structure, with microplanktonic cells (>20 μm) dominating the winter bloom during the reference period (Fig. 3d), being the diatom *Odontella aurita* the dominant species (>80% of the diatom contribution, Fig. 3e). The microplankton diatom dominance reported during the winter bloom period is consistent with other studies (Marañon et al., 2012; Harding et al., 2015) that showed a higher proportion of diatoms in communities that had high availability of resources and phytoplankton biomass. Moreover, the fact that these blooms in the SAO are almost completely dominated by large diatoms (i.e., *Odontella aurita*) agrees with the idea that estuarine-coastal waters act as diatom-producing factories that provide huge amounts of high-value food to consumers and regulate the global silica cycling (Agustí et al., 2015). During the pre- and post-bloom periods, however, nanoplanktonic cells (2–20 μm; i.e., mostly unidentified flagellates) were the most conspicuous (Fig. 3d). Even more, a survey carried out during the summer of 2006 in the study area (Villafañe et al., 2008) determined high biodiversity of picoplankton (<2 μm) using HPLC techniques, with chlorophytes, cyanobacteria and cryptophytes being the most representative groups and accounting up to 30% of the total phytoplankton biomass; thus picoplankton, although not evaluated in this study, might be numerically important in the area when diatoms are not dominant. Dinoflagellates never contributed for an important share (<2% of total abundance, with a maximum concentration of ~60 cells mL^{-1}), but it is worth to mention that *Alexandrium tamarense*, found in the samples mostly during the post-bloom is responsible for red tide events (Gayoso, 2001). The low contribution of dinoflagellates found in our study and also in a recent meta-analysis (Carstensen et al., 2015) can be attributed to the fact that they are poor competitors, as compared with fast-growing diatoms such as *O. aurita*. Moreover, a previous work (Smayda and Reynolds, 2003) reported that dinoflagellates are not able to compete with diatoms because of their low nutrient uptake capacities and their low growth rates under the replete-nutrient conditions as found in coastal waters. Also, a study carried out in the Baltic Sea proposed that dinoflagellates are only relevant contributors to the community when they develop alternative biotic strategies other than photosynthesis to obtain carbon and/or nutrients, i.e. mixotrophy or allelopathic interference (Spilling and Markager, 2008). In contrast to the above described phytoplankton dynamics, during 2015 there were two significant deviations (as compared to the reference period): The first one was related to the significantly lower values of Chl-*a*, carbon biomass and cells abundance during June of 2015 as compared to June bloom characteristic of the reference period (Fig. 3a–c). Furthermore, the 2015 bloom occurred later in the season i.e., on August (Fig. 3a–c). The second deviation was related to the size structure and composition of the phytoplankton community, with microplankton and diatoms accounting for <40% dominance during June 2015 as compared to the >80% during the reference period (Fig. 3d, e). In addition, the late bloom observed during August 2015 (Fig. 3a–c) was co-dominated by

