Seasonal hotspots and offshore accumulation of phycotoxins in a subtropical semi-enclosed bay: Insights from Qinzhou Bay, Beibu Gulf

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Abstract

Phycotoxins produced by harmful algae pose increasing risks to coastal ecosystems and aquaculture activities, yet their dynamics in subtropical semi-enclosed bays remain poorly understood. In this study, the spatiotemporal distribution, composition, and potential sources of phytoplankton-associated phycotoxins in Qinzhou Bay (South China Sea) were investigated based on monthly surveys from November 2021 to November 2022. Both paralytic shellfish toxins (PSTs) and lipophilic marine toxins (LMTs) were widely detected, with GTX analogues, pectenotoxin-2 (PTX2), and homo-yessotoxin (hYTX) as dominant components. Toxin occurrence showed pronounced seasonality, with higher prevalence in May and June. Spatially, elevated toxin levels were consistently observed in open waters outside the bay, suggesting that hydrodynamic conditions favor the accumulation of toxigenic phytoplankton. Combined morphological and molecular analyses identified *Alexandrium* spp. and *Gymnodinium* sp. as key PST producers, whereas *Dinophysis* and *Protoceratium reticulatum*, *Gonyaulax spinifera*, and *Lingulodinium polyedra* were identified as potential sources of LMTs. The decoupling between toxin occurrence and cell abundance highlights the importance of improving sampling strategies and identification methods for toxigenic dinoflagellates. These results reveal distinct seasonal windows and offshore hotspots of phycotoxin occurrence and provide a critical baseline for future monitoring and risk management in aquaculture-dominated coastal systems.

Keywords: harmful algal blooms; phycotoxin; paralytic shellfish toxin; lipophilic marine toxin; Beibu Gulf

1. Introduction

Coastal eutrophication and the increasing occurrence of harmful algal blooms (HABs) have become major environmental challenges in marine ecosystems worldwide, raising growing concerns about ecological risks and seafood safety (Anderson et al., 2002; Griffith and Gobler, 2020). Qinzhou Bay, located in the northern Beibu Gulf of the northwestern South China Sea, represents a typical coastal system undergoing rapid environmental change under increasing anthropogenic pressure. This semi-enclosed bay encompasses the Maowei Sea, receives substantial nutrient inputs from multiple rivers, including the Maolingjiang, Qinjiang, and Dalanjiang rivers, which may promote terrestrial inputs and enhance primary productivity in coastal waters. In recent decades, intensified human activities, such as coastal development and aquaculture expansion, have further altered the regional biogeochemical conditions. As a consequence, the frequency, spatial coverage, and ecological impacts of HABs in Beibu Gulf have increased significantly (Xu et al., 2019), making it an emerging hotspot of HAB occurrence in the South China Sea.

As an important aquaculture regions in the Beibu Gulf, Qinzhou Bay supports extensive mariculture activities, particularly shellfish farming in intertidal and nearshore regions (Chen et al., 2011; Zhang et al., 2022). The northern Maowei Sea with high-intensity aquaculture activities has undergone continuing changes in the marine environment and marine ecosystem (Gu et al., 2015; Li et al., 2017; Zheng et al., 2012). During which, the occurrence of HABs and associated phycotoxins in such regions is of particular concern, as toxin-producing phytoplankton can directly affect aquaculture organisms and lead to toxin accumulation in seafood. It has been reported that paralytic shellfish toxins (PSTs) in shellfish from the Beibu Gulf have occasionally exceeded regulatory limits, posing potential risks to seafood safety and human health (Xu et al., 2021b). Therefore, elucidating the occurrence and dynamics of phycotoxins in this aquaculture-dominated region is critical for both ecosystem management and aquaculture sustainability.

To date, research on HABs in the Beibu Gulf has mainly focused on bloom-forming species of *Phaeocystis globosa*, with studies addressing bloom mechanisms (Cheng et al., 2023; Zhu et al., 2023), phytoplankton community structure (He et al., 2023; Wang et al., 2021), and historical bloom records (Xu et al., 2019). Additionally, it should be noted that several toxigenic dinoflagellates, including *Alexandrium*, *Ostreopsis*, and *Gambierdiscus*, have been identified in Beibu Gulf (Gu et al., 2022; Xu et al., 2021a), suggesting the potential for diverse toxin production. Investigations on phycotoxins have primarily focused on bivalve mollusks and phytoplankton in Beibu Gulf, during which multiple lipophilic toxin groups, such as gymnodimine (GYM), pectenotoxin 2 (PTX2), homo-yessotoxin (homo-YTX), 13-desmethyl-spirolide-C (SPX), azaspiracid 2 (AZA2), and neurotoxins domoic acid (DA), have been detected (Ji et al., 2022, 2026; Liu et al., 2020).

Despite these advances, the current understanding of phycotoxin dynamics in the semi-enclosed bay remains incomplete. The existing studies in the South China Sea have focused on toxin occurrence in open sea region of Beibu Gulf (Ji et al., 2026) and Daya Bay (Jiang et al., 2017; Liu et al., 2021a, b), providing limited insight into the toxin profiles and spatiotemporal dynamics in the coastal region. Therefore, a comprehensive investigation into the spatio-temporal dynamics of phycotoxins is urgently needed in this important aquaculture region. Furthermore, the linkage between toxigenic phytoplankton assemblages and toxin composition has not been systematically resolved, constraining the ability to identify key toxin-producers and to interpret spatiotemporal variability in toxin dynamics. Given that phytoplankton represent the original source of marine phycotoxins, a comprehensive investigation of phytoplankton-associated toxins is essential. The results would enable a more mechanistic understanding of toxin production, distribution patterns, and their ecological implications in this region.

Addressing these issues, the present study conducted a year-round investigation of phycotoxins in phytoplankton communities in Qinzhou Bay. Net-concentrated phytoplankton samples were collected during monthly cruises from November 2021 to November 2022, and multiple toxin groups, including PSTs and lipophilic marine phycotoxins (LMTs), were analyzed using liquid chromatography–tandem mass spectrometry (LC–MS/MS). In addition, potential toxin-producing species were identified through a combination of morphological identifications and high-throughput sequencing approaches. This study provides the first year-round, phytoplankton-based assessment of phycotoxins in Qinzhou Bay. The findings from this study will provide new insights into their spatiotemporal dynamics and supporting future risk assessment and monitoring strategies in this important aquaculture bay region.

2. Materials and methods

2.1 Study area and sample collection

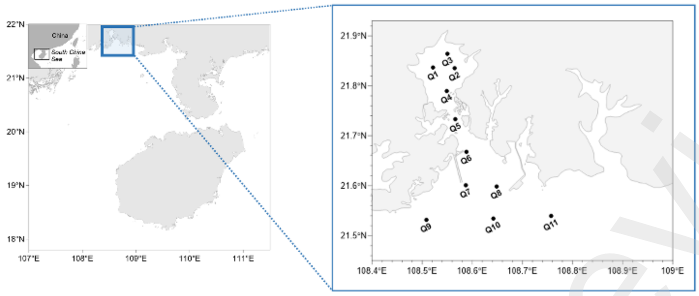

Figure 1. Illustration of the study region with sampling sites in Beibu Gulf. Monthly investigations were carried out from November 2021 to November 2022.

Field investigations were conducted in Qinzhou Bay, located in the northern Beibu Gulf of the South China Sea (108.52–108.76°E, 21.53–21.84°N). A total of ten cruises were carried out from November 2021 to November 2022, covering multiple sampling sites inside and outside the bay (Fig. 1).

Phytoplankton samples for toxin analysis and morphological identification were collected by concentrating approximately 200 L of subsurface seawater (~3 m depth) using a plankton net (20 µm mesh size). The concentrated phytoplankton was subsequently filtered onto 1.2 µm glass-fiber filters (GF/C, Whatman) and stored at −20 °C until analysis. Samples for morphological identification were preserved with Lugol's iodine solution and kept in the dark until examination.

For molecular analysis, a total of 2 L of surface seawater were prefiltered through a 200 µm mesh and subsequently filtered onto 0.4 µm polycarbonate membranes (Millipore, USA) at each site. The filters were immediately stored at −80 °C prior to

DNA extraction and sequencing analysis.

2.2 Reagents and standards

Certified reference standards of PSTs and LMTs were obtained from the National Research Council Canada (NRC, Canada). Individual toxin standards, including gonyautoxins (GTXs), decarbamoyl gonyautoxins (dcGTXs), saxitoxin (STX) and its analogues (dcSTX and NEO), and N-sulfocarbamoyl toxins (C-toxins) for PSTs, as well as okadaic acid (OA), dinophysistoxins (DTXs), pectenotoxins (PTXs), gymnodimine (GYM), yessotoxins (YTXs), azaspiracids (AZAs), and cyclic imines (CIs) for lipophilic phycotoxins, were used for identification and quantification.

