THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Fabro, E., B. Krock, A.I. Torres, F.E. Paparazzo, I.R. Schloss, G.A. Ferreyra, and G.O. Almandoz. 2018. Toxigenic dinoflagellates and associated toxins in San Jorge Gulf, Argentina. *Oceanography* 31(4):145–153, https://doi.org/10.5670/oceanog.2018.417.

DOI

https://doi.org/10.5670/oceanog.2018.417

Toxigenic Dinoflagellates and Associated Toxins in San Jorge Gulf, Argentina

By Elena Fabro, Bernd Krock, Américo I. Torres, Flavio E, Paparazzo, Irene R. Schloss, Gustavo A. Ferreyra, and Gastón O. Almandoz

ABSTRACT. The occurrence of harmful algal blooms (HABs) is a global problem, and particularly in San Jorge Gulf (SJG), Argentina, which supports important fisheries, HABs represent a risk to human health. We studied the diversity and distribution of toxigenic dinoflagellates in the SJG using toxin detection and quantification, and assessed the connections between cell densities, toxins, and oceanographic parameters. Phytoplankton net samples were taken for microscopic and liquid chromatography-tandem mass spectrometry (LC-MSMS) analyses during an expedition aboard R/V *Coriolis II* in February 2014. Solid phase adsorption toxin tracking (SPATT) devices were also deployed to determine the presence of dissolved lipophilic toxins in seawater. Toxigenic dinoflagellate species and associated toxins showed different distribution patterns in the north and the south SJG. *Protoceratium reticulatum* and *Dinophysis acuminata*, together with yessotoxin and pectenotoxins, were predominantly detected in the northern SJG, mainly associated with low-nutrient, warmer waters. By contrast, *Alexandrium catenella* and paralytic shellfish toxins showed the highest relative abundances in the southern SJG, associated with high-nutrient, low-temperature waters. Cellular toxin content was also differently affected by environmental parameters, highlighting the complexity of HABs in this area. Spirolides were detected by SPATT for the first time in the SJG, suggesting the occurrence of *A. ostenfeldii*.

INTRODUCTION

Planktonic microalgae comprise an essential component of the world ocean. As main primary producers, they form the bases of food webs. However, in some cases, the proliferation of phytoplankton involves the presence of toxigenic species, for example, dinoflagellates or diatoms, that can form harmful algal blooms (HABs; Hallegraeff, 2004; Lassus et al., 2016). During HABs, filtering animals such as mussels may accumulate high levels of phycotoxins, and due to their accumulation through the food web, deliver these toxins to shellfish consumers, including humans (Van Dolah, 2000). In recent decades, HABs have become well known because of their apparent spatiotemporal increase, their negative effects on human health, and associated economic losses, especially related to fisheries and aquaculture (Lassus et al., 2016).

Phycotoxins include a large variety of compounds that are classified as lipo- and hydrophilic based on solute characteristics identified by various extraction methods. Within each group there are different compounds, or analogues, that share some chemical characteristics. The proportions of each analogue of the producing cells define different toxin profiles (Gerssen et al., 2010).

Some of the common syndromes that may affect human consumers are diarrhetic shellfish poisoning (DSP) caused by lipophilic-toxins (DST) produced by some *Dinophysis* species, such as okadaic acid (OA) and dinophysistoxins (DTX). Paralytic shellfish poisoning (PSP) is caused by paralytic shellfish toxins (PST), such as saxitoxin (STX) produced by some *Alexandrium* species, and amnesic shellfish poisoning (ASP) caused by domoic acid (DA), produced by diatoms. There are also other toxins that do not appear to affect humans but that show toxicity in laboratory rodents, so they represent a potential risk; these include yessotoxins (YTX) produced by *Protoceratium reticulatum* and *Gonyaulax spinifera*, pectenotoxins (PTX) produced by some *Dinophysis* species, and spirolides (SPX) produced by *Alexandrium ostenfeldii* (Lassus et al., 2016).

The San Jorge Gulf (SJG) on the Atlantic coast of Argentina is a very important region for fisheries and seafood production, especially scallops (Bogazzi et al., 2005). Several PSP events have been recorded there in recent years, including two human fatalities associated with *Alexandrium catenella* (Sastre et al., 2013; as *A. tamarense*), which was found at high concentrations during spring (Akselman, 1996; Carreto et al., 2007; Pérez et al., 2013, as *A. tamarense*). Likewise, positive values of PST in the viscera of shellfish are commonly reported (Ciocco et al., 2006), and a high diversity of PST analogues was recorded in recent years from plankton samples by applying liquid chromatography coupled to tandem mass spectrometry (LC-MS/MS; Krock et al., 2015; Fabro et al., 2017). DST producers, such as *Dinophysis acuminata* and *D. tripos*, are also frequently observed in SJG coastal waters (Akselman, 1996; Gracia Villalobos et al.,

2015). Finally, YTXs, a group of toxins that has not been linked to human intoxications, but presents cardiotoxicity in mice after intraperitoneal injection (Aune et al., 2002), were recently detected from *Protoceratium reticulatum* natural populations and cultured strains from the SJG (Akselman et al., 2015).

Previous studies on this subject are scarce and confined to a few coastal monitoring sites (Pérez et al., 2013; Sastre et al., 2013) or to sampling that only partially covered the SJG area (Krock et al., 2015; Fabro et al., 2017). The extensive sampling carried out during the joint Canadian-Argentinian R/V *Coriolis II* expedition in 2014 allowed the first integrated analysis of the diversity and distribution of toxigenic dinoflagellates in the study area as well as exploration of the possible connection between dinoflagellate distribution and environmental parameters.

MATERIALS AND METHODS

Sampling

The Canadian R/V *Coriolis II* expedition was carried out in austral summer from January 30 to February 15, 2014, at 20 sampling stations (~45°–47°S, 65–67°W; Figure 1). Thirteen plankton sampling stations were located on north-south transects at three different distances from the coast (G stations) and at six stations centered in the southern frontal zone of the gulf (F stations). In addition, seven samples were taken at a fixed station located at the central mouth of the gulf about every two hours (SF1–SF14) for two days, and another sample was taken at the same station after one week (SF 15).

At each station, seawater samples were collected at the surface fluorescence maximum, immediately below the pycnocline, and near the bottom by a rosette system equipped with 12 Niskin bottles. Temperature, salinity, density, fluorescence, and depth profiles were obtained in situ using a Sea-Bird SBE-9 CTD. Nitrate, nitrite, phosphate, and silicate were measured after the cruise using an autoanalyzer (Skalar Analytical V.B., 2005a,b,c) at Centro para el Estudio de Sistemas Marinos (CESIMAR) in the Centro Nacional Patagónico (CENPAT), Argentina (Torres et al., 2018, this issue). Nitrate and nitrite were measured together for expression as inorganic nitrogen.

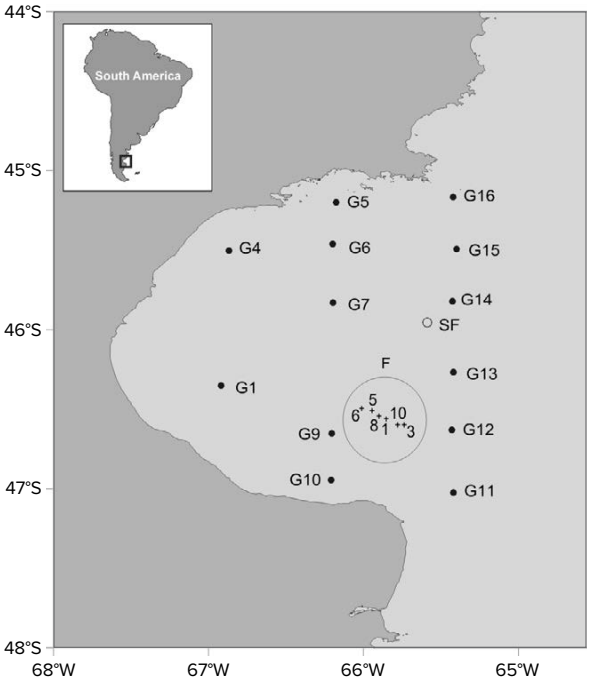

FIGURE 1. Map of the study area showing the analyzed sampling stations. G = Grid stations. SF = Fixed station. F = Frontal stations.

