

Time-varying environmental control of phytoplankton in a changing estuarine system



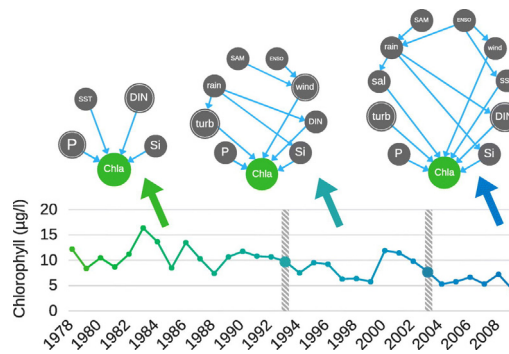
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HIGHLIGHTS

- Increasing influence of multiple environmental drivers produces changes on the temporal variability of species.
- The intensity and hierarchy of drivers acting upon organisms within alternative regimes of variability may differ.
- We identified regimes of variability of phytoplankton and depicted cascading effects of multiple drivers in each period.
- The number of factors driving the response of phytoplankton increased along time and produced the erosion of productivity patterns.
- The hierarchy and interactions of drivers changed over time, revealing that management policies require constant update.

GRAPHICAL ABSTRACT



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ABSTRACT

Estuaries are among the most valuable aquatic systems by their services to human welfare. However, increasing human activities at the watershed along with the pressure of climate change are fostering the co-occurrence of multiple environmental drivers, and warn of potential negative impacts on estuaries resources. At present, no clear understanding of how coastal ecosystems will respond to the non-stationary effect of multiple drivers. Here we analysed the temporal interaction among multiple environmental drivers and their changing priority on shaping phytoplankton response in the Bahía Blanca Estuary, SW Atlantic Ocean. The interaction among environmental drivers and the number of significant direct and indirect effects on chlorophyll concentration increased over time in concurrence with enhanced anthropogenic stress, changing winter climate and wind patterns. Over the period 1978–1993, proximal variables such as nutrients, water temperature and salinity, showed a dominant effect on chlorophyll, whereas in more recent years (1993–2009) climate signals (SAM and ENSO) boosted indirect effects through its influence on precipitation, wind, water temperature and turbidity. Turbidity emerged as the dominant driver of chlorophyll while in recent years acted synergistically with the

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concentration of dissolved nitrogen. As a result, chlorophyll concentration showed a significant negative trend and a loss of seasonal peaks reflecting a pronounced reorganisation of the phytoplankton community. We stress the need to account for the changing priority of drivers to understand, and eventually forecast, biological responses under projected scenarios of global anthropogenic change.

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1. Introduction

Estuaries harbour vast socioeconomic resources, i.e., food production and nutrient recycling, and are among the most valuable aquatic systems by their services to human welfare (Costanza et al., 2014). These ecosystems, however, face increasing pressure due to the co-occurrence of environmental stressors emerging from climate change and urban development at the watershed (Scavia et al., 2002; Bulleri and Chapman, 2010; Cloern et al., 2016). In recent years, several studies have accounted for the prevalence of complex relationship between co-occurring environmental drivers; for instance, the joint effect of drivers may amplify (synergisms) or decrease (antagonisms) the effect of individual signals (Crain et al., 2008; Brown et al., 2013; Nöges et al., 2016). Environmental conditions affect interannual variations in plankton structure and abundance (Liu et al., 2013; Barton et al., 2016; Defriez et al., 2016), although the interaction is discontinuous over the time scale (deYoung et al., 2008; Bopp et al., 2013). In this scenario, managers must face the dilemma of reducing the effect of dominant drivers acknowledging that such dominance may change in the future, and that their management actions may elicit unexpected biological responses.

Short-lived, marine phytoplankton act as sentinels of coastal ecosystem changes. Common responses of phytoplankton to such environmental changes are modifications in the temporal and spatial distribution of species (Casini et al., 2008; Kromkamp and van Engeland, 2010; Molinero et al., 2013). While some organisms may acclimate, others may not be able to tolerate the present and future environmental rate of change and will be locally excluded, ultimately affecting ecosystem services (Boyd et al., 2016). The interactive effect of multiple environmental signals has been studied through the analysis of sustained observations of marine environments (e.g. Mieszowska et al., 2014; Firth et al., 2015; Gieswein et al., 2017). This approach allows evaluating the temporal evolution of habitat control on species and can inform managers on potential modifications of driver hierarchy.

The Bahía Blanca Estuary is located in a semi-arid region at the boundary of the Pampas and Patagonia. Wide seasonal variability of environmental conditions promotes marked seasonal peaks of plankton abundance in summer and winter-early spring. The estuary presents relatively high turbidity due to the effect of tides, winds and waves on the extensive tidal flats which occupy nearly 50% of the estuarine area. In recent years, the estuary has faced heavy anthropogenic pressure derived from substantial dredging and ship traffic that fostered marked modifications in the coastal habitat. Concurrently, the region has experienced climate-driven environmental changes encompassing warmer winters and extreme dry periods (Aravena and Luckman, 2009; Guinder et al., 2010), along with persistent positive anomalies of the Southern Annular Mode (SAM), which are associated with stronger-than-normal westerlies over the mid-high-latitudes and weaker westerlies in the mid-latitudes (Marshall, 2003). The combined effect of both, climate and anthropogenic pressure has been suggested as precursor of structural changes in phytoplankton communities (Guinder et al., 2010, 2013). Accordingly, recent modelling approaches have shown that severe eutrophication magnify climate effects on microplankton dynamics (López Abbate et al., 2015) while invasive species and climate, respectively, enhanced top-down and bottom-up controls on winter blooming species (Guinder et al., 2016). Global climate signals such as ENSO and SAM indirectly shape the abundance and timing of phytoplankton blooms through their effect on local climate; for instance,

winter climate conditions in the Basque coast are largely influenced by the North Atlantic Oscillation (NAO), which shapes water temperature, stratification and mixing, and therefore, indirectly influences inter-annual variations of phytoplankton biomass (Villate et al., 2008). Likewise, El Niño years promote a decrease on phytoplankton biomass and species replacement through their effect on nutrient concentration and river runoff in the Río de la Plata Estuary (Sathicq et al., 2015).

The aim of this study is to quantify the effect of multiple drivers, from large-scale climate signals, such as El Niño-Southern Oscillation (ENSO) and SAM, to local environmental conditions, on phytoplankton within alternative regimes of variability. For this purpose, we employed long-term records of chlorophyll in the Bahía Blanca Estuary, SW Atlantic Ocean, and identified significant direct and indirect effects of multi-scale variables, and further evaluated driver hierarchy and interactions within consecutive periods based on boosted regression trees (BRT), generalised linear models (GLM) and structural equation modelling (SEM). We test the hypothesis that the increasing number of co-occurring environmental drivers promotes changes on their hierarchical relationships and that such changes modify the dominance of phytoplankton drivers along time.