HPLC-grade methanol, acetonitrile, and ammonium hydroxide used in this study were purchased from Merck (Darmstadt, Germany). HPLC-grade formic acid and acetic acid were obtained from Macklin Biochemical (Shanghai, China). Ultrapure water was produced using a Milli-Q water purification system (Milli-Q Reference, Millipore, USA). Solid-phase extraction cartridges, including Supelclean LC-18 (3 mL, Supelco, USA) and Strata-X (60 mg, Phenomenex, USA), were used for sample purification.

2.3 Toxin analysis

2.3.1 Analysis of paralytic shellfish toxins

PSTs were extracted and analyzed based on previously reported methods with minor modifications (Lin et al., 2022). Briefly, phytoplankton samples were extracted using 0.05 M acetic acid and sonicated for 5 min (100 W, 50% pulse duty cycle). The extracts were subsequently purified using octadecyl-bonded silica solid-phase extraction cartridges (Supelclean LC-18, 3 mL, Supelco, USA), which were preconditioned with methanol followed by ultrapure water. PSTs were eluted with water and subjected to instrumental analysis.

Chromatographic separation was performed using an Ultimate 3000 HPLC system (Thermo Fisher Scientific, USA) coupled with a QTRAP 4500 mass spectrometer (AB Sciex, Germany). A TSK-gel Amide-80 column (250 mm × 2.0 mm, 5 μm; Tosoh Bioscience, USA) was used for separation. The detailed elution method was referred to Lin et al. (2022). Mass spectrometric detection was conducted in positive electrospray using multiple reaction monitoring (MRM) mode.

2.3.2 Analysis of lipophilic marine toxins

LMTs were extracted and determined following previously described procedures with slight modifications (Liu et al., 2017). Briefly, phytoplankton samples were extracted with methanol and purified using Strata-X solid-phase extraction cartridges (60 mg, Phenomenex, USA) to reduce matrix interference. The raw extract was diluted to approximately 30% (v/v) methanol with Milli-Q water and loaded into the cartridge, then washed with 3 mL of methanol/water (20:80, v/v). The cartridge was dried under vacuum for 1 min, then eluted with methanol containing 0.3% (v/v) ammonium hydroxide. The purified extracts were filtered through 0.22 μm membrane before analysis.

Instrumental analysis was carried out using an Ultimate 3000 HPLC system (Thermo Fisher Scientific, USA) coupled with a QTRAP 4500 mass spectrometer (AB Sciex, Germany). Chromatographic separation was achieved on a Waters

XBridge C18 column (150 mm × 3.0 mm, 3.5 μm) with a corresponding guard column. Multiple toxins were detected in both positive and negative electrospray ionization modes using MRM.

2.4 Identification of toxigenic species

2.4.1 Morphological identification

Phytoplankton samples preserved with Lugol's iodine solution were examined using an inverted optical microscope (Axiovert, Zeiss, Germany) at 400× magnification. Species identification was conducted based on morphological characteristics following established taxonomic references. Particular attention was given to potentially toxigenic genera, including *Alexandrium*, *Gymnodinium*, *Dinophysis, Protoceratium*, and *Gonyaulax*. Cell abundance was estimated for each species.

2.4.2 High-throughput sequencing and bioinformatic analysis

Total genomic DNA extraction, sequencing, purification and bioinformatic analysis of filtered phytoplankton samples were performed using previously described methods (Chen et al., 2019). The V4 region of the 18S rRNA gene was amplified using a pair of specific primers from eukaryotes, and sequencing was performed on an Illumina platform.

Raw sequencing data were processed using standard bioinformatic workflows. Paired-end reads were merged, quality-filtered, and clustered into operational taxonomic units (OTUs) at a 97% similarity threshold. Based on the annotation results, phytoplankton operational taxonomic units (OTUs) assigned to the parasitic dinoflagellates were excluded. Representative sequences were taxonomically assigned against a reference database using a naïve Bayesian classifier.

The relative abundance of phytoplankton taxa was calculated based on sequence reads, with particular emphasis on toxigenic groups. The combined use of molecular and morphological approaches allowed for a more reliable identification of potential toxin-producing species in the study area.

2.5 Statistical analysis

Mass spectrometry data were processed using Analyst 1.6.2 and MultiQuant 3.0. Distribution patterns of phycotoxin components were processed with Surfer 13 (Golden Software, USA). Linear correlation analysis was performed using GraphPad Prism 9.0 (GraphPad Software, USA) and R software (version 4.2.0). Pearson correlation analysis was applied to examine relationships between toxin concentrations and abundance of potential toxigenic dinoflagellate species using all year-round data, and only samples with toxin concentrations above the limit of detection (LOD) were included. Correlation analyses were performed using paired datasets across all sampling sites and periods. The relationships were assessed using Pearson's correlation coefficient (r), and statistical significance was defined at $p < 0.05$.

3. Results

3.1 Occurrence and composition of phycotoxins in Qinzhou Bay

Multiple phycotoxins were widely detected in phytoplankton samples collected from Qinzhou Bay throughout the survey conducted from November 2021 to

November 2022. During the study period, both PSTs and multiple LMTs were identified across the sampling campaigns (Fig. 2). Apparent temporal variations in toxin composition were also observed over the sampling period. Higher toxin diversity was generally recorded during warmer months from May to August, while relatively lower levels were observed in colder seasons.

Among PSTs, gonyautoxins (GTXs) and decarbamoylgonyautoxins (dcGTXs) were the dominant components, whereas saxitoxin (STX) was not detected. The composition of PSTs showed moderate variability among sampling periods, dcGTX3 accounted for nearly half of the PSTs in May, while it was below the level of detection by LC-MS in October (Fig. 2A). GTX4 was consistently detected in May, June, and October. Additionally, LMTs were also frequently detected in Qinzhou Bay, including okadaic acid (OA), dinophysistoxins (DTX), pectenotoxins (PTX), yessotoxins (YTX). Among LMTs, pectenotoxin 2 (PTX2) and homo-yessotoxin (hYTX) were the most prevalent compounds, followed by diarrheic shellfish toxins (DSTs), including okadaic acid (OA) and dinophysistoxins-1 (DTX1) (Fig. 2B). The evident variability in toxin composition might indicate dynamic changes in toxin-producing phytoplankton communities over time.

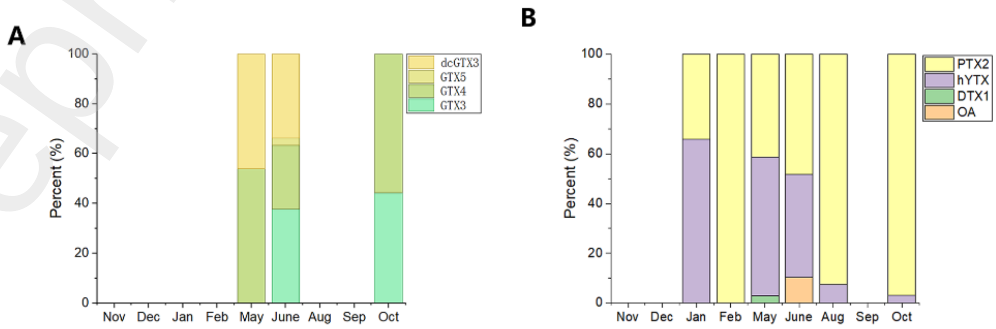

Figure 2. Toxin composition of paralytic shellfish toxins (PSTs) and lipophilic marine toxins (LMTs) in Qinzhou Bay during the annual survey from November 2021 to November 2022. GTX3/4/5: gonyautoxin 3/4/5; dcGTX3: decarbamoylgonyautoxin 3; PTX2: pectenotoxin 2; hYTX: homo-yessotoxin; SPX: 13-desmethyl-spirolide-C; OA: okadaic acid; DTX1: dinophysistoxins-1.

3.2 Spatial distribution of phycotoxins from phytoplankton in Qinzhou Bay

The spatial distribution of phycotoxins in Qinzhou Bay exhibited clear heterogeneity for various toxins. Elevated toxin concentrations were primarily observed in open waters outside Qinzhou Bay (Fig. 3), although peaking at different sites for PSTs and LMTs. In contrast, inshore sites generally showed lower toxin levels.