Plankton samples were collected by vertical net tows through the upper 20 m of the water column with a 20 µm mesh Nitex net for both plankton and phycotoxin analysis. Each net haul was adjusted to 1 L with 0.2 µm filtered seawater, of which 100 mL were fixed with Lugol solution for species determination. The rest was sequentially filtered through Nitex meshes of 200, 50, and 20 µm by gravity filtration and the material obtained from each mesh was resuspended in 45 mL of filtered seawater in 50 mL centrifugation tubes. Material from each fraction was split into three aliquots; 30 mL were collected for extraction of DSP and PSP toxins (15 mL each), and 15 mL were fixed with Lugol solution for enumeration of toxic species to compare cell densities and toxin abundances in field samples. Aliquots designated for toxin analysis were centrifuged at 3,220 × g for 15 minutes at room temperature. After centrifugation, pellets were stored at −20°C. Given that no dinoflagellates larger than 200 µm are considered to be potential phycotoxin producers, this size-fraction was not considered in this study.

Phytoplankton Analysis

Cell abundance of toxic dinoflagellates in net tow concentrates was determined by counting 1 mL of Lugol fixed samples using Sedgewick-Rafter chambers (LeGresley and McDermott, 2010) with an inverted microscope (Leica DMIL LED). The whole chamber was usually counted, or ≥10 random fields in the case of high cell abundance. Cell densities were expressed as cells per net tow (cells NT^{-1}), which corresponds to the total net harvest concentrate diluted up to 1 L. As 1 mL of total net material was used for semi-quantitative calculations, the limit for detection of the counting method was 1,000 cells NT^{-1}. Further morphological examination was made with a phase contrast/differential interference contrast Leica DM2500 microscope equipped with a Leica DFC420C camera, and two scanning electron microscopes (Jeol JSM-6360 LV SEM and FEI Quanta).

Toxin Analysis of Plankton Net Samples

Cell pellets from the plankton net tow size fractions were obtained through centrifugation (3,220 × g, 15 min at 4°C), suspended in 500 µL methanol, and subsequently homogenized with 0.9 g of lysing matrix D by reciprocal shaking at maximum speed (6.5 m s^{-1}) for 45 s in a Thermo Savant Bio101 FastPrep instrument. After homogenization, the samples

were centrifuged at 16,100 × g at 4°C for 15 min. Supernatants were transferred to spin-filters (0.45 µm pore size) and centrifuged for 30 s at 800 × g, followed by transfer to autosampler vials. Multiple lipophilic toxins were analyzed using LC-MS/MS, as described in Krock et al. (2008). At station G14, no data on lipophilic toxins were available due to sample degradation.

Toxin Cell Quotas

Cell quotas of toxins were obtained from net samples and total toxin content was estimated from two size fractions (20–50 µm and 50–200 µm) divided by the total number of cells of the possible toxin producer for each toxin co-occurring in the samples in the same pooled fractions. Based on the precision and accuracy estimates of cell counting methods reported in ICES (2006), only those samples with cell abundances >10,000 cells NT^{-1} were considered for cell quota calculations. Additionally, cell quotas of the different toxins were estimated from samples containing only one putatively toxigenic species for each toxin, or where a single toxigenic species represented >90% of the potentially toxigenic cells.

Solid Phase Adsorption Toxin Tracking (SPATT)

Solid Phase Adsorption Toxin Tracking devices (SPATT bags) were conditioned in methanol for 24 hours and then attached to sediment traps at the fixed station. Three SPATT bags per trap were deployed for one week at two different depths (40 m and 70 m), then released, retrieved, and kept at −4°C until they could be analyzed.

Salt was removed from the SPATT bags by rinsing with deionized water. SPATTs were subsequently dried on filter paper for 1 h at 50°C in a drying oven. Dry SPATTs were then opened, resins were collected in 50 mL centrifugation tubes, and 25 mL of methanol were added, and the tubes were left overnight for extraction of lipophilic toxins. The next day resin and methanol were transferred into chromatographic glass columns (27 cm length, 13 mm ID, packed with a 2 cm layer of quartz wool and 1 cm of quartz sand), and the centrifugation tubes were rinsed with an additional 15 mL methanol. Methanol was eluted dropwise from the column until the liquid reached the top column layer and subsequently another 65 mL were added to each column for complete extraction of toxins. Extracts of replicate SPATTs were combined and methanol was removed in a rotary evaporator to a final volume of approximately 0.5 mL. The concentrates were transferred to HPLC vials and adjusted with methanol to 1 mL. The final solution for LC-MS/MS measurement was prepared by dilution 1:10 (v:v) with methanol.

Data Analysis

Nonparametric Spearman's correlation analyses were employed to determine the relationship between cell density of the toxigenic species and toxin abundances, as well as between toxin cell quotas and environmental parameters. Canonical correspondence analysis (CCA) and associated Monte Carlo tests were performed using Canoco 4.5 software to explore the association between species distribution (after square root transformation) and the following environmental parameters: temperature, salinity, bottom depth, silicate, phosphate, and nitrate + nitrite (the latter expressed as inorganic nitrogen concentration). Temperature, salinity, and nutrient concentrations were estimated as the average values measured from the surface to 20 m depth.

RESULTS

Toxigenic Dinoflagellates and Associated Toxins in Plankton Samples

Microscopic and toxin analyses revealed the presence of several toxigenic dinoflagellates and phycotoxins. The toxigenic dinoflagellate species included *Alexandrium catenella*, *Protoceratium reticulatum*, *Dinophysis acuminata*, and *Gonyaulax spinifera* (Figure 2), and YTX, PTX-2, PTX-2sa, and eight PSP analogues—N-sulfocarbamoyl (C1/C2), gonyau-toxins 1/4 (GTX-1/4), gonyau-toxins 2/3 (GTX-2/3), saxitoxin (STX), and neoSTX (NEO)—were detected.

Alexandrium catenella was the most abundant toxigenic species (average = 437,500 cells NT^{-1}), representing 50% of the total toxigenic dinoflagellate cells. In addition, it was present at all stations except for G7. PSP toxins were detected

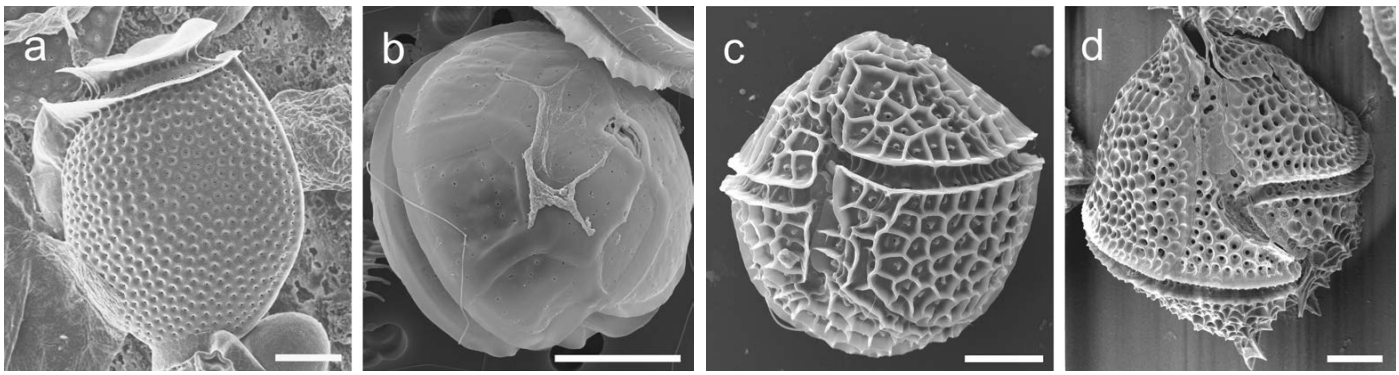

FIGURE 2. Scanning electron microscope images of the toxigenic dinoflagellate species detected in net samples. (a) *Dinophysis acuminata*, (b) *Alexandrium catenella*, (c) *Protoceratium reticulatum*, and (d) *Gonyaulax spinifera*. Scale: 10 µm.

