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Harmful Algae

Increase in records of toxic phytoplankton and associated toxins in water samples in the Patagonian Shelf (Argentina) over 40 years of field surveys

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ABSTRACT

Historical records (1980–2018) of potentially toxic phytoplankton and phycotoxins on the Argentine Continental Shelf (35°S-56.5°S) and adjacent ocean waters were systematically reviewed from scientific literature to assess their abundance and diversity over spatial and temporal scales. Records increased from 124 in the period 1980–1992 to 638 in 2006–2018, and the scanned area expanded from coastal to offshore waters including the shelf-break front. *Alexandrium* was the most reported genus (54%) during 1980–1992 and *Pseudo-nitzschia* (52%) during 1993–2005. By 2006–2018, a higher diversity was documented: *Alexandrium* (20%), *Dinophysis* (32%), *Pseudo-nitzschia* (31%), and the most recently described potentially toxic dinoflagellates of the family Amphidomataceae (8%). Likewise, a wider spectrum of phycotoxins was documented in the last decade, with lipophilic (LSTs) and paralytic shellfish toxins (PSTs) as the most recorded. Increased records are related to intensified monitoring, more detailed taxonomic analyses and more sensitive chemical techniques for marine biotoxin detection. This quantitative assessment brings light to the widespread occurrence of HABs along contrasting areas of the Patagonian Shelf and sets the basis for ecosystem risk evaluation. Moreover, comparison of toxic phytoplankton reported in the SW Atlantic with those in similar temperate seas in the North Atlantic and the Pacific Ocean, disclose ocean basin differences in strain toxicity of *A. ostenfeldii*, *D. tripos* and *Azadinium* species.

1. Introduction

Harmful Algal Blooms (HABs) of toxin-producing phytoplankton are natural events globally occurring which pose a risk to ecosystems and public health, often leading to wildlife mass mortalities, economic losses, and human intoxication or even death through ingestion of contaminated seafood (Anderson et al., 2015). In temperate regions, HABs commonly occur in spring and summer in response to multiple environmental drivers at different spatial and temporal scales, primarily seasonal changes in light and water column structure, nutrients and grazing pressure (Smayda, 1997) and often enhanced by coastal eutrophication (Smayda, 2008) and pollution (Paerl et al., 2018; Griffith and Gobler, 2020). Moreover, widespread effects of climate-induced changes in the ocean such as warming, deoxygenation, intensified stratification and extreme weather events have been ascribed as drivers of rising HABs, both in empirical and observational studies (Bindoff et al., 2019; Trainer et al., 2020). Phycotoxins are natural metabolites synthesized by certain species of phytoplankton and the most diverse producers belong to the dinoflagellates. Most phycotoxins are intracellular and are transferred to higher trophic levels through their accumulation within the food web (Díaz et al., 2022), while other bio-active compounds are exuded into the environment with lytic effects on other protists (Tillmann and Hansen, 2009) or ichthyotoxic effects (Long et al., 2021). Despite the longstanding scientific interest in understanding HABs, the ecological role of biotoxins such as grazer deterrents and allelochemicals are still in the early stage of research (Xu and Kiørboe, 2018; Blossom et al., 2019; Long et al., 2021).

In a global framework, assessment of the databases OBIS and HAEDAT of harmful algae has disclosed large-scale increasing trends in HABs attributed to intensified monitoring efforts related to aquaculture activities; for instance in the Mediterranean Sea (Zingone et al., 2021) and in the global seas (Hallegraeff et al., 2021). Moreover, growing detection of novel biotoxins in recent years such as goniodomins, GDs (Krock et al., 2018), and identification of their phytoplankton producers e.g. *Alexandrium pseudogonyaulax* (Kremp et al., 2019) and *A. taylorii* (Tillmann et al., 2020) highlight the increasing interest in studying these

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natural hazards and the yet underexplored biodiversity and functional traits of marine protists.

Compared to the coasts of North America and Europe, HAB species and phycotoxins in the southern hemisphere remain relatively understudied, even when first records of HABs go back 50 years in Latin America and the Caribbean (Sunesen et al., 2021). It is worth noting that global databases often have low resolution for some areas because regional monitoring data are not regularly loaded. In the particular case of the Argentine Sea in the Southwestern South Atlantic Ocean, the first documented HAB was in austral spring 1980 when two fishermen died after the consumption of contaminated shellfish with paralytic shellfish toxins (PSTs) (Carreto et al., 1981). This toxic event was caused by *Alexandrium catenella*, initially described as *Gonyaulax excavata* and later renamed as *A. tamarense* group 1. Thereafter, recurrent massive blooms of *Alexandrium* have been registered in the Patagonian Gulfs (Gayoso, 2001; Gayoso and Fulco, 2006) and the Beagle Channel (Almandoz et al., 2019). Further, mass mortalities of whales and marine birds (Uhart et al., 2008; Wilson et al., 2015), and fishes of commercial interest (Montoya et al., 1996) were reported along the Argentine coast associated with toxic events. In addition, shellfish harvesting closures due to toxin outbreaks also led to economic losses (Sunesen et al., 2014).

In recent years, a variety of potentially toxic phytoplankton species and associated phycotoxins (Almandoz et al., 2017; Fabro et al., 2016; 2019; Guinder et al., 2018; 2020; Tillmann et al., 2019) have been detected along the Patagonian Shelf-Break Front (PSBF). This large marine ecosystem is recognized as one of the most productive of the World Seas and provides feeding and spawning habitat for numerous animals in the pelagic and benthic realms (e.g. fishes and squids, marine mammals and scallops banks) (Martinetto et al., 2019). This permanent front characterized by a pronounced thermal gradient and high phytoplankton biomass in spring and summer (García et al., 2008; Marrari et al., 2017) supports diverse fishing resources, hence the presence of toxic species implies a risk for ecosystem services and human health. The particular hydrographic characteristics of the PSBF are driven by the interaction between the complex bathymetry and energetic boundary currents: the Malvinas Current and the Brazil Current (Piola et al., 2018; Artana et al., 2021). The time-mean pathways and variability of ocean currents determine HAB propagation and expansion, which together with mesoscale eddies or upwelling events lead nutrient loads into the system and phytoplankton biomass accumulation (Smayda, 2002; Giddings et al., 2014). The PSBF offers an ideal scenario to study the connectivity of toxic phytoplankton in the Atlantic Ocean.

The aim of this study is the provision of a comprehensive analysis of spatial and temporal trends in historical records (1980–2018) of potentially toxic phytoplankton in contrasting ecosystems along the Argentine Continental Shelf, from temperate to subpolar regions. This work relies on a database constructed by the extraction and harmonization of qualitative and quantitative data from the scientific literature and technical reports, considering only phytoplankton species that are potential producers of shellfish poisoning toxins, and the phycotoxins detected in water samples. Further, we assessed the abundance range of the most frequent species over the ca. 40 years of HABs studies, to contribute to the understanding of regional species-specific bloom thresholds. In the context of increasing HAB reports, mapping toxic species and their toxins at regional scales is important to assess environmental risk, set early alarm systems and track potential biogeographical shifts in their occurrence.

2. Materials and methods

2.1. Study area

Data of potentially toxigenic phytoplankton was gathered from available literature and reports dealing with the Argentine Continental Shelf (35–56.5°S), between La Plata River in the north and the Drake Passage in the south, covering coastal ecosystems (estuaries, gulfs, bays

and the Beagle Channel), middle shelf and shelf-break areas, and adjacent ocean waters including the Burdwood Bank (Fig. 1).