2. Materials and methods

2.1. Study area

Field data was collected from the inner area of the Bahía Blanca Estuary (38°42'–39°25'S, 61°50'–62°22'W) in the Southwestern Atlantic coast, Argentina (Fig. 1). The estuary covers an area of ca. 3000 km² while its drainage area extends to 19,000 km². The distance between the head of the estuary and its mouth, where estuarine waters meet the Atlantic Ocean, is approximately 60 km. The water column is shallow and vertically homogeneous, and shows higher salinity at the head than at the mouth of the estuary (i.e. inverted salinity gradient), as it experiences low influence from continental drainage (annual mean 2.7 m³ s⁻¹), restricted water circulation (tidal velocities between 0.69 and 0.77 m s⁻¹) and a relatively long residence time (ca. 30 days) (Perillo et al., 2001). The outlet of permanent freshwater tributaries, Sauce Chico, Saladillo de García and Napostá Creeks, are located near the head of the estuary, in the northern shore (Fig. 1). Maximum freshwater discharge occurs in spring and summer (Melo et al., 2003). The basin is characterized by the presence of extensive low-slope tidal flats, which represent half of its total area, and numerous tidal channels oriented NW–SE (Perillo et al., 2001).

The estuary offers shelter habitats for crustaceans, demersal fish and migratory birds (Blanco et al., 2006; Hoffmeyer et al., 2009). Recently, the estuary has been incorporated to the Western Hemisphere Shorebird Reserve Network (WHSRN). Human induced habitat modifications in the last decades include eutrophication (e.g. Marcovecchio et al., 2009; Dutto et al., 2012), chemical pollution (e.g. La Colla et al., 2015; Oliva et al., 2015), riverine habitat loss (Pratolongo et al., 2013), dredging (Perillo et al., 2001; Zilio et al., 2013), hypoxia (Dutto et al., 2012; López Abbate et al., 2015) and the introduction of invasive species (Berasategui et al., 2009; Fiori et al., 2016). Around 0.75 m³ s⁻¹ of untreated sewage is casted away in the middle reach of the estuary. This volume, along with other minor sewage subsidiaries represents 23% of total freshwater received by the estuary.

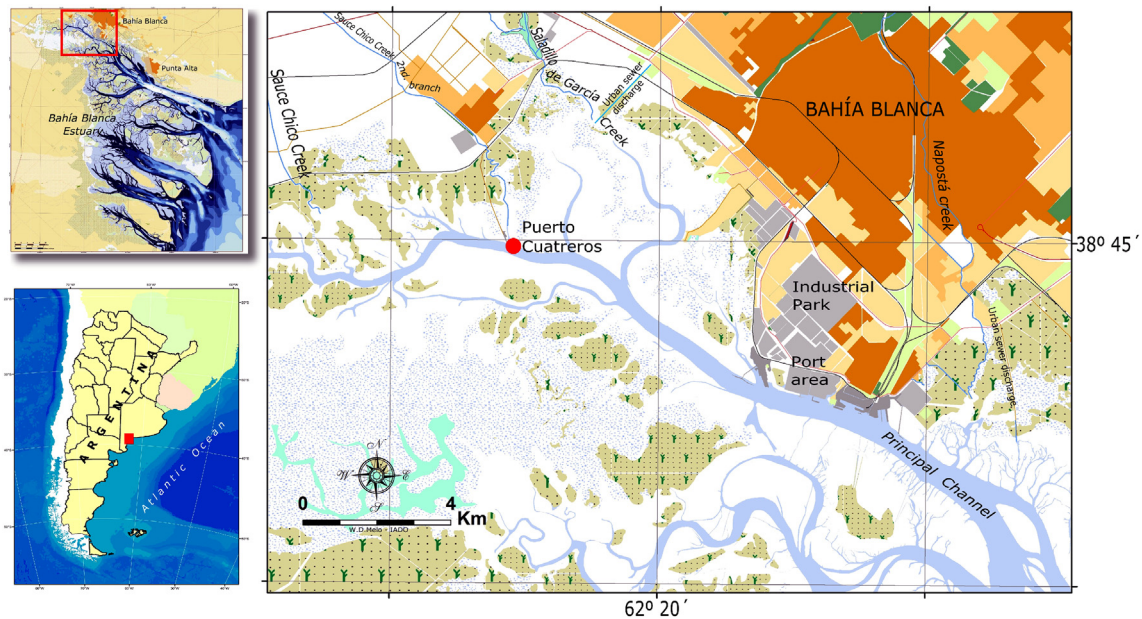


Fig. 1. Map of the Bahía Blanca Estuary, SW Atlantic Ocean, showing the location of the sampling site "Puerto Cuatrerros". Main tributaries, sewer discharge points, industrial and port areas (grey area) and the main urban centers (orange area) are also shown. Dredging operations take place periodically in the port area and in the Principal Channel. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Data collection

Chlorophyll concentration was selected as a proxy to display the long-term pattern of phytoplankton biomass. Water samples were taken from the surface layer at Puerto Cuatrerros (38°50'S, 62°20'W) (Fig. 1), on a fortnightly basis since January 1978 to December 2009 from a pier at high tide and around noon time, using a van Dorn Bottle (2.5 l). Sea surface temperature (SST), salinity and turbidity were simultaneously measured using a digital multi-sensor Horiba U-10. The number of observations of chlorophyll, SST, salinity and turbidity included in this study was 1008 for each variable. Chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) was quantified by the extraction with acetone 90% at a controlled temperature and then refrigerated in the dark at 4 °C for 24 h. Then the samples were centrifuged and the supernatant separated. The pigment concentration was determined by spectrophotometry (Jenway 6715 UV-Vis) using the equations of Lorenzen (1967). For simplicity, we here refer to chlorophyll *a* as chlorophyll. Dissolved inorganic nutrient concentrations (nitrate, nitrite, phosphate and silicate) were determined following the methods described in Spetter et al. (2015). The concentration of dissolved inorganic nitrogen (DIN) was expressed as the sum of nitrate and nitrite. Samples for nutrients determination were generally taken together with chlorophyll samples, however, a sampling discontinuation occurred from January 1987 to April 1988. Therefore, a total of 966 samples of each dissolved inorganic nutrient were available for this study. Data on monthly wind speed and direction were obtained from the National Weather Service (<http://www.smn.gov.ar>), while monthly precipitation records (i.e. monthly rainfall level) were obtained from a station adjacent to the estuary in the Bahía Blanca City, and provided by the Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS-CONICET). The total number of precipitation, wind speed and wind direction observations was 384 for each parameter. Significant linear trends in chlorophyll and explanatory variables were evaluated with linear regression models.