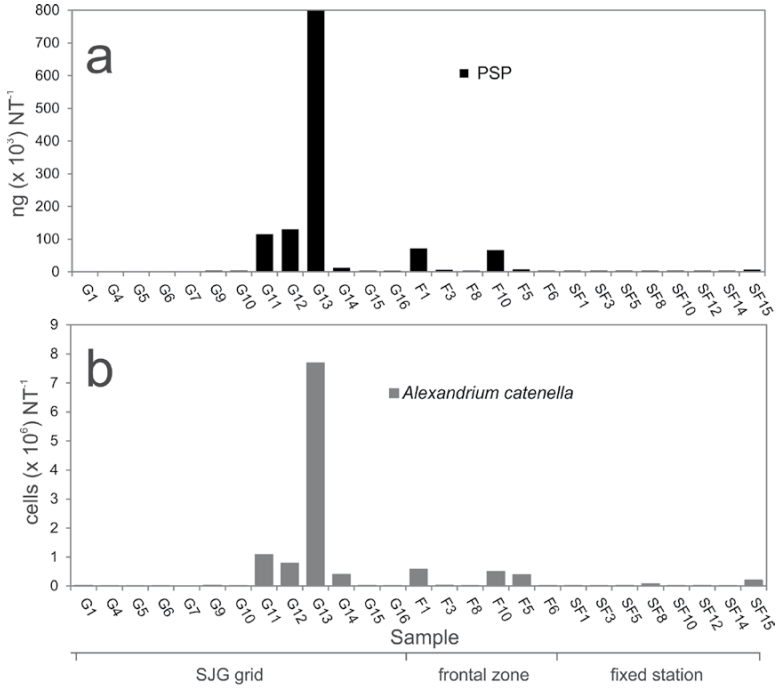

FIGURE 3. Bars represent total PSP (paralytic shellfish poisoning) toxin abundances expressed as ng (× 10^5) NT^{-1} (a) and cellular densities of *Alexandrium catenella* expressed as cells (× 10^6) NT^{-1} (b), detected in net samples.

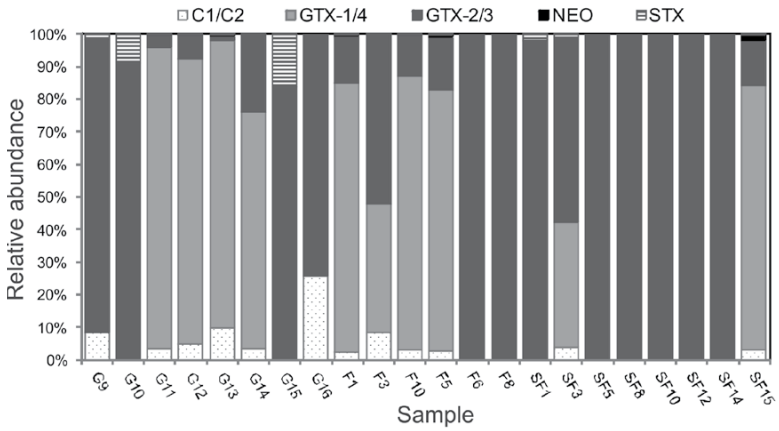

FIGURE 4. PSP (paralytic shellfish poisoning) toxin profiles detected in net samples. C = N-sulfocarbamoyl toxins. GTX = gonyautoxins. NEO = neo-saxitoxin. STX = saxitoxin.

TABLE 1. Results of correlation between cell quotas of the different toxigenic species found and environmental parameters. Significant values are presented in bold type.

	D. acuminata	*A. catenella*	*P. reticulatum*
Temperature	−0.26	**−0.84**	0.26
Salinity	−0.30	**−0.76**	**0.54**
Inorganic nitrogen	**0.75**	**0.78**	−0.39
Phosphate	**0.79**	**0.75**	0.09
Silicate	0.11	0.39	0.07

at almost all stations with *A. catenella* cell presence (Figure 3), showing a significant high correlation with cell densities ($r = 0.8$; $p < 0.05$). No PST were detected in only five samples where *A. catenella* abundances were lower than 17,000 cells NT^{-1}. Although several PSP analogues were detected, GTX dominated all profiles: GTX-2/3 at 65% of the stations and GTX-1/4 at the remaining 35% (Figure 4).

Total estimated PSP toxin cell quotas of *A. catenella* ranged from 3 pg $cell^{-1}$ to 284 pg $cell^{-1}$ (average = 85 pg $cell^{-1}$, n = 12). Maximum values were detected in samples collected in the southern SJG. We found significant and positive correlations between cell quotas and nutrient concentrations (inorganic nitrogen and phosphate but negative correlations between cell quotas and salinity and temperature (Table 1).

The DSP producer *Dinophysis acuminata* was also observed at all stations, except for G7, representing 6% of the total toxigenic cells with an average density of 54,700 cells NT^{-1}. Two toxins related to *D. acuminata* were detected, PTX-2 and PTX-2sa, showing a significant correlation with this species density ($r = 0.6$; $p < 0.05$). Although both analogues were found with equal frequency, PTX-2 abundances were always higher (Figure 5). Total PTX (PTX-2 plus PTX-2sa) toxin cell quotas of *D. acuminata* ranged from 0.3 to 1.7 pg $cell^{-1}$ (average = 0.5 pg $cell^{-1}$, n = 20), and were positively correlated with inorganic nitrogen and phosphate concentration (Table 1).

P. reticulatum was highly abundant at 70% of the sampling stations, representing 43.5% of the total toxigenic species, with average cell densities of 379,463 cells NT^{-1}. *G. spinifera*, the other potential YTX producer found in this study, was the least common of the toxigenic species (present in 40% of the samples) and showed the lowest average cell densities (618 cells NT^{-1}), representing less than 1% of the toxigenic cells (Figure 6). Although a significant and positive correlation was found between YTX abundances and cell densities of both species, the correlation coefficient was higher for *P. reticulatum* ($r = 0.94$; $p < 0.05$) than for *G. spinifera* ($r = 0.58$; $p < 0.05$). In addition, *G. spinifera* represented less than 3% of the YTX producer cells in all samples. Therefore, cell quotas were only estimated for *P. reticulatum*, ranging between 0.4 pg $cell^{-1}$ and 4.2 pg $cell^{-1}$ (average = 1.2 pg $cell^{-1}$, n = 13). Maximum values corresponded to samples collected in the northern SJG. YTX cell quotas showed significant and positive correlation with salinity (Table 1).

Association Between Toxigenic Species and Environmental Parameters

Figure 7 summarizes CCA results for toxigenic taxa cell density and environmental data in the biplot of the first two axes. The associated permutation test showed that axes 1 and all canonical axes were statistically significant ($p < 0.05$). The ordination axes 1 and 2 accounted for 84.7% and 5.8% of the cumulative variance in the species data. Inorganic nitrogen concentration, depth, salinity, and temperature explained the largest proportion of the total variance, as indicated by the length of their arrows in Figure 7.

