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Seasonality of phytoplankton community and dynamics of autotrophic carbon in a cold temperate port (Argentina)

Romina Vanessa Barbosa [a,b], Silvana Halac [c], Evangelina Schwindt [d] and Marcos Tatián [a,e]

aUniversidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Ecología Marina, Córdoba, Argentina; bUniv Brest, CNRS, IRD, Ifremer, LEMAR, Plouzané, F-29280, France; cCentro de Investigaciones en Ciencias de la Tierra (CICTERRA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) – Universidad Nacional de Córdoba (UNC), Avenida Vélez Sarsfield 1699, Córdoba, Argentina; dInstituto de Biología de Organismos Marinos (IBIOMAR-CONICET), Blvd. Brown 2915, Puerto Madryn, Chubut, Argentina; eConsejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA)

ABSTRACT
The changes within and between seasons in phytoplankton composition and abundance determine the carbon biomass available for upper levels of the food web. Temporal changes in phytoplankton community and environmental parameters in a port in Puerto Madryn, Southwest Atlantic were analysed. During an annual period (2011–2012), samples of surface seawater were collected approximately monthly. We determined phytoplankton community structure (species composition and abundance) and biomass (determined by carbon content and chlorophyll *a* (Chl *a*)). Water temperature, salinity and transparency were measured when sampling the surface water and local meteorological data were considered. The main groups observed were diatoms (Bacillariophyta; the most abundant during the concentration peaks of Chl *a*), dinoflagellates (Dinophyta) and flagellates, which mainly included species of Cryptophyta and Chlorophyta. Diatoms exhibited blooms in March (summer–autumn) and September (spring), represented by *Skeletonema costatum* and *Pseudo-nitzschia* spp. respectively. Dinoflagellates contributed to the highest carbon biomass, with peaks in January (summer) and April (autumn), exemplified by *Prorocentrum micans* and *Scrippsiella acuminata*, respectively. Temporal differences in community composition were related to the seasonal changes in temperature, solar irradiance, precipitation, salinity and wind velocity. The environmental conditions seem not only to determine the species composition but also cell size distribution: nanoplanktonic (≤ 20 μm) species dominated mainly during late spring, summer and early winter while microplanktonic species (> 20 μm) during late winter and early spring. Our results showed within-season changes and show that not only Chl *a*, but also carbon content can be considered, as the former is a biased estimator of phytoplankton biomass. This study provides the first seasonally resolved estimation in the area of the carbon biomass available for upper levels of the food web and a necessary information for future scenarios prediction.

HIGHLIGHTS
- Two diatom blooms were followed by an increase in dinoflagellate abundance.
- Annual environmental conditions drive the phytoplankton community structure.
- First seasonally estimation of autotrophic biomass availability for Patagonian trophic web.

Introduction

Despite representing only 1% of the planet's autotrophic biomass, phytoplankton is responsible for 45% of annual primary production, which constitutes a short-term carbon storage (Falkowski *et al.*, 2004). The amount of primary production is related to the phytoplankton diversity, i.e. its composition and abundance, and its temporal dynamics (Vallina *et al.*, 2014). Thus, phytoplankton composition and dynamics are fundamental for the short-term carbon storage in the oceans; the Southern Ocean is the region with the poorest availability of data (Majkut *et al.*, 2014).

The composition and abundance of phytoplankton communities depend on the interactions between seasonal variation of solar irradiance, nutrients, stratification of the water column and grazing, among others. In nutrient-rich areas, the phytoplankton seasonal cycle is driven by light availability (Haraguchi *et al.*, 2015). Therefore, different phytoplankton species dominate at different times of year, depending on environmental conditions, which determines the annual succession of species as well as the inter-annual changes (Miller, 2004). Fluctuations in the environmental variables that influence phytoplankton are more pronounced in areas of medium and high latitudes, where seasonality is highly marked. For instance, seasonal variations in solar irradiance intensity and thermal stratification of water bodies are pronounced in temperate zones (Kaiser *et al.*, 2011). The winds can break the thermal stratification, mixing the water column. In turn, the state of the water column (stratified or mixed) partly determines the possibility of nutrient

availability and therefore, influences the composition and abundance of phytoplankton. Likewise, the occurrence of abundance peaks or blooms is determined by the seasonal physicochemical and meteorological variables. However, the interaction of all these factors plus local events creates a high variety of scenarios and understanding the wide range of bloom patterns is still a challenge (Carstensen et al., 2015; Rumyantseva et al., 2019).

Phytoplankton can influence the species richness and biomass of higher trophic levels, therefore, the carbon biomass of planktonic organisms is a fundamental parameter in ecosystem models. Temporal and spatial variations of exported primary production can be quantified and predicted if the carbon content of planktonic organisms is known (Menden-Deuer & Lessard, 2000). Thus, the study of these organisms can often help to understand the phenomena that occur at higher levels of the food web.

Data on the composition and biomass of the phytoplankton community is especially important in Patagonia. The spring phytoplankton blooms are comparable to those of very productive areas worldwide (Garcia et al., 2008). The phytoplankton of this region is the basis for a large stock of commercially valuable fish and invertebrates, e.g. hake and prawns (Caille et al., 1997) and also benthic organisms (Tatián et al., 2010; Schwindt et al., 2014, 2020; Giachetti et al., 2019). This region also represents the destination for annual wildlife migrations and a feeding place for numerous birds and mammals, e.g. the southern right whale (Eubalaena australis) (Rowntree et al., 2001).

Phytoplankton distribution has been studied along the coasts of the Southwest Atlantic (e.g. Gonzalez-Silvera et al., 2006; Dogliotti et al., 2014) and its composition documented (Sabatini et al., 2012; Antacli et al., 2018; D'Agostino et al., 2018; Guinder et al., 2018). Although environmental variables have a very noticeable influence on the development of different phytoplankton groups in the Argentine Patagonian coast (Gayoso, 2001), data on seasonal changes in phytoplankton community composition are scarce, especially at monthly resolution (e.g. Gonçalves-Araujo et al., 2016; D'Agostino et al., 2018). In particular, ports where constant human activities distort the natural environmental conditions, impacting on the composition of phytoplankton communities, are poorly studied (López Abbate et al., 2017; Santinelli et al., 2018). Evidence of anthropogenic activities was observed as an increase of chlorophyll a (Chl a), at some sites in Nuevo Gulf, including ports (Esteves et al., 1997). High ammonium concentrations (> 2 μM)

(Hasan, 2003; Santinelli, 2008; Paparazzo et al., 2013) and changes in species dominance and community composition of the beach-cast macroalgae (Piriz et al., 2003) have been reported. However, there are few studies on the annual phytoplankton community variation in this gulf and in other Patagonian coastal ecosystems (e.g. Gayoso, 2001; Santinelli, 2008; D'Agostino et al., 2018).

