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RESEARCH ARTICLE

# First insights into the distribution and diversity of toxic dinoflagellate cysts in the surface sediments of Dakhla Bay (African Atlantic coast): relationships with environmental factors and mollusk intoxication events

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## Abstract
Dakhla Bay, situated on the African Atlantic coast, has witnessed sporadic harmful algal blooms (HABs) caused by toxic dinoflagellate species over the past two decades. In this study, we investigated the distribution, abundance, and diversity of dinoflagellate cysts, with a focus on potentially toxic species that develop in this ecosystem where such data are lacking. Sediment samples were collected in April 2018 through coring at 49 stations distributed across the bay. The highest abundance of dinoflagellate cysts was recorded at 304 cysts/g dry sediment, observed at the inner part of the bay, indicating that this area is the preferential zone for cyst accumulation. Pearson's tests revealed significant positive correlations ($P < 0.05$) between cyst abundance and the water content, organic matter, and fine fraction (< 63 μm) of the sediment. Cyst morphotypes of potentially toxic dinoflagellate species known to produce saxitoxins, such as *Alexandrium minutum*, *Alexandrium tamarense* species complex, *Gymnodinium catenatum*, and yessotoxins, such as *Lingulodinium polyedrum* and *Gonyaulax* cf. *spinifera*, were identified in the sediment of Dakhla Bay. These findings were further supported by our long-term monitoring period (2005–2018), underscoring the presence of these HAB species in Dakhla Bay. During our survey, sporadic mollusk

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**Highlights**

- The abundance of cysts (with up to 304 cysts/g dry sediment) was significantly and positively correlated with water content, organic matter, and the fine fraction (< 63 μm) of the superficial sediment. These factors are the main drivers of cyst distribution in Dakhla Bay.
- Cyst morphotypes of five potentially toxic species known to produce saxitoxins (*Alexandrium minutum*, *Alexandrium tamarense* species complex, *Gymnodinium catenatum*) and yessotoxins (*Lingulodinium polyedrum* and *Gonyaulax* cf. *spinifera*) were identified in the sediment of Dakhla Bay.
- The long-term monitoring period (2005–2018) of harmful dinoflagellate species confirms the role of cysts in the development of Harmful Algal Blooms (HABs) and the sporadic occurrence of paralytic, lipophilic, and amnesic shellfish poisoning in mollusks.
- *Gambierdiscus* sp. was observed at St43 closed to Dunablanca in the inner part of the Dakhla bay; these genera are often associated to Ciguatera disease.
- This study highlights the usefulness of cyst analysis in assessing the diversity of HAB species and evaluating associated sanitary risks.

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intoxication events were recorded at station PK25 for the grooved razor shell *Solen marginatus* and at station Boutelha for the oyster *Crassostrea gigas*. Paralytic shellfish toxin concentrations exceeded the sanitary threshold (80 µg STX di-HCl eq/100 g of shellfish meat) only twice, in December 2006 and January 2007 at station PK25. Contamination by amnesic shellfish toxins occurred sporadically but never reached the sanitary threshold of 20 µg/g of shellfish meat. Lipophilic shellfish intoxication occurred multiple times in the two investigated areas. These observations suggest that the cysts of the identified HAB species germinated and inoculated the water column, resulting in the observed intoxication events. Relatively low levels of intoxication could be attributed to the moderate abundances of cysts, which may reduce the seeding capacity. This could be explained by the significant interaction of Dakhla Bay with the Atlantic Ocean, characterized by hydrological dynamics that impede the deposition and accumulation of cysts in the bay's sediments. This study reaffirms the importance of investigating dinoflagellate cysts in assessing the diversity of HAB species and evaluating associated sanitary risks.

**Keywords** Dakhla Bay · African Atlantic coast · Dinoflagellate cysts · Mollusk intoxication

## Introduction

Phytoplankton species are the primary producers in aquatic ecosystems and are highly responsive to environmental changes (Liu et al. 2012). Dinoflagellates represent significant constituents of the phytoplankton community in coastal ecosystems. During their life cycle, approximately 10% of dinoflagellate species produce resting cysts capable of withstanding physical, chemical, and biological stressors. The production of these cysts is influenced by various biological and environmental factors, including temperature, salinity, and nutrient availability (De Vernal et al. 2001; Harland 1983; Pospelova et al. 2002; 2005; 2008; Pospelova and Kim (2010); Rochon et al. 1999; Zonneveld et al. 2013). Dinoflagellate cysts could serve as biological indicators of past environmental conditions such as eutrophication (Matsuoka 1999; Marret and Zonneveld 2003; García-Moreiras et al. 2018; Li et al. 2017; 2019; 2020; Sala-Pérez et al. 2020; Rodrigues et al. 2022), pollution loads (Liu et al. 2012; Pospelova et al. 2005; Sætre et al. 1997), and blooms of toxic species (Matsuoka et al. 2003). Cyst assemblages may serve as a tool for forecasting the potential risks associated with harmful algal blooms (HABs) and the occurrence of shellfish intoxication events (Dale 2001; Stock et al. 2007; Satta et al. 2013; Anderson et al. 2014; Tang et al. 2021; Persson et al. 2023). Over 200 dinoflagellate species are capable of producing resting cysts associated with the maintenance, termination, and recurrence of HABs (Shin et al. 2011; Tang and Gobler 2012; Bravo and Figueroa 2014; Mudie et al. 2017; Brosnahan et al. 2019). Dinoflagellate cysts are considered indicators and effective tracers of primary productivity, reflecting changes in the water environment and phytoplankton communities (Dale 2001; Zonneveld and Pospelova 2015; Brosnahan et al. 2019).

Dakhla Bay, located on the Atlantic coast of Morocco, stands as one of the largest bays in Northwest Africa and serves as one of the most productive natural marine areas, offering significant ecological, biological, and socio-economic services (Zidane et al. 2008). This bay holds a pivotal status as the primary national area for shellfish production, notably for the oyster *Crassostrea gigas*, and for harvesting the razor clam *Solen marginatus*. Moreover, it holds recognition as one of the most prominent tourist sites in Morocco. The distinctiveness of Dakhla Bay, characterized by its semi-enclosed nature with one opening to the sea, and its predominance of muddy areas (Anhichem and Benbrahim 2020; El Asri et al. 2018; Zidane et al. 2008; 2017), facilitates the hosting of fine sediments where dinoflagellate cysts could potentially be deposited.

Events involving paralytic shellfish toxins (PSTs) resulting from blooms of the neurotoxic *Gymnodinium catenatum* have been recorded in Moroccan Atlantic waters since 1969, leading to several intoxication incidents. Regrettably, in 1994, these events resulted in the deaths of four individuals in Casablanca (Bourhilli 1982; Taleb et al. 2003; Tber 1983). To safeguard consumers from potential intoxication, phycotoxin and toxic phytoplankton monitoring was established by the INRH (Institut National de Recherche Halieutique: Moroccan National Institute of Fisheries Research) in 1996 along the Mediterranean and Atlantic coasts of Morocco, covering a total of 3500 km. From 1998 to 2016, multiple instances of shellfish contamination with paralytic shellfish toxins (PSTs) were reported in various Mediterranean and Atlantic Moroccan coastal areas, yet no cases of severe human intoxication were reported during this period (Abouabdellah et al. 2008; 2011; Naouli et al. 2018; Rijal Leblad et al. 2020; Aboualaalaa et al. 2022).

The present study offers, for the first time, a comprehensive description of the species composition, distribution, and abundance of resting dinoflagellate cysts in sediments of a Northern African Atlantic ecosystem (Dakhla Bay, Morocco). Additionally, it presents a historical record (2005–2019) of the principal potentially toxic genera and species (*Alexandrium* sp., *Dinophysis* sp., *Gymnodinium* *catenatum*, and *Pseudo-nitzschia* sp.) thriving in the waters of Dakhla Bay and the associated intoxication events caused by PSTs, lipophilic shellfish toxins (LSTs), and amnesic shellfish toxins (ASTs). The main objectives of this study were to assess the spatial distribution, abundance, and diversity of dinocysts throughout Dakhla Bay and to identify the primary environmental parameters influencing their distribution.

Additionally, we aimed to investigate the long-term temporal variations of the main harmful toxic phytoplankton species in relation to PST, LST, and AST intoxication events in shellfish at two monitored stations: one associated with *Solen marginatus* harvesting (PK25) and the other with *Crassostrea gigas* cultures (Boutelha). Such data are currently lacking in Northern African Atlantic marine ecosystems and are therefore crucial for understanding the global spread of toxic dinoflagellates and the seeding capabilities of their cysts. These events are significant in the context of global warming and increasing anthropogenic activities.

## Materials and methods

### Study area

The Moroccan Atlantic coast in Northwest Africa boasts several lagoons, estuaries, and bays with significant potential for aquaculture development. Dakhla Bay (23° 35′ N and 16° W) is an embayment situated along the Atlantic coast of southern Morocco. Stretching 37 km in length and with a width ranging between 10 and 12 km, the bay features depths varying from 6 to 20 m (Orbi et al. 1995). Renowned as the primary national area for shellfish production, particularly of the Pacific oyster *Crassostrea gigas*, Dakhla Bay ranks among the largest natural bays in Northwest Africa. It is situated in a region characterized by a typical desert climate. However, Dakhla Bay experiences significant oceanic influence, primarily due to interactions between the cold Canary current and subtropical ridge currents (Orbi et al. 1999). Currents within Dakhla Bay are bidirectional and can be very strong, reaching intensities of 1 m/s near the bay's inlet and surrounding area during spring tides (Hilmi et al. 2017). The study area is separated from the Atlantic Ocean by the peninsula of Oued Ed-Dahab and is naturally divided into three sections: the outer, central, and inner bays. Bathymetry gradually increases from both shores toward the middle of the bay, reaching depths of 20 m (Orbi et al. 1995). Classified as a site of biological and ecological interest under the Protected Areas Master Plan of Morocco, Dakhla Bay has been recognized as a RAMSAR site (wetland of international importance) since 2005 (RAMSAR 2016). The upwelling, resulting in nutrient-rich waters, is confined to the western boundary of Dakhla Bay.