A. catenella dominated the toxigenic dinoflagellate assemblages in the southern SJG (Figure 8), mainly associated with high nutrient concentration (i.e., inorganic nitrogen and phosphate) and lower temperatures and salinity. *P. reticulatum* proportions were higher in the northern SJG (Figure 8), associated with higher temperatures and salinity and lower nutrient concentrations. *D. acuminata* did not show such a clear association with the analyzed variables, although it was mainly related to warmer conditions found at northern coastal stations.

Lipophilic Toxins Detected from SPATT

Total toxin amounts detected from SPATT at 40 m were ~11 times higher than the abundances detected from SPATT at 70 m (Figure 9). YTX, PTX-2, PTX2-sa, dinophysistoxin-1 (DTX-1), okadaic acid (OA), and gymnodimine (GYM) were detected at both depths, while spirolide-1 (SPX-1) was found only at 70 m. YTX was the dominant toxin at 40 m depth, representing 75% (2,240 ng) of total toxin content, followed by PTX-2 (15%). At 70 m, the contribution of the different toxins was more homogeneous, with maximum proportions exhibited by DTX-1 (26%) and YTX (22%). GYM and SPX-1 were detected in very low abundances (<15 ng).

DISCUSSION AND CONCLUSIONS

Various phycotoxins (e.g., PST, PTX, and YTX analogues) were frequently observed in plankton samples collected in the SJG during austral summer 2014, showing a significant correlation with three toxigenic dinoflagellate species: *A. catenella*, *D. acuminata* and *P. reticulatum*, respectively.

The finding of *A. catenella* as the most abundant species coincided with previous studies in the area (Akselman, 1996; Pérez et al., 2013; Sastre et al., 2013, as *A. tamarense*); moreover, it was the

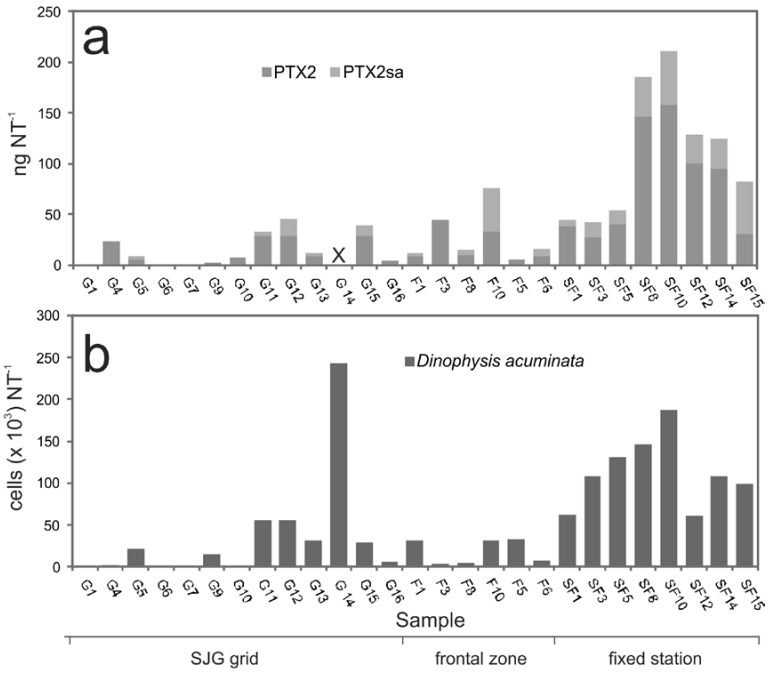

FIGURE 5. Bars represent PTX (pectenotoxins) abundances expressed as ng NT^{-1} (a) and cellular densities of *Dinophysis acuminata* expressed as cells ($\times 10^3$) NT^{-1} (b), detected in net samples. X = no lipophilic toxins measured due to sample degradation.

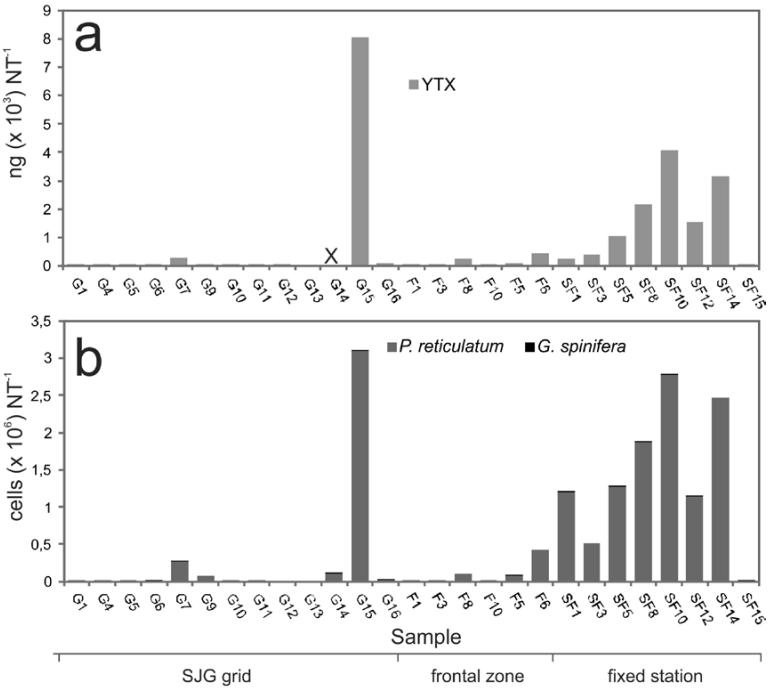

FIGURE 6. Bars represent YTX (yessotoxins) abundances expressed as ng ($\times 10^3$) NT^{-1} (a) and cellular densities of *Protoceratium reticulatum* and *Gonyaulax spinifera* expressed as cells ($\times 10^6$) NT^{-1} (b), detected in net samples. X = no lipophilic toxins measured due to sample degradation.

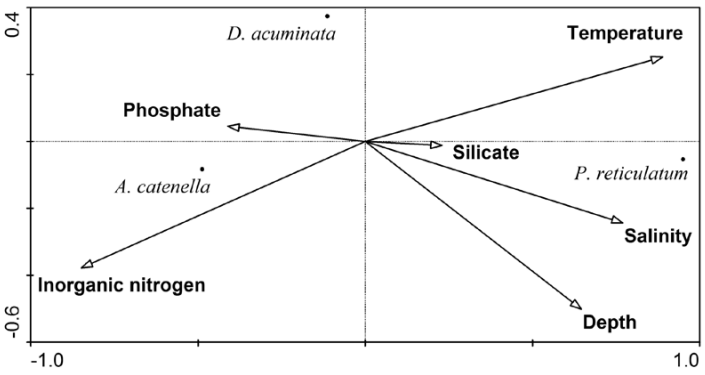

FIGURE 7. Biplot showing CCA (canonical correspondence analysis) results for cell density of toxigenic taxa and environmental data.

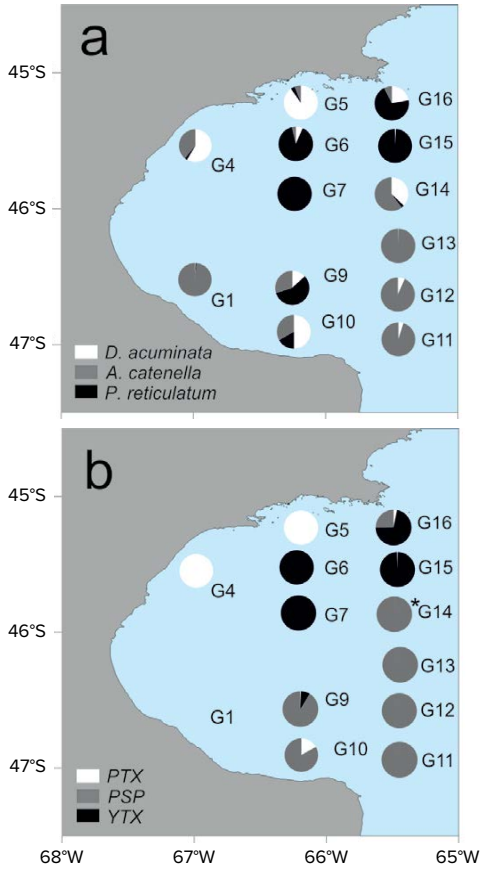

FIGURE 8. Proportions of toxigenic dinoflagellate species (a) and related toxins (b) found in net samples at SJG grid stations. Note that no lipophilic toxins were measured at station G14 due to sample degradation.