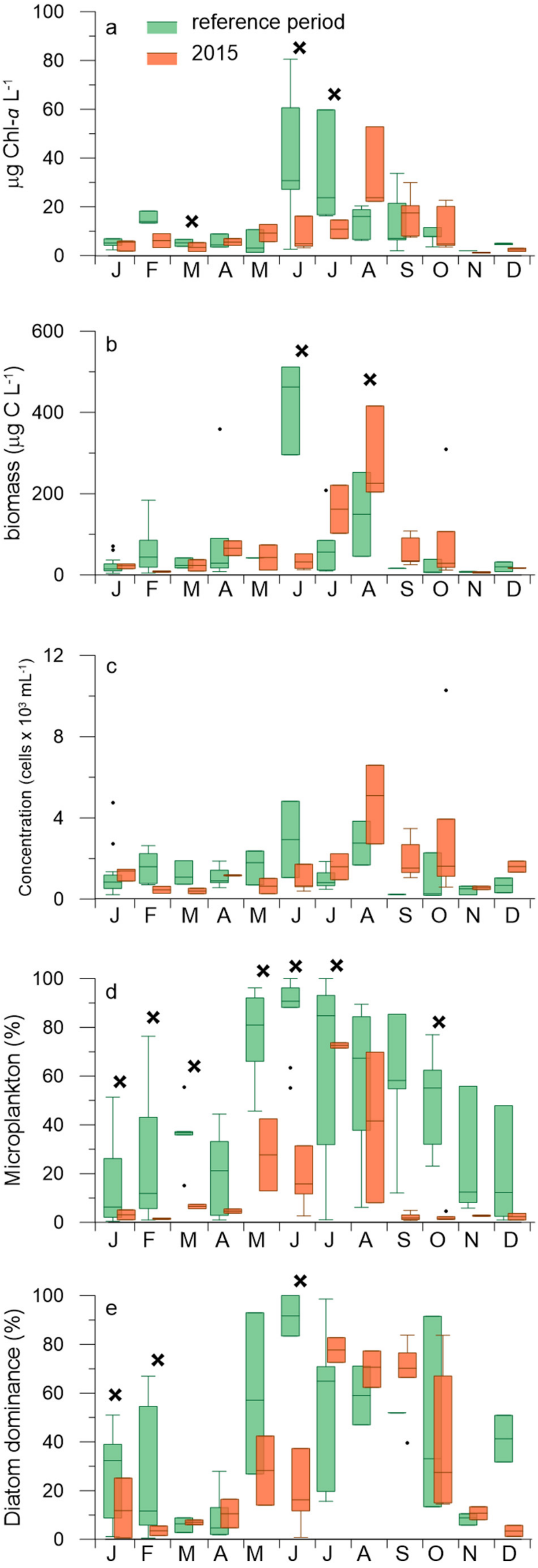

Fig. 3. Box plots showing the monthly median, first and third quartiles, together with 1.5 of the interquartile range (IQR) and outliers, for both the reference period and the year 2015 for: a) Chl-*a* concentration (in μg Chl-*a* L^{-1}), b) Phytoplankton biomass (in μg C L^{-1}); c) Total phytoplankton abundance (in cells $\times$ 10^3 mL^{-1}), d) Percentage of microplankton (>20 μm) and, d) Percentage of diatom contribution. The X indicates significant differences between the reference period and the year 2015.

nanoplanktonic diatoms such as *Thalassiosira* species (10–20 μm in diameter) together with *O. aurita*.

It was proposed for the study area (Villafañe et al., 2004; Helbling et al., 2005) that the stratification of the water column (i.e., shallow upper mixed layer, UML) during the winter was the key factor for the development of the intense phytoplankton blooms observed during the reference period. The underlying mechanism that allowed the growth of phytoplankton was such that stratification resulted in higher solar radiation availability during this low-light period, allowing the cells to take full advantage of nutrients. On the other hand, the intense vertical mixing due to the strong winds - characteristic of mid-latitudes of the SAO - precluded the development and/or the maintenance of the bloom during the rest of the year (e.g., spring and summer). This is in agreement with a recent survey of 86 estuarine-coastal sites that showed that the occurrence of blooms did not follow a response pattern across gradients of temperature, salinity or nutrient concentrations; rather, the wind direction and/or speed was the main variable directly related to the bloom occurrence and its timing (Carstensen et al., 2015). The differences in the stratification (due to differences in wind conditions) throughout the annual succession during the reference period are also seen in the C/Chl-*a* ratio, that had significantly higher values during the June bloom (value of 18) in spite of the relatively low irradiance during winter, as compared to the rest of the year (values <8). These values, although somehow lower than in other parts of the World's ocean (i.e., 15–176; Sathyendranath et al., 2009) reflect the relatively deep mixing for most of the year, and the low-light history of these cells. In June of 2015 however, the C/Chl-*a* ratio was <5, supporting the view that the strong northerly winds mixed the water column, thus exposing the phytoplankton to relatively low solar radiation levels. During August 2015 (bloom period) the irradiance was higher and thus the C/Chl-*a* ratio during this month also increased (value of ca. 15).