Phytoplankton carbon biomass is fundamental to the food web and its variation is tightly related to the phytoplankton community structure and their changes along the year. Hence, knowledge of the phytoplankton community structure and dynamics provides a baseline that allows monitoring of areas with a rich and diverse fauna, such as the area in which our study site is located (Almirante Storni Pier, Nuevo Gulf). This area belongs to a Natural Protected Area but has important port developments with increasing anthropogenic impact. This study aims to analyse the annual variation of phytoplankton composition and abundance, as well as the variation in the autotrophic carbon biomass, to infer the influence of environmental variables as the principal controlling factors on the phytoplankton communities through an annual cycle.

In the context of global climate change and increasing port development, this study will provide baseline information and tools for future predictions in the region. It is one of the first regional investigations of the monthly temporal changes in carbon biomass from phytoplankton communities, which may potentially contribute to other trophic levels.

Materials and methods

Study area

Nuevo Gulf (Argentina, Southwest Atlantic, 42°49′S, 65°04′W) is an enclosed system of about 2500 km^2 with relatively little exchange with the open Atlantic Ocean (Fig. 1; Rivas & Beier, 1990). The gulf does not receive freshwater run-off from rivers, thus salinity is stable around 34 psu. The water column is generally mixed, except in summer, when the thermocline is situated around 20–30 m. Southwesterly winds predominate all year and have been associated with upwelling/downwelling events (Esteves et al., 1992; Dellatorre et al., 2012). Average wind velocity is 15–35 km h^{-1}, with maxima during summer (Gayoso, 2001; Dellatorre et al., 2012). The sampling location, the Almirante Storni Pier (42°44′S, 65°01′W; Fig. 1) is a touristic, industrial and fishing port situated in Puerto Madryn city (115 000 inhabitants). The pier is in a wave-protected area, with a semidiurnal tidal
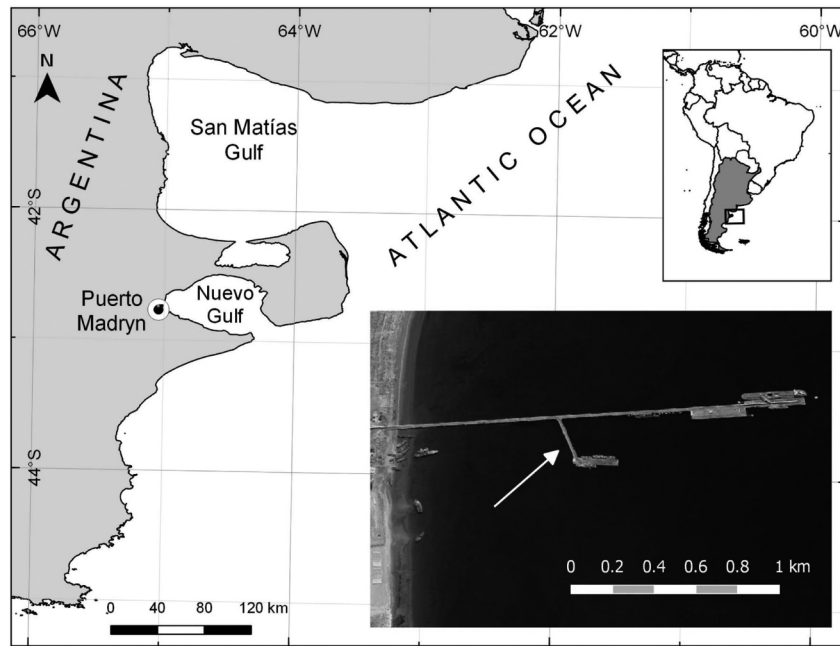
Fig. 1. Map of northern Patagonia, showing the location of Puerto Madryn Port in Nuevo Gulf; inset showing position in South America. Satellite image (Google Earth) indicates the sampling site (white arrow) (from Giachetti *et al.*, 2020)

regime and a mean tidal amplitude of 5 m (Servicio de Hidrografía Naval, 2019). The depth at high tide is < 9 m (Giachetti *et al.*, 2019).

Environmental variables

Environmental variables were obtained ~ monthly from October 2011 to September 2012. The physico-chemical parameters sea surface water temperature (SSWT, °C), salinity (pps) and transparency (m) were measured in triplicate at the time of water sampling. SSWT and salinity were measured with an ALTRONIX TPA-IV sensor, and transparency was determined with a Secchi disc (Secchi, 1866). Transparency was excluded from statistical analyses due to the lack of data from May to July.

The meteorological variables precipitation (mm), wind velocity and incident solar photon irradiance were obtained from the automatic meteorological station (EMA) of CENPAT-CONICET, ~7 km from the study site (42°47'12"S, 65°00'28"W). Solar irradiance was obtained with a pyranometer (Li-Cor Series Li-200), which measures 280–2800 nm wavelengths and represents a day's energy as:

$$Wh\ m^{-2}\ day^{-1} = [E]/[t]\ [t]\ /[l]\ [t]$$

where $[E]/[t]\ [t]$ is Wh = $J\ s^{-1} * 3600\ s$; and $[l]\ [t]$ is $m^2\ day^{-1}$.

To investigate the effects of incident solar irradiance and precipitation on the phytoplankton community, the prior 8 days before sampling were considered. For wind effects, due to the short time lags between high wind velocity and small-scale upwelling/downwelling events, ~5–6 hours, in the

study area (Dellatorre *et al.*, 2012), hourly mean wind velocity on the sampling day was determined.

Annual phytoplankton variation

Three replicate water samples were collected, approximately monthly from October 2011 to September 2012 (except February 2012 due to meteorological conditions). Sampling was performed during high tide (~7 m depth in the port), ~2 m below the surface. The water column is usually mixed and no vertical stratification occurs. Samples were taken by scuba diving. For microscopic observations, samples were fixed in Lugol's solution (0.3% final concentration, v:v; Sournia, 1978) and stored in 1 l dark glass bottles. Additional water samples for Chl *a* determinations were obtained, stored at 4°C in darkness and transported to the laboratory within 3–5 h.

To determine the phytoplankton composition and abundance, samples were analysed in an inverted microscope (Iroscope SI-PH). A drop of Rose bengal was added to each sample to better distinguish between organic and inorganic particles (Villafañe & Reid, 1995). Phytoplankton abundance (cell l^{-1}) was estimated by the Utermöhl method. Samples were settled for ~48 h; after settling, the supernatant was carefully removed for species identification and quantification. Triplicate samples were observed along the entire chamber, using 200× magnification for microplankton cells (> 20 μm) and along transects delimited in the chamber with 400× magnification for nanoplankton (≤ 20 μm). To be considered a representative sample, a mean of at least 50 cells of the most common species had to be present. Most of the observed cells were

identified at the genus level, except for some nano-planktonic cells which were identified at class level (e.g. flagellates). All cells were counted, differentiating size ranges for further biomass estimation. Identifications were achieved following Tomas (1997) and Balech (1988).