### Sediment, phytoplankton collection, and environmental parameter measurements

The sampling was conducted from the 10$^{th}$ to the 16$^{th}$ of April 2018 using a cylindrical plastic core sampler (47 cm long, 5 cm wide). Forty-nine stations covering the entire bay were randomly sampled (Fig. 1), with three replicates taken for each station. The surface layer of the sediment cores (3 cm) was sliced out and kept at 4 °C until analysis. Physicochemical parameters of the water column, including temperature (°C), salinity, pH, and dissolved oxygen (mg/l), were measured in the sub-surface of the water column (− 50 cm) using a multiparametric probe (HANNA Hi 9829). The concentrations of nitrites ($NO_2^-$), nitrates ($NO_3^-$), and phosphates ($PO_4^{3-}$) were determined by chemical analysis following the seawater analysis method described by Aminot and Chaussepieds (1983).

### Cyst extraction and identification

For their quantification, resting dinoflagellate cysts were isolated from the sediment fractions using a gradient density method with Ludox CLX, following the procedures outlined in Genovesi et al. (2007) and Yamaguchi et al. (1995), utilizing 1 g of sediment. The concentrated cysts were then examined in a sedimentation chamber using an inverted photonic microscope (Leica DM IRB), with photographs taken at × 40 magnification. Cyst identification was conducted following the guidelines provided by Matsuoka and Fukuyo (2000) and the works of Mudie et al. (2017), Zonneveld et al. (2013) and Zonneveld and Pospelova (2015).

### Phytoplankton analysis

Seawater samples were collected from the water column during the high tide period using polyethylene bottles. Phytoplankton samples were fixed with Lugol's solution (final concentration 1% v/v). Subsequently, the samples were allowed to settle for 24 h following the Utermöhl method (Utermöhl, 1958). Species identification and enumeration were conducted utilizing an inverted photonic microscope (Leica DM IRB). Algal taxa were identified referencing various keys provided by Balech (1988), Dodge (1982, 1985), Sournia (1986), and Tomas et al. (1996). Microphytoplankton abundances were expressed as cells per liter (cells/l).

### Mollusk intoxication events

In the framework of the RSSL (Réseau de Surveillance de la Salubrité du Littoral: Coastal Health Monitoring Network)

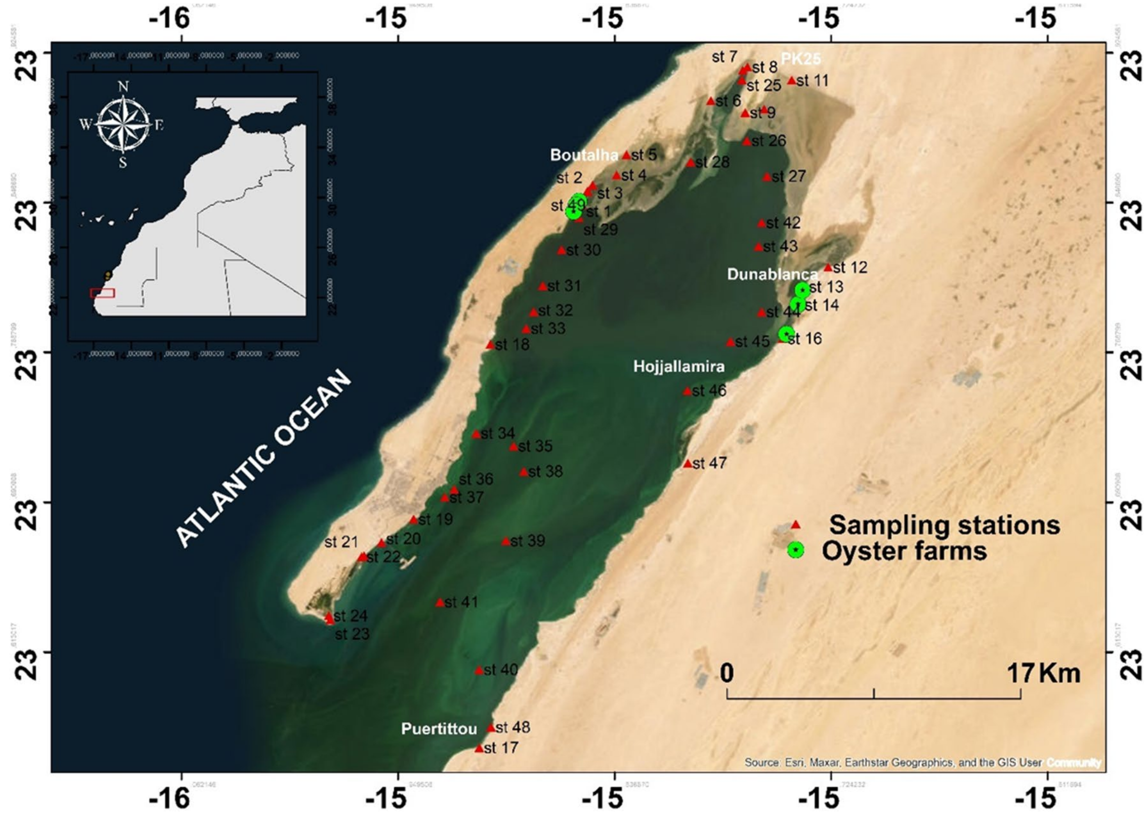



**Fig. 1** Study area and location of sampling stations (ST1 to ST49) in Dakhla Bay (Southern Morocco, African Atlantic Ocean). Sampling stations of phytoplankton (PK25, Boutalha, Dunablanca, Hojjamira) corresponding to culture and harvesting of mollusks

survey, oysters *Crassostrea gigas* and razor clams *Solen marginatus* were sampled every 2 weeks at the Boutalha GH and PK5 stations, respectively. Mollusk samples were placed in a cooler with ice blocks until they reached the laboratory. The samples were then processed for AST, PST, and LST analyses.

### Amnesic shellfish toxin (domoic acid) analysis

The concentrations of domoic acid (DA) were determined by high-performance liquid chromatography (HPLC). The instrumental setup (Shimadzu 10vp type) included a SCL-10vp controller, a LC-10ADvp quaternary pump, a CTO-10vp column oven, a SIL-10ADvp autosampler, a SPD-M10Avp photodiode array detector, a Vydac C18 column (250 × 4.6 mm, with 5 µm), and a guard cartridge (Vydac C18, 5 µm). DA analysis was conducted monthly and during periods of high *Pseudo-nitzschia* abundance (> $10^5$ cells/l). It was measured in the whole meat of the sampled mollusks following Quilliam's (1995) protocol.

Analyses in triplicate were performed using approximately 100 g of shellfish meat (ten to fifteen individuals were required to obtain such an amount of meat). After being shredded and homogenized, 4 g of meat was added to 16 mL of solvent extraction (methanol–water, 1:1) and homogenized (Ultra Turrax for 3 min at about 10,000 rpm). The homogenate was centrifuged at 4000 rpm for at least 10 min to obtain the supernatant. The latter was analyzed under the following chromatographic conditions: mobile phase flow rate of 1 ml/min, detector wavelength of 242 nm, injection volume of 20 µl, and an oven temperature for the column of 40 °C. The DA contents of the samples were determined with a detection limit of 0.3 µg/g.

### Paralytic shellfish toxin intoxication analysis using bioassays

Analyses of PST toxicity were conducted using the mouse bioassay method outlined in the AOAC method (1990). Briefly, 100 g of homogenized mollusk tissues was mixed with 100 ml of 0.1 M hydrochloric acid and boiled for 5 min; the pH was then adjusted to 2–3, and the sample was centrifuged for 15 min at 3000 rpm. One milliliter of the supernatant was injected intraperitoneally into three 20-g albino mice. The reported values are expressed in µg STX di-HCl Eq. /100 g of mollusk meat.

### Lipophilic shellfish poisoning analysis

The analyses of lipophilic toxins (including okadaic acid, pectenotoxin, and azaspiracid group toxins) were conducted by extracting these toxins from shellfish samples using acetone and dichloromethane (DCM). The extracts were then washed with dichloromethane and water. After evaporation of the DCM, the resulting residue was solubilized with a 1% solution of tween 60. One milliliter of the extract was injected into the intraperitoneal cavity of Suisse albino mice weighing between 19 and 21 g. A positive result was indicated by the death of two or three mice injected with the solution during a 24-h observation period. These analyses were performed following the method outlined by EURLMB (EU Harmonised SOP MBA Lipophilic Version 4, Vigo, Spain).

## Sediment analyses

### Water contents

The water contents were determined after drying subsamples of 20 g at 100 °C for 7 days until all the water was evaporated. The water contents were then calculated using the following formula:

$$H_2O\% = \frac{[Ww - \mathrm{Wd}]}{Ww} * 100$$

Ww = wet weight, Wd = dry weight.

As suggested by Cho and Matsuoka (2001), the cysts were expressed as cysts per gram of dry sediment using the following formula: Cysts/g DS = Cysts/g of wet sediment/[1- (water content/100)].

### Organic matter contents

To determine the organic matter (OM) contents of the sediments, subsamples of 20 g were dried at 450 °C for 12 h. The resulting dry samples were weighed and the new dry weight (Wd1) was recorded. The percentages of OM were calculated using the following formula, as outlined by Byers et al. (1978).

OM %= $\frac{[Wd - \mathrm{Wd1}]}{Wd1} * 100$

### Granulometry

For the grain size analyses, 100 g of sediment samples from the 49 stations were dried at 40 °C for 48 h and then sieved through meshes ranging from 2 mm to 63 µm. The grain size distributions were obtained using the method described by Bellair and Pomerol (1977).