2.2. Systematic search and literature filter

All available literature on potentially toxigenic phytoplankton and/ or phycotoxins ever described in water samples in the area (since first documentation in Carreto et al., 1981) was consulted using Google Scholar, ResearchGate and other institutional platforms. Some specific work not accessible on the web such as doctoral or master theses (e.g. Cadaillón, 2012) were directly requested from the authors. The literature revision for the data extraction was performed until March 2022, and by then, no publications describing new records of potentially toxic phytoplankton –in water samples– were found in the study area beyond 2018. Among all the spectra of HAB species, here only phytoplankton species that potentially produce shellfish poisoning toxins were considered (toxins which are transferred through the food web mainly through filter-feeding bivalves). This excludes ichthyotoxic phytoplankton species that do not produce shellfish toxins (e.g. *Chattonella marina*), benthic species, cyanobacteria, and high biomass phytoplankton blooms that lead to hypoxia. In addition, phycotoxins measured in animal tissues like shellfish or marine mammals (e.g. D'Agostino et al., 2015; Goya et al., 2020; Cadaillón et al., 2022) were not considered in this assessment, because sampling and data interpretation are not comparative with algae/toxins concentration in water samples . A total of 112 downloaded articles were filtered for metadata collection (Fig. 2), keeping only those that were specifically focused on potentially toxic phytoplankton in water samples –collected with bottle, hose and/or with phytoplankton net (e.g. Fabro et al., 2017; Guinder et al., 2018; Tillmann et al., 2019)–, and those based on general phytoplankton community composition but with specific quantification of HAB species (e.g. Esteves et al., 1997; Antacli et al., 2018; Santinelli et al., 2018). After the addition of an unpublished dataset of toxins from an expedition carried out in spring 2016 in El Rincón shelf area, the systematic revision of the literature resulted in a total of 82 studies considered for the construction of the database (**supplementary table S1**).

2.3. Data extraction and organization

Selected studies were thoroughly reviewed and the explicit numeric data were extracted from tables, maps, graphics or text body. Thereafter, data were organized in a table, where each row corresponded to a taxonomic species or to a specific toxin at a particular date and sampling station. Columns corresponded to the following variables: [1] species name, [2] genus, [3] cell abundance, [4] binary presence/absence, [5] toxin name, [6] syndrome produced, [7] toxin level, [8] month, [9] season, [10] year, [11] latitude, [12] longitude and [13] area of collection, and [14] bibliographic reference. When available, additional environmental information was extracted including surface water temperature, salinity and nutrient concentrations, and information of intoxication or mortality episodes. The potentially toxigenic dinoflagellates *Amphidoma languida* and species of the genus *Azadinium* were merged into the "Amphidomataceae" group, due to eventual difficulties in their taxonomic identification using traditional microscopy (see Tillmann et al., 2019).

2.4. Data analyses

Using the software *R* (package: *dcast*), the first table was restructured to a new format in which each row corresponded to a particular water sample, and all species, toxins and environmental data were variables (columns). By creating a unique variable with the spatial-temporal-ID of each water sample, we grouped samples from identical sampling stations published in different articles focused on particular species or groups of species. For instance, Almandoz et al. (2017) and Fabro et al.
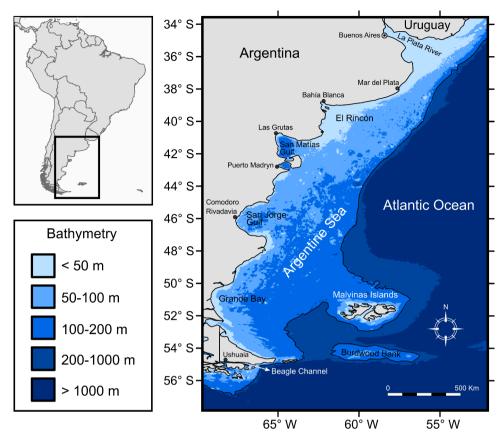
Fig. 1. Study area showing the location of the Argentine Sea in the Southwestern South Atlantic. The bathymetry and the main geographical areas are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
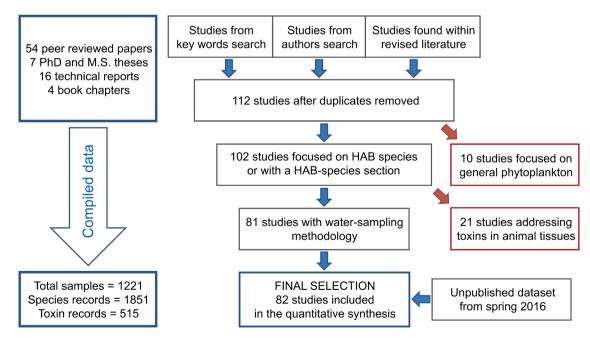

Fig. 2. Workflow of the selection of articles for the assessment of historic records of potentially toxic phytoplankton in the Argentine Sea. Blue arrows indicate consecutive steps and red arrows indicate neglected articles, which were not related to toxic phytoplankton in water samples. On the left, an overview of total articles and data collected is displayed.
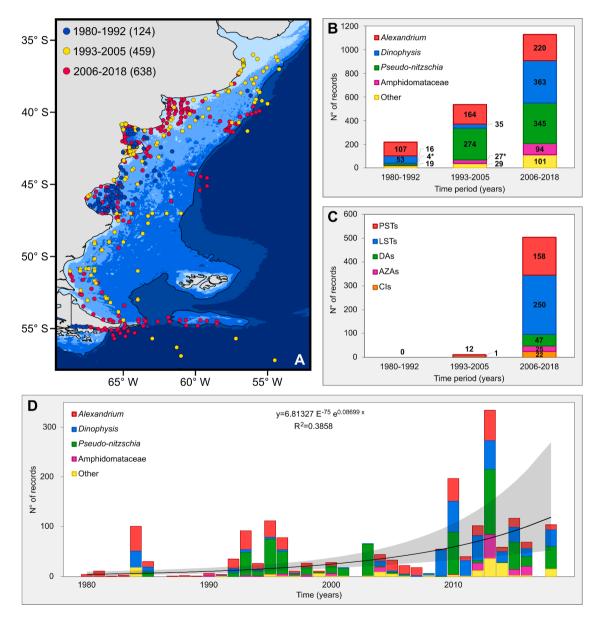
(2016) published results separately of *Pseudo-nitzschia* spp. and *Dinophysis* spp., respectively, collected in the same oceanographic expedition along the shelf onboard R/V Bernardo Houssay in austral summer 2013. Likewise, from the cruise onboard R/V B. Houssay in austral spring 2015 in El Rincón shelf area, Guinder et al. (2018) focused on *Alexandrium* spp. and other producers of lipophilic toxins, while Tillmann et al. (2019) focused on the Amphidomataceae group and azaspiracids. Thus, species, toxins and environmental variables at each

station were successfully paired through the collected literature.

To evaluate the spatial and temporal evolution of records of all potentially toxic species and phycotoxins in water samples, a roadmap was built covering the period 1980–2018, considering their proportions over three 13-year intervals: 1980–1992, 1993–2005 and 2006–2018. A temporal trend was estimated between the log-transformed number of species records and time (years) with a linear regression model, which disclosed an exponential relation. Trends for phycotoxin records over time were not assessed since most reports were densely concentrated in a few years ($n = 7$) within a short time period (2012–2016). Maps of potentially toxic species abundance and maps of phycotoxin content were built to assess their spatial distribution. Further, regarding the large extension of the studied area and its wide heterogeneity in terms of geomorphology/hydrology, we analyzed the proportions of species by subregions/ecosystems, including estuarine areas, gulfs, shelf-break frontal area and open ocean waters.

Finally, we assessed the abundance range of the most frequent species in the Patagonian Shelf over the 39 years of HAB records. Although data on cell-toxin quota were not available in most cases, the analysis of population density in the field may provide hints about potential development of HABs at a regional scale. For this, we estimated for each species, the mean $\pm$ 2 standard deviations ($\bar{X} \pm 2SDs$) of their log-transformed abundance (cells L^{-1}), which encompasses 95.4% of the data. Thereafter, we suggested the upper 2SD of each log-abundance ranking as the species-specific threshold of exceptionally high regional abundance (2.2% of the data). Normal distribution was tested with a Q-Q Plot using *R* (function "qqp" of the package *car*).