To evaluate the phytoplankton community, biomass of carbon and Chl *a* were estimated. The phytoplankton carbon concentration, i.e. the biomass (mg C m^{-3}) for each species was estimated from its biovolume and carbon content depending on the taxonomic group, following Menden-Deuer & Lessard (2000). To do this, species biovolume was estimated by shape assimilation to known geometric forms, according to Hillebrand *et al.* (1999). Main cell dimensions of 10 (in the case of the less frequent species) to 50 cells per species (in the case of the most frequent species) were measured with a calibrated microscope ruler. When it was not possible to measure cell height, the length/width ratio was used to determine the missing parameters of the target cells (Cornet-Barthaux *et al.*, 2007). When different sizes were observed within a species or morphotype, organisms were classified into several cell size classes. The Chl *a* concentration (mg m^{-3}) was determined by filtering 500–1000 ml of the additional water samples through a Whatman GF/F filter (47 mm) and extracting the photosynthetic pigments in acetone 90% for 20 h under cold and dark conditions. Chl *a* extracted from water samples were measured by the fluorometric method (Holm-Hansen *et al.*, 1965).

Statistical analysis

A redundancy analysis (RDA) was performed to evaluate the relationship between the community composition, in terms of abundance, and the environmental conditions along the studied period. RDA is a multivariate linear regression (i.e. multiresponse), in which results of fitted values are represented in a principal component analysis (PCA) (Borcard *et al.*, 2011a). The RDA was carried out after applying a Hellinger transformation of the data, which allows the structure of the data to be retained without overweighting rare species (Legendre & Gallagher, 2001). To ensure a better interpretation of the RDA analysis, only species or genera with abundances higher than 1.5×10^2 cells l^{-1} were used. Species with lower abundances were aggregated as a group, i.e. other diatoms, other dinoflagellates or other flagellates. The environmental variables incorporated in the analysis were: SSWT, wind velocity, solar irradiance, precipitation and salinity. To avoid multicollinearity between variables, the variance inflation factor (VIF) was calculated (Graham, 2003) and only variables with VIF < 10 were used in the final model (Craney & Surles, 2002). The variables included in the final model were selected based on a forward model selection using permutation tests with the ordiR2step function, from the R "vegan"

package (Oksanen *et al.*, 2019). The statistical significance of the final RDA and of each individual canonical axis was tested with 999 permutations and the proportion of the variance explained was adjusted by multiplying by R^2_{adj} (Borcard *et al.*, 2011a). The final model used a correlation biplot representation (scaling 2), which reflects the correlations between response and explanatory variables (i.e. species variables and environmental variables), as well as between response variables themselves, by the angles between them (i.e. arrows in the plot) (Borcard *et al.*, 2011b).

A variance partitioning analysis from the RDA was used to evaluate how much of the variation of the community was related to each environmental variable. This analysis was performed following the method proposed by Borcard *et al.* (1992) and improved by Peres-Neto *et al.* (2006) in R using the "varpart" function from the Vegan package (Oksanen *et al.*, 2019). All analyses were performed in R software (R Core Team, 2019).

Results

Environmental variables

A marked variation in SSWT was observed, with the maximum in December (2011) and the minimum in July and August (2012) (Fig. 2a, Supplementary table S1). The variation in solar irradiance was similar to that of the SSWT, with maximum values in austral spring and summer (Fig. 2a, Supplementary table S1). For the wind velocity, higher values were recorded in December (2011), which corresponded with the estimated lower value of water transparency (Fig. 2b, Supplementary table S1). Salinity was lowest from January to April (2012), which coincided with the highest precipitation (January and March 2012; Fig. 2c, Supplementary table S1).

Total cell abundance, biomass and Chl a

The total cell abundance varied between 0.45×10^5 and 3.87×10^5 cell l^{-1}, with the highest peak in March and another, less pronounced peak, in September (Fig. 3, Supplementary table S2). Biomass ranged from 4.2 (October) to 101.5 mg C m^{-3} (January), with a second peak of 43.4 mg C m^{-3} in April (Fig. 3, Supplementary table S2). The Chl *a* concentrations were 0.3–2.6 mg m^{-3} with the lowest values in August and higher values in December–April. The Chl *a* annual trend of variation was quite different from the abundance and biomass patterns (Fig. 3, Supplementary tables S2 and S3).