Specifically, various compounds of PSTs (GTX4, GTX3, GTX5, dcGTX3) showed similar spatial trends, with highest concentrations detected at site Q10 in June (Fig. 4), and decreasing concentrations in the inner bay throughout the investigation. However, LMTs displayed a patchy distribution pattern, with higher concentrations detected at different sites. Among LMTs, PTX2 consistently dominated across most sampling time points and peaked at the west region (site Q7) outside the bay in June 2022, with low concentrations of hYTX detected at site Q10 and Q11, and trace diarrhetic shellfish toxins (OA and DTX1) were detected at the central and external bay (Fig. 5). Notably, certain hotspots (site Q7, Q10, Q11) with elevated toxin levels were repeatedly observed during multiple sampling campaigns, suggesting the persistence of favorable conditions for the growth of toxigenic dinoflagellates in the sea regions outside Qinzhou Bay.

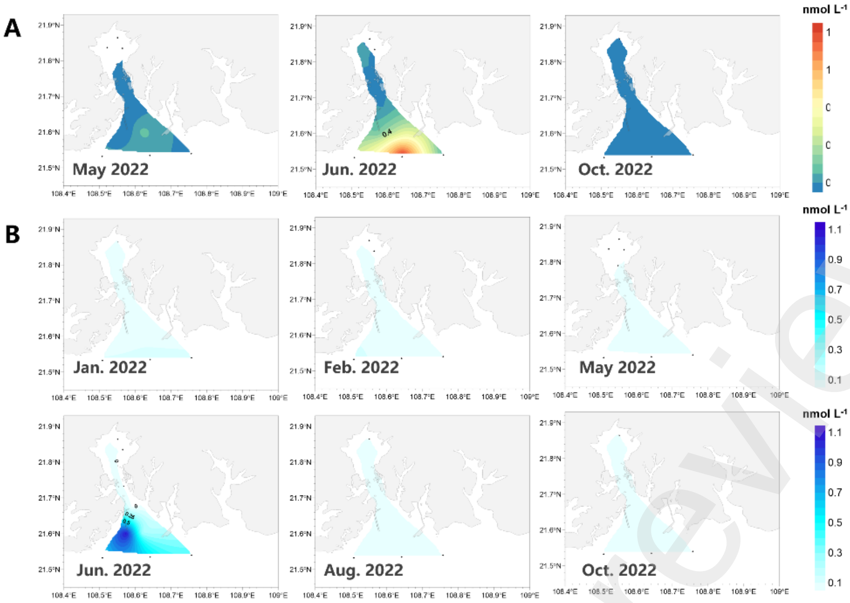

Figure 3. Spatial distribution of total paralytic shellfish toxins (A) and lipophilic marine toxins (B) in Qinzhou Bay during the annual survey from November 2021 to November 2022.

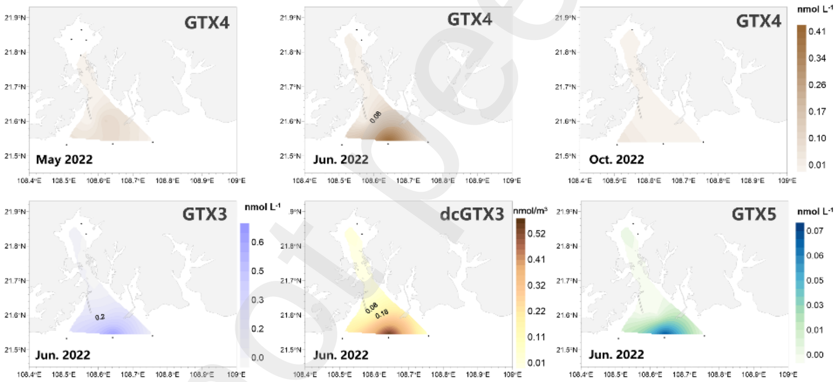

Figure 4. Spatial distribution of various components of paralytic shellfish toxins (PSTs) in Qinzhou Bay during the annual survey from November 2021 to November 2022. GTX3/4/5: gonyautoxin 3/4/5; dcGTX3: decarbamoylgonyautoxin 3.

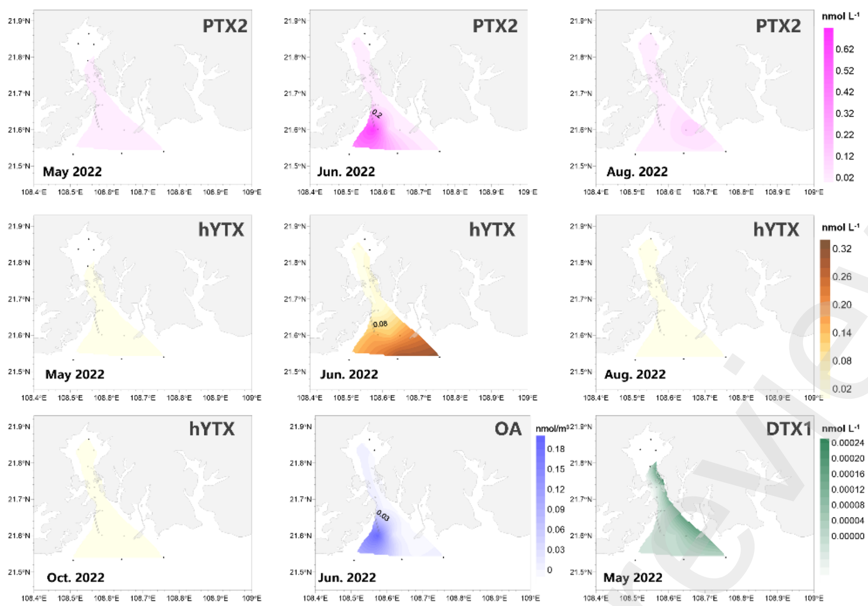

Figure 5. Spatial distribution of various components of multiple lipophilic marine toxins (LMTs) in Qinzhou Bay during the annual survey from November 2021 to November 2022. PTX2: pectenotoxin 2; hYTX: homo-yessotoxin; SPX: 13-desmethyl-spirolide-C; OA: okadaic acid; DTX1: dinophysistoxins-1

3.3 Temporal variation of phycotoxins from phytoplankton in Qinzhou Bay

Pronounced temporal variations in phycotoxin occurrence were observed throughout the investigation period from November 2021 to November 2022, with differences in PSTs and LMTs. Overall, toxin concentrations and diversity were higher in May and June, while relatively lower levels were recorded in winter, indicating the favorable environment for the proliferation of toxigenic microalgae in late spring and early summer.

According to the investigation results, PSTs exhibited distinct seasonal fluctuations, which were prevalent in May and June, except for the low content in October, and not detected in other months (Fig. 6A). In contrast, LMTs displayed relatively broader temporal distributions, their concentrations also tended to increase in June with elevated temperature, and presented in most months except for December and September (Fig. 6B).

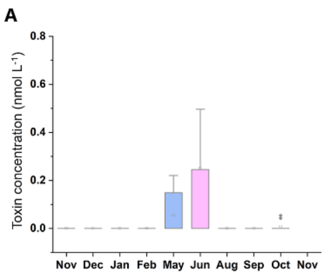

Figure 6. Temporal variation of paralytic shellfish toxins (A) and lipophilic marine toxins (B) in Qinzhou Bay during the annual survey from November 2021 to November 2022.

3.4 Relationships between phycotoxins and toxigenic dinoflagellate species

In this study, toxigenic dinoflagellate species from phytoplankton samples collected in four seasons were identified using high-throughput sequencing and bioinformatic analysis, and potential toxigenic dinoflagellate species responsible for PSTs and various lipophilic phycotoxins were identified. The dominant toxic dinoflagellates identified in several sampling sites were listed in Table 1. In general, several toxigenic dinoflagellates, including *Alexandrium* spp., *Prorocentrum* spp., *Gymnodinium* sp., *Gonyaulax* sp., *Dinophysis* sp., were identified across the sampling sites, showing pronounced spatial and temporal variability.

Table 1. Potential toxigenic dinoflagellate species identified by high-throughput sequencing during the investigation in Qinzhou Bay.

Month	Sampling Site	Potential toxigenic dinoflagellate species
June 2022	Q7	*Prorocentrum micans*, *Alexandrium leei*, *Alexandrium catenella*, *Prorocentrum* sp., *Gymnodinium* sp.
June 2022	Q9	*Alexandrium leei*, *Prorocentrum* sp., *Alexandrium catenella*, *Prorocentrum micans*, *Gymnodinium* sp.