2.3. Detection of phytoplankton structural changes

To evaluate temporal modifications of the environmental influence on phytoplankton, we first identify shifts on the linear trend of

chlorophyll time series. Piecewise linear breakpoints were employed to identify significant fluctuations on the mean and variance (i.e. non-stationarities) by using the R-package *strucchange* (Zeileis et al., 2002). The identification of segments with particular mean and variance, allowed us splitting the time-series into period with a particular regime of variability. The number of breakpoints was set so that the confidence interval of each point did not overlap. To gain robustness on the identification of breakpoints and therefore on the detection of the main regimes of variability, we reproduced the analysis using an alternative approach, the Rodionov regime shift algorithm (Rodionov, 2004). Previous to this analysis, fortnightly records of chlorophyll were screened and averaged to obtain monthly values. Sampling gaps in 1985 (12 months), 2008 (8 months) and 2009 (6 months) were interpolated by a spline function. We used the cubic algorithm for the calculation of the spline that passes through every data point by the linkage of individual polynomials (Akima, 1970). For this analysis, seasonality was removed by applying a 365-day low-pass Loess filter.

Once the significant changes on the chlorophyll time series were identified, we evaluated the phenology and species composition of phytoplankton within each period. To do so, we first assessed the annual cycle of chlorophyll concentration by Generalised Additive Models (GAM), using mean monthly records as a function of time (months). Monthly records of chlorophyll were fitted with a logit link function using the R-package *mgcv*. Subsequently, the strength of seasonal productivity events was investigated by wavelet analysis using the Morlet wavelet function, which best describes time series with unknown frequencies (Cazelles et al., 2008). We used the averaged wavelet power spectrum (i.e. intensity of variance) in each period to represent the dominant mode of chlorophyll variability. Finally, to assess structural changes in the phytoplankton community in each period, we compiled the existing quantitative data of phytoplankton species from previous studies (Gayoso, 1998, 1999; Popovich and Gayoso, 1999; Pettigrosso et al., 1997; Popovich et al., 2008; Guinder et al., 2010).

2.4. Driver hierarchy and interactions

The hierarchical order of variables explaining chlorophyll within each period was established according to its relevance on predicting the response of chlorophyll by applying regression trees (Breiman

et al., 1984; De'ath and Fabricius, 2000). This technique allows to model the relationships between data interacting nonlinearly, and is based on the recursive partitioning of the predictor space until data fragments can fit simple models. We here used BRT which combines simple models (trees) to gain predictive power and allows to identify interactions between explanatory variables (Elith et al., 2008). We constructed models in each period following the guidelines in Feld et al. (2016) and using the R-packages gbm and dismo. The following regional and local scale variables producing direct effects on chlorophyll were selected as explanatory variables to build the BRT models: SST, salinity, wind speed, turbidity and dissolved inorganic nutrients. This set of variables is referred to as “proximal variables”. For the sake of clarity and to avoid collinearity, wind direction was not included in BRT, GLM and SEM models as it showed significant correlation with wind velocity. No direct link between precipitation and chlorophyll was stated, but both variables were indirectly linked through turbidity and nutrients (Gunder et al., 2009; Spetter et al., 2015). The relative variable importance was obtained by ranking the deviance explained by individual predictors. BRT models in the first, second and third periods comprised 138, 128 and 80 samples, respectively. Interaction among explanatory variables was computed with the R-function gbm.interactions. Single and pairwise variables candidates yielded by BRT, were used to generate GLM, which allows to quantify the standardized effect size (SES) of interactions (Feld et al., 2016). All individual additive terms and significant interactions ($p < 0.05$) were included in the GLM model. The best model was selected by comparing the Akaike information criterion (Burnham and Anderson, 2002). Confronting SES of pairwise interactions with the additive effect of individual variables, allowed us to classify interaction as additive, antagonistic and synergistic (Piggott et al., 2015).

2.5. Quantification of driver effects

To quantify the effects of environmental forcing, and their co-variations, on chlorophyll concentration within each period we used SEM. This method has proved useful to detect mediating effects of explanatory variables, allowing to test multiple interactions behind the observations (Grace, 2006). We first constructed the theoretical model by ranking the explanatory variables from global to regional and local scale, thus assuming causal relationships (Fig. 2). Primary patterns of atmospheric variability over the Southern Hemisphere, SAM and ENSO, were employed to assess the influence of large-scale climate modes on the local scale variables (Vera et al., 2004; Menéndez and Carril, 2010). Both climate signals are known to co-vary during austral summer (Fogt et al., 2010), therefore they were set as covariates in the model. Moreover, the SAM index showed persistent dominance of positive values in the last three decades, which are related with a higher-than-normal mean sea level pressure and weaker westerlies in mid-latitudes (Wang and Cai, 2013). The SAM-Marshall index, based on the difference of mean sea-level pressure between the latitudes 40°S and 65°S, was selected for the analysis as it reduces the influence of spurious trends of reanalysis products (Marshall, 2003). The temporal evolution of ENSO was assessed by the SST averaged anomaly in the Niño 3.4 region (Niño3.4 index) in the central-east region of the Tropical Pacific Ocean (5°N–5°S, 170°–120°W) (Trenberth, 1997). Regional and local scale variables driving the response of chlorophyll, were set as SST, salinity, wind speed, turbidity and dissolved inorganic nutrients; DIN, phosphate and silicate. All explanatory variables were standardized to zero mean and unit standard deviation. Collinearity between drivers was checked by the variance inflation factor (Zuur et al., 2007). Spurious up-weighting of SST due to autocorrelation was avoided by removing the annual pattern with a 365-day low-pass Loess filter. The temporal evolution of sediment extraction by dredging is shown with the aim to scrutinize the synchrony of broad-scale operations with water column turbidity, but was not included in the model as data availability was restricted to yearly mean values. Volume of