Fig. 3. (A) Number of water samples in which toxic phytoplankton species and/or phycotoxins were detected over the period 1980–2018. The time frame was divided in three 13-year intervals: 1980–1992 (blue circles, 124 observations), 1993–2005 (yellow circles, 459 obs.) and 2006–2018 (red circles, 638 obs.). **(B)** Number of records of the most frequent toxic phytoplankton genera, the family Amphidomataceae, and other toxic algae (Other) namely: *Gonyaulax spinifera, Prorocentrum lima, Protoceratium reticulatum* and *Gymnodinium catenatum* over the three 13-year periods. *Dinoflagellates of the family Amphidomataceae were detected in the shelf-break front (i.e. Akselman and Negri 2012; Akselman et al., 2014) before their taxonomic description in 2009 (Tillmann et al., 2009). **(C)** Number of records of phycotoxins detected in water samples over the three 13-year intervals: PSTs: Paralytic shellfish toxins, LSTs: Lipophilic toxins, DA: Domoic acid, AZAs: Azaspiracids, and CIs: Cyclic imines. **(D)** Annual trend of the number of records of potentially toxic phytoplankton. The black line shows the positive, exponential trend over time. Shaded area indicates the confidence intervals of the model. The model equation and R^2 value are shown.

3. Results

Data compilation of potentially toxic phytoplankton species and phycotoxins from scientific literature resulted in a total of 1221 water samples over the period 1980–2018, including 1851 records of potentially toxic species and 515 records of phycotoxins (Fig. 2). From the total water samples, 69.8% were collected during austral spring and summer (October-March). When all samples were plotted in a map over three consecutive 13-year periods (Fig. 3A), spatial and temporal trends were evident, that is expansion of the sampled area from coastal to offshore waters and a 5.1-fold increase in the number of records from the period 1980–1992 (124) to 2006–2018 (638) (with 459 records in the middle period 1993–2005). Early studies (1980–1992) were more localized in the San Jorge Gulf, the Northern Patagonian Gulfs and the Beagle Channel, while recent studies (2006–2018) appeared more frequently in shelf waters, especially in the area of El Rincón and the shelf-break front. The number of potentially toxic phytoplankton species mentioned in the literature increased from 1 in 1980 to 25 by 2018. *Alexandrium* was the most reported genus (54%) during 1980–1992 followed by *Dinophysis* (27%), and *Pseudo-nitzschia* (52%) in 1993–2005 followed by *Alexandrium* (31%) (Fig. 3B). By the period 2006–2018, higher diversity of toxigenic phytoplankton was documented: *Dinophysis* (32%), *Pseudo-nitzschia* (31%), *Alexandrium* (20%), and the most recently described dinoflagellates of the family Amphidomataceae (8%) (Fig. 3B). Other potentially toxic phytoplankton species completed the spectrum of the last period (9%), namely *Gonyaulax spinifera*, *Prorocentrum lima*, *Protoceratium reticulatum* and *Gymnodinium catenatum* (Fig. 3B). Phycotoxins were not studied in water samples during the first period of records of HAB species (1980–1992) (Fig. 3C), and only paralytic shellfish toxins (PSTs) and domoic acid (DA) were detected in the second period, in the year 2000 and 2005, respectively. Conversely, over recent years (2006–2018) the scanning of different phycotoxins was intensified, resulting in the characterization of five groups of toxins: PSTs (31.5%), lipophilic toxins (LSTs, 49.8%), DA (9.4%), azaspiracids (AZAs, 5.0%) and cyclic imines (CIs, 4.4%) (Fig. 3C). The number of records of species showed an increasing trend over time ($p > 0,001$), with a good fit to an exponential relation (slope = 0.087; $R^2 = 0.384$; Fig. 3D). The potential phytoplankton producers and their associated phycotoxins and syndromes registered in the Argentine Sea are shown in Table 1. Pictures of common toxin-producing phytoplankton in the Argentine Sea are shown in Fig. 4.

From the 25 toxic species identified during 1980–2018, nine species corresponded to the genus *Pseudo-nitzschia* (34.3% of total records), six to *Dinophysis* (24.4%) and two to *Alexandrium* (26.6%) (Fig. 5 and Table 1). Altogether these three genera and the Amphidomataceae group (6.7% with four toxic species: *Azadinium dexteroporum*, *Az. poporum*, *Az. spinosum* and *Amphidoma languida*) accounted for 92.0% of the total records. The remaining 8.0% corresponded to the species: *Gonyaulax spinifera*, *Protoceratium reticulatum*, *Prorocentrum lima*, and *Gymnodinium catenatum* (Fig. 5 and Table 1).

Most common phycotoxins detected over the period 1980–2018 were LSTs (48.5% of total records), mainly represented by pectenotoxins (PTXs) and yessotoxins (YTXs). Only three records of diarrhetic shellfish toxins (DSTs): okadaic acid (OA) and dinophysistoxins (DTXs) (Table 1), were detected in water samples in 2016. The second most abundant phycotoxins were PSTs (33.0%), mainly represented by gonyautoxins (GTXs) and C-1/2, followed by neosaxitoxin (NEO) and saxitoxin (STX) (Fig. 6). Other phycotoxins in the period were DA (9.3%), AZAs (4.9%), and CIs (4.3%) (Fig. 6).

Potentially toxic species were documented widespread in the Patagonian Shelf, but most records were concentrated in coastal areas (Fig. 7). PSTs producing species (Fig. 7A) were mostly reported at low latitudes below 47.5°S in the Patagonian Gulfs and El Rincón area. In particular *A. catenella* was also notably abundant in the Beagle Channel (55°S). Amphidomataceae group (Fig. 7B) resembled the distributional pattern of PSTs producing species, reported in coastal and offshore

Table 1
Summary of toxin producing phytoplankton species and their associated phycotoxins and syndromes, registered in the Argentine Sea, SW South Atlantic, over the period assessed in this study (1980–2018).

Producer	Toxin - Syndrom	
Alexandrium catenella, Gymnodinium catenatum →	**Paralytic Shellfish Poisoning (PSP)** Saxitoxin (STX) and derivatives	
A. ostenfeldii →	**Spiroimine Shellfish Poisoning (SSP)** Cyclic imines (CIs: SPXs and GYMs)	
Prorocentrum lima →	**Diarrhetic Shellfish Poisoning (DSP)** Okadaic acid (OA) Dinophysistoxins (DTXs)	**Lipophilic toxins** (**LSTs** in this study)
Dinophysis acuta, D. caudata →		
D. acuminata, D. tripos, D. forti, D. norvegica →	Pectenotoxins (PTXs) (not diarrheagenic)	
Protoceratium reticulatum, Gonyaulax spinifera	Yessotoxins (YSTs)	
Azadinium spinosum, Az. poporum, Az. dexteroporum, Amphidoma languida,	**Azaspiracid Shellfish Poisoning (AZP)** Azaspiracids (AZAs)	
Az. luciferelloides (toxicity not confirmed)		
Pseudo-nitzschia australis, P. pseudodelicatissima, P. fraudulenta, P. multiseries, P. pungens, P. turgidula, P. calliantha.	**Amnesic Shellfish Poisoning (ASP)** Domoic acid (DA)	

waters and mainly in lower latitudes. Regarding DSTs and DA producing species (Fig. 7C and 7D, respectively), they were more dispersed across the Patagonian Shelf. Records of the least documented species *Dinophysis fortii* ($n = 2$), *Pseudo-nitzschia delicatissima* ($n = 4$) and *P. seriata* ($n = 5$) were included in "*Dinophysis* spp." and "*Pseudo-nitzschia* spp.", respectively, together with other non-identified species of these genera.

In agreement with the distribution of toxin-producing phytoplankton species, records of phycotoxins in water samples (Fig. 8) were also more abundant in coastal regions, with the highest levels in the Patagonian Gulfs and El Rincon shelf area, the Beagle Channel, and the northern part of the shelf-break. Some discrepancies raised when comparing the distribution of the potential toxin-producing species (Fig. 7) and the expected phycotoxins associated with them (Fig. 8), which did not necessarily co-occur in a certain area or at a sampling station. For instance, the distribution of CIs and the potential producer detected *A. ostenfeldii* (Fig. 8A and 7A), the Amphidomataceae group and AZAs (Figs. 7B and 8B), yessotoxins concentrated in the San Jorge Gulf while their producers were wider distributed (Fig. 8C and 7C), and *Pseudo-nitzschia* species and DA (Figs. 7D and 8D). As shown in Fig. 3C, the first records of AZAs in water samples were in recent years, when these toxins were detected in two out of four oceanographic cruises planned for their scanning along the middle and outer shelf. In both cruises (spring 2013 and 2016), AZAs were detected at low levels (<2.19 ng L^{-1}).