June 2022	Q11	*Prorocentrum* sp., *Alexandrium tamiyavanichii*, *Prorocentrum micans*, *Alexandrium leei*, *Dinophysis* sp.,
Jan. 2022	Q9	*Alexandrium leei*, *Alexandrium affine*, *Gymnodinium* sp., *Alexandrium ostenfeldii/minutum*, *Prorocentrum* sp., *Karenia selliformis*, *Gonyaulax spinifera*
Feb. 2022	Q11	*Gonyaulax spinifera*, *Protoceratium reticulatum*, *Prorocentrum micans*, *Alexandrium tamiyavanichii*, *Prorocentrum* sp., *Alexandrium* leei, *Dinophysis* sp.,
Dec. 2021	Q7	*Prorocentrum* sp., *Alexandrium leei*, *Gonyaulax spinifera*, *Karenia selliformis*, *Prorocentrum micans*, *Protoceratium reticulatum*, *Alexandrium affine*
May 2022	Q4	*Alexandrium leei*, *Alexandrium tamiyavanichii*, *Prorocentrum micans*, *Dinophysis* sp., *Lingulodinium polyedra*, *Gonyaulax spinifera*

Moreover, toxigenic dinoflagellate species were also identified and counted by morphological methods using an inverted optical microscope, then the relationships between toxin concentrations and the abundance of toxigenic dinoflagellate species were analyzed. During the investigation in Qinzhou Bay, dinoflagellates *Alexandrium* spp. (*Alexandrium catenella*, *Alexandrium tamarense*, and *Alexandrium* sp.) and *Gymnodinium catenatum* accounted for STX-group toxins, *Prorocentrum lima* and *Prorocentrum micans*, which were responsible for diarrhetic shellfish toxins, were determined. Elevated concentrations of PSTs were generally observed in samples where *Alexandrium* spp. were present, with GTX analogues representing the dominant toxin components. According to the linear correlation analysis, the concentration of PSTs was related to the abundance of various *Alexandrium* species, while the concentration of okadaic acid was not significantly correlated to the abundance of the potential toxigenic dinoflagellates *Prorocentrum lima* and *Prorocentrum micans* (Fig. 7). Besides, *Dinophysis* sp. was not identified by microscopic observation, which is responsible for PTX production.

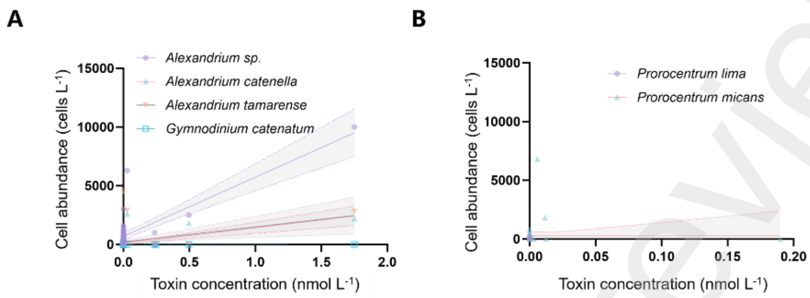

Figure 7. Relationships between toxin concentrations and the abundances of potential toxigenic dinoflagellate species during the annual survey from November 2021 to November 2022 in Qinzhou Bay. The shaded regions denote the 95% confidence intervals around the fitted regression lines. A) Linear relationship between the content of paralytic shellfish toxins (PSTs) and the abundance of *Alexandrium* spp. and *Gymnodinium* sp.; B) Linear relationship between the content of okadaic acid (OA) and the abundance of *Prorocentrum* sp.

4. Discussion

4.1 Spatiotemporal patterns of phycotoxins in Qinzhou Bay

This study provides the first comprehensive year-round characterization of phycotoxins from net-concentrated phytoplankton in Qinzhou Bay located at the northern Beibu Gulf of South China Sea. The investigation results of multiple phycotoxins revealing pronounced spatiotemporal dynamics in toxin occurrence, composition, and distribution in Qinzhou Bay. Multiple phycotoxins were widely detected, including PSTs and LMTs, with GTX analogues (GTX4, GTX3, dcGTX3), PTX2, and hYTX as dominant components (Fig. 2, 4, 5). Whereas GTX1 and GTX2 were not detected synchronously, likely due to their low abundance below the limit of detection or strain-specific toxin profiles of the causative dinoflagellates in this region. The observed distribution patterns of PSTs and LMTs may indicate that phycotoxin occurrence was influenced by specific ecological and environmental controls.

The clear seasonal increase in multiple phycotoxins during late spring to early summer (May–June) is consistent with the growth dynamics of toxigenic dinoflagellates under favorable environmental conditions. Elevated temperature, enhanced water column stratification, and increased nutrient inputs driven by river discharge likely promote dinoflagellate growth and toxin production (Griffith and Gobler, 2020). According to the survey in this study, the sea surface temperature reached 25~28°C in May 2022，at the same time, the average nitrate concentration increased to 55 μM driven by river discharge (Fig. S1), collectively facilitate the persistence of dinoflagellates (Glibert et al., 2016). Additionally, seasonal windows of the growth of dinoflagellates are often associated with intensified stratification, shifts in nutrient regimes, and coastal circulation in coastal systems. Although the relationships between environmental parameters and growth of dinoflagellates were not deeply explored in this study, the observed seasonal patterns are consistent with those well-established mechanisms of bloom dynamics in coastal ecosystems. Future studies incorporating physicochemical variables (e.g., temperature, nutrients, salinity, etc.) would allow for a more mechanistic understanding of toxin dynamics.

It should be noted that, in this study a clear spatial gradient was observed, with consistently higher toxin concentrations predominantly occurring in open waters outside the bay compared to the inner bay. This pattern suggests that hydrodynamic conditions and artificial activities may play key roles in regulating toxin distribution. Despite higher nitrogen sources in inner Qinzhou Bay compared to open waters (Fig. S2), Maowei Sea is strongly influenced by riverine inputs from Maolingjiang, Qinjiang, and Dalanjiang rivers, as well as intensive aquaculture activities. Therefore, the increased turbidity, fluctuating nutrient conditions, and potentially higher grazing pressure may constrain the accumulation of toxigenic dinoflagellates in the inner bay (Gu et al., 2015; Zheng et al., 2012). In contrast, open waters outside the bay are likely characterized by reduced disturbance and greater hydrodynamic stability, which may favor the persistence and aggregation of dinoflagellate populations and associated toxin production. Similar offshore accumulation patterns of phycotoxins have been reported in other coastal ecosystems, where stratification and hydrodynamic retention enhance bloom development (Pitcher et al., 2010). Although these mechanisms are consistent with patterns observed in other coastal systems, the present study did not directly quantify hydrodynamic conditions in Qinzhou Bay, these factors should be considered as plausible drivers rather than demonstrated causes.

4.2 Risk assessment of phycotoxins in Qinzhou Bay

The co-occurrence of multiple PSTs and LMTs observed in this study is consistent with previous reports from the South China Sea, where multiple toxin groups have been detected in both phytoplankton and shellfish, with LMTs dominated by PTX2 and hYTX (Ji et al., 2022; Liu et al., 2020). Compared with open waters of Beibu Gulf (Ji et al., 2026), Qinzhou Bay appears to exhibit relatively higher PTX2 concentrations but lower hYTX and GYM concentration (Table S1), likely reflecting differences in phytoplankton abundance and community composition.

Although phycotoxin concentrations in phytoplankton samples were generally low, their potential risks to seafood safety should not be underestimated. It has been widely acknowledged that phycotoxins can be efficiently accumulated and transformed in filter-feeding bivalves, leading to contaminated toxin levels that may exceed regulatory thresholds even under low concentrations in natural environment. This has become a major concern regarding the impacts of phycotoxins on seafood safety and public health worldwide (Anderson et al., 2002). Consumption of contaminated seafood may have various harmful effects on human health, such as neurotoxicity and cardiotoxicity (Anderson et al., 2012; Alfonso et al., 2003). In Beibu Gulf, previous studies have reported PST contamination in commercially important bivalves *Paphia undulate* and *Mytilus galloprovincialis* exceeding regulatory limits (80 μg STXeq·100 g^{-1}) by 1~3 times (Zhao et al., 2016). This study presents the first report of PSTs produced by phytoplankton in Qinzhou Bay. GTXs with higher toxicity than *N*-sulfocarbamoyl toxins (C1/2) were detected in May and June, highlighting the importance of prevention and management of PSTs-producing dinoflagellates.

Importantly, this study identifies a clear seasonal window (May–June) and offshore hotspots associated with elevated toxin levels, which represent periods and locations of increased risks for aquaculture activities. These findings provide a scientific basis for improving early warning systems, as well as optimizing monitoring strategies and risk assessment of phycotoxins in Qinzhou Bay.

4.3 Potential causative dinoflagellates of typical phycotoxins in Qinzhou Bay

Toxigenic phytoplankton, especially dinoflagellates, have expanded globally under the climate and ocean variability (Griffith and Gobler, 2020). In this study, the integration of morphological identifications and high-throughput sequencing has been performed to provide complementary insights into the potential sources of multiple phycotoxins in Qinzhou Bay. However, linking toxin profiles to specific causative species remains challenging due to ecological and methodological uncertainties.