**Table 1** Environmental parameters of the water column in Dakhla Bay measured at the sampled stations (ST1 to ST41) during April 2018

| Environmental variables | Minimum | Maximum | Mean ± SD |
|---|---|---|---|
| Temperature (°C) | 16 | 21 | 19.58 ± 0.94 |
| Salinity | 35 | 41 | 38.51 ± 1.39 |
| $O_2$ (mg/l) | 5.1 | 10.96 | 8.33 ± 1.16 |
| Ph | 7.5 | 8.56 | 7.95 ± 0.2 |
| $NO_2^-$ (mg/l) | 0.03 | 0.46 | 0.05 ± 0.09 |
| $NO_3^-$ (mg/l) | 0.2 | 9.90 | 0.47 ± 1.39 |
| $PO_4^{3-}$ (mg/l) | 1.99 | 6.2 | 2.70 ± 0.92 |

## Data analysis

### Diversity indices

The species diversity of the dinocysts was assessed through the Shannon–Wiener diversity index (H′) (Shannon and Wiener 1949) according to the following formula:

$$H' = -\sum S_i = 1\ p_i\ log\ 2p_i$$

where $S$ is the total number of cyst taxa recorded in the sample (species richness) and $p_i$ is the proportion of each cyst taxon in the sample.

The species characteristics for Dakhla Bay were examined among the taxa identified in the samples using indicator species analyses (Dufrêne and Legendre 1997). The indicator value ($I_{nd}V_al$) of each species was tested using a randomization test with 10,000 permutations. Threshold of $I_{ND}V_{AL} \geq 25\%$ and $p < 0.05$ were used as a cutoff for the indicator species (Dufrêne and Legendre 1997).

To evaluate spatial variations of cyst densities (Sokal and Rohlf 1981), Pielou's evenness ($J'$) (Pielou 1966) was calculated.

### Statistical analyses and mapping procedures

The correlations between sediment characteristics (water and OM contents, fine sediment fractions), environmental parameters (temperature, salinity, pH, dissolved oxygen, and nutrients), and cyst abundances were tested using Pearson's correlation coefficient and principal components analyses (PCA). The statistical analyses were conducted using R Core (2017). Prior to the analyses, normality was verified, and the data were log-transformed when necessary. The maps were created in ArcGIS 10.4.1 using an inverse distance weighting (IDW) method for interpolation.

## Results

### Environmental conditions

The physico-chemical characteristics of the water columns from the 49 stations sampled during April 2018 are summarized in Table 1. Salinity varied from 41 at St4, St6, St10, and St13 to 35 at St25, progressively increasing from downstream to upstream. The highest temperature (21 °C) was recorded at St10 and St12, while the lowest (16 °C) was recorded at St28; temperature followed the same increasing gradient as salinity. pH oscillated between 7.50 and 8.56. The waters of Dakhla Bay were well oxygenated, with dissolved oxygen ranging between 5.70 and 10.96 mg/l. Nitrite concentrations varied between 0.03 and 0.46 mg/l, while nitrate fluctuated from 0.20 to 9.90 mg/l. Phosphate contents exhibited significant variability, with a maximum recorded at St20 (6.2 mg/l) and a minimum of 1.99 mg/l at stations 1, 2, 3, 4, and 5. The water percentages of the sediment samples were also heterogeneous (mean 25.10 ± 17.48%) and peaked at a maximum of 72.78% at St32 (Fig. 2a). OM contents ranged from 0.25 to 9.15%, with maxima observed in the center and north of the bay (Fig. 2a). Granulometry varied from sandy (upstream) to sandy-silt or silt (downstream) (Fig. 2b).

### Dinoflagellate cyst assemblages and distribution

The dinoflagellate cyst densities ranged between 0 and 304 cysts/g DS, with an average of 17.55 cysts/g DS (Fig. 3). The highest density was recorded at station 27 in the PK25 zone, which is surveyed by the monitoring program as it is exploited for razor clam *S. marginatus* harvesting. The species richness of the cysts ranged from 0 to 13 at St43 near the oyster park. The highest cyst diversity index (H′ = 2.65) was recorded at the same station. Pielou's evenness index ranged from 0 to 0.99, with an average of 0.85, indicating relative stability of dinoflagellate assemblages in the study area.

Eighteen cyst morphotypes belonged to four orders: Gonyaulacales (six species), Peridiniales (seven species), Gymnodiniales (three species), and Thoracosphaerales (two species) (Fig. 4). The cyst assemblages were dominated by a few species (Fig. 5): *Lingulodinium polyedrum* (38.33%); *Protoperidinium* sp. (17%); *Scrippsiella trochoidea* (14%); *Gonyaulax spinifera* (5.33%); *Gymnodinium catenatum* (3.33%); and *Alexandrium minitum* (2%). According to the indicator species analysis (IndVal) (Table 2), five dinoflagellate cyst assemblages characterized Dakhla Bay. The cyst density distribution map shows two areas with the highest cyst densities. The first one is

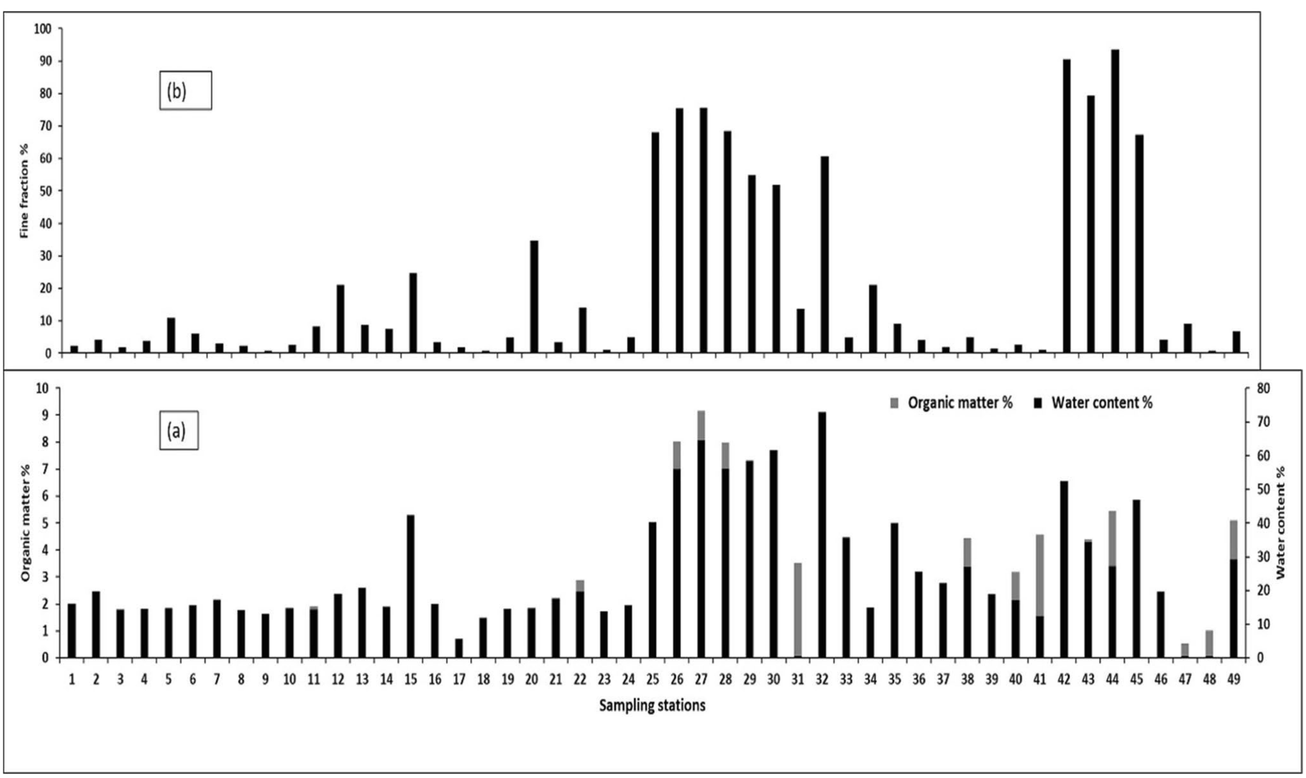



**Fig. 2** Spatial distribution in percent (%) of water content (**a**), organic matter (**a**), and fine fraction (**b**) in the superficial sediment of the sampling stations in Dakhla Bay (April 2018)

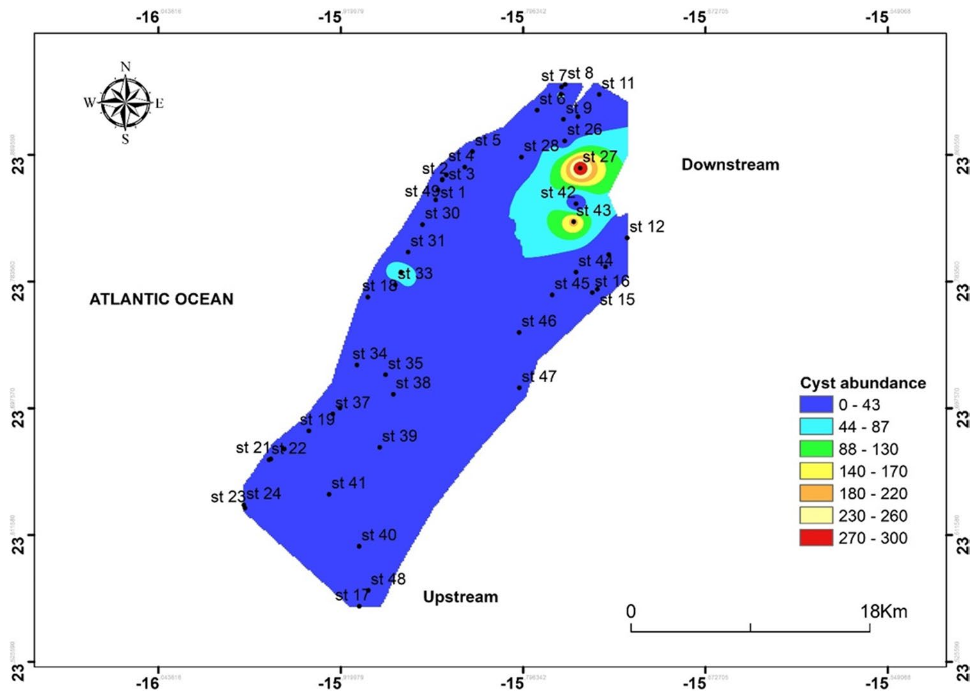



**Fig. 3** Spatial distribution of resting cysts and their abundance (RC/g dry sediment) in the superficial sediment of Dakhla Bay (St, station)

located in the northern part of the lagoon, St43 with 190 cysts/g DS, near an important oyster farm (Dunablanca), and the second one at St27 with 304 cysts/g DS, located in the PK25 zone where razor clams are harvested (Fig. 3).