The phytoplankton dynamics also depends on other variables such as solar radiation (Platt and Jassby, 1976; Mitchell et al., 1991; Cloern, 1996), temperature (Sobrino and Neale, 2007; Yvon-Durocher et al., 2015) and nutrients (Paerl, 2007; Lancelot and Muylaert, 2011). Thus we analyzed and compared the patterns of these variables during 2015 and the reference period to evaluate if there were changes that may also accounted for the lack of a bloom during June 2015. The mean daily doses for surface solar radiation i.e., PAR (400–700 nm) and for ultraviolet radiation (UVR, 280–400 nm) during 2015 were comparable to the reference period with the exception of a few months (June to August) when they were slightly, but significantly lower in the former (data not shown). These differences in solar radiation doses were so small that we consider that they were not enough to solely explain the lack of a phytoplankton bloom during June 2015, but they contributed to decrease the irradiance received by the cells in the water column. Nevertheless, previous experimental and modeling results indicate that a critical light intensity is needed to trigger a phytoplankton bloom (Siegel et al., 2002; Sommer and Lengfellner, 2008).

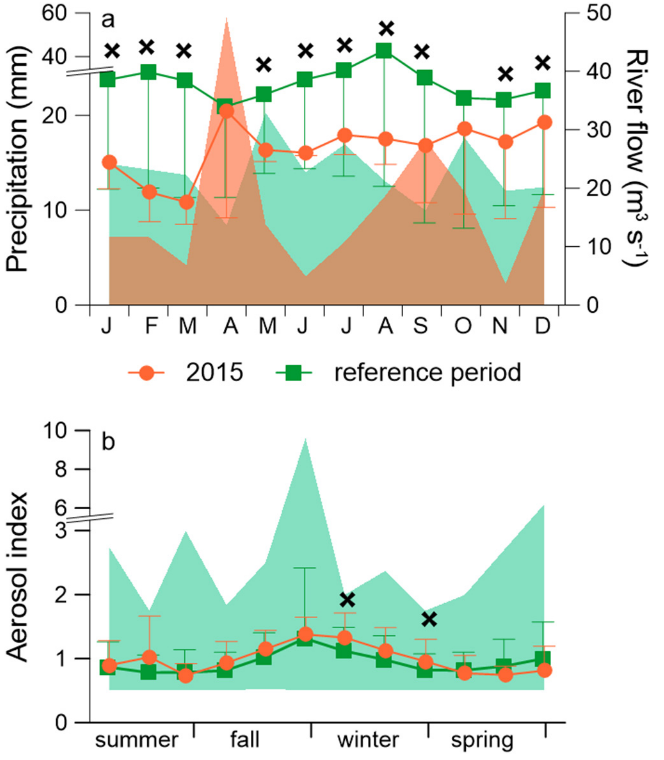

Fig. 4. a) Monthly precipitation (in mm, symbols and deviations) and river flow (in $m^3\ s^{-1}$, shaded areas) for the reference (green) and 2015 periods (orange); b) Daily aerosol index (AI) for the reference period (green squares) and year 2015 (orange circles); the shaded green area covers the maximum and minimum values for the reference period. The X represents significant differences between the reference period and the year 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the water column however, solar radiation is further reduced by the presence of dissolved and suspended organic material from riverine and eolic origin, and it is expected that their amounts will increase in the future due to the growth of cities and their associated economic activities (Rabalais et al., 2009; Cloern et al., 2016). In the study area, the monthly precipitation values (Fig. 4a) during 2015 were in general lower than during the reference period, and this might be associated with the 2015 El Niño event that caused less precipitation than the average in the Patagonian area (https://www.ncdc.noaa.gov/sotc/global/201513). This pattern was also observed (Fig. 4a) in the river flow (with the