For PSTs, the detection of *Alexandrium catenella*, *Alexandrium tamarense*, *Alexandrium* sp. and *Gymnodinium catenatum*, together with the positive relationship between *Alexandrium* spp. abundance and concentrations of PSTs (Fig. 7A), supports their roles as primary PST-producers in Qinzhou Bay. This finding is consistent with the common knowledge that *Alexandrium* species are major producers of saxitoxin-group toxins in marine environments, as well as *Gymnodinium catenatum*, and *Pyrodinium bahamense* var. compressum (Anderson et al., 2012). During the survey, the abundance of *Alexandrium* sp. could be up to 10000 cells L^{-1} determined by microscopic identification. However, species-level identification based solely on morphological characteristics is constrained by the presence of cryptic species complexes. In Beibu Gulf, *Alexandrium tamiyavanichii* with lower toxin production (4.6 fmol/cell) has been identified as one of the PST-producing species based on molecular evidence (Xu et al., 2021b), which may partly explain the low concentrations of PSTs observed in this study.

In contrast, the identification of toxin-producing dinoflagellates for LMTs remains more complex. As the dominant lipophilic toxin in Qinzhou Bay, PTX2 is typically associated with dinoflagellates in genus *Dinophysis* (Reguera et al., 2012). However, *Dinophysis* spp. were not consistently observed under microscopic identification, despite being detected through high-throughput sequencing. This apparent decoupling between toxin occurrence and observable cell abundance is well documented and may reflect the unique ecological characteristics of *Dinophysis* species. These organisms are known to produce high cellular toxin content and often grow in thin layers within the water column, making them more difficult to detect by conventional sampling methods (Fux et al., 2010; Séchet et al., 2021). In this way, even low cell abundances of *Dinophysis* may contribute significantly to PTX presence in the environment. Moreover, methodological limitations in molecular approaches further contribute to the uncertainties in species identification of *Dinophysis* spp. The V4 region of the 18S rRNA gene used in this study has limited resolution for discriminating closely related species within genera *Dinophysis* (Anonymous, 2022). It should be noted that, discrepancies between morphological and molecular biological methods may arise due to differences in sampling biases, detection sensitivity, and DNA persistence among phytoplankton species (De Vargas et al., 2015). In this study, the samples for morphological and molecular analysis were collected separately, which may also contribute to the discrepancies between the two methods.

For YTXs, several potential producers, including *Protoceratium reticulatum* (*Gonyaulax grindleyi*), *Gonyaulax spinifera*, and *Lingulodinium polyedra* (*Gonyaulax* *polyedra*), were identified through high-throughput sequencing (Table 1), which were consistent with previous studies (Rhodes et al., 2006; Paz et al., 2004; Suzuki et al., 2007; Amzil et al., 2008). Additionally, the detection of potential cyclic imine-producing species such as *Karenia selliformis* and *Alexandrium ostenfeldii* suggests the presence of emerging toxin risks in this region (Ji et al., 2022). Although cyclic imine toxins (e.g. GYMs and SPXs) were not detected during the investigation in this study, emerging risks of cyclic imine contamination in bivalves in the Beibu Gulf have been proposed (Ji et al., 2022). Further culture-based and molecular investigations are required to confirm toxin production by these dinoflagellate species.

4.4 Implications for monitoring strategies and future research

The coastal waters of the South China Sea have been considered to contain more lipophilic groups and to have higher lipophilic phycotoxin content than other sea regions in China (Wang et al., 2023). The results of this study have important implications for phycotoxin monitoring and management in semi-enclosed sea region. The fundamental data on multiple phycotoxins would provide important guidance for aquaculture practices in Qinzhou Bay, where intensive mariculture activities were distributed in the inner Maowei Sea and outer bay (Xu et al., 2021b). There are two main types of aquaculture activities in Qinzhou Bay, including culture pounds in nearshore areas of Maowei sea (mainly shrimp, crab, and fish), and natural open culture farms in open estuaries and shallow regions (mainly commercial shellfish) (Zhang et al., 2020). Due to the increasing intensity of aquaculture activities in this region, continuous regular monitoring is strongly encouraged.

According to this study, the pronounced seasonal variability suggests that monitoring efforts should be intensified in May and June (Fig. 4, 5), when toxin diversity and concentrations are highest. Targeted monitoring during this period would enhance early warning capabilities for harmful algal bloom events. In addition, the spatial heterogeneity observed in this study indicated that open waters outside the Qinzhou Bay represented important hotspots for toxin occurrence. Therefore, shellfish aquaculture activities in the open waters may pose more severe risks from phycotoxins than the inner pound aquaculture. Moreover, monitoring programs focusing solely on aquaculture areas in Maowei Sea may underestimate regional toxin dynamics. It's suggested to incorporate sampling stations from open water into routine monitoring frameworks to improve comprehensive risk assessment and management.

For the monitoring strategy of toxigenic dinoflagellates, this study highlights the mismatch between toxin detection and phytoplankton observations and calls for improved sampling methods. Conventional sampling method for phytoplankton in surface water may underestimate species, such as *Dinophysis*, that exhibit vertical patchiness or low abundance in the water column. The integration of vertical profiling, more targeted sampling and molecular techniques would improve detection and provide a more comprehensive understanding of toxigenic species, rather than relying solely on surface seawater sampling. Furthermore, species isolation and toxin profile analysis would more accurately resolve relationships between toxin–producing microalgae and toxin dynamics.

Future research should focus on estimating the influence of key environmental drivers on toxin production, elucidating toxin bioaccumulation processes in typical aquaculture species, and isolating and charactering local toxin-producing strains. These efforts will contribute to a more mechanistic understanding of phycotoxin dynamics and support the development of effective monitoring and management strategies in coastal aquaculture systems.

5. Conclusions

This study provides the first year-round assessment of phytoplankton-associated phycotoxins in the subtropical Qinzhou Bay and reveals clear spatiotemporal patterns in toxin occurrence, toxin composition, and potential phytoplankton sources. Multiple toxin groups, including PSTs and LMTs, co-occurred in the study area, with GTX analogues, PTX2, and hYTX as dominant components.

Phycotoxin dynamics exhibited strong seasonality, with pronounced increases in May and June, highlighting a critical temporal window associated with enhanced dinoflagellate activities. Spatially, consistently higher toxin concentrations in open waters indicate that hydrodynamic and environmental conditions outside the bay favor the persistence and accumulation of toxigenic dinoflagellates. The integration of morphological and molecular approaches enabled the identification of key toxigenic dinoflagellates, although mismatches between toxin occurrence and cell abundances suggest that low-abundance or vertically distributed species (e.g., *Dinophysis* spp.) may play a disproportionately important role in toxin production.

From a management perspective, the identified seasonal peaks and offshore hotspots represent periods and areas of elevated ecological and aquaculture risks. These findings highlight the higher contamination risks of shellfish aquaculture in the open waters of Qinzhou Bay, and emphasize the need to improve monitoring strategies by incorporating offshore stations and refining sampling and determination approaches of toxigenic dinoflagellate samples.

Overall, this study advances the understanding of phycotoxin dynamics in subtropical coastal systems in South China Sea and provides important scientific basis for enhancing monitoring frameworks and risk management associated with HABs in the aquaculture region of Beibu Gulf. These findings contribute to a broader understanding of phycotoxin dynamics in subtropical coastal systems worldwide.

Data availability

Data will be made available on request.