## Distribution of harmful dinoflagellate species

Among the 18 dinoflagellate morphotypes of cysts detected in the surface sediments of Dakhla Bay (Fig. 5), five are considered to be potentially toxic. Specifically, the *A. tamarense* species complex, *A. minutum*, and *G. catenatum* are known as PST producers (Anderson et al. 2012; Rijal Leblad et al. 2020), while the *G. spinifera* complex and *L. polyedrum* have been shown to cause toxic blooms in the Northern Adriatic Sea (Pistocchi et al. 2012). Among these, *L. polyedrum* cysts dominated the assemblages in the sediments of Dakhla Bay.

## Relationships between dinocyst assemblage descriptors and environmental variables

The abundance of dinocysts showed significant and positive correlations with the following sediment characteristics: OM ($r = 0.54$; $p < 0.05$), water content ($r = 0.50$; $p < 0.05$), and fine fractions (0–63 µm) ($r = 0.52$; $p < 0.05$). The PCA revealed that the density of dinocysts was significantly correlated with these sediment characteristics (Fig. 6). Axes 1 and 2 of the PCA accounted for 51.4% of the correlation between dinocyst densities and the aforementioned sediment characteristics. No correlation was observed between cyst distribution and the measured physicochemical characteristics of the water column (temperature, salinity, pH, $O_2$, nutrients).

## Phytoplankton diversity during the sampling period (April 2018)

During our study (in situ sampling performed at April 2018), the microphytoplankton community consisted of three groups, namely diatoms with 35 species, which comprised the dominant taxa (between 51 and 98%) (Fig. 7; Supplementary Table 1), followed by dinoflagellates (1.49 to 40.24%), and finally silicoflagellates (0 to 8.66%). The microphytoplankton abundance ranged from 1400 to 28,520 cells/l. The inventory of dinoflagellates showed the presence of 21 species dominated by *Prorocentrum micans* (37%), *Scrippsiella trochoidea* (24%), and *Alexandrium* sp. (20%). The potentially toxic species found in Dakhla Bay were *Alexandrium* sp. (including *A. minutum* and *A. tamarense* species complex) with up to $5.76 \times 10^3$ cells/l; *Dinophysis* sp. (maximum of 100 cells/l), *Pseudo-nitzschia* sp. (maximum of $2.9 \times 10^3$ cells/l), *Gymnodinium catenatum* (maximum of 200 cells/l), *Gambierdiscus* sp. (maximum of 40 cells/l), *Lingulodinium polyedrum* (maximum of 40 cells/l), and *Gonyaulax spinifera* (maximum of 40 cells/l) (Supplementary Table 1).

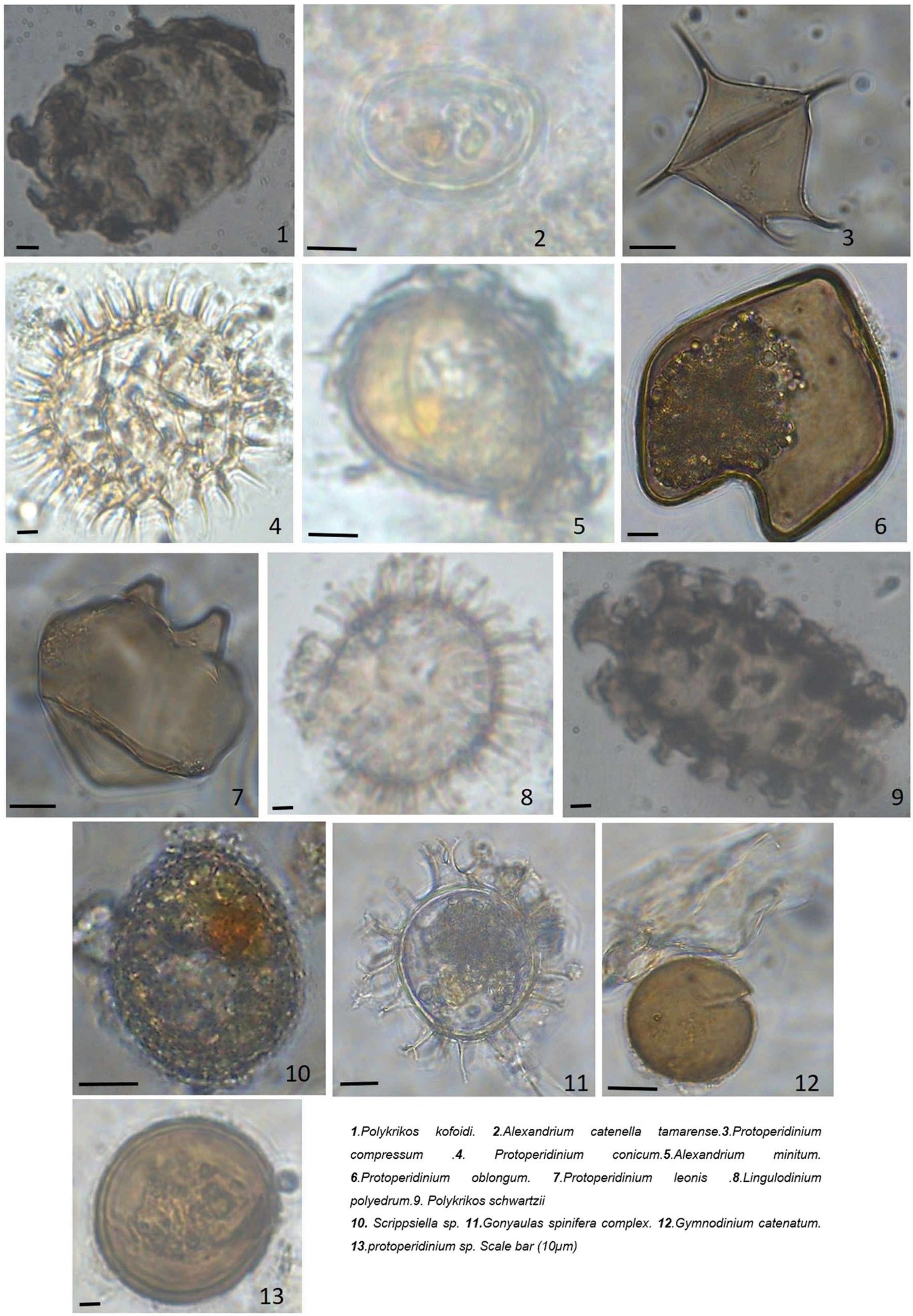



**Fig. 4** Photographs taken by a light microscope of cyst morphotypes collected from superficial sediment in Dakhla Bay, Morocco

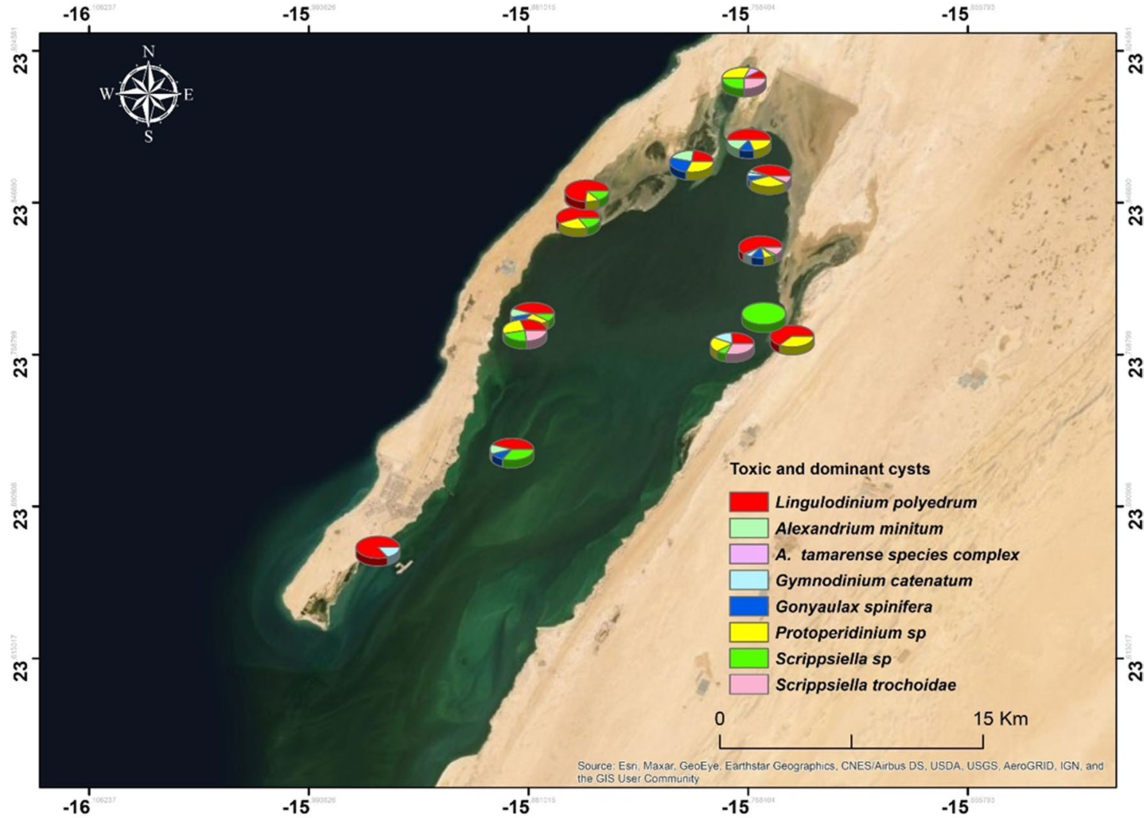



**Fig. 5** Spatial distribution of the main and potentially toxic dinoflagellate species, identified by morphotype cysts in the superficial sediments of Dakhla Bay (April 2018)