Total records of potentially toxic species and phycotoxins were mainly concentrated in coastal ecosystems in between 38°S and 47°S, from El Rincón area (ER) to the San Jorge Gulf (SJG) (Fig. 9), where the most sampled areas were the Northern Patagonian Gulfs (NPG) (42.0% of total records), ER (13.2%) and the SJG (12.4%) (Fig. 9A). Notably, in some areas with relatively low monitoring efforts like South of Valdés Peninsula (SVP) and the shelf-break front (SBF), some species showed higher abundance than in more monitored areas. For instance, the mean abundance of *Alexandrium* in SVP ($\bar{X} = 91,509$ cells L^{-1}) was greater than in NPG ($\bar{X} = 38,591$ cells L^{-1}), even though most records of this genus were from the latter region ($n = 29$ and $n = 196$, respectively) (Fig. 9B). Similarly, Amphidomataceae showed the highest abundances in the (northern) SBF followed by the ER shelf area in the same latitudes, notably surpassing the abundances detected in other regions with
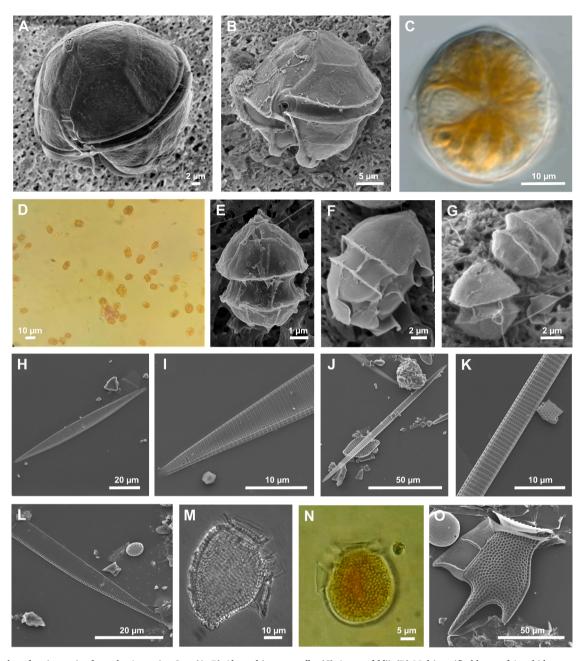
Fig. 4. Examples of toxic species from the Argentine Sea. (**A, B**) *Alexandrium catenella*; (**C**) *A. ostenfeldii*; (**D**) Multispecific bloom of Amphidomataceae (and other dinoflagellates); (**E**) *Azadinium dexteroporum*; (**F, G**) *Azadinium* sp., H, I) *Pseudo-nitzschia australis*, (**J, K**) *P. pungens*; (**L**) *P. fraudulenta*; (**M**) *Dinophysis norvegica*; (**N**) *D. acuminata*; (**J**) *D. tripos*. Contributions: A, B, E-G, M, O, Elena Fabro; H-L: Gastón Almandoz, C: photo from Guinder et al. (2018); D: Photo from the oceanographic cruise "Agujero Azul" (41.8°S-61.3°W) onboard RV Víctor Angelescu in November 2021 (Ramírez, F.J. – Ferronato, C.); **N**: Photo from the oceanographic cruise Beagle-Burdwood onboard RV Puerto Deseado in December 2016 (Guinder, V.A.).

sustained monitoring systems (e.g. the Beagle Channel).

Lastly, the most frequently documented toxigenic species over the period 1980–2018 were *Alexandrium catenella* ($n = 334$ records), *Dinophysis acuminata* ($n = 178$), Amphidomataceae ($n = 110$), *Pseudo-nitzschia pungens* ($n = 85$), *Pseudo-nitzschia australis* ($n = 71$), *Pseudo-nitzschia pseudodelicatissima* ($n = 71$), *Dinophysis tripos* ($n = 65$), *Pseudo-nitzschia fraudulenta* ($n = 48$), and *Alexandrium ostenfeldii* ($n = 42$) (Fig. 10). The threshold of unusual high population abundance in the region, estimated as the mean + two standard deviation ($\bar{X}+2SD$) of the log-transformed abundances of each species (red dot in Fig. 10), was maximal for *P. pseudodelicatissima*: 2.5×10^6 cells L^{-1}, followed by *A. catenella* and *P. australis* with thresholds one order of magnitude below: 2.5 and 2.1×10^5 cells L^{-1}, respectively. The minimum values corresponded to *D. acuminata* (15,000 cells L^{-1}), *D. tripos* (13,000 cells

L^{-1}), and *A. ostenfeldii* (2700 cells L^{-1}).

4. Discussion

4.1. Increased number of records of toxic phytoplankton in the Patagonian Shelf

Distribution of potentially toxic phytoplankton and shellfish toxins on the basis of four decades of field surveys revealed a trend of an increasing number of records of species, and a rise in the number of phycotoxins identified in water samples in the last years. In addition, a spatial expansion of the monitored area became evident, first alongshore from the Patagonian Gulfs and the Beagle Channel with frequent monitoring, towards other coastal and inner shelf areas such as El
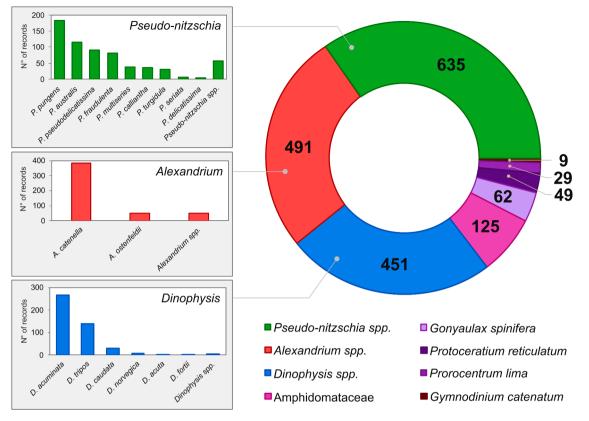
Fig. 5. Number of records of potentially toxic phytoplankton species in the Argentine Sea over the period 1980–2018.
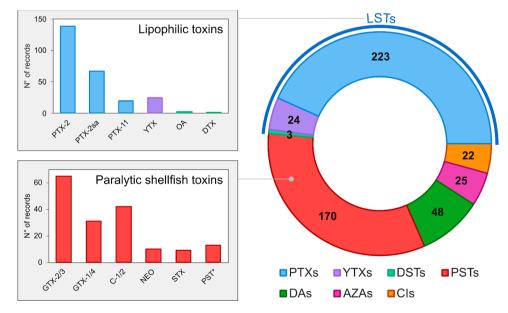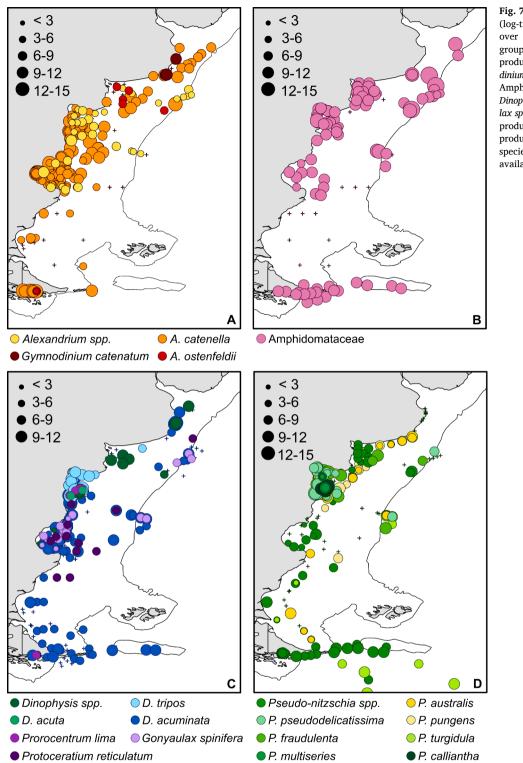