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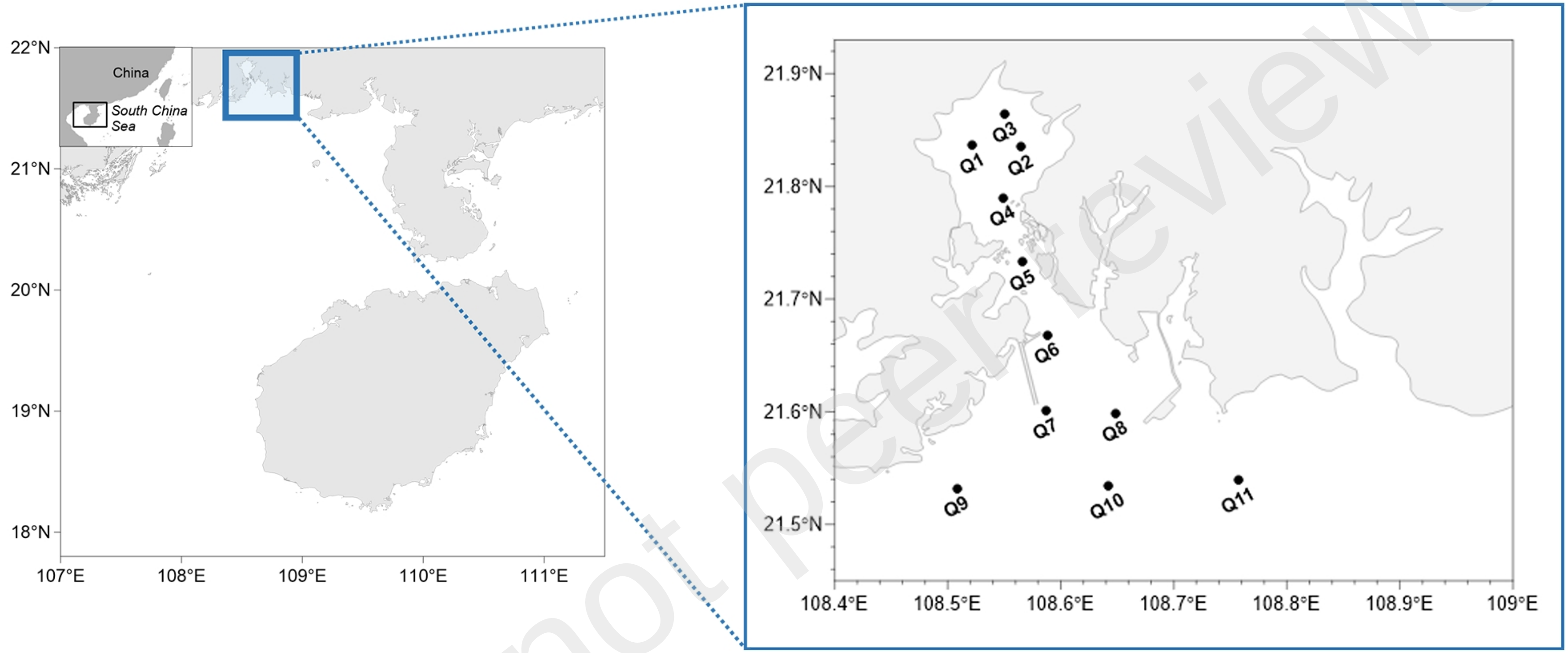
22°N
21°N
20°N
19°N
18°N
107°E
108°E
109°E
110°E
111°E
China
South China Sea
21.9°N
21.8°N
21.7°N
21.6°N
21.5°N
108.4°E
108.5°E
108.6°E
108.7°E
108.8°E
108.9°E
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Q1
Q2
Q3
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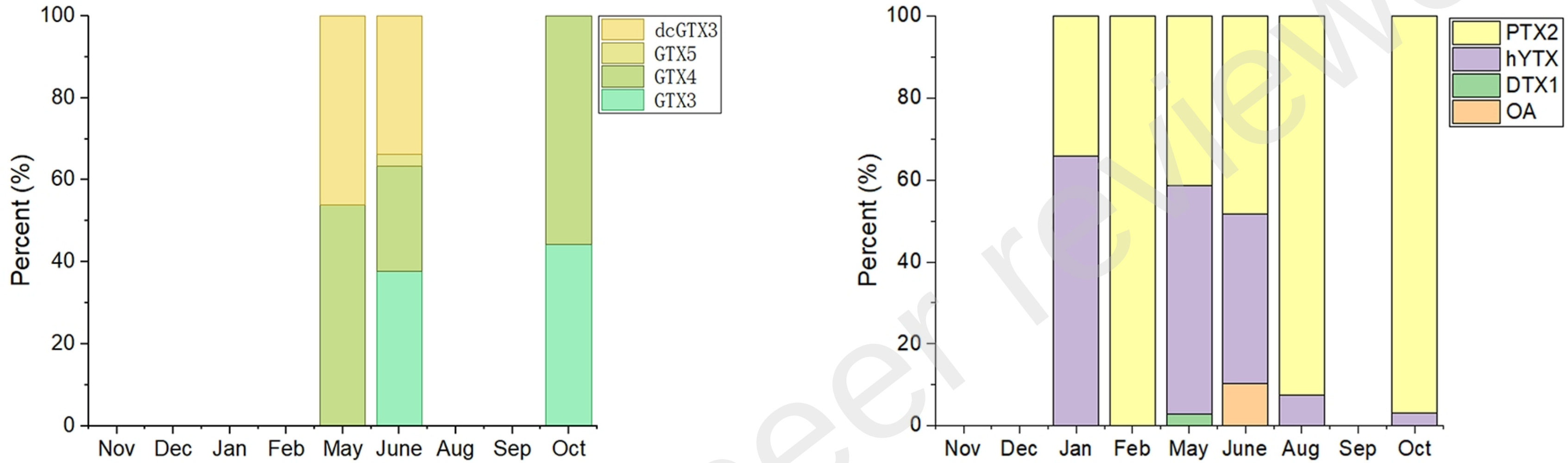
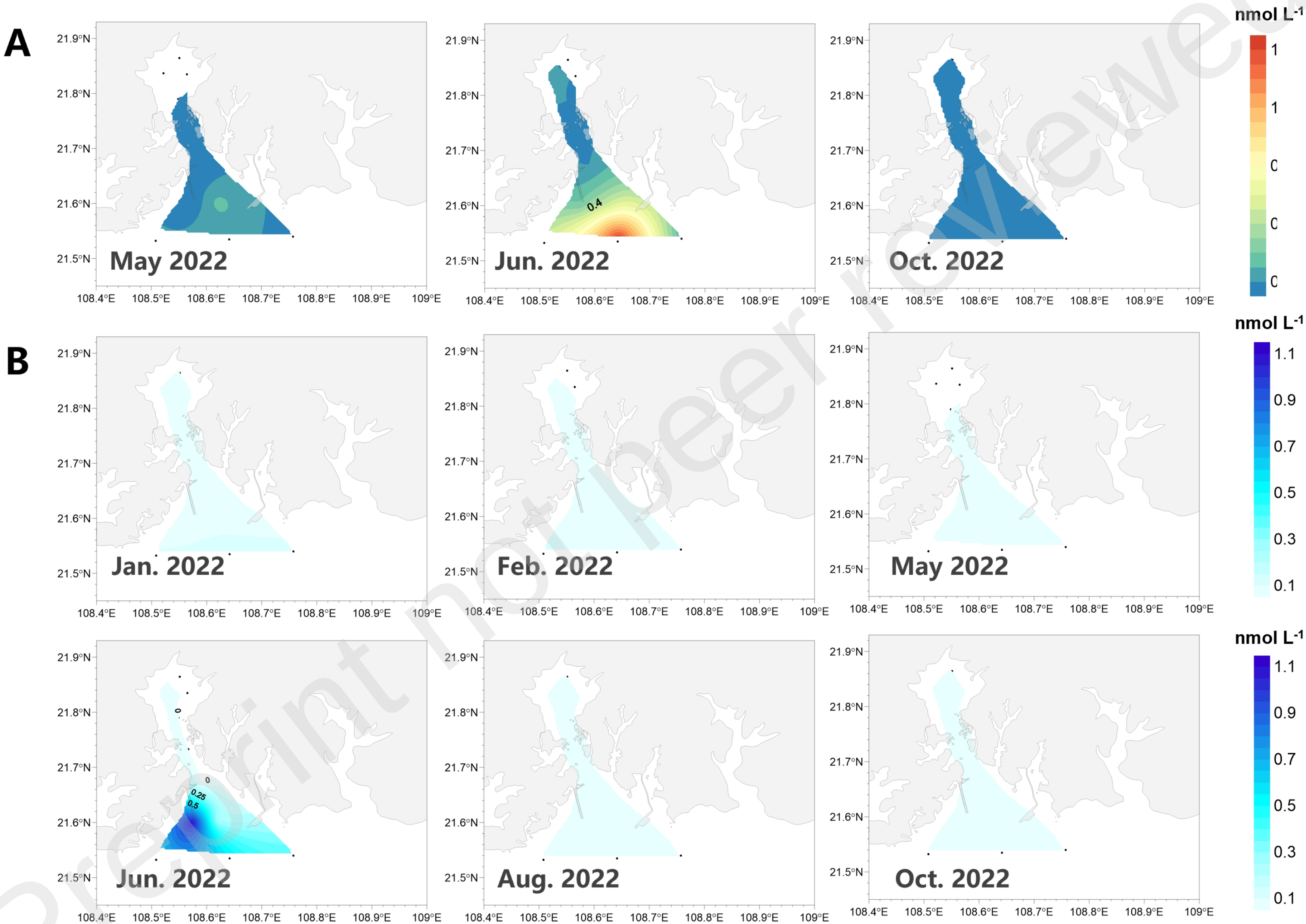
Q5
Q6
Q7
Q8
Q9
Q10
Q11