**Table 2** Cyst indicator species for Dakhla Bay based on indicator values (IndVal ≥ 25%). Codes of significance **0.01, *0.05

| Species | IndVal | *P* value |
|---|---|---|
| *Protoperidinium* sp. | 65.7 | 0.003** |
| *Lingulodinium* sp. | 63.6 | 0.009** |
| *Scrippsiella* sp. | 60.0 | 0.002** |
| *Scrippsiella trochoidea* | 49.0 | 0.019* |
| *Alexandrium minitum* | 44.7 | 0.048* |

## Long-term variations of HAB species and intoxication events of bivalves from 2005 to 2018

Several potentially toxic dinoflagellate species were identified along with the neurotoxic diatom *Pseudo-nitzschia* sp. at Dakhla Bay during the long-term monitoring period. Species belonging to the *Alexandrium* genus (*A. minutum*, *A. tamarense* species complex) dominated the surveyed stations (Fig. 8) from 2005 to 2018, except at the Hojjalamira station (Fig. 8). The second most represented genera were *Dinophysis* and *Gymnodinium*. Other recorded noxious dinoflagellates included *L. polyedrum*, *Protoperidinium* sp., *and Gonyaulax* sp. *Alexandrium* species were detected in seawater during all the PST events from 2005 to 2018 at PK25 and Boutelha, suggesting that species of this genus could have been related to the observed PST intoxication of the mollusks (Figs. 9, 10). The other species that may have been related to the PST intoxication included *G. catenatum*, which reached concentrations of up to 10,000 cells/l at PK25 in 2009.

The PST concentrations at PK25 exceeded the sanitary threshold by double on the 1st of November 2006 with 118.5 µg STX di-HCL eq/100 g mollusk meat and on the 1st of December 2006 with 238 µg STX di-HCL eq/100 g. This corresponded to *Alexandrium* cell density of 49,400 cells/L, which was the maximum density registered during the 2003–2019 survey (Figs. 9, 10). In the Boutelha GH zone, the PST levels never exceeded the sanitary threshold in *C. gigas* but twice registered significant values of 42 and 53 µg STX di-HCL eq/100 g of mollusk meat on December 1st, 2006, and January 1st, 2007, with *Alexandrium* cell densities of 18,800 cells/l and 7160 cells/l, respectively.

*Dinophysis* species, which are usually associated with LSTs, were present in all surveyed areas of Dakhla Bay, with a more frequent presence in Hojallamira and Puertito (Fig. 10). Lipophilic shellfish toxins were detected several

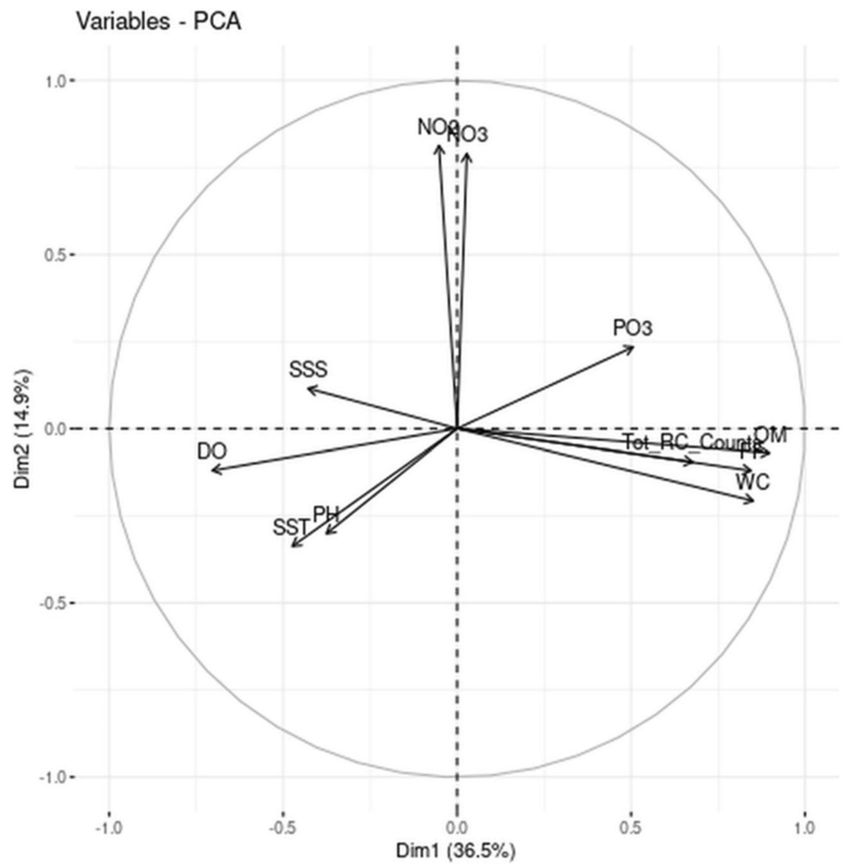



**Fig. 6** Principal component analysis (PCA) applied to dinocyst density (TRC counts) and the environmental factors (T temperature, Sal salinity, DO dissolved oxygen, pH, WC water content, FF fine fraction, OM organic matter). Nutrients: $NO_2^-$, $NO_3^-$, $PO_4^{3-}$ (axes F1 and F2 = 51.4%)

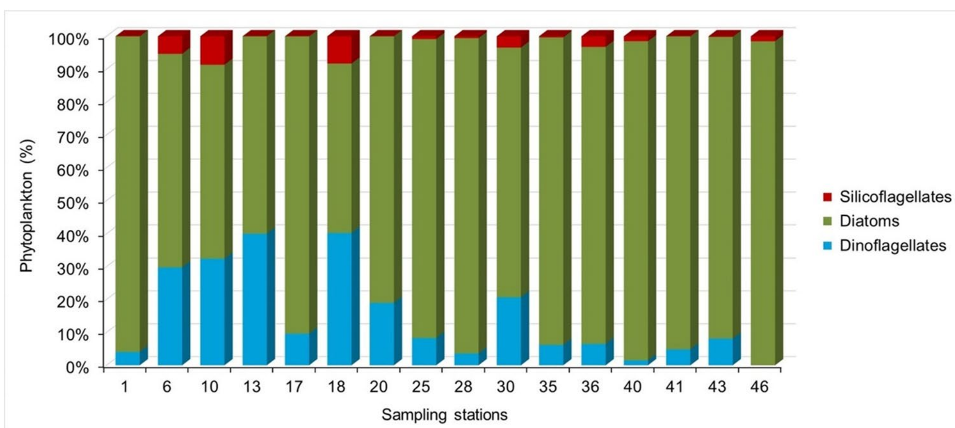



**Fig. 7** Distribution of the main taxonomic groups of phytoplankton in the water column of Dakhla Bay during the sampling period of April 2018

times in October–November 2013, November 2016, and March 2017, mainly in the PK25 area (in the razor clam *S. marginatus*) and in Boutalha GH (in the oyster *C. gigas*) (Table 3). The lipophilic intoxication of the mollusks in Dakhla Bay was likely due to the presence of *Dinophysis* species in the water column in 2005, 2006, 2014, and 2017, with concentrations of up to 79,040 cells/l on the 1st of November 2017 at Boutelha. At PK25, the maximum concentration was 13,400 cells/l, registered on the 1st of December 2005. At Boutelha, *C. gigas* were intoxicated (positive mouse bioassay test) only seven times sporadically during the entire survey period from 2005 to 2018.

*Pseudo-nitzschia* species were present at all stations but reached concentrations exceeding $2 \times 10^6$ cells/l and $5 \times 10^6$ cells/l at Boutelha and PK25, respectively, on the 1st of March 2014. At Boutelha GH, the levels of ASTs were below the sanitary threshold (20 µg DA/g mollusk meat) during the entire survey. The maximum registered value in this area was 5.32 µg DA/g mollusk meat on the 1st of March 2014 when *Pseudo-nitzschia* species were