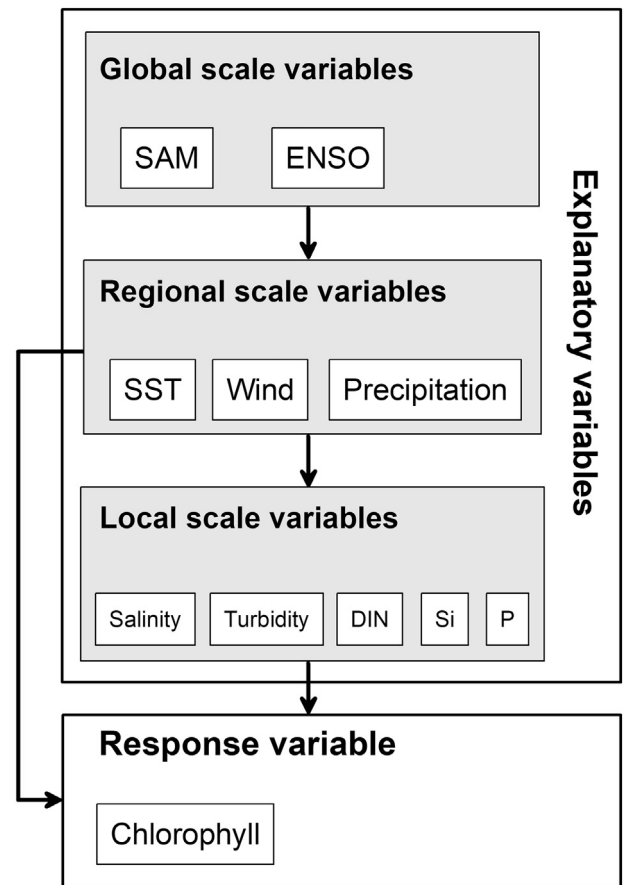


Fig. 2. Theoretical model of the direct and indirect effects of explanatory variables on the concentration of chlorophyll. Explanatory variables used in SEM specification, were categorized into global, regional and local scale variables, thus assuming causal relationships among predictive variables.

sediment extraction by dredging were provided by the Secretary of Ports and Waterways (<http://www.sspvvn.gov.ar/sspvvn/>) and the Bahía Blanca Port Management Consortium (<http://puertobahia blanca.com/>).

The response of lower ranked variables (local and regional scale variables) was tested in each period in order to calculate the strength of links along the time series. Path coefficients were determined by simple and partial multivariate regression and Monte Carlo permutation tests (1000 replicates), while the Bayesian Information Criterion (BIC) and Chi-square values were used to assess the robustness of models (Alsterberg et al., 2013). Path analysis was performed using the R-library lavaan.

3. Results

3.1. Long-term structural changes of phytoplankton

The assessment of long-term structural changes in the chlorophyll time series revealed three different regimes of variability; 1978–1993, 1993–2003 and 2003–2009 (Fig. 3a). The long-term variation of chlorophyll showed a significant annual rate of decline of 1% ($p < 0.001$) corresponding to a yearly decrease of $0.26 \mu\text{g l}^{-1}$. The rate of change in the first, second and third periods was 0.03, 0.72 and 2.14%, respectively. The rate of chlorophyll decline in the last period (2003–2009) was three-fold higher than the observed in the previous period (1993–2003), and such change was preceded by a 680% increase of sediment extraction due to dredging (Fig. 5I).

The annual cycle of chlorophyll concentration in the analysed periods is shown in Fig. 3b. The mean annual concentration of chlorophyll

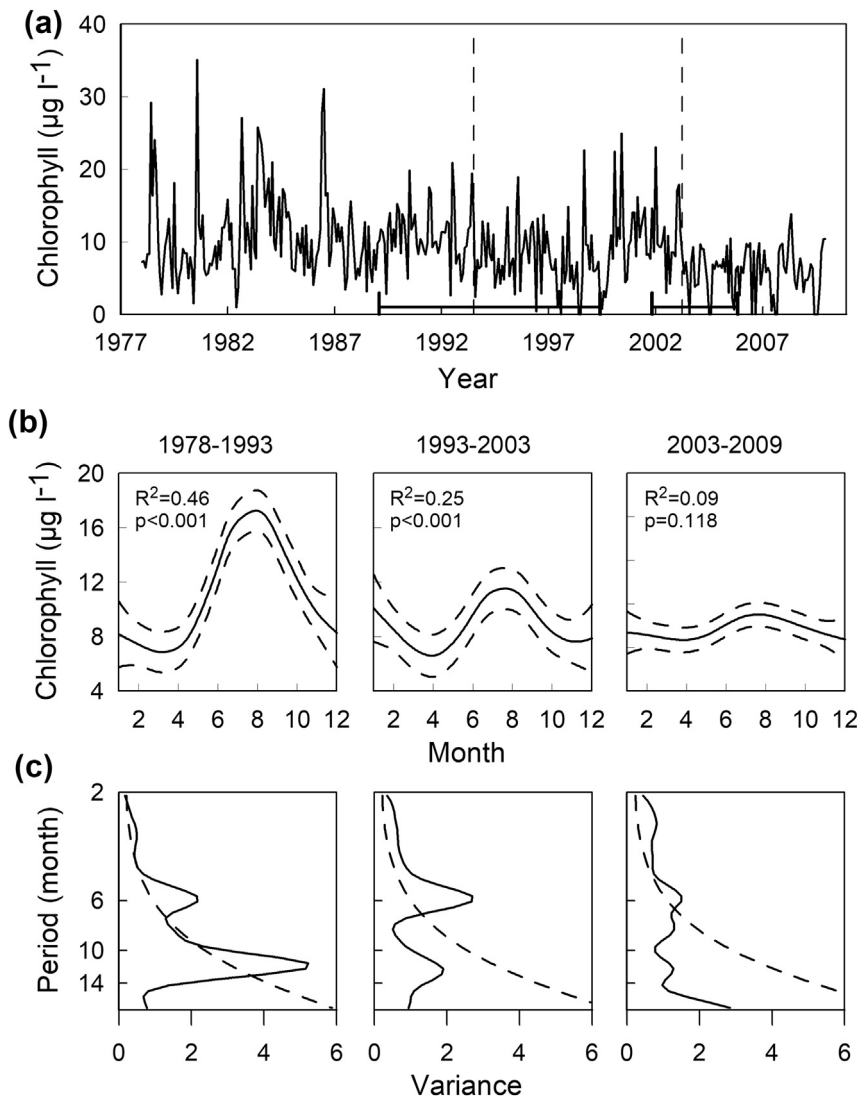


Fig. 3. Long-term variation of chlorophyll in the Bahía Blanca Estuary over the period 1978–2009. a) The interannual variation of non-seasonal chlorophyll showed a significant annual rate of decline of 1% ($R^2 = 0.397$, $p < 0.001$) and was subdivided into three different periods delimited by two breakpoints in 1993 and 2003 (dashed lines). Horizontal bars denote 95% confidence limits for breakpoints. b) GAM estimates of monthly mean chlorophyll annual patterns in the three periods. Adjusted R^2 and p -values are indicated inside the plots. c) Global power spectrum of chlorophyll concentration showing the dominant periodicities in the three periods. During the first period, the signal was characterized by two significant annual productivity events with a strong dominance of the 12-month periodicity (winter bloom). This pattern shifted towards an enhancement of the 6-month (summer bloom), which constituted the main annual event. In the third period, chlorophyll periodicity was blurred while significant values were found at lower periodicities.

in the first, second and third periods was 10.92 ± 7.54 , 8.85 ± 5.75 and $5.66 \pm 3.20 \mu\text{g l}^{-1}$, respectively. The continuous wavelet spectrum of chlorophyll time series captured the seasonal productivity events corresponding to the winter and summer blooms (Fig. 3c). During the first period, the signal was characterized by two significant events with a strong dominance of the 12-month periodicity (winter bloom). This pattern shifted towards an enhancement of the 6-month periodicity (summer bloom) in the second period. In the third period, the seasonal pattern was blurred while significant values were found at periodicities <6 month (Fig. 3c).