Fig. 6. Number of records of phycotoxins in the Argentine Sea over the period 1980–2018. Individual species of lipophilic toxins (LSTs) and paralytic shellfish toxins (PSTs) are shown in the left charts. PSTs* embrace those paralytic toxins not identified up to the specific molecular level. DA: Domoic acid. CI: Cyclic imines. AZAs: Azaspiracids.
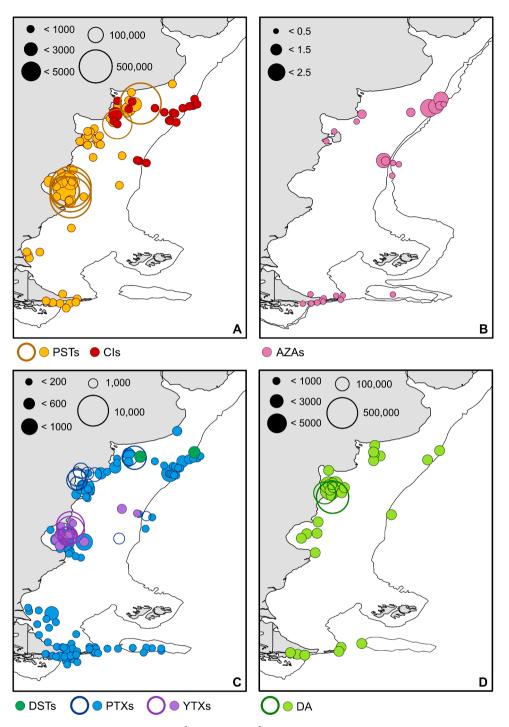
Rincón and Grande Bay with more sporadic monitoring. Lately, sampling events shifted towards the middle shelf and the shelf-break zone, with discrete sampling through sporadic oceanographic cruises. Sustained long-term monitoring systems of phytoplankton species producers of shellfish poisoning toxins have been carried out since the early 1980s in coastal waters of San Matías Gulf, Valdés Peninsula and San Jorge Gulf (Esteves et al., 1997; Gayoso, 2001; Gracia-Villalobos et al.,

2015) and the Beagle Channel (Goya and Maldonado 2014; Almandoz et al., 2019; Cadaillón et al., 2022), related to aquaculture activities. More recently, monitoring extended to the northern part of the Patagonian Shelf-Break Front, site of exploitation of the Patagonian scallop *Zygochlamys patagonica*. This fishery, with ~5000 t disembarked per year and pricing of 9000 USD t^{-1} represents 5% of the total Argentinian fishery exports (Campodónico et al., 2019). In consequence, unbalanced

Fig. 7. Geographic distribution and abundance (log-transformed cells L^{-1}) of toxigenic species over the period 1980–2018. The species are grouped according to the phycotoxins they produce. **(A)** *Alexandrium* species and *Gymnodinium catenatum* (PSTs producers). **(B)** Amphidomataceae (AZAs producers). **(C)** *Dinophysis* species, *Prorocentrum lima, Gonyaulax spinifera* and *Protoceratium reticulatum* (LSTs producers). **(D)** *Pseudo-nitzschia* species (DA producers). Crosses indicate the presence of the species when no data of abundance was available.

monitoring efforts have led to substantial differences in the number of records of HAB species among different ecosystems, as disclosed in Fig. 9. Moreover, in mid-shelf zones rich in biodiversity and fishing resources (Ferronato et al., 2021) and in the extensive Patagonian Shelf-Break Front, PSBF (Martinetto et al., 2019) (Fig. 9), oceanographic cruises including phycotoxins scanning only began in the last decade: 2012–2018. This "snapshot" monitoring system (a total of eight cruises), has augmented the records of phycotoxins. For instance, the highly abundant and multispecific blooms of Amphidomataceae (Akselman
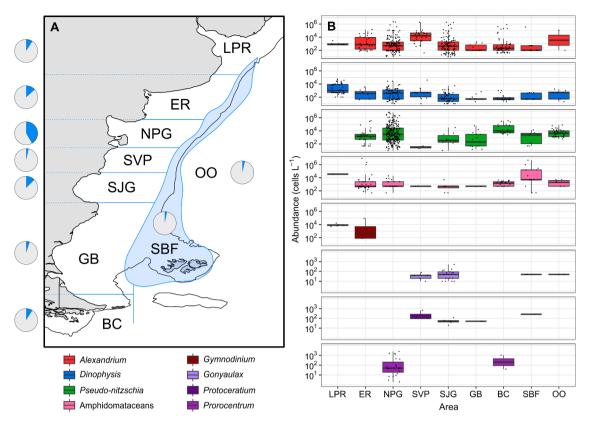
and Negri, 2012) and azaspiracids in different regions of the PSBF (Fabro et al., 2019; Tillmann et al., 2019; Guinder et al., 2020), the wide dispersion across the shelf of different potentially toxic *Pseudo-nitzschia* spp. and domoic acid (Almandoz et al., 2017; Guinder et al., 2018), *Alexandrium catenella* and *A. ostenfeldii* and their associated toxins (Fabro et al., 2017; Guinder et al., 2018), and *Dinophysis* spp. and lipophilic toxins (Fabro et al., 2016) including high levels of pectenotoxins in open ocean waters over the Burdwood Bank (Guinder et al., 2020). These findings support the idea that dominance of HABs in

Fig. 8. Geographic distribution and abundance (in ng net tow^{-1}; AZAs in ng L^{-1}) of phycotoxins registered in water samples over the period 1980–2018. **(A)** Paralytic shellfish toxins (PSTs) and Cycloimines (CIs). **(B)** Azaspiracids (AZAs), only represented by AZA-2. **(C)** Lipophilic toxins: Diarrhetic shellfish toxin (DSTs), pectenotoxins (PTXs) and yessotoxins (YTXs). **(D)** Domoic acid (DA).

coastal areas might be an anthropocentrically biased perception, because most human activities associated with aquaculture occur alongshore while open ocean waters are rarely screened for phycotoxins. However, growing observational data has confirmed that offshore waters are rich in toxin-producing phytoplankton. This is particularly true in the wide Patagonian Shelf, where the shelf-break front is located ~200 to ~900 km offshore and recent surveys have confirmed the occurrence of numerous HAB species. The complex oceanographic conditions of the PSBF and adjacent offshore regions result from the interplay between wind stress, different water masses in the shelf, the steep shelf slope and energetic edge currents (e.g. Malvinas), which

induce upwelling of nutrient-rich waters and promote phytoplankton outbreaks in spring (e.g. García et al., 2008; Carreto et al., 2016). In general, frontal shelf zones have been ascribed as "pelagic seed banks" for toxic dinoflagellates which develop advantageous traits to bloom over other phytoplankton groups (Smayda, 2008). This seems to be the case of the small dinoflagellates of the Amphidomataceae group that bloom in different areas along the PSBF, while no coastal blooms of Amphidomataceans have been registered. Still a large area of the PSBF and adjacent ocean waters in the South Atlantic remains unexplored, leading to open questions regarding trans-oceanic plankton connectivity and redistribution of toxic species driven by ocean currents, eventually

Fig. 9. (A) Proportion of samples per region (light blue in the pie charts) with records of toxin-producing phytoplankton and/or phycotoxins from the total water samples over the period 1980–2018. LPR: La Plata River area, ER: El Rincón shelf area, NPG: North Patagonian Gulfs, SVP: South of Valdés Peninsula, SJG: San Jorge Gulf, GB: Grande Bay, BC: Beagle Channel, SBF: Shelf Break Front, and OO: Open ocean. **(B)** Box plots of abundance (in cells L^{-1}) of the phytoplankton genera reported in different regions of the Argentine Sea. Note the different scale of the y-axes in the last three subpanels.
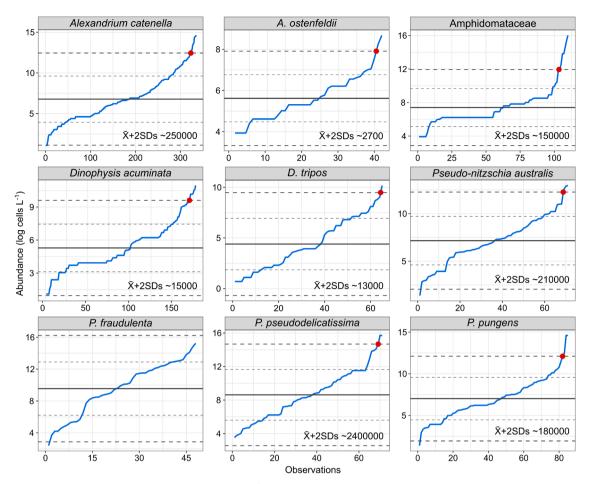
overcoming natural geographical barriers.