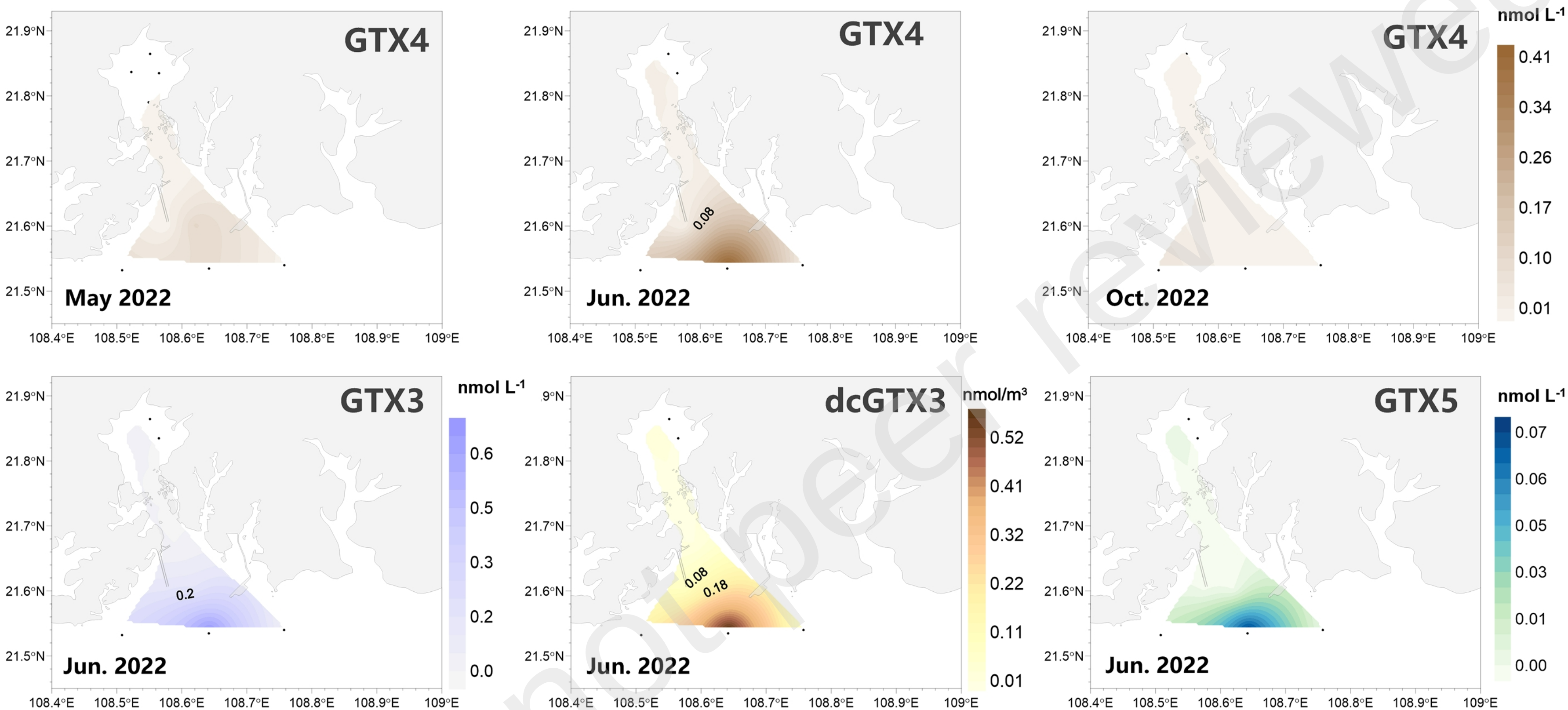
A

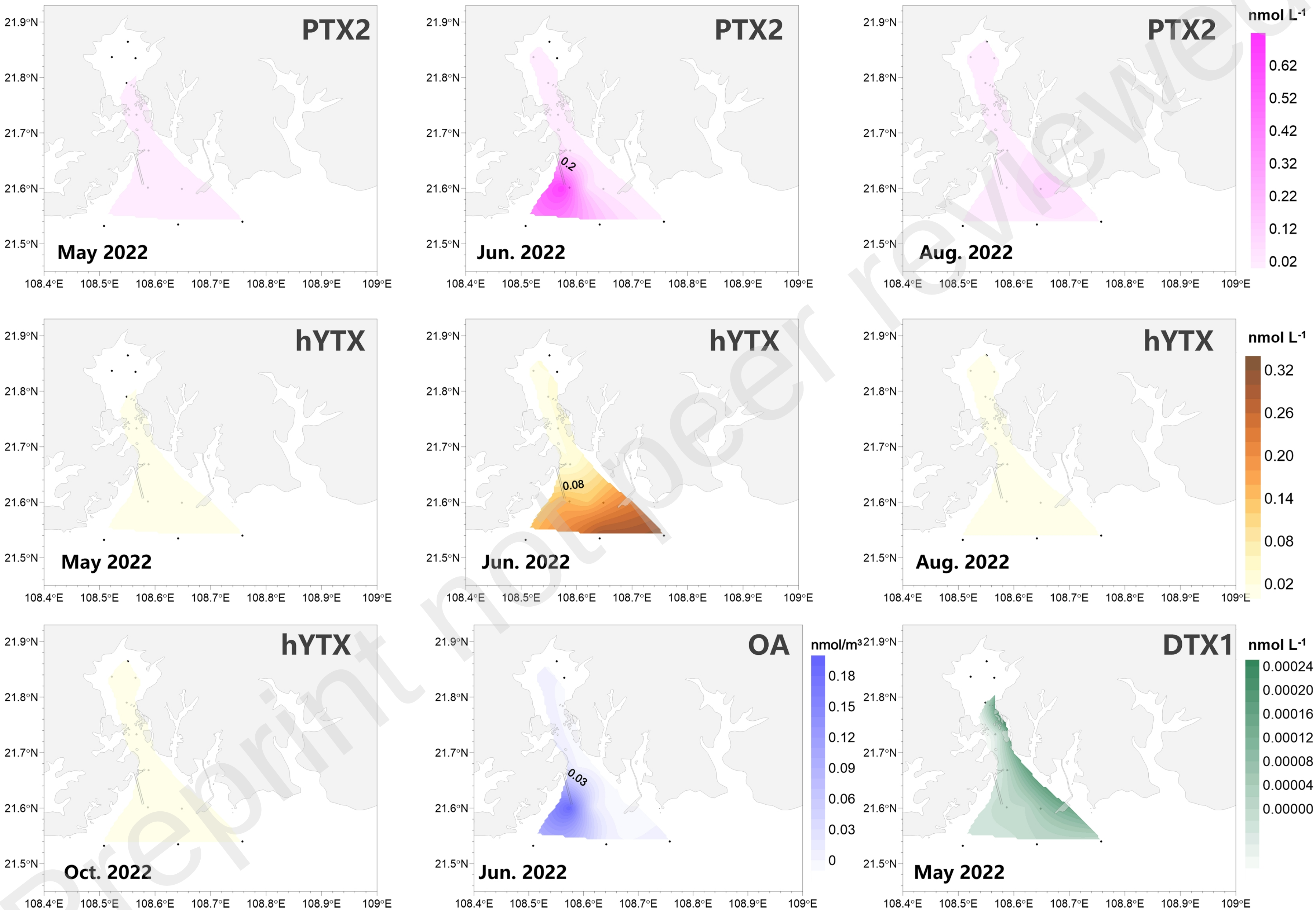
B



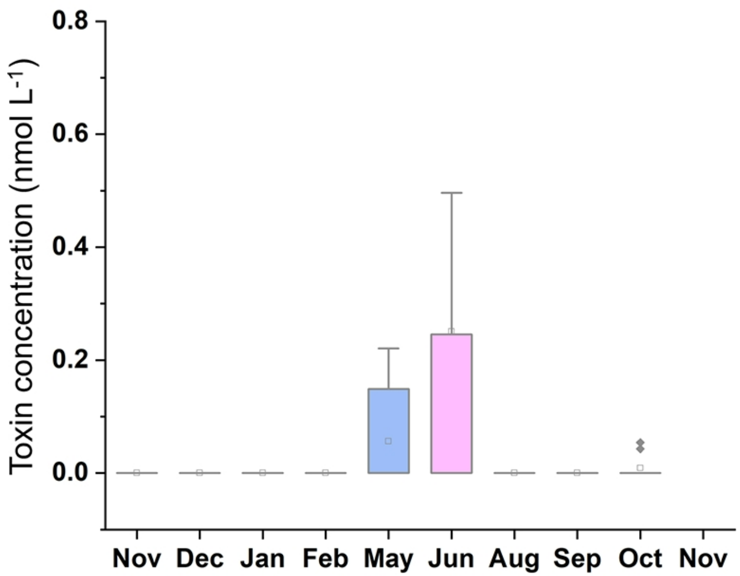
Percent (%)
100
80
60
40
20
0
Nov
Dec
Jan
Feb
May
June
Aug
Sep
Oct
dcGTX3
GTX5
GTX4
GTX3
PTX2
hYTX
DTX1
OA