The first and second periods were characterized by the dominance of winter blooming diatoms, in particular, *Thalassiosira curviseriata* and other species of the genus *Thalassiosira* and *Chaetoceros* (Fig. 4). The abundance of these species substantially declined during the third period, whereas other smaller diatoms, such as *Cyclotella* sp. and *Chaetoceros* sp., were dominant during the last period. In addition, the small blooming diatom *Thalassiosira minima* showed a progressive abundance increase in the warm season since its first record in the early 1990s, strengthening the bimodal regime.

3.2. Long-term evolution of environmental drivers

The influence of regional climate and infrastructure development in the watershed was perceived as significant interannual linear trends ($p < 0.05$) in most of environmental variables (Fig. 5). This was noticed either on the whole time series: SAM index, winter temperature, wind direction, DIN, phosphate and sediment extraction (Fig. 5b, c, g, h, i, l), or in the second half of the time series: winter salinity, wind speed and turbidity (Fig. 5d, f, k). No significant trend was found in the Niño3.4 index, precipitation and silicate (Fig. 5a, e, j).

The temporal variations of sediment extraction due to dredging (Fig. 5l) showed two major milestones that resulted from broad-scale operations conducted to improve navigation of large ships (i.e. deepening and straightening of waterway). The first occurred during the years 1989–1991, and was related to the deepening of the port area in the inner reach of the estuary. During this period, the annual mean of removed sediment increased temporarily from $105,786 \text{ m}^3 \text{ yr}^{-1}$ to $1,393,030 \text{ m}^3 \text{ yr}^{-1}$. The second deepening began in 1999 and

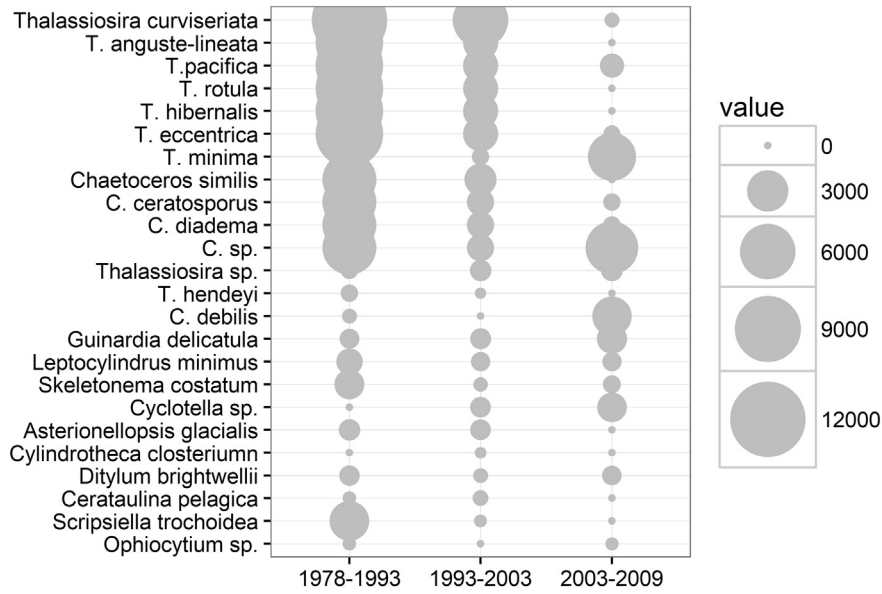


Fig. 4. Cell abundance ($\text{cell l}^{-1} \times 10^3$) of phytoplankton species averaged from discontinuous observations within each period. Scale bar is shown next to the figure.

corresponded to a conspicuous increase in the annual removal of bottom sediment, which shifted from $228,330 \text{ m}^3 \text{ yr}^{-1}$ to $2,657,919 \text{ m}^3 \text{ yr}^{-1}$. The rate of sediment removal remained high until the end of the period investigated, and a new dredging technique, based on water jet injection, was launched in the early 2000s to maintain harbour basin in the inner reach. The onset of this period was paralleled by the shift towards lower intensity NW winds and a significant increase of water turbidity at a yearly rate of 4% (Fig. 5k).

3.3. Driver hierarchy and interactions

BRT identified and ranked pairwise interactions between explanatory variables in the three periods investigated. The results given by BRT were employed to build GLM models, which confirmed four significant interactions; one in the first period (DIN:salinity), one in the second period (DIN:wind) and two in the third period (DIN:salinity and DIN:turbidity) (Fig. 6). R^2 values of BRT models were 0.60, 0.29 and 0.26 in the first,