Contribution of the main phytoplankton groups

The relative contribution of the main taxonomic groups to the total abundance varied depending on the season (Supplementary table S4). Bacillariophyta (diatoms)
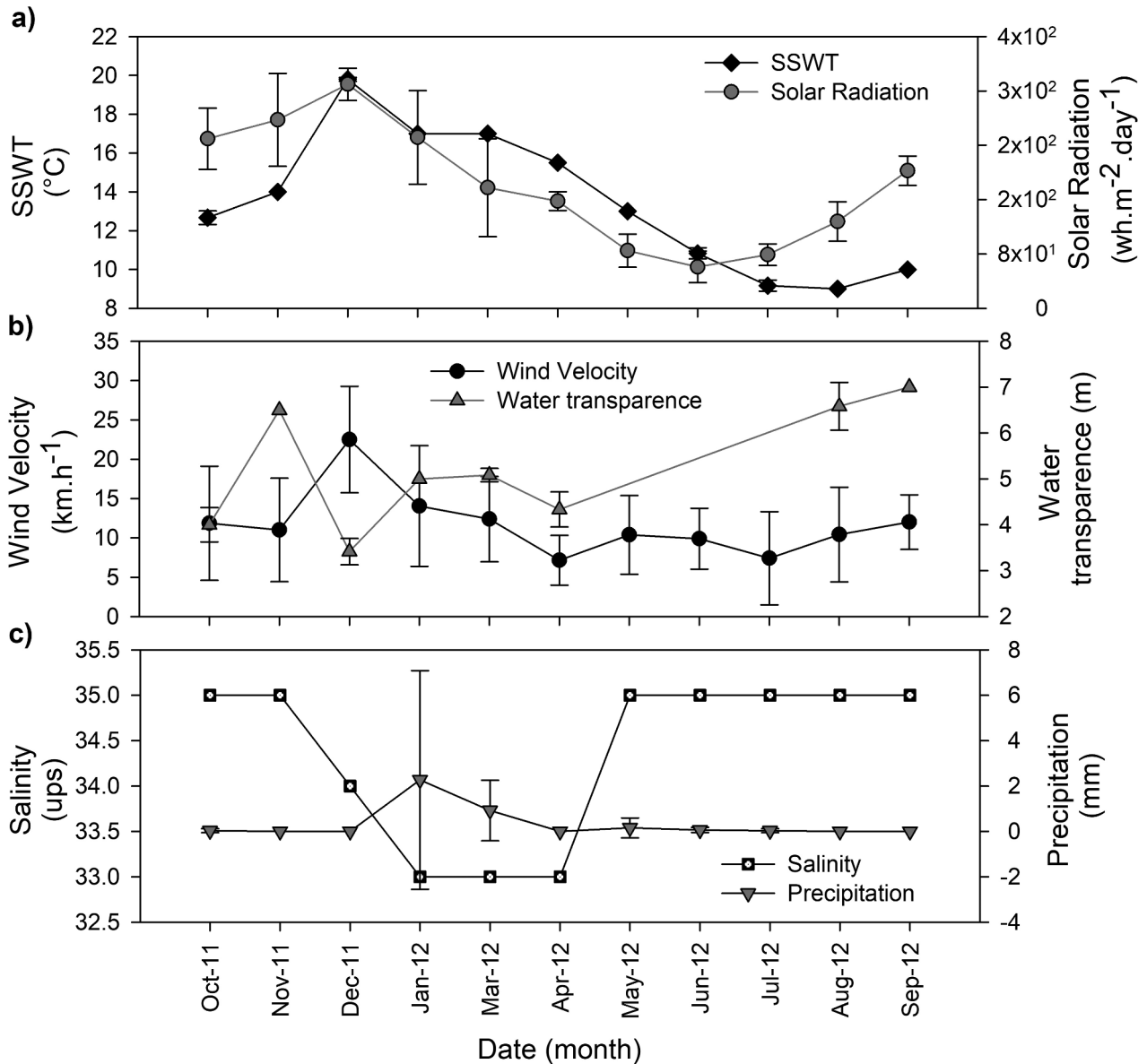
Fig. 2. Temporal variation of environmental variables: (a) Water temperature (°C) and irradiance (Wh m^{-2} day^{-1}), expressed as mean ± SD; (b) Wind velocity (km h^{-1}) expressed as mean ± SD and water transparency (m); (c) Salinity (psu) and precipitation (mm), in the Almirante Storni Port (Nuevo Gulf). Black and white symbols are represented on the right and the left axis respectively. Solar irradiance, wind velocity and precipitation were obtained from the automatic meteorological station (CONICET-CENPAT). Note that February was not represented due to the lack of samples.

dominated during the two peaks of phytoplankton cell abundance, in March and September (~92%; Fig. 4a). Flagellates, mainly species of Cryptophyta and Chlorophyta, had their maximum contribution from October to December and during June, reaching up to 73% of the total abundance (Fig. 4a). Dinophyta (dinoflagellates) were less abundant than the other two groups, but dominated during January and April, accounting for 63% and 49% of the total cell concentration, respectively (Fig. 4a). However, in terms of biomass, dinoflagellates contributed more to the phytoplankton community biomass than diatoms and flagellates (Fig. 4b). The three main phytoplanktonic groups were clearly differentiated through the year by their abundance, but also by their size distribution (Supplementary fig. S1). Almost all species of dinoflagellate were microplankton (> 20 μm), except for

Gyrodinium stuariale, Heterocapsa niei and some cysts. Diatoms included nanoplanktonic species (≤ 20 μm; 62.7%) during most parts of the year, but there were other species corresponding to the microplanktonic fraction, especially in late winter and early spring (37.3%) (Supplementary fig. S1). Most of the flagellates studied corresponded to the nanoplanktonic fraction, except for some species of Dictyochophyceae and Euglenophyceae.

Species succession

The most abundant species at the beginning of the study (October–December) were Chlorophyta and Cryptophyta flagellates (Fig. 5, Supplementary table S4). As the annual cycle progressed, other species appeared and some of them became dominant, e.g.
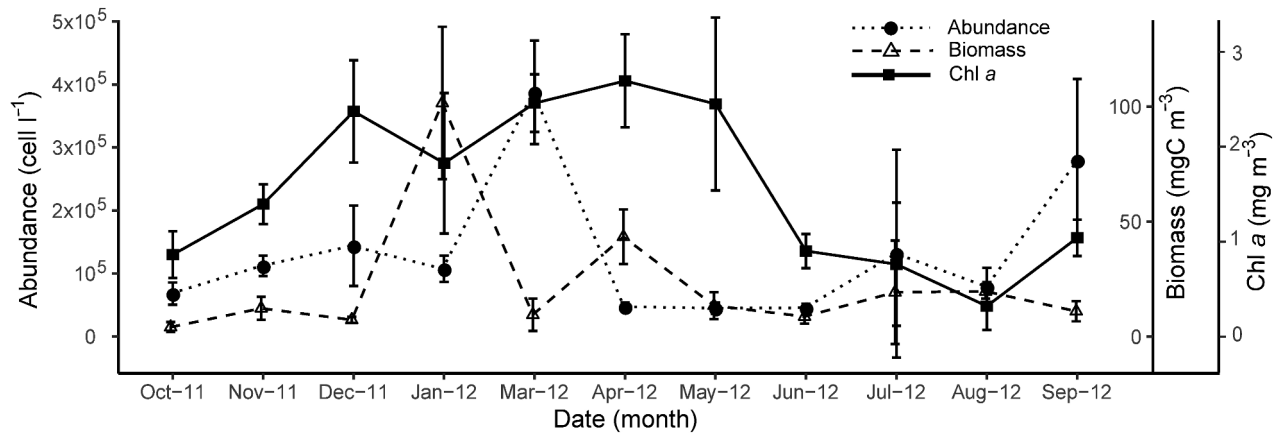
Fig. 3. Temporal variation of cell abundance, phytoplankton biomass and Chl *a* from October 2011 to September 2012, Almirante Storni Port (Nuevo Gulf). Chl *a* and phytoplankton biomass are represented on the right axis. The values represent the mean ± SD. Note that February was not represented due to sampling problems.
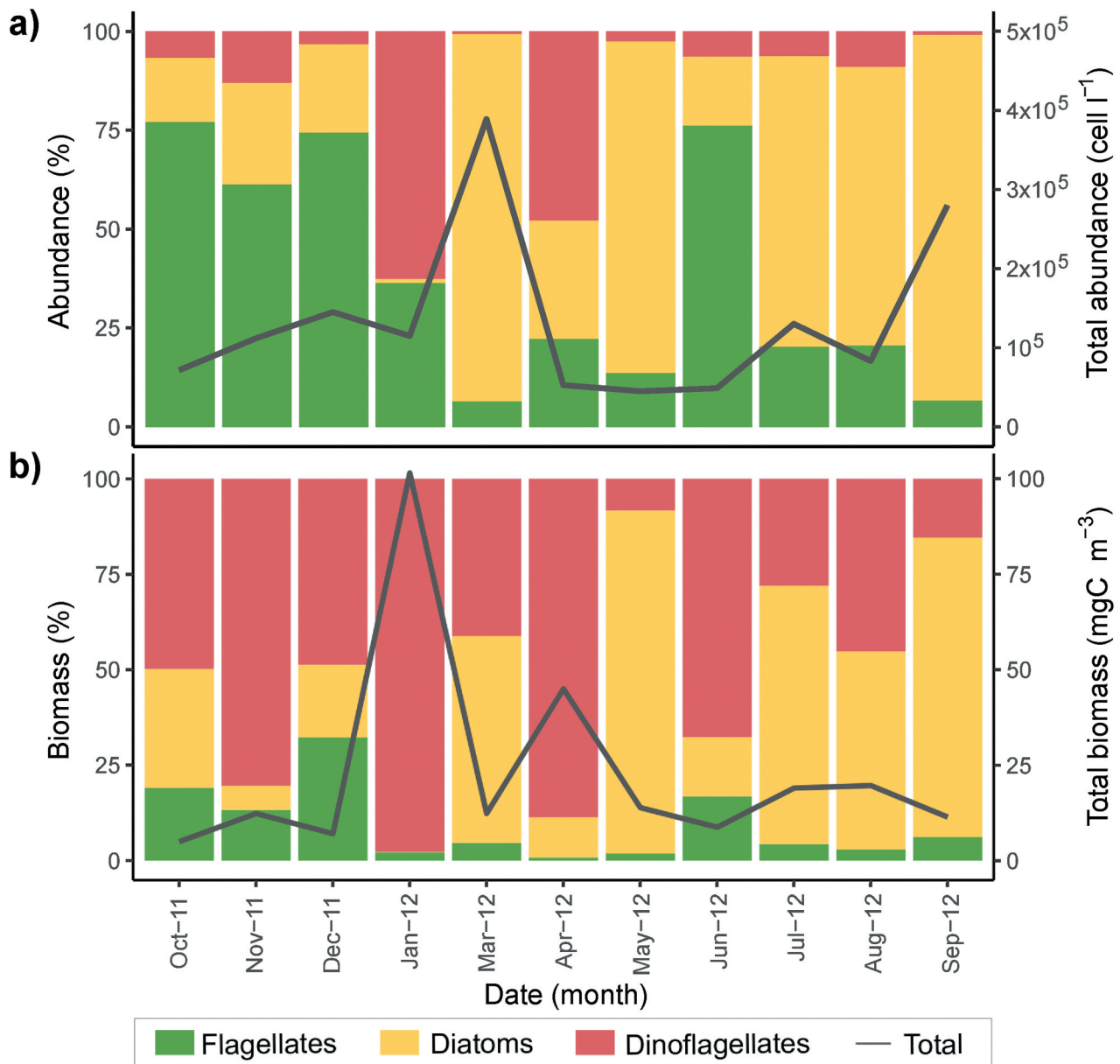