exception of April and September 2015) that had a yearly mean of 26.8 $m^3\ s^{-1}$ (SD $=$ 4.5) and 37.9 $m^3\ s^{-1}$ (SD $=$ 2.6) during the year 2015 and the reference period, respectively. The river flow is controlled by the Florentino Ameghino Dam and this is why there is little or no correlation in the monthly means between precipitation and river flow. It could argued that as the river flow and precipitation were lower in 2015 than in the reference period, lower amounts of dissolved and particulate materials would be dumped into the coastal areas, thus counteracting somehow the lower solar radiation levels determined during winter in 2015. However, if there was a decrease in the amount of materials carried by the river, this was not reflected in the C/Chl-*a* ratio (as mentioned above) that during June 2015 was low (<5), highlighting for the low-light history of the cells. The other source of particulates (eolic aerosols i.e., dust and smoke Acker and Leptoukh, 2007), estimated through the monthly mean aerosol index (AI), varied between 0.7 and 1.4 (Fig. 4b) for both, 2015 and the reference period; the only exceptions were July and September of 2015, when the AI values were significantly higher than during the reference period. However, a particular event gave rise to a maximum reference AI of ca. 10 during June 2011, when the Puyehue volcano erupted in the Andes (~700 km west from Bahía Engaño) but ashes reached soon the study area, as aerosols in general (and the Patagonian dust in particular) can travel long distances over the continents and seas such as the SAO region (Johnson et al., 2011; Li et al., 2010). This event resulted in a decrease in the underwater radiation levels in the study area; however, it did not affect photosynthesis and growth during the bloom period (Villafañe et al., 2013).

Nutrients are also essential for photosynthesis and growth, and in the coastal SAO they originate from local upwellings (Pisoni et al., 2014), river inputs (mainly associated to anthropogenic activities i.e., agricultural and land use; Giraud et al., 2008) and dust deposition from eolic origin (Jickells and Moore, 2015; Song et al., 2016). Thus it can be argued that the reduced precipitation and river flow during 2015 would decrease the amount of nutrients brought into the coastal areas, potentially modifying the dynamics of the bloom. However, and although there were differences in the nutrient concentrations between