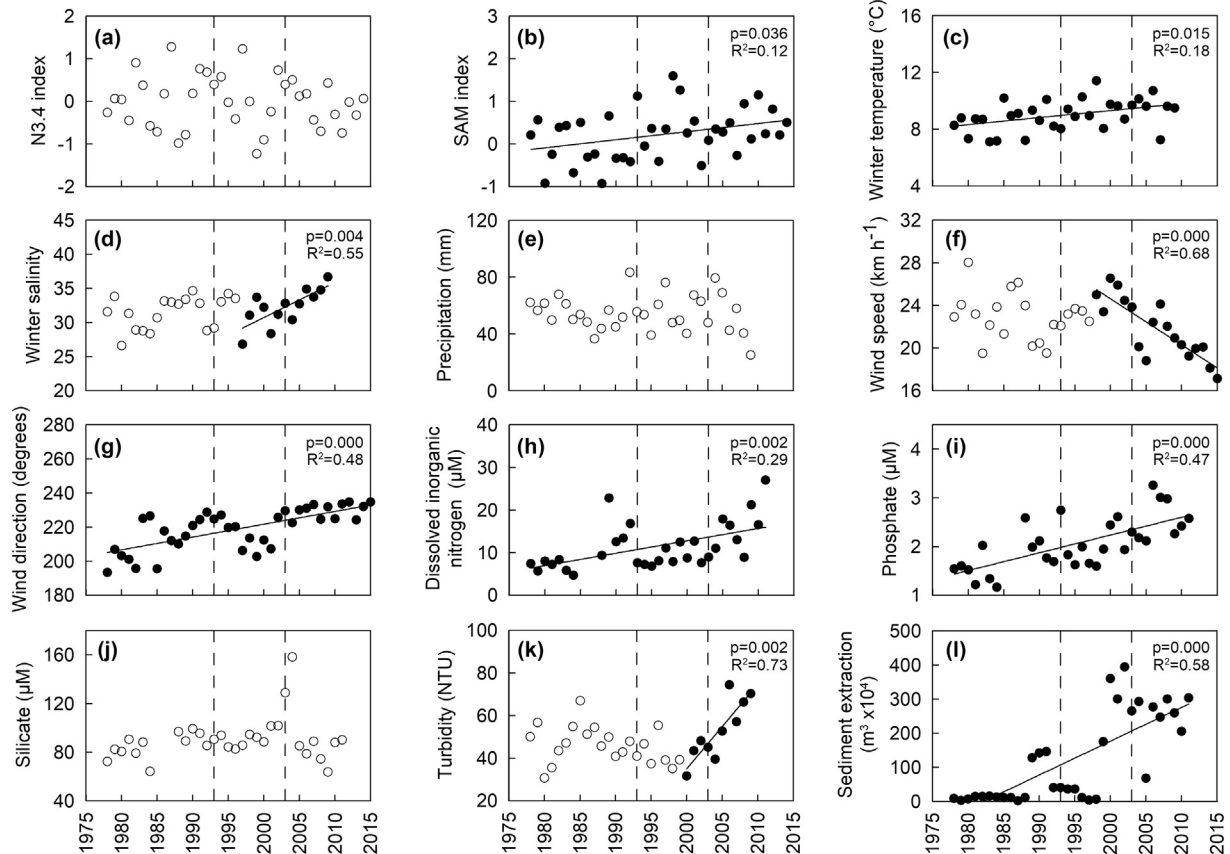


Fig. 5. Annual means of environmental variables in the Bahía Blanca Estuary over the period 1978–2009. Variables showing significant linear trends are indicated by filled (black) dots and a linear fit. R^2 and p -values are indicated inside the plots. Dashed lines delimit different regimes of variability of chlorophyll.

second and third periods, respectively, while in the GLM models, R^2 values were 0.43, 0.14 and 0.16 in the first, second and third periods, respectively.

The ranking of driver importance unveiled a changing dominance of drivers among the three periods (Fig. 7). Indeed, BRT revealed a dominant role of nutrients during the first period. This was followed by a predominant effect of turbidity, wind speed and nutrients, while during the last period, turbidity and nutrients were the main descriptors of chlorophyll, although a larger evenness in the importance of remaining variables was emphasized (Fig. 7).

3.4. Interactions among the environmental matrix

SEM models uncovered that the strength of links in the network founded by climate signals (SAM and ENSO) and the environmental matrix markedly changed and displayed a conspicuous increase of significant interactions over time (Fig. 7, Table 1). During the first period, 1978–1993, chlorophyll variability responded to the direct influence of proximal variables, such as nutrients and SST, while precipitation and salinity appeared linked with climate variability, as denoted by the Niño3.4 index. The configuration observed in the years 1993–2003 displayed a conspicuous increase of direct and indirect effects on chlorophyll. Besides the direct effect of nutrients, wind and turbidity also displayed a significant influence on chlorophyll, while precipitation and global scale variables (SAM and ENSO) indirectly shaped chlorophyll through their influence on turbidity and nutrients and on wind speed, respectively. During the third period, the SEM results pointed out cascading effects from global scale to regional and local scale variables, enhancing the environmental complexity, as depicted by the number of direct and indirect effects acting on chlorophyll. The

proximal variables, i.e. nutrients, SST and salinity, showed a significant direct effect, whereas the climate forcing (SAM and ENSO) promoted an increase of indirect effects through its influence on precipitation, wind and SST.

4. Discussion

4.1. Time-varying hierarchical relationships of drivers shaping the response of phytoplankton

During the studied period (1978–2009), we identified three regimes of variability of chlorophyll characterized by the progressive decline of chlorophyll concentration and the erosion of seasonal peaks, which shifted from the typical unimodal productivity pattern to a bimodal regime. The negative progress of chlorophyll was opposed to the positive trend in the surrounding shelf area of the Southwestern Atlantic Ocean (Gregg and Rousseau, 2014; Marrari et al., 2016), where the exposure to anthropogenic disturbance is lower and the phytoplankton productivity is fostered by the confluence of mesoscale currents and the associated marine fronts (Acha et al., 2004). Winter blooming diatoms were gradually excluded while the summer blooming diatom *T. minima* and other non-blooming species gained relevance in the phytoplankton community. Results showed that the response of phytoplankton was determined by complex hierarchical relationships among multi-scale drivers. The number of direct and indirect drivers of chlorophyll increased progressively, revealing that complex hierarchical relationships in ecosystems exposed to rapid rate of change may predict biotic responses more precisely than generalizable linear models. As climate and anthropogenic activities exerted a growing pressure in the ecosystem, the hierarchy of drivers drastically changed; the typical dominance of nutrients concentration and water temperature as main drivers of phytoplankton, shifted to the dominance of turbidity and wind velocity, whereas climate signals (SAM and ENSO) boosted indirect effects through its influence on precipitation, wind, water temperature and turbidity.

The influence of complex hierarchical relationships among drivers was shown by the joint effect of turbidity, local winds and climate modes on chlorophyll concentration during recent years. Wind pattern is an important factor affecting turbidity in coastal plains estuaries. In fact, the shear stress in the tidal flats produced by waves in the Bahía Blanca Estuary is shaped by the direction and intensity of winds (Piccolo et al., 2008). The observed shift towards low intensity NW winds, probably contributed to the increase of water turbidity in the third period, as NW winds are known to produce longer fetch and high energy waves because of their alignment with the azimuth of the estuary (Perillo and Sequeira, 1989; Pratolongo et al., 2010). The sustained effect of NW winds on wave energy, boosts the transport of fine sediments from tidal flats to the water column, and contribute to the increase on water turbidity. Both NW winds and the intensification of dredging operations in the second and third periods may have interfered on the recurrent reduction of winter water turbidity, which favoured the development of the phytoplankton bloom (Guinder et al., 2009). Similar interactive effect of dredging and winds have been identified as potential drivers of phytoplankton in Limfjorden, Denmark (Riemann and Hoffmann, 1991). In fact, among the main effects of dredging on coastal ecosystems is the potential increase in bottom shear stress that enhances bottom sediment erosion and the consequent water turbidity (Winterwerp et al., 2001).