4.2. Potential human-related causes and environmental drivers of the trend

Historically, the study of HABs focused on coastal areas primarily due to the easier access to the sampling sites and the need for regular control of water quality related to aquaculture and other human activities such as tourism and artisanal fisheries. As a result, more intensified monitoring has led to an apparent trend of increasing records of HABs frequency and their intensity in some regions (Díaz et al., 2019; Zingone et al., 2021; Hallegraeff et al., 2021). The increase in frequency and geographical expansion of toxigenic phytoplankton records on the Patagonian Shelf disclosed in this study are in agreement with large-scale regional assessments in other seas that rely on global databases like HAEDAT, OBIS, CARPHA and AREC and complemented with local records, such as in the coasts of the USA (Anderson et al., 2021), Chile (Díaz et al., 2022) and Latin America and the Caribbean (Sunesen et al., 2021). Notably, according to the global assessment of Hallegraeff et al. (2021), the OBIS dataset displayed a reduced number of HABs in Latin America in recent years, while Sunesen et al. (2021) found that HAEDAT events in Latin America have increased from rare to almost yearly since 1990. This discrepancy could be due to the sparse sampling resolution of the databases, and highlights the need for their update with local monitoring systems, as well as the need for national unification of databases especially in countries with large sea extension and with diverse coastal ecosystems such as Argentina. In this sense, this study may work as an archetype of quantitative data gathering, harmonization and analysis at a high-resolution regional scale.

It is worth noting that the available data over 40 years of studies in the Patagonian Shelf were not evenly collected, which hinders the detection of natural trends in HABs and their attribution to environmental drivers. The data were collected in a biased way, as some studies were based only on (i) the detection and quantification of specific toxin-producing species: e.g. *Alexandrium* (Gayoso and Fulco, 2006), *Pseudo-nitzschia* spp. (Almandoz et al., 2017) or *Dinophysis* spp. (Fabro et al., 2016) without considering other phytoplankton groups, (ii) intense monitoring in particular areas focused on specific toxic phytoplankton (Sunesen et al., 2009) (Fig. 9), (iii) long-term coastal monitoring systems (Sastre et al., 2018) or discrete "snapshot" sampling on oceanographic cruises on the shelf and shelf-break front (Akselman et al., 2015; Tillmann et al., 2019), and (iv) different approaches for species taxonomy and evaluation of toxin production (e.g. isolation of strains, DNA analysis and microscopy; Guinder et al., 2018). Taking under consideration all this biased sampling, the analysis of the dataset constructed here suggests that the rise of HAB records in the Argentine Sea seems to be the result of the growing awareness about the risk of these natural threats for ecosystem services and human health, which resulted in more frequent sampling in the early years in order to assure food safety. More recently, in the early 2000s, an increase of scientific interest became evident focusing more on taxonomy of toxic species, their ecophysiology, associated biogeographical shifts, and bloom drivers, especially with recent studies expanding towards the outer shelf (e.g. Akselman et al., 2015; Fabro et al., 2017). In addition, trends of rising toxin records may be related to the implementation of more sophisticated techniques (e.g. liquid chromatography coupled to tandem mass spectrometry LC-MS/MS), and taxonomical studies (scanning electron microscopy and phylogenetic studies) for the detection, identification and quantification of previously undiscovered phycotoxins and their producers in the region. For instance, the recent description of new spirolides produced by strains of *Alexandrium ostenfeldii* isolated from the PSBF, whose population in the Argentine Sea (first genetic characterization for the

Fig. 10. Ranking distribution of the abundance (log-transformed cells L^{-1}) of the most frequent species over the period 1980–2018. The solid gray line indicates the mean log-abundance of each species, and the dashed gray lines indicate one and two standard deviations (1SD and 2SD, respectively) from the mean. The red circle in the log-abundance curve indicates the regional bloom threshold ($\bar{X} + 2SD$) which acquires 2.2% of the total data. The value of the species bloom threshold in cells L^{-1} is shown in each panel.

South Atlantic Ocean), turned out to be a separate phylogenetic group from other *A. ostenfeldii* strains in the World Seas (Guinder et al., 2018). Similarly, the detection of azaspiracid-2 (AZA-2) and *Azadinium luciferelloides* as the potential producer in highly abundant blooms of Amphidomataceae in El Rincón area (Tillmann and Akselman, 2016), or the first detection of yessotoxins in plankton samples and the confirmation of their production by strains of *Protoceratium reticulatum* isolated from the San Jorge Gulf (Akselman et al., 2015) were the result of the application of advanced analytical techniques in this field.

Apart from the anthropogenic factors biasing the knowledge of the occurrence of HAB species and associated phycotoxins, climate-related changes in the ocean such as more frequent extreme storms and marine heatwaves, and shifts in the intensity of ocean currents, together with co-occurring eutrophication and pollution, may have led to more frequent and severe outbreaks of HABs in coastal areas along with a higher concern and monitoring efforts to alert about these events (Griffith and Gobler, 2020; Trainer et al., 2020; Anderson et al., 2021). In this regard, the recent detection of novel toxic species in the Patagonian Shelf, i.e. *Prorocentrum texanum* (Sunesen et al., 2020), or potentially toxic species, i.e. *Pseudo-nitzschia brasiliana* (Almandoz et al., 2017) and *Alexandrium* aff. *minutum* (Fabro et al., 2017) warns about the risk of the potential geographical expansion of HAB species from lower latitudes in response to ocean warming (Bindoff et al., 2019). In particular, the Southwestern Atlantic region has been identified as a warming hotspot where sea surface temperature is increasing faster compared to other regions (Hobday et al., 2016; Risaro et al., 2022), likely driving the southward displacement of the Brazil-Malvinas

Confluence (BMC). Although the data collected here do not allow the detection of geographical changes or to know for certain whether there are new phytoplankton species in the region, the expansion of other marine organisms in the coasts of Uruguay and North of Argentina likely related to warmer surface waters in the SWA (Franco et al., 2020) calls for further investigation on this topic when more observations become available. In a similar latitudinal range in the Pacific Ocean, a poleward shift of the population of *Dinophysis acuta* has been observed in the southernmost regions of the Chilean coast, causing severe impacts on the ecosystems as the only producer of okadaic acid in this region (Díaz et al., 2022).