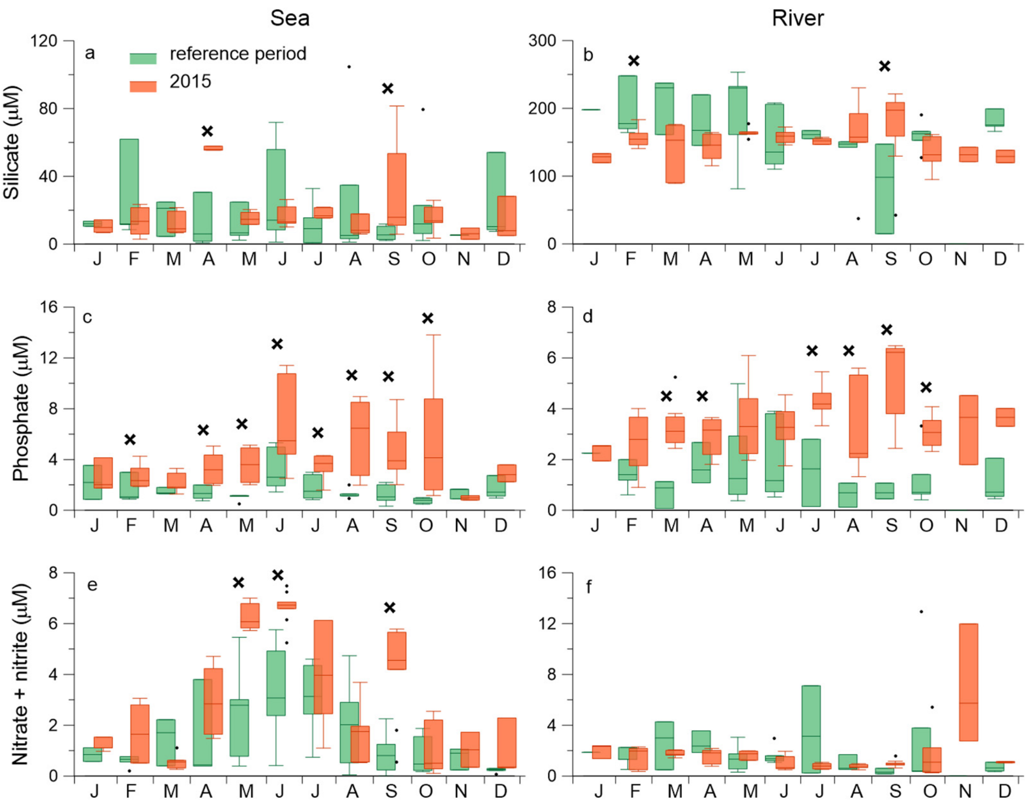

Fig. 5. Box plots showing the monthly median, first and third quartiles, together with 1.5 of the interquartile range (IQR) and outliers, for both the reference period and the year 2015 for: a, b) Silicate concentration (in µM), at sea and river, respectively. c, d) Phosphate concentration (in µM), at sea and river, respectively. e, f) Nitrite + nitrate concentration (in µM), at sea and river, respectively. The X represents significant differences between the reference period and the year 2015.

2015 and the reference period (Fig. 5) they were probably not the main drivers behind the changes in the phytoplankton dynamics. Silicate concentrations were always higher in the river than in the sea (Fig. 5a, b) but high values were observed at the sea during April and September 2015, coinciding with the two peaks of river flow (Fig. 4a) during this year. This increase in silicate, however, was not reflected in the dominance of diatoms or in the relative proportion of microplankton (Fig. 2d, e). In the case of nitrogen and phosphorus (Fig. 5c–f), and despite their high variability throughout the year, their patterns during the reference years and during 2015 in both the river and the sea were rather similar, for most of the time. This suggests little use of nutrients within the estuary, and that much of them, transported by the river, reached the ocean. However, significantly higher values in 2015 (as compared with the reference period) were determined for phosphate, both in the river and the sea (Fig. 5c, d), and nitrite + nitrate at the seawater end of the estuary (Fig. 5e), with values that sometimes surpassed the maximum registered during the reference period reported here. The high amounts of phosphate are probably related to the more intense use of land (i.e., agricultural activities and excessive use of fertilizers; Kopprio et al., 2015), mainly in the form of organophosphates (Antolini, 2012). On the other hand, the high amounts of nitrogen observed at the sea end of the estuary, that far exceeded those registered in the river, may originate from the fish processing factories (Arvanitoyannis and Kassaveti, 2008) located at the mouth of the river (Chiarandini Fiore et al., 2013). Overall, we conclude that nutrients were not limiting throughout the year; even more, during 2015 their concentrations were in general higher than during the reference period therefore, the lack of a bloom during June 2015 was not directly related to nutrients availability.

Finally, we evaluated the water temperature patterns during 2015 and the reference period. At the sea end of the estuary, higher temperatures were determined during 2015, as compared with the reference period, mainly in summer and fall (Fig. 6). Thus seawater was warmer