Fig. 4. Temporal variation of the percentage contribution of the three main taxonomic groups (see legend) to the total cell abundance (a) and biomass (b) from October 2011 to September 2012, Almirante Storni Port (Nuevo Gulf). (February not represented due to lack of samples).
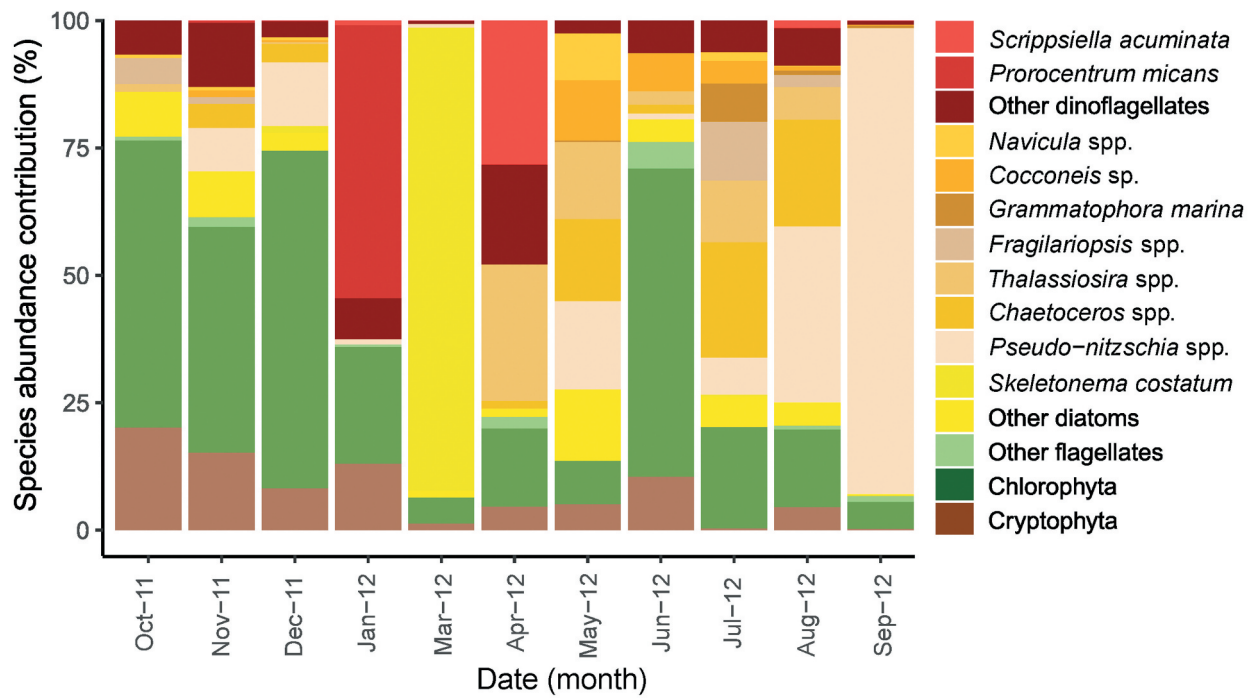
Fig. 5. Temporal variation of the percentage of contribution of the main species to the total cell abundance of the phytoplankton community from October 2011 to September 2012, Almirante Storni Port (Nuevo Gulf). "Other diatoms" include *Guinardia* spp., *Leptocylindrus* spp., *Pleurosigma* spp. and species detailed in Supplementary tables S4 and S5. "Other dinoflagellates" include *Oxytoxum* sp., *Gonyaulax* sp., *Gymnodinium* spp., *Gyrodinium* sp., *Tripos* spp., and species detailed in Supplementary tables S4 and S5. "Other flagellates" include dictyochophyceans and euglenophyceans. (February not represented due to lack of samples).

the dinoflagellate *Prorocentrum micans* in January, and the diatoms *Skeletonema costatum* and *Thalassiosira* spp. in March and April respectively. During April, the dinoflagellate *Scrippsiella acuminata* and, in lower concentrations, *Tripos* spp., *Gyrodinium* spp. and *Heterocapsa niei* were also found (Fig. 5, Supplementary tables S4 and S5). Flagellates constituted the most abundant components of phytoplankton community in June. The diatoms *Chaetoceros* spp. and *Pseudo-nitzschia* spp. started to increase in May, reaching the highest abundance in September.