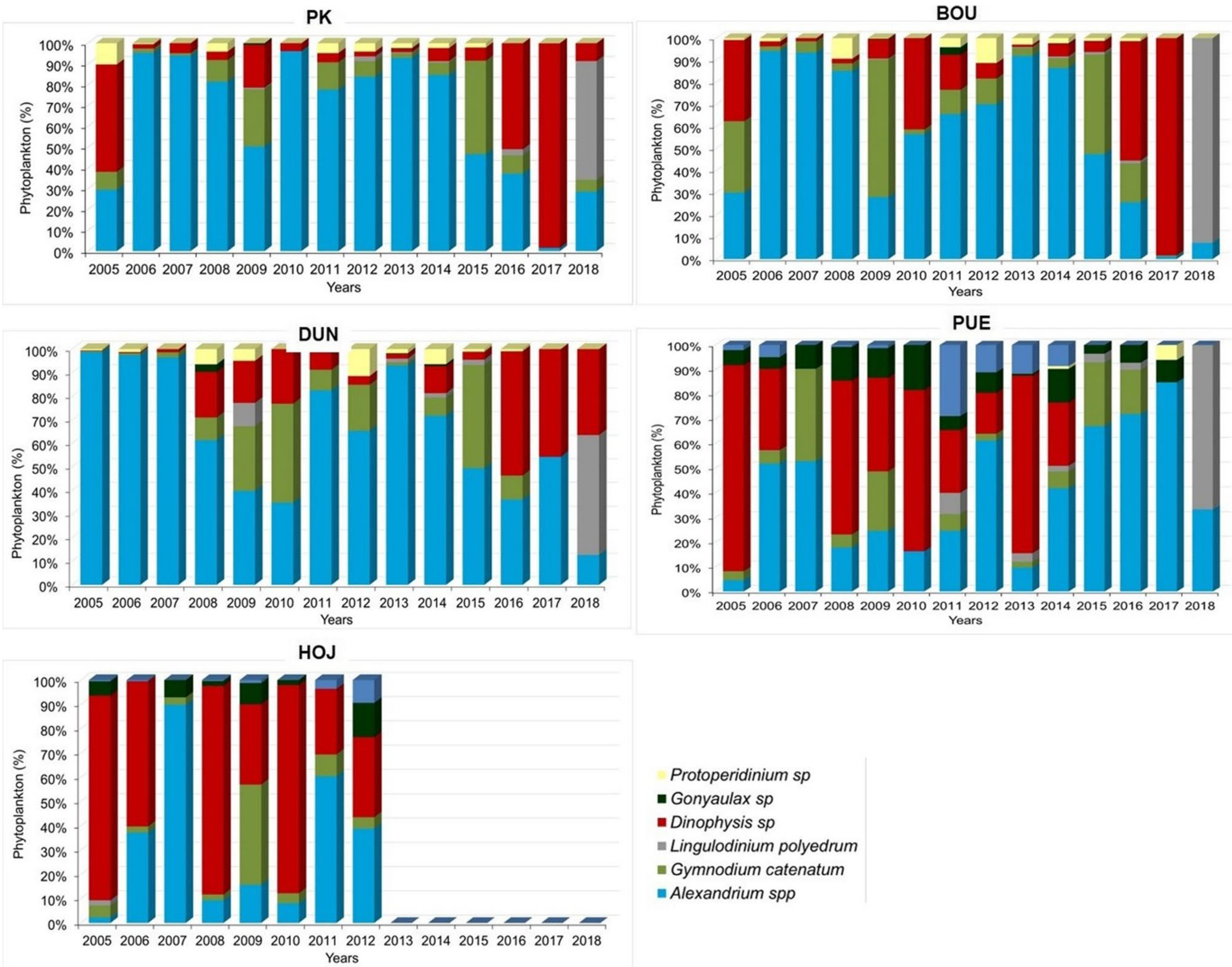



**Fig. 8** Temporal variations of potentially toxic phytoplankton species in Dakhla Bay from 2005 to 2018 at PK25 (PK), Boutalha (BOU), Dunablanca (DUN), Puertittou (PUE), and Hojjallamira (HOJ). Phytoplankton monitoring at Hojjallamira ended in 2013

observed with the highest densities. Similarly, the AST values measured at PK25 were below the sanitary threshold during the whole survey period with concentrations not exceeding 4.98 µg DA $g^{-1}$ measured in *S. marginatus* on the $1^{st}$ of August 2008 (Fig. 10).

## Discussion

This study represents the first investigation into dinoflagellate cysts in surface sediment from a large bay on the African Atlantic coast. The measurements conducted enabled the assessment of the distribution, abundance, and diversity of dinoflagellate cyst species in the southern Atlantic, where such data are previously unrecorded (Joyce et al. 2005; Holzwarth et al. 2007; Chaira et al. 2021). The findings indicate that cyst densities in Dakhla Bay are moderate compared to other ecosystems, as detailed in Table 4. Cyst densities did not surpass 304 cysts/g of dry sediment (DS), and were significantly lower than those reported for other semi-confined areas, such as Izmir Bay in Turkey with up to 9944 cysts/g DS (Aydin et al. 2015), Daya Bay in the South China Sea with up to 819 cysts/g DS (Li et al. 2019), and Bizerte Lagoon in Tunisia with up to 20,000 cysts/g DS (Fertouna-Bellakhal et al. 2014; Zmerli-Triki et al. 2017).

However, the cyst abundances in Dakhla Bay are comparable to those observed in other lagoon ecosystems, such as Ghar El Melh Lagoon (Mediterranean, Tunisia) with up to 229 cysts/g DS (Dhib et al. 2016), Oualidia Lagoon (Atlantic coast, Morocco) with up to 293 cysts/g DS (Chaira et al. 2021), Mellah Lagoon (Algeria) with up to 315 cysts/g DS (Draredja et al. 2020), and Cabras Lagoon in Sardinia (Italy) with up to 287 cysts/g wet sediments (WS) (Satta et al. 2014). Nevertheless, cyst densities in Dakhla Bay exceeded those found in Homa Lagoon

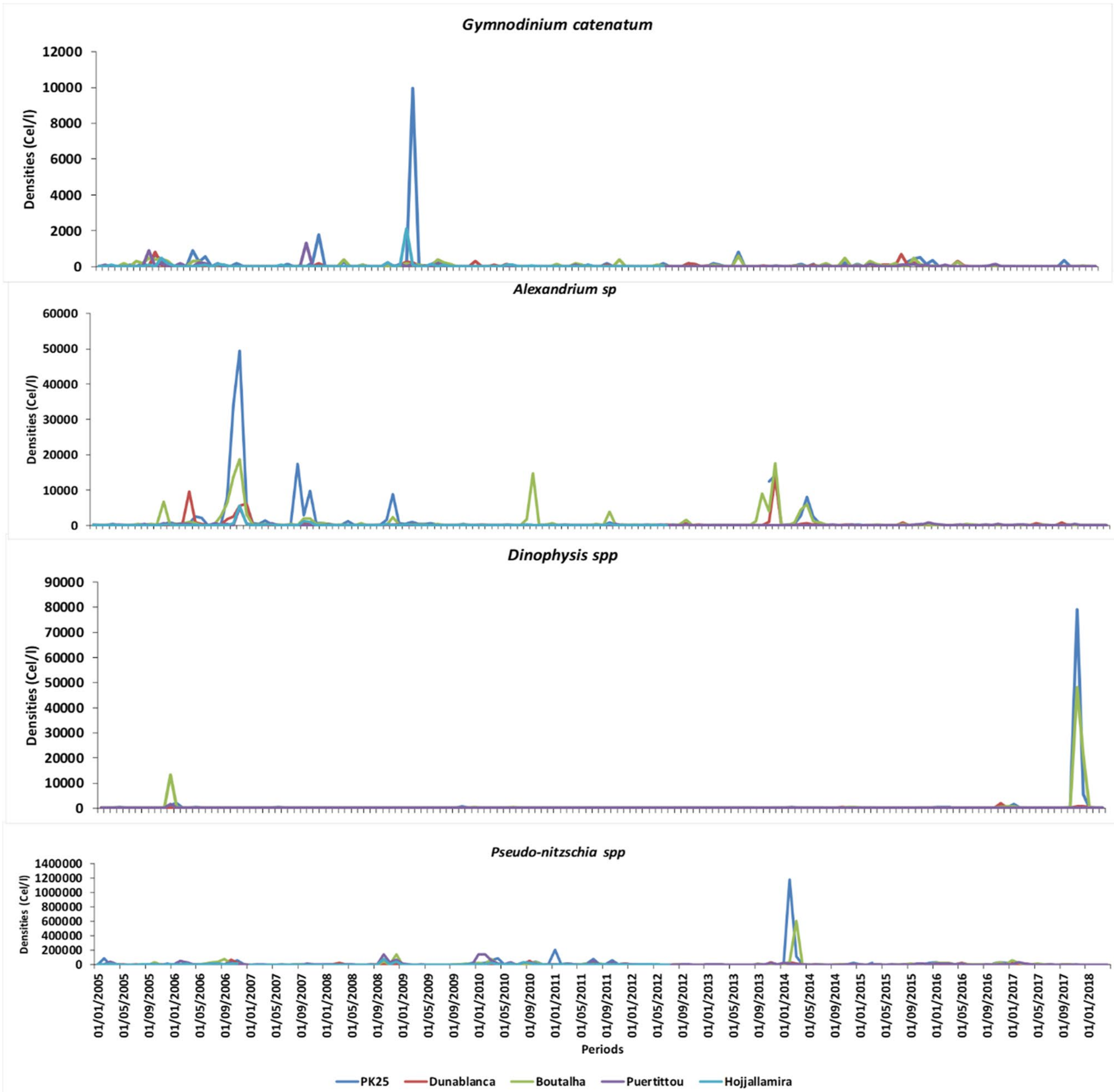



**Fig. 9** Temporal variations of potentially toxic dinoflagellates, including *Gymnodinium catenatum*, *Alexandrium* sp., *Dinophysis* sp., and *Pseudo-nitzschia* sp., observed in Dakhla Bay from 2005 to 2018 at PK25 (Pk), Boutalha GH (Bo), Dunablanca (Dun), Puertittou (Puer), and Hojjallamira (Hoj). The data were provided by the RSSL monitoring network of toxic phytoplankton species. Monitoring in Hojjallamira ended in 2013

(Turkey) with up to 71 cysts/g WS (Aydin et al. 2014) and Boughrara Lagoon (Tunisia) with up to 132 cysts/g DS (Keskes et al. 2020). The wide range of dinoflagellate cyst abundances along the western boundaries of the African subcontinent, varying from 139 to 75,000 cysts/g DS (Table 4), is attributed to the intensive upwelling characteristic of this region (Targarona et al. 1999; Sprangers et al. 2004; Holzwarth et al. 2007).