4.3. Most common phycotoxins and their potential producers in the Patagonian Shelf: LSTs and PSTs

Lipophilic (LSTs) and paralytic shellfish toxins (PSTs) were the most abundant groups of phycotoxins documented in water samples in the Patagonian Shelf over the 40 years of HAB studies. Together, they represented up to 81.5% of all the toxin records. PSTs were essentially associated with *Alexandrium* species in the Argentine Sea, with *A. catenella* as the most abundant (regional bloom threshold ~250,000 cells L^{-1}, Fig. 10) and widely distributed: from La Plata River (~35°S) to the Beagle Channel (~55°S) and from coastal to offshore waters. This is in agreement with the global monitoring of HAB species, where toxic *Alexandrium* species causative of paralytic shellfish poisoning (PSP) have been registered worldwide in coastal ecosystems from tropical to polar regions (Anderson et al., 2012). On a global scale, *A. catenella* has

been the most problematic and probably the most studied HAB species. In Argentina, most records of *A. catenella* were concentrated in the Patagonian Gulfs between 40°S and 47°S. Initially, monitoring efforts in coastal waters focused on this species as it has been responsible of highly toxic outbreaks since the early 80 s. Recurrent blooms of *A. catenella* in austral spring and summer in the Patagonian Gulfs (Esteves et al., 1996; Sastre et al., 2013) and in the Beagle Channel (Carreto et al., 1981; Benavides et al., 1995) were associated with high PSTs accumulation in mussels, and in some cases led to fish, bird, marine mammal, and human mortalities (Carreto et al., 1981; Benavides et al., 1995; Montoya et al., 1996). Likewise, since the first observation of *A. catenella* in the coast of Chile (Guzmán et al., 1975), this species has caused repeated intense blooms, in occasions associated with human fatalities and massive economic losses (Díaz et al., 2019). Conversely, in Argentina, the highest values of PSTs in water samples ($> 500,000$ ng net tow^{-1}) documented in the San Jorge Gulf (Fabro et al., 2018a), were not related with PSP events on marine biota or human health.

Alexandrium ostenfeldii, the other PSTs producing *Alexandrium* species in the Argentine Sea, was documented in plankton samples in relatively low abundances compared to *A. catenella*, and was reported only in northern Patagonia and the Beagle Channel. Further investigation is needed to understand the low population density of *A. ostenfeldii* (regional bloom threshold ~2700 cells L^{-1}, Fig. 10) in the Argentine Sea, as it was notably below the bloom levels in northern European Seas, in the order of 1 to 5×10^6 cells L^{-1} (Kremp et al., 2009; Burson et al., 2014; Van de Waal et al., 2015). This difference may indicate that *A. ostenfeldii* is indeed a low background concentration species in the Southwestern Atlantic Shelf, or that monitoring effort has not been enough to capture short-living extraordinary blooms. In fact, note in Fig. 10 that this species shows the least number of observations in plankton samples, suggesting low prevalence or low monitoring. *A. ostenfeldii* has been associated with PSTs in Patagonian Gulfs (Fabro et al., 2017), El Rincón area and in the shelf-break front (Guinder et al., 2018). However, the strains in Beagle Channel did not produce PSTs, but they were proven to produce spirolides (SPXs; Almandoz et al., 2014). All these recent studies brought light to the different toxin profiles of *A. ostenfeldii* in the Argentine Sea, which differ in the production of PSTs, and also in the production of cyclic imines (CIs): SPXs and gymnodimines (GYMs). In addition, it is worth noting that SPXs have been detected in mussels along the coastline of the Argentine Sea (Turner and Goya, 2015), suggesting that *A. ostenfeldii* may be widely distributed in the pelagic realm, but monitoring efforts in water samples are scarce to evaluate its distribution and potential risk of HAB occurrence. These findings highlight the need to go further in the understanding of strain-specific toxin profiles and toxicity, likely related to species geographical distribution and local environmental and biological conditions (Long et al., 2021; Otero and Silva, 2022). Finally, *Gymnodinium catenatum*, another PST-producing species was documented for the first time in the Argentinian coast in 1962 by Balech (1964), although was first cited as toxigenic species in coastal waters of El Rincón area (Akselman et al., 1998; Montoya et al., 2006; Sunesen et al., 2014), and its toxin profile was characterized only once in a bloom (up to 89,000 cells L^{-1}) in autumn 2003 (Montoya et al., 2006). Certainly, intensified monitoring and more research on ecological aspects are needed to fully assess potential risk of blooms of PST-producing species in the Patagonian Shelf.

Of the historical group of diarrheic shellfish poisoning toxins, here operationally named lipophilic toxins (LSTs), pectenotoxins (PTXs) were the dominant component and were only produced by species of the genus *Dinophysis*, widely distributed in the Argentine Sea. Conversely, the diarrhetic toxins okadaic acid (OA) and dinophysistoxins (DTXs) were rarely found (Fabro et al., 2018a). *D. acuminata* was the most widespread and abundant species, followed by *D. tripos*, essentially restricted to the North Patagonian Gulfs where it reached the highest bloom abundances (Sastre et al., 2018), over the regional bloom threshold of 13,000 cells L^{-1} (Fig. 10). In a similar latitudinal range

along the Chilean coast, PTXs are also the dominant LSTs mainly produced by the prevalent species *D. acuminata* and *D. acuta*, while *D. tripos* is frequently an accompanying species (Díaz et al., 2022). In this region of the Southeast Pacific, *D. acuta* is the most harmful *Dinophysis* species associated with outbreaks of OA and PTXs in shellfish (Díaz et al., 2022). Notably, the association of high abundances of *D. tripos* with PTX-2sa in plankton samples in the Argentine Sea was striking, because PTX-2sa is regarded as a hydrolysis product of PTX-2 in the aquatic environment and in higher trophic levels such as mussels (Otero and Silva, 2022). Nevertheless, this formation path was discarded for many PTX-2sa detections in the Argentine Sea, where it was proposed as synthetized *de novo* by *D. tripos* (Fabro et al., 2015). In addition, even though PTX-2sa is presumably innocuous, it was proven that it can be a good predictor of outbreaks of more severe toxins, like mussel contamination with DTX-1 (Mackenzie, 2019). This reinforces the importance of monitoring strain-specific toxicity at local and regional scales for developing effective early alarm systems, even when some toxins do not directly affect human health but do have negative impacts on ecosystems and their services.

After PTXs, the second most reported LSTs in the Argentine Sea were yessotoxins (YTXs). Two potential YTX-producers reported in the Argentine Sea were *Gonyaulax spinifera* and *Protoceratium reticulatum*, both widely distributed but with relatively low abundances (< 510 and 660 cells L^{-1}, respectively, Akselman, 1996; Fabro et al., 2018b). Only *P. reticulatum* was associated with YTXs in plankton samples (cell quotas between ~2 and 12 pg cell^{-1}) (Akselman et al., 2015; Fabro et al., 2018b), and YTX production was confirmed in strains isolated from the San Jorge Gulf in 2012 (Akselman et al., 2015). *P. reticulatum* was documented in different areas of the shelf between 47°S and 49°S (Antacli et al., 2018) and all along the PSBF in autumn, spring and summer (Akselman et al., 2015; Fabro et al., 2018b) but with low prevalence (11 out of 120 sampled stations in two expeditions). However, abundant cyst beds of this species were found in frontal zones and near La Plata River (Akselman et al., 2015; Antacli et al., 2018), highlighting the relative importance of *P. reticulatum* over other species in its potential to inoculate the water column. *P. reticulatum* is also widely distributed along the coast of Chile (Díaz et al., 2022), where viable cyst beds are located in latitudes between 40 and 48°S, and vegetative cell blooms reach abundances of nearly 400,000 cells L^{-1} with cell quotas of 0.2–0.4 pg YTXs cell^{-1} (Rossi and Fiorillo, 2010). In the Argentine Patagonian Shelf, abundant viable cysts of *P. reticulatum* in plankton and benthic reservoirs, along with the high cell quota of YTXs, warn about the potential risk of harmful blooms of this species in productive areas such as the PSBF.