Relationship between annual phytoplankton variation and environmental variables

The RDA model for cell abundance was significant (F = 2.47; p = 0.001; R^2_{adj} = 0.28) and included SSWT, salinity, solar irradiance, precipitation and wind velocity as significant environmental variables (Fig. 6). The two first axis were significant (999 permutations, p < 0.05) and explained 21% of community composition variation between samples. The variance partitioning analysis indicated that each variable explained between 3.3–6.6% of the total variability of the community composition (SSWT 6.6%; precipitation 4.9%;

salinity 6.4%; wind velocity 3.3% and solar irradiance 3.6%).

In the biplot representation from the RDA model, axis 1 separated mainly samples corresponding to March and April (left side) from the other months (right side) whereas axis 2 separated autumn and winter samples (top) from spring and summer (bottom). Bottom samples were related to higher SSWT, precipitation, solar irradiance and wind velocity (Fig. 6).

Discussion

Overview of phytoplankton community composition

Our results showed a complex set of factors relating to the phytoplankton community composition in the study site. This was particularly evident in the different responses displayed not only by the dominant taxonomic groups, but also by the nanoplanktonic and microplanktonic species. In general, nanoplankton dominated during late spring, summer and early winter. In contrast, microplankton dominated during late winter and early spring, when calm weather conditions prevailed. These findings are in agreement with results obtained in several studies on the Patagonian coast which characterized the seasonal phytoplankton community composition (Helbling *et al.*, 2001; Barbieri *et al.*, 2002; Villafañe *et al.*, 2004; Marcoval
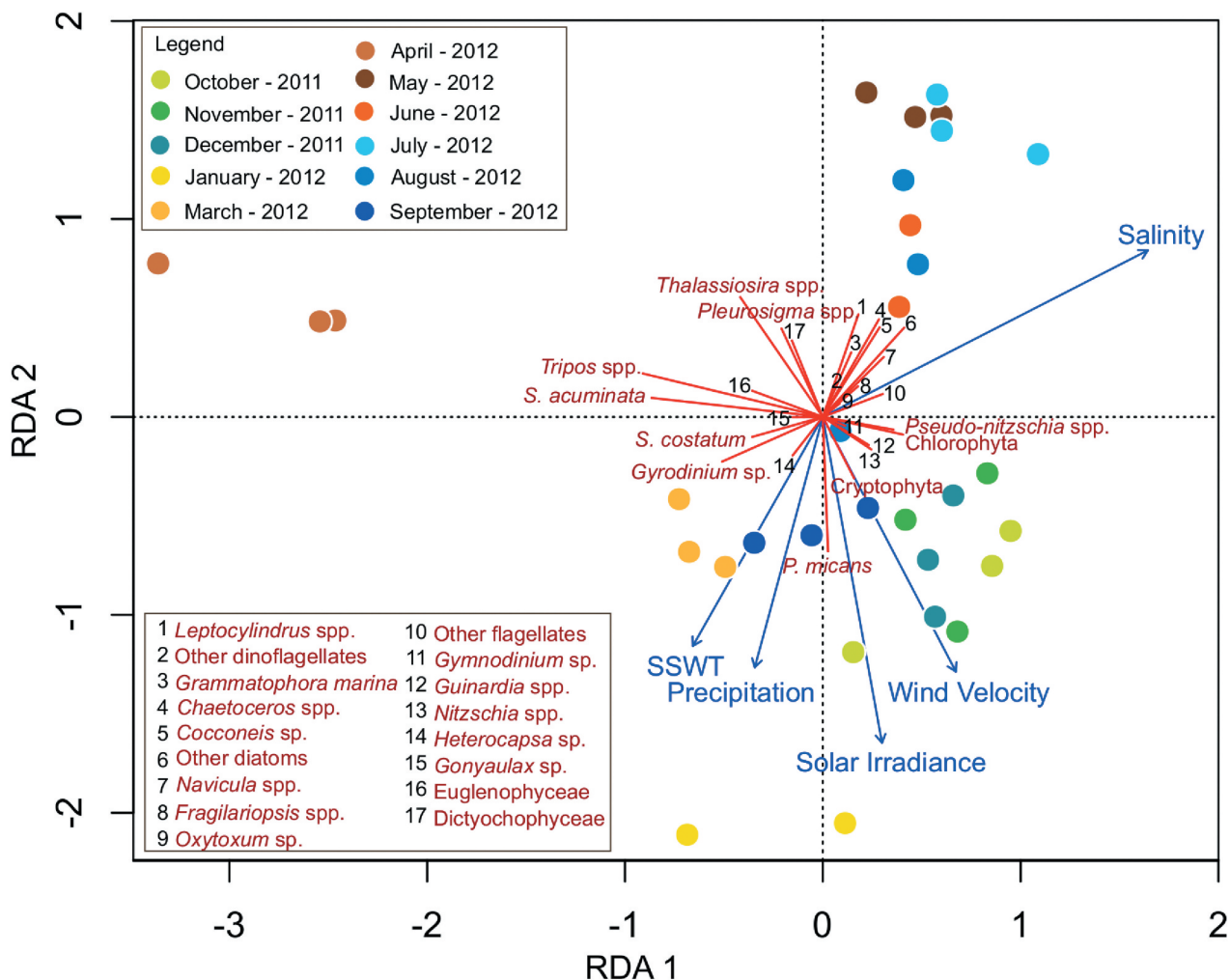
Fig. 6. RDA biplot of phytoplankton species abundance from Almirante Storni Port (October 2011–September 2012). Sample scores are plotted with different colours corresponding to each month (see legend) and environmental variables are represented by arrows, showing the correlations between them and with species (scaling 2). SSWT: sea surface water temperature. For details of the 'other diatoms', 'other dinoflagellates' and 'other flagellates' refer to the Supplementary tables S4 and S5.

et al., 2008; D'Agostino *et al.*, 2018; Saad *et al.*, 2019). Our study of temporal variation in the phytoplankton community composition showed a non-synchronous response among its three main features analysed: cell abundance, carbon biomass and Chl *a* content.