In the Mediterranean Sea, high cyst abundances have been attributed to factors such as river plumes and eutrophic coastal waters (Aydin et al., 2011; Elshanawany et al. 2010; Fertouna-Bellakhal et al. 2014). To a certain degree, the moderate abundance of dinocysts in Dakhla Bay may be attributed to the timing of sampling in April, which likely coincides with a spring bloom when cysts are recruited from the sediments. Additionally, the considerable openness of

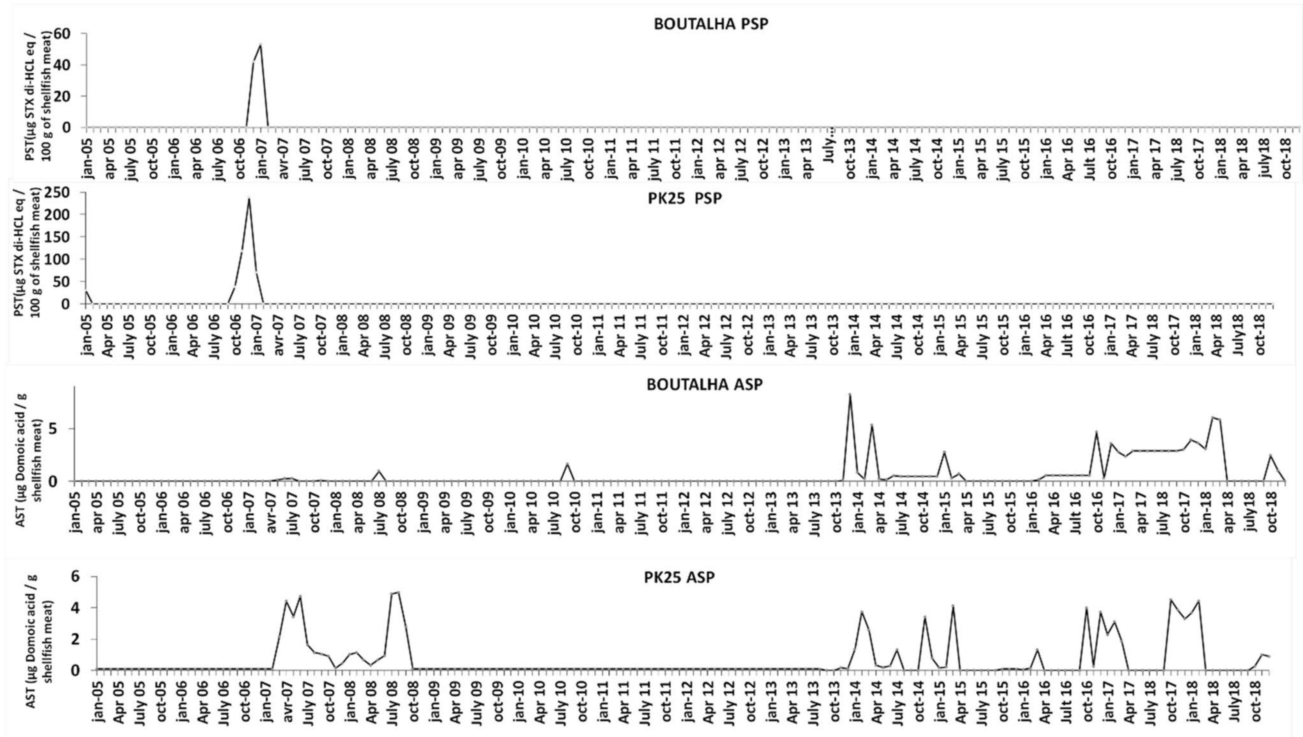
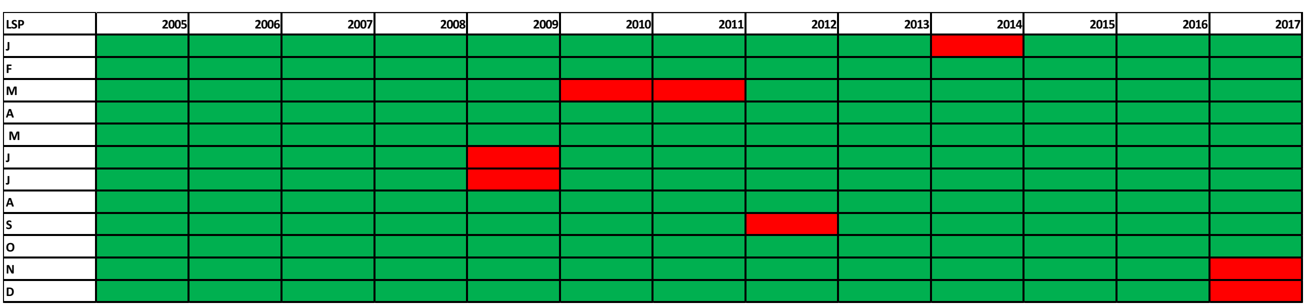



**Fig. 10** Temporal variations in the concentrations of the amnesic shellfish toxin, domoic acid (µg DA/g of shellfish meat), and paralytic shellfish toxins (µg STX di-HCl eq/100 g of shellfish meat) measured in the oyster *Crassostrea gigas* cultivated at Boutelha GH and in the razor clam *Solen marginatus* harvested at PK25, Dakhla Bay (Atlantic Ocean, Morocco)

**Table 3** Events of positive mousse bioassay for lipophilic shellfish toxins in the razor clam *Solen marginatus* harvested in PK25 and in the oyster *Crassostrea gigas* cultivated in Boutalha, Dakhla Bay (Atlantic Ocean, Morocco)




Boutalha

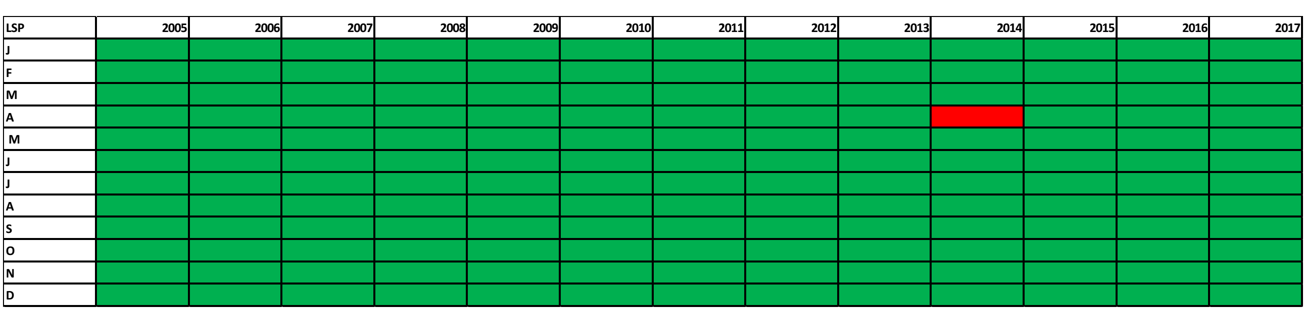


**Table 4** Summary data on dinoflagellate cyst densities observed in various marine ecosystems worldwide, sourced from the literature. Key: *DS* dry sediment, *WS* wet sediment

| Location | Country | Density | Reference |
|---|---|---|---|
| Mediterranean | | | |
| Ghar El Melh Lagoon | Tunisia | 0–229 cysts/g DS | Dhib et al. (2016) |
| Bizerte Lagoon | Tunisia | 0–20000 cysts/g DS | Fertouna-Bellakhal et al. (2014) |
| Boughrara Lagoon | Tunisia | 65–132 cysts/g DS | Keskes et al. (2020) |
| Homa Lagoon | Turkey | 15–71 cysts/g DS | Aydin et al. (2014) |
| Arenys de Mar. Harbor | Spain | 480–10679 cysts/cm$^3$ WS | Satta et al. (2010) |
| Olbia Gulf | Italy | 20–5484 cysts/cm$^3$ WS | Satta et al. (2010) |
| Syracuse Bay | Italy | 43–828 cysts/g DS | Rubino et al. (2010) |
| Cabras lagoon | Italy | 46–287 cysts/g DS | Satta et al. (2014) |
| Santa Giusta Lagoon | Italy | 144–2317 cysts/g DS | Satta et al. (2014) |
| Corru S'Ittiri Lagoon | Italy | 61–1072 cysts/g DS | Satta et al. (2013) |
| Thau Lagoon | France | 16–234 cysts/g DS | Genovesi et al. (2013) |
| Izmir Bay | Turkey | 41–3292 cysts/g DS | Aydin et al. (2011) |
| Mellah lagoon | Algeria | 1–315 cysts/g DS | Draredja et al. (2020) |
| Asia | | | |
| Bolinao | Philippines | 31–1484 cysts/g DS | Baula (2011) |
| Manila Bay | Philippines | 30–793 cysts/g DS | Azanza et al. (2004) |
| Sunda Shelf | China | 86–817 cysts/g DS | Kawamura (2004) |
| Daya Bay | China | 400–13000·cysts/g DS | Wang et al. (2004) |
| Daya Bay | China | 79–819 cysts/g DS | Li et al. (2019) |
| Tokyo Bay | China | 240–8380 cysts/g DS | Matsuoka et al. (2003) |
| Sishili Bay | China | 122–1322 cysts/g DS | Liu et al. (2012) |
| Southern coast | Korea | 173–1276 cysts/g DS | Shin et al. (2011) |
| Visakhapatnam harbor | India | 11–1218 cysts/g DS | D'Silva et al. (2013) |
| Bengal Bay | India | 0 to 1660 cysts/g DS | Uddandam et al. (2017) |
| Gulf of Thailand and East Coast of Peninsular Malaysia | | 12–56 cysts/g DS | Lirdwitayaprasit (1997) |
| Ambon Bay | Eastern Indonesia | up to 12,000 cysts/g DS | Likumahua et al. (2021) |
| Pacific Ocean | | | |
| Northeastern Pacific Ocean | Thailand/Malaysia | 100–35000 cysts/g DS | Pospelova et al. (2008) |
| Vancouver Island Atlantic Iberian Margin | Canada | 154–113,483 cysts/g DS | Radi et al. (2007) |
| Atlantic Ocean | | | |
| Gullmar Fjord, | Sweden | 4000–7000·cysts/g DS | Harland et al. (2006) |
| Saldanha Bay | South Africa | 0–366 cysts/ml sediment | Joyce et al. (2005) |
| North Canary Basin | NW Africa | 139 to 75 000 cysts/g DS | Targarona et al. (1999) |
| Oualidia lagoon | Morocco | 0–293 cysts/g DS | Chaira et al. (2021) |
| Dakhla Bay | Morocco | 0–304 cysts/g DS | Present study |

Dakhla Bay to the ocean, coupled with the presence of muddy sediments predominantly in the inner part of the bay, suggests that the hydrodynamic and sedimentary conditions may not favor extensive cyst deposition. Furthermore, a long-term survey (2005–2018) of dinoflagellates, particularly *Alexandrium*, *Gymnodinium*, and *Lingulodinium*, which produce the cysts found in Dakhla Bay's sediments, revealed that the densities of vegetative cells were moderate compared to other ecosystems. This could explain the observed moderate densities of cysts in our study area. The spatial distribution of dinoflagellate cysts in Dakhla Bay highlights two regions with the highest densities (Fig. 3). The first is located at St27 in the PK25 area, and the second at St43 near the Dunablanca area, adjacent to a large oyster farm, with cyst densities reaching up to 304 cysts/g DS and 190 cysts g DS, respectively. These regions are positioned in the inner part of the bay, characterized by weak hydrodynamics (Hilmi et al. 2017). The abundance of dinocysts demonstrated a significant positive correlation ($p < 0.05$) with muddy sediments (< 63 µm) and high levels of water and organic matter (OM) content. These findings align with previous research on dinoflagellate cysts in sediment, which has underscored the relationship between cyst abundances and sediment characteristics (Anderson et al. 2005; Anglès et al. 2010; Gayoso 2001; Genovesi et al. 2013; Horner et al. 2011; Joyce et al. 2005; Yamaguchi et al. 1996).