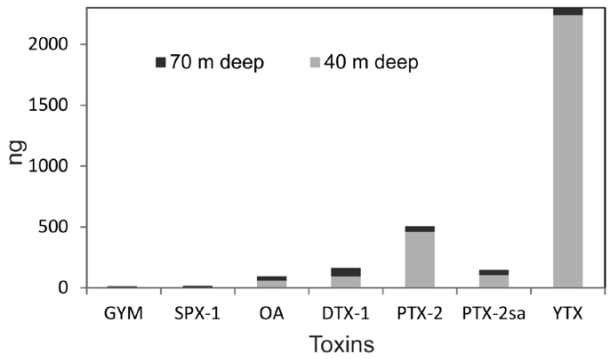

FIGURE 9. Lipophilic toxins detected from SPATT (Solid Phase Adsorption Toxin Tracking) at 40 m and 70 m.

only *Alexandrium* species found in net samples by microscopic observations. However, the detection of SPX in SPATT suggested the occurrence of *A. ostenfeldii* in the SJG. The presence of this species, which is the only known SPX producer (Cembella et al., 2001; Franco et al., 2006), has recently been detected in the Beagle Channel (Almandoz et al., 2014) and in Argentinean slope waters (Fabro et al., 2017).

Eight PSP analogues were detected in net samples: STX, NEO, GTX-1/4, GTX-2/3, and C-1/2; however, PSP profiles were mostly dominated by GTX-2/3 and to a lesser extent by GTX-1/4. Previous research on toxins in the SJG is scarce, but PSP profiles from what is available were also dominated by GTX-2/3 and GTX-1/4 (Krock et al., 2015; Fabro et al., 2017). The predominance of GTX analogues in PSP profiles is quite alarming considering that GTXs are the most toxic analogues for vertebrates (Wiese et al., 2010). In this sense, GTX-1 was the main PSP toxin detected in mussels during monitoring programs in the SJG, associated with *A. catenella* and 10 cases of human PSP intoxication, two of which resulted in fatalities (Sastre et al., 2013, as *A. tamarense*).

Total PSP cell quotas estimated in this study were high (average of 85 pg cell^{-1}) compared with previous reports on SJG field samples collected during spring (<0.8 pg cell^{-1}; Fabro et al., 2017), and were also higher than those recorded for two *A. catenella* isolates from the same area (60 pg cell^{-1} and 74 pg cell^{-1}; Krock et al., 2015). Maximum values in the present study were detected in the southern frontal area and minimum values in coastal waters. Similarly, Montoya et al. (2010) found that *A. catenella* (as *A. tamarense*) strains isolated from the Valdés Peninsula frontal system showed higher cell quotas than those isolated from coastal zones, leading those authors to conclude that differences in regional *A. catenella* toxicity could be due to isolate-specific responses to environmental conditions. They also found a positive correlation between nitrate concentration and toxin content, and a negative correlation between toxin content and temperature, which is consistent with our observations. The southern SJG is characterized by tidal mixing of nutrient-rich shelf waters with cold, low-salinity waters of a branch of the Patagonian current (Fernández et al., 2005; Palma et al., 2008; Matano et al., 2010). These oceanographic characteristics seem to provide specific conditions for PSP production in the southern SJG (i.e., lower temperatures and salinities, high nutrient input, and a weakly stratified water column).

D. acuminata was the only DSP producer found in the SJG, while *D. caudata* and *D. tripos*, which were previously reported for the area (Akselman, 1996; Gracia Villalobos et al., 2015), were not observed during this expedition.

D. acuminata cell densities showed a significant correlation with PTX-2 and PTX-2sa concentrations, whereas no DSP toxins were detected in plankton samples. This coincides with previous studies in the Argentinean Sea that showed the main toxins from *Dinophysis* profiles to be PTX, while OA and its derivatives (DTX) are rarely found (Fabro et al., 2015, 2016; Gracia Villalobos et al., 2015; Krock et al., 2015). Despite the absence of DSP toxins in plankton samples, OA and DTX-1 were detected in the seawater by SPATT sampling during the present study, suggesting that DSP toxins are indeed part of SJG *Dinophysis* profiles. Previous studies detected OA and DTX-1 in mussels using liquid chromatography with fluorescence detection (LC-FD) during a DSP outbreak in northern Buenos Aires Province that was related to *D. acuminata* (Sar et al., 2012). Moreover, recent monitoring programs in the San Matías and San José Gulfs, located ~550 km north of the SJG, reported positive mouse bioassays for DST related to the presence of *D. tripos* (Gracia Villalobos et al., 2015). It is also important to consider that SPATT accumulates toxins present in seawater during long time periods (a week in the case of this study), while analyses of phytoplankton samples measure toxins inside the cells of their producers at the moment of the sample collection, which highlights the importance of applying both methods in a complementary way to assess lipophilic-toxin diversity in the study area.

Toxin cell quotas of *D. acuminata* in this study (0.3–1.7 pg cell^{-1}) were lower than those previously reported from waters near the slope adjacent to the SJG (22 pg cell^{-1}; Fabro et al., 2016). The positive correlation between PTX cell quotas and nutrients is consistent with the observations of Hattenrath-Lehmann and Gobler (2015), who suggested that enhanced loading of nitrogen and organic matter in coastal zones is likely to promote toxic *Dinophysis* blooms.

The lipophilic neurotoxin YTX was frequently detected in the area (present in 66% of samples). Previous reports from the SJG associated YTX detection with the presence of *P. reticulatum*, while *Gonyaulax spinifera*, the other YTX producer present in the Argentinean Sea, has not been clearly associated with YTX detection (Akselman et al., 2015; Fabro, 2018). The high correlation between *P. reticulatum* cell density and YTX concentration observed in the present study also suggests that *P. reticulatum* is the main YTX producer in the SJG. Field YTX cell quotas estimated for *P. reticulatum* in this study were lower (0.4–4.2 pg YTX cell^{-1}) than those obtained under culture conditions for *P. reticulatum* strains isolated from the SJG (9.1–10.2 and 3–7 pg YTX pg cell^{-1}; Akselman et al., 2015; Houghton et al., 2016), and slightly lower than those estimated during spring from another field study (2.2–6.5 pg cell^{-1}; Fabro, 2018). Estimated *P. reticulatum* YTX content was positively correlated with salinity, in agreement with results from experiments performed with batch cultures of this species from the Adriatic Sea: Guerrini et al. (2007) showed that toxin release from cells decreased as salinity increased, leading to a higher YTX content inside the cells. Likewise, analysis of a *P. reticulatum* strain isolated from the North Sea showed that the YTX cell quotas increased with increasing salinity during the stationary phase at 20°C (Röder et al., 2012).

The occurrence of toxigenic dinoflagellate species and their toxins showed marked differences in the northern and southern areas of the SJG, respectively characterized as nutrient poor and nutrient rich areas (Torres et al., 2018, this issue). The northern SJG was mainly dominated by *P. reticulatum* and YTX and by *D. acuminata* and PTX, whereas the southern SJG was dominated by *A. catenella* and PST. A similar north-south distribution pattern was observed in abundance and composition of microbial and zooplankton communities during the *Coriolis II* expedition (Latorre et al., 2018, in this issue; Giménez et al., 2018, in this issue). CCA results indicated that the distribution of toxigenic dinoflagellate species was mostly determined by nutrients and temperature. Accordingly, inorganic nitrogen and phosphate increased from north to south or almost southeast (Torres et al., 2018, in this issue), with an increasing concentration gradient of these nutrients toward the southern frontal area (Rivas and Pisoni, 2010).