Annual variation of total cell abundance, carbon biomass and Chl *a* related to the community composition

The seasonal variation in total cell abundance was as is generally observed in temperate regions, with two blooms of diatoms, in autumn and spring, followed by an increase of dinoflagellates. Similarly, Santinelli *et al.* (2018) registered peaks in diatom abundance in autumn and spring, although D'Agostino *et al.* (2018) only observed a peak in spring in the Nuevo Gulf (Supplementary fig. S2a and table S2). The biomass also varied seasonally, and its peaks were associated with increasing dinoflagellate abundance in January and April. Although dinoflagellates were

not numerically dominant, their higher carbon content (Menden-Deuer & Lessard, 2000) and relatively high volume resulted in peaks of carbon biomass. Higher dinoflagellate abundances were previously reported in the region, e.g. during winter and summer in San Antonio Bay (Saad *et al.*, 2019) and during late spring and summer in Nuevo Gulf (Santinelli, 2008; D'Agostino *et al.*, 2018) (Supplementary fig. S2b). Both diatoms and dinoflagellates represent high quality of food for other trophic levels, since they have a high content of long-chain essential fatty acids (Winder *et al.*, 2017). This result highlights the availability of high phytoplankton quality supporting the high biodiversity of the Península Valdés Natural Protected Area UNESCO reserve.

High values of Chl *a* were previously recorded in the study area during autumn (Gayoso & Fulco, 2006; Marcoval *et al.*, 2008; Santinelli, 2008) (Supplementary fig. S2b, Supplementary table S2), reaching up to 2 mg m^{-3} (Gayoso, 2001). Our results showed peaks of Chl *a* in autumn (March and April), but also in summer

(December and January), with more than 2 mg m^{-3} in most of these cases. The former period seems to be related to an increase of *Skeletonema costatum*, and the latter to the increase in bigger species with a high biomass, particularly the dinoflagellates *Scrippsiella acuminata, Tripos* spp. and *Prorocentrum micans* and a high density of nanoflagellates (Chlorophyta and Cryptophyta). Conversely, high Chl *a* associated with abundant microplanktonic cells, has been observed during winter in Bahia Engaño (Barbieri *et al.*, 2002; Villafañe *et al.*, 2004), located in southern Nuevo Gulf.

Chl *a* peaks were only coincident with the peaks of abundance and/or carbon biomass during some months (January and March), indicating that Chl *a* was more related to the community composition than the total cell abundance or carbon biomass. This mismatch has previously been observed in Nuevo Gulf (Santinelli *et al.*, 2018) and in sub-Antarctic areas, where diatom cell abundance and biomass did not correlate with Chl *a* (Olguín & Alder, 2011). Although Chl *a* concentration has traditionally been used as an estimation of potential primary production (López Abbate *et al.*, 2017; Cañavate, 2019), there is a decoupling between the phytoplankton carbon biomass and Chl *a* related to the species composition (Winder & Cloern, 2010). One possible cause is identification using a light microscope, where resolution does not allow differentiation between photosynthetic and non-photosynthetic dinoflagellates and flagellates. This decoupling could also be explained by variability of the ratio between cellular carbon and Chl *a* content, which is mainly driven by nutrients and light conditions (MacIntyre *et al.*, 2000; Arteaga *et al.*, 2016). Besides, it is important to consider that total Chl *a* also includes the picophytoplankton (0.7–2 µm), which can account for a high percentage of the total Chl *a* but represent low carbon biomass (Cotti-Rausch *et al.*, 2020). The picophytoplankton fraction was not analysed in the present study. An increase of picophytoplankton could explain the high estimation of Chl *a* during May (~1.8 mg m^{-3}) when no particular abundance or biomass increase were detected for other fractions. These results highlight the importance of measuring both carbon biomass and Chl *a*, as the latter is a biased estimator of phytoplankton biomass (Cullen, 1982).

Species succession as response of the seasonal variation of environmental conditions

Our results showed a phytoplankton community characterized by variation in seasonal abundance and species composition determined by the environmental conditions, typical of temperate regions. For instance, SSWT has a crucial influence as a structural factor for phytoplankton communities, mostly in temperate latitudes, but also on the salinity of the water (Antacli *et al.*, 2018). It is likely that salinity, as well as altering phytoplankton community structure, may also influence the nutritional value of these assemblages (Cañavate, 2019).

The seasonal variation of phytoplankton community along an environmental gradient, from spring–summer to autumn–winter periods can be observed in the RDA results (axis 2; Fig. 6). Highest SSWT, solar irradiance and precipitation were associated with some species forming blooms, as the dinoflagellate *P. micans* and the diatom *S. costatum*. Since *S. costatum* is a nanoplanktonic species (estimated volume: 355 µm^3), the bloom of nanoplanktonic diatom species could be promoted during lower salinity periods. In general, nanoplanktonic species have higher efficiency in nutrient utilization than bigger species, reaching a faster population growth under oligotrophic conditions, as were reported during summer and autumn in the studied area (Marcoval *et al.*, 2008; Halac *et al.*, 2011). In contrast, the second bloom of diatoms occurred in September and was represented by the macroplanktonic species *Pseudo-nitzschia* spp. (250–1200 µm^3). This suggests that well-differentiated controlling factors determine nano- and microplanktonic diatom blooms. A similar pattern was previously reported in the proximity of our study site. For instance, blooms of diatoms were observed during March and September, the dominant species being *Chaetoceros socialis* and *Pseudo-nitzschia* spp., respectively (Gayoso, 2001; Santinelli, 2008).

Pseudo-nitzschia spp. blooms frequently occur at the Nuevo Gulf associated with elevated temperature and salinity (Almandoz *et al.*, 2017; D'Agostino *et al.*, 2018). Furthermore, many reports have associated *Pseudo-nitzschia* spp. blooms to coastal upwelling, due to mesoscale events and windy conditions (Parsons & Dortch, 2002; Kudela *et al.*, 2005; Díaz *et al.*, 2014). This explains the association of *Pseudo-nitzschia* spp. with higher wind velocity observed in our results (see RDA biplot in Fig. 6). *Pseudo-nitzschia* includes harmful species and stress due to silica and phosphate limitation has been related to higher levels of domoic acid production (Bates *et al.*, 1991; Pan *et al.*, 1996; Fehling *et al.*, 2004; Schnetzer *et al.*, 2007). The lack of nutrient concentration data limits our interpretation about the potential domoic acid production associated with *Pseudo-nitzschia* spp. blooms. However, we hypothesize that windy conditions could avoid nutrient limitation and domoic acid production in the study area (e.g. Díaz *et al.*, 2014).