The presence of dinoflagellate cysts in sediments is influenced by several environmental factors, including the proportion of fine particles in the sediment (typically ranging from 20 to 50 µm), the organic matter content, and the hydrodynamics of the marine area where the cysts are deposited (Harland et al. 2006; Fertouna-Bellakhal et al. 2015; Casabianca et al. 2020; Nogueira et al. 2022; Rodríguez-Villegas et al. 2021; Balaji-Prasath et al. 2022; Salgado et al. 2023). Dinoflagellate cysts behave similarly to fine silt particles (Dale 1983), and previous studies have demonstrated correlations between dinoflagellate cysts and sediment mud content, particularly with particles not exceeding 63 µm in size (Yamaguchi et al. 2002). The fine fraction of sediments in coastal areas is significantly influenced by hydrodynamics (Fertouna-Bellakhal et al. 2014; Li et al. 2019, 2020; Zmerli-Triki et al. 2014). In confined bays and lagoons, water currents significantly influence the spatial distribution and abundance of cysts (Genovesi et al. 2013; Joyce et al. 2005; Matsuoka and Fukuyo 2000). Hilmi et al. (2017) noted that the hydrodynamics and water circulation in Dakhla Bay are primarily driven by tides and winds. The currents within Dakhla Bay exhibit a bidirectional flow, with particularly strong intensity near the bay's inlet and surrounding areas, reaching speeds of up to 2 m/s during spring tides. In contrast, during neap tides, the current intensity diminishes to less than 0.6 m/s, particularly in the central and northern regions of the bay, where the highest cyst densities (≥ 190 cysts/g DS) were observed.

The long-term monitoring (2005–2018) of potentially toxic phytoplankton species in the mollusk-rearing and harvesting areas of Dakhla Bay, conducted by the INRH, demonstrated the recurrent but sporadic development of species from the *Alexandrium*, *Gymnodinium*, *Dinophysis*, and *Pseudo-nitzschia* genera, which were likely responsible for the observed PSTs, LSTs, and AST intoxications of bivalves (Fig. 10). Potentially neurotoxic *Alexandrium* species exhibited significant spatial and temporal variations without any increasing trend from 2005 to 2018 (Fig. 9). The recorded densities of *Alexandrium* reached up to 2500 cells/l in May and June of 2006, with a peak of 208,000 cells/l observed in December 2005. Abouabdellah (2018) demonstrated a correlation between the presence of *A. minutum* in the waters of Dakhla Bay and shellfish toxicity incidents in the PK25 area. Furthermore, Abouabdellah (2012) reported that mouse bioassay tests conducted on shellfish revealed intoxication events occurring only in December 2006 and January 2007. During this period, *S. marginatus* was intoxicated for 5 weeks (≥ 1215 µg STX di-HCL eq/kg of fresh meat), with PST levels exceeding the established sanitary threshold (INRH, 2012–2017). Our survey also identified another PST-producing species, *G. catenatum*, exhibiting moderate densities and a single peak of $10^4$ cells/l in 2009 in the PK25 area. Over the past decade, *G. catenatum* has been associated with severe intoxication events (up to 13,000 µg STX di-HCL eq/kg of shellfish meat, which is 16 times higher than the established sanitary threshold) affecting cockles (*Acanthocardia tuberculata*) in the western Mediterranean, even at moderate densities (Rijal Leblad et al. 2020; Aboualaalaa et al. 2022). Furthermore, Abouabdellah (2012) reported that mouse bioassay tests conducted on shellfish during December 2006 and January 2007 revealed intoxication events. During this period, the razor clam *S. marginatus* experienced intoxication for 5 weeks, with PST levels exceeding 1215 µg eq STX di-HCL eq/kg of fresh meat, surpassing the established sanitary thresholds (INRH, 2012–2017). Our survey also identified another PST-producing species, *G. catenatum*, exhibiting moderate densities with a peak density of 104 cells/; in 2009 in the PK25 area. Over the past decade, *G. catenatum* has been linked to severe intoxication events affecting cockles in the western Mediterranean, even at moderate cell concentrations (Rijal Leblad et al. 2020; Aboualaalaa et al. 2022).

Lipophilic shellfish toxin (LST) intoxication events were more frequent than those related to PSTs and ASTs in Dakhla Bay, as shown in Fig. 10. *Dinophysis* species, commonly associated with LSTs, were present at all surveyed stations, with notable concentrations at Hojallamira and Puertito (Fig. 10). In 2017, the maximum concentrations of *Dinophysis* cells reached 80,000 cells per liter. Intoxication events involving ASTs occurred in 2007 and 2008, persisting throughout both years. There was no evident correlation between the densities of *Pseudo-nitzschia* and AST intoxication events; notably, a significant bloom of this neurotoxic diatom occurred in 2014 at PK25 and Dunablanca, with concentrations reaching $10^6$ cells/l, yet no intoxications of the exploited mollusks were recorded during this event. During our survey, *Gambierdiscus* sp. was observed at St43 closed to Dunablanca in the inner part of the bay (Supplementary Table 1). Many species of this genera produced ciguatoxins which cause Ciguatera (CG) poisoning (Litaker et al. 2010). Several outbreaks of CG have been reported in the central northeast Atlantic Ocean (Canary Islands) (Pérez-Arellano et al. 2005) not far from Dakhla.

## Conclusion

This study represents the first investigation of dinocyst assemblages in relation to the environmental characteristics of a bay on the Western African Atlantic coast. We identified the presence of 18 dinocyst species, exhibiting a relatively high species diversity (2.65) and evenness index (0.99), which indicates the relative stability of the dinoflagellate assemblages. The total cyst densities varied from 0 to 304 cysts/g of dry sediment (DS) and displayed clear spatial variations, with densities increasing from the mouth of the bay toward its central and northern parts. Our findings enhance the understanding of the diversity and abundance of cyst-producing dinoflagellates. Notably, the diversity of cysts in the sediments corresponded with that of dinoflagellate species in the water column, underscoring the crucial role of deposited cysts in initiating and sustaining algal blooms in Dakhla Bay.

The relatively low levels of PSTs, LSTs, and ASTs in the shellfish at the two investigated stations in Dakhla Bay could be attributed to the moderate abundances of cysts, which reduce the seeding capacity of HAB species. This situation may arise from the bay's extensive exposure to the Atlantic Ocean, whose hydrological dynamics could impede the deposition and accumulation of cysts in the bay's sediments, except in its inner regions. This study underscores the value of cyst investigations in assessing the diversity of HAB species and in evaluating the sanitary risks associated with HABs.

Monitoring programs should incorporate studies of cyst communities as an early warning system for HABs. These studies can also support precautionary management policies aimed at preventing harm to human health and mitigating economic losses in aquaculture farms. Future research in the Bay of Dakhla will include conducting cyst germination experiments to obtain vegetative cells. Monoclonal cultures of potentially toxic species will be established, enabling ribotyping, characterization of toxin profiles, and ecophysiological studies that are crucial for understanding their population dynamics.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11356-024-34451-y.

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**Author contribution** Karima chaira: investigation, data curation, formal analyses, writing.

Hassan Rhinane: project administration.

Btissam Ennaffah: conceptualization, project administration.

Mina Dellal: phytoplankton analyses.

Rachid Abouabdellah: toxins analyses.

Sanae Ammari: phytoplankton analyses.

Fatima zohra Bouthir: data acquisition.

Reqia Sagou: phytoplankton and toxins analyses.

Samir Benbrahim: funding acquisition.

Anas Yassir: data acqusition.

Hinde Abdelouahab: statistics.

Estelle Masseret: data analyses, writing.

Mohamed Laabir: conceptualization, supervision, project administration, funding acquisition, writing.

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## Declarations

**Ethical approval** Hereby, I Mohamed Laabir and co-authors consciously assure that for the manuscript "First insights into the distribution and diversity of harmful dinoflagellate cysts in the surface sediments of Dakhla Bay (African Atlantic coast): Relationships with environmental factors and mollusc intoxication events," the following is fulfilled:

1) This material is the authors' own original work, which has not been previously published elsewhere.
2) The paper is not currently being considered for publication elsewhere.
3) The paper reflects the authors' own research and analysis in a truthful and complete manner.
4) The paper properly credits the meaningful contributions of co-authors and co-researchers.
5) The results are appropriately placed in the context of prior and existing research.
6) All sources used are properly disclosed (correct citation). Literally copying of text must be indicated as such by using quotation marks and giving proper reference.
7) All authors have been personally and actively involved in substantial work leading to the paper, and will take public responsibility for its content.

The violation of the Ethical Statement rules may result in severe consequences.

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I agree with the above statements and declare that this submission follows the policies of Solid State Ionics as outlined in the Guide for Authors and in the Ethical Statement.

10 October 2023, Montpellier.

Mohamed Laabir, PhD.

**Consent to participate** This study is not concerned by this statement.

**Consent for publication** All authors consent to publish their data in the submitted study of Chaira et al.

**Competing interests** The authors declare no competing interests.

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