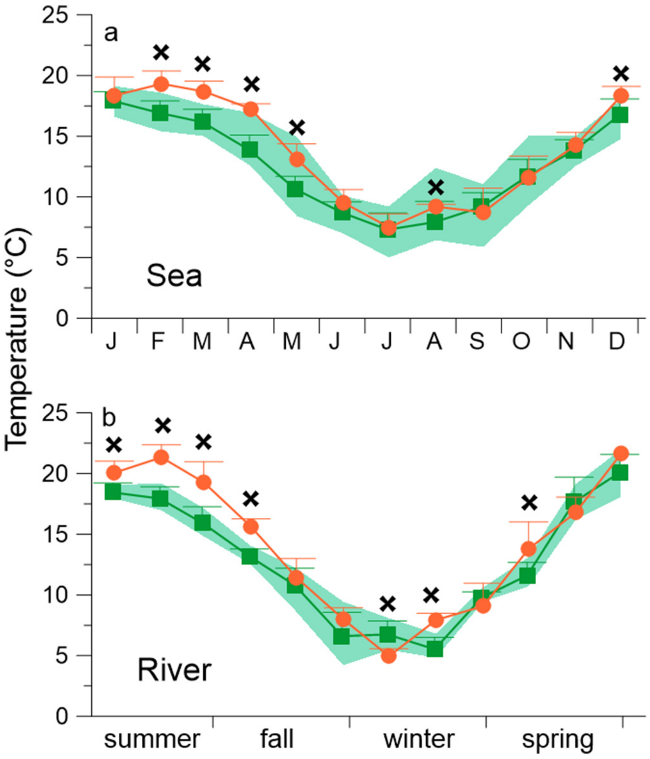

Fig. 6. Monthly temperature (°C) average (±SD, vertical lines) for seawater and river during the reference (green squares) and 2015 periods (orange circles). The green shaded areas cover the maximum and minimum values for the reference period. The X represents significant differences between the reference period and the year 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

during August 2015 than in the past (Fig. 4b) and this temporally coincided with the maximum Chl-*a* and cell abundances observed (Fig. 3b, c). This slight, but significant increase in temperature during August 2015 might partially explain the changes in the phytoplankton size structure towards a higher proportion of small nanoplankton species (Fig. 3d). This is in agreement with other studies (Winder and Hunter, 2008; Lewandowska and Sommer, 2010) that determined the key role of temperature in shaping the size structure of the community. In particular, other studies conducted in the SAO (north of Bahía Engaño) reported changes in the phytoplankton community towards the dominance of small diatoms such as *Cyclotella* and *Thalassiosira* that were associated to the combined effects of increased water temperature and changes in precipitation patterns (Guinder and Molinero, 2013).

4. Conclusions

SAO coastal areas deserve much attention due to their high productivity and their key role as breeding and nursery areas for species of ecological and economical interest. This is an under-sampled area as compared to other parts of the World's ocean, so our work presented here add relevant information about recent changes in wind patterns and how this affected the phytoplankton dynamics in this coastal system. The delay of the annual phytoplankton bloom in Bahía Engaño during 2015, as well as the reduction in its intensity clearly highlight for an important influence of physical mechanisms as disturbance agents that can disrupt the balance between phytoplankton division and grazer consumption (Behrenfeld and Boss, 2014). In the coastal SAO, wind provides by itself the necessary mechanism to trigger or to delay blooms. These changes in the timing and intensity of the bloom, tied to shifts in the size structure of the bloom community towards smaller cells, can alter the subsequent ecosystem feedbacks due to the coupling predator (zooplankton) - prey (phytoplankton), negatively impacting the food quality and quantity for the zooplankton community and thus, the energy transference to higher trophic levels.

This work allowed us to establish a starting point for temporal patterns and variability of different biotic and abiotic factors for the last decades, and it constitutes the first step to understand potential changes that are expected for the future. It is obvious, from the type of data obtained so far (with important gaps in time and effort to collect the data), the necessity of implementing more rigorous and new monitoring and control programs over long-term. Such programs should consider other variables related with climate (e.g. winds) and/or human-being activities (e.g. amount of nutrients of anthropogenic origin, effluents from fisheries, agricultural fertilizers) to obtain more precise predictions that would allow policymakers and environmental managers to take decisions based on solid empirical evidences.

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