After the diatom blooms ended, dinoflagellates increased their abundance, probably due to their high physiological diversity, that allows them to grow under low nutrient conditions (Smayda, 2002). For instance, mixotrophy allows some species to be autotrophic or heterotrophic, depending on

environmental conditions (Stoecker, 1999; Burkholder et al., 2008). *S. acuminata, Tripos* spp., *Gyrodinium* spp. and *Heterocapsa niei* were the main dinoflagellate species after the first bloom of diatoms in March. On the other hand, *P. micans* was the main dinoflagellate after the second diatom bloom in September, showing its highest abundance during January, as was previously observed in the Nuevo Gulf (Gayoso, 2001; Esteves et al., 1997; Halac et al., 2011; D'Agostino et al., 2018). Another factor that could favour *P. micans* growth is the high solar irradiance during December and January (Fig. 2a). *P. micans* has higher resistance and better acclimation to high solar irradiance (Marcoval et al., 2008; Halac et al., 2014).

During winter (August), cell abundance was low, with higher abundance of the diatoms *Pseudo-nitzschia* spp., *Chaetoceros* spp., *Thalassiosira* spp. and *Fragilariopsis* spp. Microplanktonic cells have a low area/volume ratio and consequently low efficiency in nutrient assimilation; thus, their growth would be optimum under high nutrient concentrations, as found on the Patagonian coast during winter (Esteves et al., 1992; Gayoso, 2001; Santinelli, 2008). Furthermore, during this season, low wind velocity allows water column stratification (Helbling et al., 1994; Barbieri et al., 2002) and the cells stay trapped in the upper layers. Our data showed an opposite relationship between the microplanktonic diatoms and wind velocity, contrarily to the turbulence effect on microplankton dominance suggested by Saad et al. (2019) in San Antonio Bay. However, other factors such as solar irradiance, which was not high enough to reduce photosynthetic efficiency, could allow the microplanktonic diatom cells to grow faster than other phytoplankton (Villafañe et al., 1991, 2004).

At the study region, most nanoplanktonic cells are present when the water stratification breaks down due to high wind velocity and vertical mixing takes place, generally during spring and summer (Helbling et al., 2001; Buma et al., 2001; Marcoval et al., 2008). High winds can produce micro-upwelling events that are observed in this area with wind velocities higher than 20 km h^{-1} (Esteves et al., 1992; Dellatorre et al., 2012). Our data indicated that not only high wind velocity, but also low water transparency support the possibility of a particularly mixed water column. These environmental conditions could promote the growth of chlorophytes and cryptophytes, the principal component of nanoplanktonic flagellates from October to December, as suggested by the RDA results.

The seasonal variability of the community composition was not fully explained by the environmental conditions evaluated. This suggests that additional variables are also driving succession patterns and may produce faster changes even in the same season,

which are not captured when analysing a representative month of a season. Species nutritional requirements might also explain the differences in the taxonomic and size distribution of the phytoplankton communities. Besides, information on nutrient concentrations could complement the explanation about the causes of these differences. In coastal areas, nutrient concentrations are enhanced by anthropogenic nutrient-laden fresh water (Cloern, 2001). In Victoria Harbour (Hong Kong), a river estuary discharge increased NO_3 and SiO_4 concentrations, while continuous year-round discharge of sewage effluent resulted in high NH_4 and PO_4. Besides anthropogenic activities, port areas are particularly vulnerable due to their shallow water column and the presence of weak water currents that increase the residence time of pollutants (Pestorić et al., 2018). In Nuevo Gulf, the main factors increasing eutrophication are fishery effluents discharge (Gil et al., 2015) and urban sewage effluents from Puerto Madryn city (Gil, 2001; Díaz et al., 2002; Torres et al., 2004). Although the sewage discharge was closed in 2005 (Torres & Caille, 2009), recorded nutrient levels from spring 2009 onwards did not change relative to previous reports from this season in the area (Gil et al., 2015).

Importance of phytoplankton community description and monitoring

The rapid response of the phytoplankton community to environmental conditions makes its monitoring a key feature for assessing water quality. Temporal comparisons of the phytoplankton abundance and composition are essential for understanding changes in water quality and ecosystem functioning. Comparison of the observed community dynamics with previous and/or future studies could also help to clarify the role of primary producers in sustaining the biodiversity present in the area. Other methods could complement the present approach to overcome some limitations associated with microscopic identification, such as the difficulty of differentiating between photosynthetic and non-photosynthetic dinoflagellates and flagellates.

Over longer time scales, there are expected changes in phytoplankton communities due to global warming, mainly in the timing of spring blooms and biomass peaks as responses to temperature (Sommer & Lengfellner, 2008). Consequently, an increase in temperature due to global warming could affect the food chain in the region, not only by modifying the potential biomass available but also efficient energy transfer from primary to fish production (Sommer & Lengfellner, 2008). Despite the importance of phytoplankton for the entire food web, scarce information and the lack of monitoring make it difficult to assess, predict and validate the effects of global warming on phytoplankton communities.

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Disclosure statement

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Supplementary information

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at https://doi.org/10.1080/09670262.2021.1995630

Supplementary table S1. Environmental conditions during the study period from October 2011 to September 2012 in Almirante Storni Port, Nuevo Gulf (Argentina).

Supplementary table S2. Mean and standard deviation of the abundance of phytoplankton cells, carbon biomass and chlorophyll a (Chl a) registered in this study together with the cell abundance and Chl a registered in previous studies from Santinelli (2008) and D'Agostino et al. (2018) in Nuevo Gulf (Argentina).

Supplementary table S3. Raw data of measured Chlorophyll a in each sample replicate and the corresponding monthly mean and standard deviation from October 2011 to September 2012, in Almirante Storni Port, Nuevo Gulf (Argentina).

Supplementary table S4. Raw data of all sample replicates with cells abundance, carbon biomass and size class (micro and nano plankton) by species/morphotype. Species/morphotype mean volume and the estimated carbon biomass are detailed.

Supplementary table S5. Phytoplankton taxa identified from October 2011 to September 2012, in Almirante Storni Port, Nuevo Gulf (Argentina). (*) taxa with low abundance included as "Other diatoms", "Other dinoflagellates" or "Other flagellates" in figures and statistical analyses.

Supplementary figure S1. Temporal variation in abundance contribution (percentage) of taxonomic groups, differentiating microplankton and nanoplankton fraction from October 2011 to September 2012, in Almirante Storni Port (Nuevo Gulf).

Supplementary figure S2. Temporal variation in phytoplankton abundance (a) and Chl a (b) in Nuevo Gulf observed during different time periods (indicated in the legend) by diverse research references. Data expressed as mean and standard deviation (bars). Santinelli (2008) and D'Agostino et al. (2018) data is presented as the seasonal mean abundance and Chl a.

ORCID

Romina Vanessa Barbosa http://orcid.org/0000-0003-1793-8444
Silvana Halac http://orcid.org/0000-0002-7919-0382
Evangelina Schwindt http://orcid.org/0000-0001-6693-9828
Marcos Tatián http://orcid.org/0000-0002-9092-9184

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