The association of *A. catenella* with high inorganic nitrogen concentrations might be related to its trophic strategy, as unlike other mixotrophic species of the genus, this species is autotrophic (Blossom et al., 2012). The other two main species observed in this study (*D. acuminata* and *P. reticulatum*) have the capacity to feed on microalgae or bacteria (Reguera et al., 2012; Nielsen and Kiørboe, 2015), which might give them some advantage in low nitrate environments. Moreover, it was established that *A. catenella* is not a good competitor for nitrate at low concentrations (Collos et al., 2004), so other species might be favored under such circumstances. This was also observed in natural assemblages of *A. catenella* and *D. acuminata* from South Africa, where the temporal succession was related to different strategies used by these species for nitrogen uptake (Seeyave et al., 2009).

Distribution of the toxigenic species might also be related to water column stratification, given that this is a key factor in nutrient dynamics. During summer, stratified waters were usually observed in the northern SJG, where the surface layer is separated from nutrient-rich bottom waters by a well-defined pycnocline. By contrast, the mixed southern area was characterized by the input of nutrients from deeper waters to the surface (Torres et al., 2018, in this issue). Moreover, it was recently established that ammonium uptake rates of *D. acuminata* were significantly higher than those of any other nitrogen source, indicating a preference for ammonium over nitrate (Hattenrath-Lehmann and Gobler, 2015), which might have allowed *D. acuminata* to dominate in more stratified, recycling

environments toward the north and center of the SJG. This is consistent with some studies that show *Dinophysis* blooms can be related to cell accumulation forced by stratification (Swanson et al., 2010; Sjöqvist and Lindholm, 2011). In contrast, Hattenrath-Lehmann et al. (2013) found an association of high *Dinophysis* densities with higher temperature and salinity, but not with water column stratification, probably due to the characteristics of the system studied: a shallow, well-mixed, and never strongly stratified area of New York waters.

Finally, *A. catenella* distribution might also be related to the location of the frontal area in the southern SJG, as Smayda and Reynolds (2001) characterized this species as a "frontal zone taxon." Likewise, maximum abundances of the genus *Alexandrium* from Argentina were estimated from stations at frontal zones (Carreto et al., 1986, as *Gonyaulax excavata*). Collos et al. (2004) suggested that *A. catenella* is possibly adapted to large single inputs of nutrients associated with low frequency phenomena such as frontal disturbances.

Although it is usually considered a cold-water species (Balech, 1988), *P. reticulatum* was associated here with higher temperatures, showing maximum cell abundances between 14°C and 16°C. Experiments performed with a clonal isolate from the SJG showed the highest cell division rate at 20°C and the lowest at 10°C, suggesting successful adaptation of *P. reticulatum* to higher temperatures (Houghton et al., 2016). Likewise, Akselman et al. (2015) reported spatio-temporal progress in the presence of the motile stage of *P. reticulatum* with the onset of the warm season. Moreover, during a *P. reticulatum* bloom in northern Chile, an upwelling relaxation coincided with increase of coastal water temperature to values near 22°C (Álvarez et al., 2011). All of this evidence suggests that *P. reticulatum* is more a temperate- than a cold-water species.

This work is the first integrated analysis of the diversity and distribution of toxigenic dinoflagellates and the environmental conditions that lead to their accumulation during late summer in San Jorge Gulf. In summary, several toxigenic species co-occurred in the SJG during summer, showing marked spatial differences as a result of environmental variability. Cellular toxin content was also differently affected by environmental parameters, highlighting the complexity of HABs in this area.

REFERENCES

Akselman, R. 1996. *Estudios ecológicos en el Golfo de San Jorge y adyacencias (Atlántico sudoccidental). Distribución, abundancia y variación estacional del fitoplancton en relación a factores fisico-químicos y la dinámica hidrográfica.* PhD Dissertation, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 234 pp.

Akselman, R., B. Krock, T.J. Alpermann, U. Tillmann, M. Borel, G.O. Almandoz, and M. E. Ferrario. 2015. *Protoceratium reticulatum* (Dinophyceae) in the austral southwestern Atlantic and the first report on YTX-production in shelf waters of Argentina. *Harmful Algae* 45:40–52, https://doi.org/10.1016/j.hal.2015.03.001.

Almandoz, G.O., N.G. Montoya, M.P. Hernando, H.R. Benavides, M.O. Carignan, and M.E. Ferrario. 2014. Toxic strains of the *Alexandrium ostenfeldii* complex in southern South America (Beagle Channel, Argentina). *Harmful Algae* 37:100–109, https://doi.org/10.1016/j.hal.2014.05.011.

Álvarez, G., E. Uribe, R. Díaz, M. Braun, C. Marino, and J. Blanco. 2011. Bloom of the Yessotoxin producing dinoflagellate *Protoceratium reticulatum* (Dinophyceae) in Northern Chile. *Journal of Sea Research* 65(4):427–434, https://doi.org/10.1016/j.seares.2011.03.008.

Aune, T., R. Sorby, T. Yasumoto, H. Ramstad, and T. Landsverk. 2002. Comparison of oral and intraperitoneal toxicity of yessotoxins towards mice. *Toxicon* 40:77–82, https://doi.org/10.1016/S0041-0101(01)00192-1.

Balech, E. 1988. *Los dinoflagelados del Atlántico Sudoccidental*. Instituto Español de Oceanografía, Madrid, 310 pp.

Blossom, H., N. Daugbjerg, and P.J. Hansen. 2012. Toxic mucus traps: A novel mechanism that mediates prey uptake in the mixotrophic dinoflagellate *Alexandrium pseudogonyaulax*. *Harmful Algae* 17:40–53, https://doi.org/10.1016/j.hal.2012.02.010.

Bogazzi, E., A. Baldoni, A. Rivas, P. Martos, R. Reta, J.M. Orensanz, M. Lasta, and P. Dell´Arciprete. 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the Southwestern Atlantic. *Fisheries Oceanography* 14:359–376, https://doi.org/10.1111/j.1365-2419.2005.00340.x.

Carreto, J.I., H.R. Benavides, R.M. Negri, and P.D. Glorioso. 1986. Toxic red-tide in the Argentine Sea. Phytoplankton distribution and survival of the toxic dinoflagellate *Gonyaulax excavata* in a frontal area. *Journal of Plankton Research* 8:15–28, https://doi.org/10.1093/plankt/8.1.15.

Carreto, J.I., M.O. Carignan, N.G. Montoya, and D.A. Cucchi Colleoni. 2007. Ecología del fitoplancton en los sistemas frontales del Mar Argentino. Pp. 11–31 in *El Mar Argentino y sus recursos Pesqueros*. J.I. Carreto and C. Bremec, eds, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina.

Cembella, A.D., A.G. Bauder, N.I. Lewis, and M.A. Quilliam. 2001. Association of the gonyaulacoid dinoflagellate *Alexandrium ostenfeldii* with spirolide toxins in size-fractionated plankton. *Journal of Plankton Research* 23(12):1,413–1,419, https://doi.org/10.1093/plankt/23.12.1413.

Ciocco, N.F., M. Lasta, M. Narvarte, C. Bremec, E. Bogazzi, J. Valero, and J.M. Orensanz. 2006. Scallops in Argentina. Pp. 1,251–1,292 in *Scallops: Ecology and Aquaculture*, 2nd ed. S. Shumway and G.J. Parsons, eds, Elsevier, Amsterdam.

Collos, Y., C. Gagne, M. Laabir, and A. Vaquer. 2004. Nitrogenous nutrition of *Alexandrium catenella* (Dinophyceae) in cultures and in Thau Lagoon, Southern France. *Journal of Phycology* 40:96–103, https://doi.org/10.1046/j.1529-8817.2004.03034.x.