Local wind, in turn, is modulated by the displacement of the South Atlantic subtropical anticyclone (Venegas et al., 1996; Palma et al., 2004), which revealed southward movement in the last decades and promoted changes in regional wind patterns (Simionato et al., 2005; Dragani et al., 2010). The displacement and intensity of the anticyclone system are intermittently connected with ENSO (Venegas et al., 1996), which could explain the teleconnections between local wind and El Niño signal (Colberg et al., 2004). Both climate modes, ENSO and SAM,

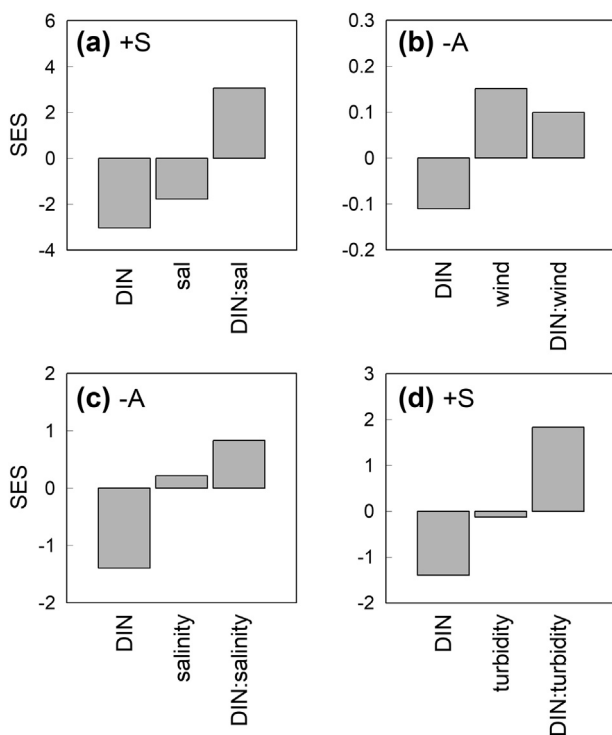


Fig. 6. Significant ($p < 0.01$) pairwise interactions of variables driving the response of chlorophyll obtained by GLM. The sign and absolute value of the standardized size effect (SES) of individual and combined drivers are used to classify the interaction; cumulative effects are classified as positive synergistic (negative synergistic) when the interactive effect is more positive (more negative) than predicted additively, while positive antagonistic (negative antagonistic) is defined when the interactive effect is less positive (less negative) than predicted additively. Positive synergistic effect (+S) occurred in the first (a) and third periods (d), while negative antagonistic (-A) occurred in the second (b) and third periods (c).

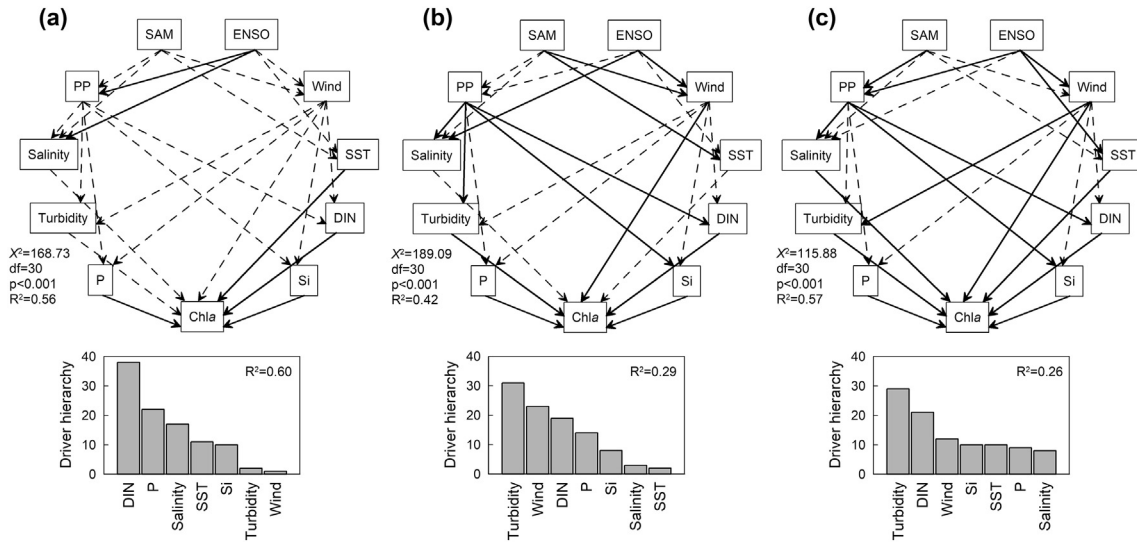


Fig. 7. Path diagrams showing significant (thick lines) and non-significant (dashed lines) interconnections between multiple environmental drivers and chlorophyll (upper panels), and the ranking of proximal variable importance driving the response of chlorophyll increased along the three periods, denoting a higher complexity within the environmental matrix. In the first period, most relevant predictors were the concentration of inorganic nutrients, while in the second and third periods, physical factors as turbidity and wind speed gained predictive power. The variables used in the model are: El Niño Southern Oscillation (ENSO), Southern Annular Mode (SAM), precipitation (PP), wind speed (wind), sea surface temperature (SST), turbidity, dissolved inorganic nitrogen (DIN), phosphate (P), silicate (Si) and chlorophyll (Chla).

shaped the response of local wind velocity during the second period (1993–2003), during which the SAM-Marshall and Niño3.4 indices showed significant correlation ($r = -0.202$, $p = 0.022$). Although part of the interannual variability of SAM is explained by ENSO signals (Fogt et al., 2010), the mechanisms driving the potential teleconnection of SAM and local wind are not clear.

These results evidence that the relationship between environmental drivers and chlorophyll may not be linear given that causal effects between predictive variables change along time regardless of the value of individual signals. Moreover, our results revealed that climate and anthropogenic stress not only modified environmental properties, but also promoted a higher interaction among environmental drivers and a higher habitat-dependency of phytoplankton. These findings underlie the need to understand hierarchical relationships among drivers within

alternative regime of variability of marine populations in coastal areas subject to rapid environmental change.

4.2. Implications for ecosystems exposed to a rapid rate of change

Several reports have shown a decline of phytoplankton biomass resulting from the combined effect of anthropogenic stress and climate forcing in estuarine systems worldwide (Nixon et al., 2009; Ensign et al., 2014). In addition to changes in phytoplankton biomass, the joint effect of multi-scale drivers may promote changes in phytoplankton phenology. For instance, warming conditions fostered the earlier onset of blooms in the English Channel (Molinero et al., 2013) and in the Western Scheldt Estuary (Kromkamp and Van Engeland, 2010). These modifications in phytoplankton blooms, in turn, challenge the survival of

Table 1
Standardized path coefficients and standard error (SE) of the structural equations models (SEM). Significant effects ($p < 0.05$) are indicated in bold.