4.4. Amphidomataceae group and Pseudo-nitzschia spp. in the Argentine sea

Amphidomataceans have been reported from multiple regions since the recent description of *Azadinium* species (Tillmann et al., 2009), including the European North Atlantic, the North Sea and the Mediterranean Sea, the Gulf of Mexico, and the Asian Pacific (see Tillmann, 2018). So far, one of the maximal historical abundances reported globally are from the shelf-break front in the Argentine Sea (between 3×10^6 and 9×10^6 cells L^{-1}), in consecutive extraordinary multi-specific blooms of Amphidomataceae species in spring 1990 and 1991, which caused water discoloration (Akselman and Negri, 2012). *Azadinium luciferelloides* was the dominant blooming species (Tillmann and Akselman, 2016) and no phycotoxin analysis was performed at that time. In contrast, in spring 2015, a multispecific bloom of Amphidomataceae was observed in the same region of the Northern Patagonia Shelf and shelf-break front, and this time azaspiracid-2 (AZA-2) was detected (Tillmann et al., 2019). Although AZAs were detected in mussels in the Argentine Sea some years before their description (Turner and Goya, 2015), the first field survey planned for their detection in plankton samples only began in 2012, followed by other expeditions in 2013,

2015 and 2016 in different seasons (spring, summer and autumn) (Fabro et al., 2019; Guinder et al., 2020; Tillmann et al., 2019). Data showed that Amphidomataceae are particularly abundant in frontal areas. Moreover, in a recent oceanographic cruise "Agujero Azul" in November 2021 onboard the R/V Víctor Angelescu, an extraordinary abundant bloom of Amphidomataceae (up to 5×10^6 cell L^{-1}) was detected in a highly productive area near the PSBF between 44°S and 46°S (unpublished data, see Fig. 4D). This evidence highlights the relevance of studying this group in the Argentine Sea concerning its high abundance (see Fig. 10) and potential to cause severe toxic outbreaks.

Amphidomatacean strains from the North Atlantic produce a wide list of AZA-variants, with AZA-1 as one of the most frequent toxins (Tillmann, 2018). Strikingly, Argentinian strains produce only AZA-2 (e. g. Turner and Goya, 2015; Fabro et al., 2019), suggesting geographical differences in the toxic potential of the populations. For instance, *Azadinium spinosum* is the most important causative agent of AZA poisoning in Europe (Salas et al., 2011) but no toxic events have been registered in Argentina associated with this species (Tillmann et al., 2019) or any other Amphidomataceae. Nowadays, more than 60 different AZAs have been identified (Krock et al., 2019), hence as long as more molecular analogues are discovered, more specific techniques and monitoring efforts are required -especially in underexplored regions. Several cases of human intoxication with AZAs in Europe and the USA have been associated with the consumption of contaminated mussels from Ireland (Twiner et al., 2014). Similarly to the blooms of Amphidomataceans in the PSBF, these dinoflagellates also form blooms in the Irish Sea shelf-break area, which can reach coastal shellfish beds by wind-driven advection (Raine, 2014). Conversely, AZAs in Chile have been detected in bivalves (López-Rivera et al., 2010), but so far *Azadinium poporum* is the only AZA producer reported in Chilean plankton samples, and in low abundance (6800 cells L^{-1}, Tillmann et al., 2017) as compared to populations in the PSBF. Surprisingly, both shelf-break areas of Chile and Argentina are influenced by currents originating in the Southern Ocean (i.e. the Humboldt Current and the Malvinas Current, respectively, running northward as branches of the Circumpolar Antarctic Current). The notable difference in the occurrence of Amphidomataceae blooms in similar latitudes in the Southeastern Pacific and the Southwestern Atlantic calls for further research to assess plankton dispersion and strain-specific toxic potential.

Finally, the most abundant domoic acid (DA) producing *Pseudo-nitzschia* species in the Argentine Sea were *P. pungens, P. australis* and *P. pseudodelicatissima*, followed by *P. fraudulenta* which did not reach regional bloom levels (Fig. 10). These species were most abundant in the North Patagonian Gulfs and the Beagle Channel, and were widely distributed in the shelf and the shelf-break front. These species are a common feature in phytoplankton assemblages in temperate to higher latitudes (Almandoz et al., 2007; 2008; Smith et al., 2018), as virtually high abundances or DA quotas have not been reported in tropical regions. *Pseudo-nitzschia* forms chains of overlapping cells which are easily recognized under light microscopy at the genus level. But their taxonomic characteristics need further examination using electronic scanning microscopy, constraining their identification to the species level in regular phytoplankton surveys. Moreover, different species usually co-occur in nature, which hinders the determination of DA cell quotas. For instance, the highest values of DA in a mixed bloom of *Pseudo-nitzschia* in the Patagonian Gulfs were associated only with the dominant species *P. australis* (Almandoz et al., 2017). Measurements of DA in plankton samples in the Argentine Sea have started in recent years, but so far, no human intoxications have been attributed to this toxin. In contrast, *Pseudo-nitzschia* are of high concern along the coast of California, USA, where blooms of ~500,000 cells L^{-1} (McCabe et al., 2016) -notably lower than the maxima for the Argentine Sea ~6.6×10^6 cells L^{-1} (Esteves et al., 1997) and the regional bloom threshold of *P. pseudodelicatissima* of 2.4×10^6 cells L^{-1} (Fig. 10)- have been associated with severe poisoning events, causing closures of fisheries and massive mortalities of seabirds and marine mammals (McCabe et al.,

2016). *P. australis* and *P. pungens* were the most abundant species responsible for the toxic event. Similarly in Argentina, a massive stranding of the southern right whale (*Eubalaena australis*) in Valdés Peninsula (Wilson et al., 2015) was likely related to the detection of DA in whale feces (D'Agostino et al., 2017), probably after trophic transfer and accumulation of DA through mesozooplankton (D'Agostino et al., 2019). In Chile, *P. australis* and *P. calliantha* are the main producers of DA, causing yearly blooms which sometimes have led to closures in shellfish harvest areas (Díaz et al., 2019). Overall, effects of chronic, low-level exposure to DA on human health could cause mild to severe symptoms (Petroff et al., 2021), suggesting that monitoring of *Pseudo-nitzschia* in plankton samples is crucial as an anticipated measure to ensure seafood safety and consumer protection.

5. Conclusions

This assessment of historical records of shellfish-toxin-producing phytoplankton in the Argentine Sea highlights the high prevalence and widespread occurrence of diverse species along contrasting ecosystems. All these species have shown different degrees of negative impacts on marine biota, ecosystem functioning and human health. Differences seem to be related to strain toxicity and magnitude of the bloom, as well as to seafood exploitation at the local scale and monitoring effort, which affect the human perception of the level of detrimental impacts. Still a large area of the Patagonian Shelf and adjacent open waters in the SW Atlantic Ocean, such as the Patagonian Shelf-Break Front remains underexplored. In this crucial hotspot of productivity, abundant multispecific blooms of Amphidomataceans raise concern for their potential to produce poisoning episodes enhanced by upwelling. In addition, HABs along the PSBF may represent a threat to adjacent regions as they are exposed to strong advection by energetic edge currents. More oceanographic cruises along with more scientific research and social awareness are essential to increase observational data. Moreover, interdisciplinary expeditions are needed to assess physical and biogeochemical conditions underpinning regional blooms and strains toxicity. Scanning surveys for phycotoxins should focus on well-known recurrent HABs in the Argentine Sea and on other phycotoxins and allelopathic compounds not yet reported in the region (e.g. goniodomins produced by *Alexandrium* spp. or novel toxins produced by *Karenia* spp.), but responsible for causing severe outbreaks in other areas of the North Atlantic Ocean or the Southeastern Pacific. Regular phytoplankton monitoring provides an early alarm for the fisheries industry and for avoiding adverse effects on human health by the implementation of mitigation actions. This kind of sampling is complementary to the measurement of toxins in seafood, because it provides information of bloom development, -population density and cell-toxin quota-, and allows their detection even when organisms have not accumulated them yet. The population thresholds proposed here could help to guide future research by reporting also low abundance harmful species that potentially may play a major role under changing environmental conditions, such as global warming or eutrophication. Overall, the comprehensive, quantitative data gathered here provide a holistic picture to compose a regional behavior with relevance at a global scale for further exploration of toxic species biogeography and ecophysiology.

CRediT authorship contribution statement

Fernando J. Ramírez: Data compilation and Curation, Data processing, Visualization, Writing original draft. **Valeria A. Guinder:** Conceptualization, Visualization, Writing original draft, Supervision. **Carola Ferronato:** Data processing, Visualization. **Bernd Krock:** Conceptualization, Visualization, Supervision.

Research Council (CONICET), Argentina [doctoral fellowship to Fernando J. Ramírez]; and the Fund for the Scientific and Technological Research (FONCYT-MINCYT), Argentina [PICT 2016–0830 to Valeria A. Guinder].

Supplementary material

The table **ST1** is a list of all the references used in this assessment for data extraction.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2022.102317.

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