Fabro, E. 2018. *Dinoflagelados toxígenos en el Mar Argentino. Diversidad, abundancia y toxinas asociadas.* PhD Dissertation, Facultad de Ciencias Naturales de la Universidad Nacional de La Plata, Buenos Aires, Argentina, 197 pp.

Fabro, E., G.O. Almandoz, M.E. Ferrario, M.S. Hoffmeyer, R.E. Pettigrosso, R. Uibrig, and B. Krock. 2015. Co-occurrence of *Dinophysis tripos* and pectenotoxins in Argentinean shelf waters. *Harmful Algae* 42:25–33, https://doi.org/10.1016/j.hal.2014.12.005.

Fabro, E., G.O. Almandoz, M.E. Ferrario, U. John, U. Tillmann, K. Toebe, B. Krock, and A. Cembella. 2017. Morphological, molecular and toxin analysis of field populations of *Alexandrium* genus from the Argentina Sea. *Journal of Phycology* 53(6):1,206–1,222, https://doi.org/10.1111/jpy.12574.

Fabro, E., G.O. Almandoz, M.E. Ferrario, U. Tillmann, A. Cembella, and B. Krock. 2016. Distribution of *Dinophysis* species and their association with lipophilic phycotoxins in plankton from the Argentine Sea. *Harmful Algae* 59:31–41, https://doi.org/10.1016/j.hal.2016.09.001.

Fernández, M., J.I. Carreto, J. Mora, and A. Roux. 2005. Physico-chemical characterization of the benthic environment of the Golfo San Jorge, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 6(85):1,317–1,328, https://doi.org/10.1017/S002531540501249X.

Franco, J.M., B. Paz, P. Riobó, G. Pizarro, R. Figueroa, S. Fraga, and I. Bravo. 2006. First report of the production of spirolides by *Alexandrium peruvianum* (Dinophyceae) from the Mediterranean Sea. Pp. 174–175 in *12th International Conference on Harmful Algae Programme and Abstracts*, Copenhagen, Denmark.

Gerssen, A., I.E. Pol-Hofstad, M. Poelman, P.P. Mulder, H.J. Van den Top, and J. De Boer. 2010. Marine toxins: Chemistry, toxicity, occurrence and detection, with special reference to the Dutch situation. *Toxins* 2:878–904, https://doi.org/10.3390/toxins2040878.

Giménez, E.M., G. Winkler, M. Hoffmeyer, and G.A. Ferreyra. 2018. Composition, spatial distribution, and trophic structure of the zooplankton community in San Jorge Gulf, southwestern Atlantic Ocean. *Oceanography* 31(4):154–163, https://doi.org/10.5670/oceanog.2018.418.

Guerrini, F., P. Ciminiello, C. Dell'Aversano, L. Tartaglione, E. Fattorusso, L. Boni, and R. Pistocchi. 2007. Influence of temperature, salinity and nutrient limitation on yessotoxin production and release by the dinoflagellate *Protoceratium reticulatum* in batch-cultures. *Harmful Algae* 6:707–717, https://doi.org/10.1016/j.hal.2007.02.006.

Gracia Villalobos, L., N. Santinelli, V. Sastre, B. Krock, and J.L. Esteves. 2015. *Dinophysis* species associated with diarrhetic shellfish poisoning (DSP) episodes in North Patagonian gulfs (Chubut, Argentina). *Journal of Shellfish Research* 34:1,141–1,149, https://doi.org/10.2983/035.034.0339.

Hattenrath-Lehmann, T., and C.J. Gobler. 2015. The contribution of inorganic and organic nutrients to the growth of a North American isolate of the