Predictor	Response	1978–1993			1993–2003			2003–2009		
		Path coefficient	SE	P	Path coefficient	SE	P	Path coefficient	SE	P
SAM	Precipitation	−2.937	2.258	0.193	0.024	0.081	0.771	0.023	0.013	0.056
SAM	Wind speed	−0.258	0.176	0.142	−0.167	0.072	0.020	0.048	0.112	0.671
SAM	Salinity	0.157	0.176	0.373	0.059	0.08	0.462	0.12	0.095	0.206
SAM	SST	0.046	0.275	0.867	0.175	0.08	0.029	0.133	0.109	0.223
Niño3.4	Precipitation	8.350	4.210	0.047	0.099	0.078	0.204	0.042	0.021	0.045
Niño 3.4	Wind speed	−0.415	0.328	0.206	−0.307	0.069	0.001	−0.241	0.113	0.034
Niño 3.4	Salinity	−0.663	0.332	0.046	−0.324	0.078	0.001	−0.11	0.096	0.253
Niño 3.4	SST	−0.316	0.512	0.537	−0.02	0.077	0.799	0.364	0.111	0.001
Precipitation	Turbidity	0.008	0.031	0.786	0.215	0.072	0.003	0.086	0.132	0.517
Precipitation	Salinity	0.002	0.007	0.743	−0.231	0.091	0.011	−0.22	0.075	0.003
Precipitation	Phosphate	0.008	0.022	0.181	0.118	0.087	0.175	−0.08	0.106	0.45
Precipitation	Silicates	0.079	0.063	0.215	0.223	0.061	0.001	0.39	0.119	0.001
Precipitation	DIN	0.009	0.024	0.719	0.184	0.087	0.035	0.221	0.116	0.056
Wind speed	Turbidity	−0.568	0.403	0.159	0.035	0.075	0.636	0.556	0.16	0.001
Wind speed	Phosphate	−0.009	0.026	0.734	0.02	0.09	0.827	0.183	0.128	0.153
Wind speed	Silicates	0.503	0.822	0.540	0.006	0.064	0.929	−0.078	0.144	0.589
Wind speed	DIN	−0.191	0.314	0.543	−0.102	0.091	0.266	−0.11	0.14	0.433
SST	Chlorophyll	−0.455	0.095	0.001	0.007	0.079	0.933	0.871	0.062	0.025
Turbidity	Chlorophyll	−0.026	0.031	0.412	−1.079	0.699	0.044	−0.094	0.043	0.029
Salinity	Chlorophyll	−0.129	0.146	0.378	−0.057	0.073	0.436	−0.043	0.012	0.046
Wind speed	Chlorophyll	−0.048	0.149	0.745	0.175	0.084	0.038	0.163	0.068	0.017
Phosphate	Chlorophyll	−1.160	0.455	0.011	0.038	0.014	0.047	0.412	0.054	0.048
Silicates	Chlorophyll	−0.039	0.015	0.012	−0.214	0.114	0.041	−0.623	0.045	0.032
DIN	Chlorophyll	−0.081	0.040	0.044	−0.194	0.083	0.019	−0.154	0.049	0.002

higher trophic levels, some of them of economic and conservative value (Thackeray et al., 2010). In the Bahía Blanca Estuary, the observed shifts on chlorophyll concentration have been concomitant with dramatic changes in harvested populations, such as the collapse of haddock fishing (López Cazorla et al., 2014). Trophic cascades resulting from warmer temperatures and anthropogenic disturbances may also promote harmful algal blooms (HAB); in the Baltic Sea, trophic cascades driven by overfishing of carnivore fish biomass (e.g. cod) favour small pelagic fish (e.g. sprat). The latter are able to deplete zooplankton biomass, thereby favouring phytoplankton growth and increasing the probability of cyanobacterial blooms under warm conditions (Casini et al., 2008).

Another important response of phytoplankton to the interplay among multivariate factors is the spatio-temporal exclusion of resident species (Breitburg et al., 1998; Crain et al., 2008; Rose et al., 2009). In the Northeast Atlantic, pronounced shifts in dominant phytoplankton groups, i.e. a decrease in large diatoms and a larger abundance of phyto-flagellates, have been reported during the middle-late 1990s with wide consequences for ecosystem functioning (Widdicombe et al., 2010). In recent years, warmer temperatures and increasing windy conditions during summer promoted larger abundances of small HAB (e.g. *Pseudo-nitzschia* spp.) and non-HAB (e.g. *Thalassiosira* spp.) diatoms (Hinder et al., 2012). Likewise, in the North Pacific, temperature and wind drove variations in phytoplankton structure by changing the proportion of diatoms-non diatoms (Chiba et al., 2012). In the Bahía Blanca Estuary, small non-blooming diatoms gained relevance in recent years at the expense of the blooming diatom, *T. curviseriata*, which dominated the winter bloom in past years.

The current rate of environmental change underlies that climate and anthropogenic stress promotes a higher interaction among drivers (Boyd et al., 2016). The relatively weak explanatory power of BRT and SEM models may be related with the inherent attributes of the dependent and explanatory variables, and with the apparent non-stationarity of chlorophyll time-series. In the first place, models presented here were not saturated, i.e. not as many explanatory variables as degree of freedom were included. Further variables may have contributed to explain the response of chlorophyll within each period. For instance, predator concentration is known to negatively affect the abundance of winter blooming species (Berasategui et al., 2009; Guinder et al., 2016). In addition, the selected dependent variable integrates unknown variability from a myriad of underlying physiological processes operating in various phytoplankton species that obscure its interpretation. In the second place, the loss of annual seasonal peaks along the chlorophyll time-series denotes a trend towards weak stationarity or enhanced stochasticity, which relentlessly drives to large model residuals. This fact may explain the decreasing explanatory power of BRT in the second and third periods. Notwithstanding, low explanatory power does not necessarily mean low predictive power, particularly when predicting field data that is usually affected by a large number of unobservable factors. The methodological ensemble employed here allowed us to detect and model time-varying relationships between drivers and plankton responses in an ecosystem heavily exposed to human stress. It can be used to investigate long-term ecological data as it provides insights on the ecological responses to increasing climate and anthropogenic stressors. We further stress on the importance of sustained ocean observation systems, which allows to discriminate between transient anomalies and persistent trends, and are thereby essential for detecting ecosystem changes. By deciphering the mechanisms behind those changes, ocean observations provide the means to progress towards long-term sustainable management of coastal marine resources. For instance, our results allowed us to understand the ecological relevance of DIN, as it exhibited interacting relationship with explanatory variables in the three periods, and in recent years, it exacerbated the effect of turbidity (synergistic effect). Focusing management actions on nutrient loading and turbidity might mitigate the impact on primary producers.

In the coming decades, developing countries will face the highest rate of coastal transformation, posing serious risks for the ecological and economic value of ecosystem assets (Seto et al., 2012). To gain resilience management of estuarine systems, conservative policies should develop a framework that takes into consideration the non-stationary behavior of driver interactions and their interplay (i.e. synergisms, antagonisms), as their growing influence in global anthropogenic changes boosts the complexity of the environmental matrix relative to coastal populations.

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