mixotrophic dinoflagellate *Dinophysis acuminate*. *Limnology and Oceanography* 60:1,588–1,603, https://doi.org/10.1002/lno.10119.
Hattenrath-Lehmann, T.K., M.A. Marcoval, D.L. Berry, S. Fire, Z. Wang, S.L. Morton, and C.J. Gobler. 2013. The emergence of *Dinophysis acuminata* blooms and DSP toxins in shellfish in New York waters. *Harmful Algae* 26: 33–44, https://doi.org/10.1016/j.hal.2013.03.005.
Hallegraeff, G.M. 2004. Harmful algal blooms: A global overview. Pp. 25–49 in *Manual of Harmful Marine Microalgae*. G.M. Hallegraeff, D.M. Anderson, and A.D. Cembella, eds, Intergovernmental Oceanographic Commission of UNESCO, Paris.
Houghton, C., M.P. Hernando, G. Malanga, B. Krock, and U. Tillmann. 2016. Temperature effects on growth, yessotoxin content, and oxidative stress of *Protoceratium reticulatum* from Argentina (South Atlantic Ocean). P. 116 in *ICHA, The 17th International Conference on Harmful Algae, Brazil 2016, Abstract Book*. October 9–14, 2016, Florianópolis Santa Catarina, Brazil.
ICES (International Council for the Exploration of the Sea). 2006. *Report of the ICES/IOC Workshop on New and Classic Techniques for the Determination of Numerical Abundance and Biovolume of HAB Species: Evaluation of the Cost, Time-Efficiency and Intercalibration Methods (WKNCT)*. August 22–27, 2005, Kristineberg, Sweden, ICES CM 2005/C:10, 30 pp.
Krock, B., C.M. Borel, F. Barrera, U. Tillmann, E. Fabro, G.O. Almandoz, M.E. Ferrario, J.E. Garzón Cardona, B.P. Koch, C. Alonso, and R. Lara. 2015. Analysis of the hydrographic conditions and cyst beds in the San Jorge Gulf, Argentina, that favor dinoflagellate population development including toxigenic species and their toxins. *Journal of Marine Systems* 148:86–100, https://doi.org/10.1016/j.jmarsys.2015.01.006.
Krock, B., U. Tillmann, U. John, and A.D. Cembella. 2008. LC-MS/MS on board ship: Tandem mass spectrometry in the search for phycotoxins and novel toxigenic plankton from the North Sea. *Analytical and Bioanalytical Chemistry* 392:797–803, https://doi.org/10.1007/s00216-008-2221-7.
Lassus, P., N. Chomérat, P. Hess, and E. Nézan. 2016. Toxic and harmful microalgae of the World Ocean. Micro-algues toxiques et nuisibles de l'océan mondial. Pp. 523 in *IOC Manuals and Guides 68* (English/French), Intl. Society for the Study of Harmful Algae (ISSHA), Intergovernmental Oceanographic Commission of UNESCO (IOC), Copenhagen, Denmark.
Latorre, M.P., I.R. Schloss, G.O. Almandoz, K. Lemarchand, X. Flores-Melo, V. Massé-Beaulne, and G.A. Ferreyra. 2018. Mixing processes at the pycnocline and vertical nitrate supply: Consequences for the microbial food web in San Jorge Gulf, Argentina. *Oceanography* 31(4):50–59, https://doi.org/10.5670/oceanog.2018.410.
LeGresley, M., and G. McDermott. 2010. Counting chamber methods for quantitative phytoplankton analysis: Haemocytometer, Palmer-Maloney cell and Sedgewick-Rafter cell. Pp. 25–30 in *Microscopic and Molecular Methods for Quantitative Phytoplankton Analysis*. B. Karlson, C. Cusack and E. Bresnan, eds, UNESCO, Paris.
Matano, R.P., E.D. Palma, and A.R. Piola. 2010. The influence of the Brazil and Malvinas Currents on the Southwestern Atlantic Shelf circulation. *Ocean Science* 6(4):983–995, https://doi.org/10.5194/os-6-983-2010.
Montoya, N.G., V.K. Fulco, M.O. Carignan, and J.I. Carreto. 2010. Toxin variability in cultured and natural populations of *Alexandrium tamarense* from southern South America: Evidences of diversity and environmental regulation. *Toxicon* 56(8):1,408–1,418, https://doi.org/10.1016/j.toxicon.2010.08.006.
Nielsen, L.T., and T. Kiørboe. 2015. Feeding currents facilitate a mixotrophic way of life. *The ISME Journal* 9:2,117–2,127, https://doi.org/10.1038/ismej.2015.27.
Palma, E.D., R.P. Matano, and A.R. Piola. 2008. A numerical study of the Southwestern Atlantic Shelf circulation: Stratified ocean response to local and offshore forcing. *Journal of Geophysical Research* 113(C11), https://doi.org/10.1029/2007JC004720.
Pérez, L.B., N. Santinelli, V. Sastre, A.A. Pérez, R. Peralta, and M. Bergalio. 2013. Morfología y presencia estacional de *Alexandrium tamarense* (Lebour) Balech en estaciones costeras del golfo San Jorge (Patagonia, Argentina). *Naturalia* 50.
Reguera, B., L. Velo-Suárez, R. Raine, and M.G. Park. 2012. Harmful *Dinophysis* species: A review. *Harmful Algae* 14:87–106, https://doi.org/10.1016/j.hal.2011.10.016.
Rivas, A.L., and Pisoni, J.P. 2010. Identification, characteristics and seasonal evolution of surface thermal fronts in the Argentinean continental shelf. *Journal of Marine Systems* 79:134–143, https://doi.org/10.1016/j.jmarsys.2009.07.008.
Röder, K., F.M. Hantzsche, C. Gebühr, C. Miene, T. Helbig, B. Krock, M. Hoppenrath, B. Luckas, and G. Gerdts. 2012. Effects of salinity, temperature and nutrients on growth, cellular characteristics and yessotoxin production of *Protoceratium reticulatum*. *Harmful Algae* 15:59–70, https://doi.org/10.1016/j.hal.2011.11.006.
Sar, E.A., I. Sunesen, A.B. Goya, A.S Lavigne, E. Tapia, C. García, and N. Lagos. 2012. First report of diarrheic shellfish toxins in mollusks from Buenos Aires Province (Argentina) associated with *Dinophysis* spp.: Evidence of okadaic acid, dinophysistoxin-1 and their acyl derivatives. *Boletín de la Sociedad Argentina de Botánica* 47:5–14.
Sastre, A.V., N.H. Santinelli, V. Willers, M.E. Solís, S. Díaz Ovejero, L.B. Pérez., A.A. Pérez, M.A. Fajardo, L. Gracia Villalobos, and G.R. Marino. 2013. Floraciones de *Alexandrium tamarense* y TPM en el Golfo San Jorge in *Proceeding of XXXIV Jornadas Argentinas de Botánica*, La Plata, Buenos Aires, Argentina.
Seeyave, S., T.A. Probyn, G.C. Pitcher, M.I. Lucas and D.A. Purdie. 2009. Nitrogen nutrition in assemblages dominated by *Pseudo-nitzschia* spp. *Alexandrium catenella* and *Dinophysis acuminata* off the west coast of South Africa. *Marine Ecology Progress Series* 379:91–107, https://doi.org/10.3354/meps07898.
Sjöqvist, C.O., and T. Lindholm. 2011. Natural co-occurrence of *Dinophysis acuminata* (Dinoflagellata) and *Mesodinium rubrum* (Ciliophora) in thin layers in a coastal inlet. *Journal of Eukaryotic Microbiology* 58:365–372, https://doi.org/10.1111/j.1550-7408.2011.00559.x.
Skalar Analytical® V.B, 2005a. Skalar Methods - Analysis: Nitrate + Nitrite - Catnr. 461-031 + DIAMOND Issue 081505/MH/99235956. Breda, The Netherlands.
Skalar Analytical® V.B, 2005b. Skalar Methods - Analysis: Phosphate - Catnr. 503-010w/r + DIAMOND Issue 081505/MH/99235956. Breda, The Netherlands.
Skalar Analytical® V.B, 2005c. Skalar Methods - Analysis: Silicate -Catnr. 563-051 + DIAMOND Issue 081505/MH/99235956. Breda, The Netherlands.
Smayda, T.J., and C.S. Reynolds. 2001. Community assembly in marine phytoplankton: Application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research* 23:447–461, https://doi.org/10.1093/plankt/23.5.447.
Swanson, K.M., L.J. Flewelling, M. Byrd, A. Nunez, and T.A. Villareal. 2010. The 2008 Texas *Dinophysis ovum* bloom: Distribution and toxicity. *Harmful Algae* 9:190–199, https://doi.org/10.1016/j.hal.2009.10.001.
Torres, A.I., F.E. Paparazzo, G.N. Williams, A.L. Rivas, M.E. Solís, and J.L. Esteves. 2018. Dynamics of macronutrients in the San Jorge Gulf during spring and summer. *Oceanography* 31(4):25–32, https://doi.org/10.5670/oceanog.2018.407.
Van Dolah, F.M. 2000. Marine algal toxins: Origins, health effects, and their increased occurrence. *Environmental Health Perspectives* 108:133–141.
Wiese, M., P.M. D'Agostino, T.K. Mihali, M.C Moffitt, and B.A. Neilan. 2010. Neurotoxic alkaloids: Saxitoxin and its analogs. *Marine Drugs* 8:2,185–2,211.

ACKNOWLEDGMENTS

The R/V *Coriolis II* expedition was jointly funded by the Ministerio de Ciencia, Tecnología e Innovación Productiva (MINCyT), the Province of Chubut, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (Argentina) and the Institut des sciences de la mer de Rimouski (ISMER). The authors thank Wolfgang Drebing (AWI) for sample extraction and toxin measurements by LC-MS/MS and Annegret Müller (AWI) for toxin extraction and analyses of PSP toxins. In addition, the friendly reception and support of the 2014 captain and crew of the *R/V Coriolis* are gratefully acknowledged. This work was partially funded by PIP 0122 (CONICET) and PICT 0576 (ANPCyT) grants, and supported by the Helmholtz-Gemeinschaft Deutscher Forschungszentren through the research program Polar regions And Coasts in the changing Earth System (PACES) of the Alfred Wegener Institut-Helmholtz Zentrum für Polar- und Meeresforschung. Finally, we thank the reviewers for their suggestions to improve this manuscript.

AUTHORS

Elena Fabro (fabroelena@yahoo.com.ar) is Postdoctoral Research Fellow, División Ficología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina, and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina. **Bernd Krock** is Senior Scientist, Alfred Wegener Institut-Helmholtz Zentrum für Polar- und Meeresforschung, Chemische Ökologie, Bremerhaven, Germany. **Américo I. Torres** is a researcher at Centro para el Estudio de Sistemas Marinos (CESIMAR), CONICET, Puerto Madryn, Chubut, Argentina. **Flavio E. Paparazzo** is a researcher at CESIMAR, CONICET, Puerto Madryn, Chubut, Argentina, and Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Chubut, Argentina. **Irene R. Schloss** is Researcher, Instituto Antártico Argentino, Centro Austral de Investigaciones Científicas (CADIC), Tierra del Fuego, Argentina; Associate Professor, Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, Québec, Canada; and Professor, Universidad Nacional de Tierra del Fuego, Ushuaia, Tierra del Fuego, Argentina. **Gustavo A. Ferreyra** is Head, CADIC-CONICET, Ushuaia, Tierra del Fuego, Argentina, and Associate Professor, Institut des sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski, Québec, Canada. **Gastón O. Almandoz** is a CONICET Researcher at División Ficología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

ARTICLE CITATION

Fabro, E., B. Krock, A.I. Torres, F.E. Paparazzo, I.R. Schloss, G.A. Ferreyra, and G.O. Almandoz. 2018. Toxigenic dinoflagellates and associated toxins in San Jorge Gulf, Argentina. *Oceanography* 31(4):145–153, https://doi.org/10.5670/oceanog.2018.417.