A
May 2022
Jun. 2022
0.4
Oct. 2022
nmol L-1
1
1
B
Jan. 2022
Feb. 2022
May 2022
nmol L-1
1.1
0.9
0.7
0.5
0.3
0.1
Jun. 2022
0
0
0.25
0.5
Aug. 2022
Oct. 2022
nmol L-1
1.1
0.9
0.7
0.5
0.3
0.1
21.9°N
21.8°N
21.7°N
21.6°N
21.5°N
108.4°E
108.5°E
108.6°E
108.7°E
108.8°E
108.9°E
109°E


GTX4
May 2022
GTX4
0.08
Jun. 2022
GTX4
Oct. 2022
nmol L-1
0.41
0.34
0.26
0.17
0.10
0.01
GTX3
0.2
Jun. 2022
nmol L-1
0.6
0.5
0.3
0.2
0.0
dcGTX3
0.08
0.18
Jun. 2022
nmol/m3
0.52
0.41
0.32
0.22
0.11
0.01
GTX5
Jun. 2022
nmol L-1
0.07
0.06
0.05
0.03
0.01
0.00
21.9°N
21.8°N
21.7°N
21.6°N
21.5°N
108.4°E
108.5°E
108.6°E
108.7°E
108.8°E
108.9°E
109°E

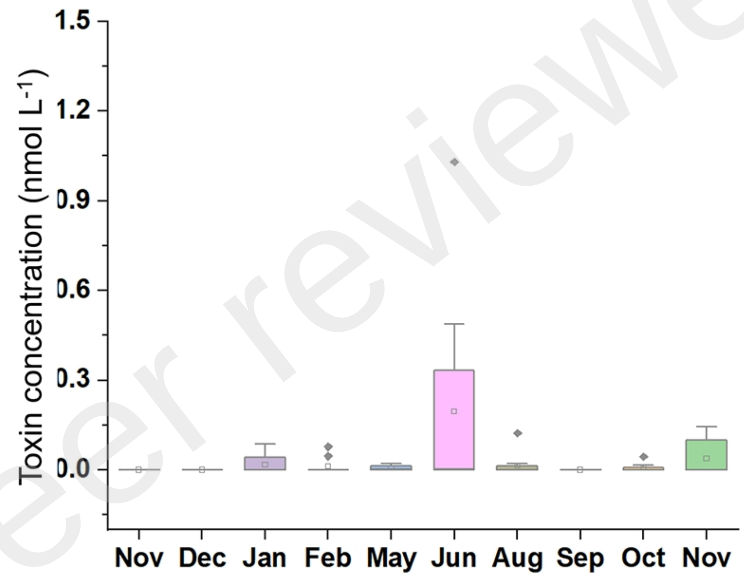

PTX2
May 2022
PTX2
0.2
Jun. 2022
PTX2
Aug. 2022
nmol L-1
0.62
0.52
0.42
0.32
0.22
0.12
0.02
hYTX
May 2022
hYTX
0.08
Jun. 2022
hYTX
Aug. 2022
nmol L-1
0.32
0.26
0.20
0.14
0.08
0.02
hYTX
Oct. 2022
OA
0.03
Jun. 2022
nmol/m3
0.18
0.15
0.12
0.09
0.06
0.03
0
DTX1
May 2022
nmol L-1
0.00024
0.00020
0.00016
0.00012
0.00008
0.00004
0.00000
21.9°N
21.8°N
21.7°N
21.6°N
21.5°N
108.4°E
108.5°E
108.6°E
108.7°E
108.8°E
108.9°E
109°E

A



0.8
0.6
0.4
0.2
0.0
Toxin concentration (nmol L-1)
Nov
Dec
Jan
Feb
May
Jun
Aug
Sep
Oct
Nov

B



1.5
1.2
0.9
0.6
0.3
0.0
Toxin concentration (nmol L-1)
Nov
Dec
Jan
Feb
May
Jun
Aug
Sep
Oct
Nov

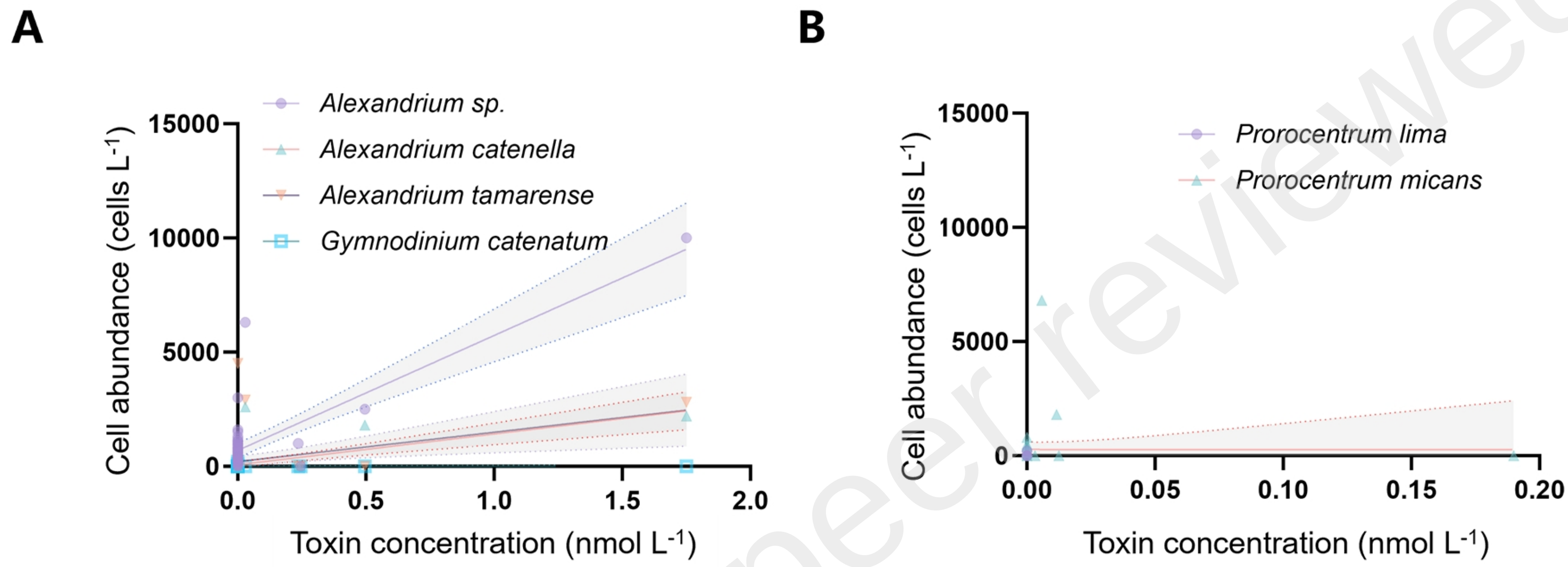

A
Alexandrium sp.
Alexandrium catenella
Alexandrium tamarense
Gymnodinium catenatum
Cell abundance (cells L-1)
15000
10000
5000
0
0.0
0.5
1.0
1.5
2.0
Toxin concentration (nmol L-1)
B
Prorocentrum lima
Prorocentrum micans
Cell abundance (cells L-1)
15000
10000
5000
0
0.00
0.05
0.10
0.15
0.20
Toxin concentration (nmol L-1)

Table 1. Potential toxigenic dinoflagellate species identified during the investigation in Qinzhou Bay.

Month	Sampling Site	Potential toxigenic dinoflagellate species
June 2022	Q7	*Prorocentrum micans*, *Alexandrium leei*, *Alexandrium catenella*, *Prorocentrum* sp., *Gymnodinium* sp.
June 2022	Q9	*Alexandrium leei*, *Prorocentrum* sp., *Alexandrium catenella*, *Prorocentrum micans*, *Gymnodinium* sp.
June 2022	Q11	*Prorocentrum* sp., *Alexandrium tamiyavanichii*, *Prorocentrum micans*, *Alexandrium leei*, *Dinophysis* sp.,
Jan. 2022	Q9	*Alexandrium leei*, *Alexandrium affine*, *Gymnodinium* sp., *Alexandrium ostenfeldii/minutum*, *Prorocentrum* sp., *Karenia selliformis*, *Gonyaulax spinifera*
Feb. 2022	Q11	*Gonyaulax spinifera*, *Protoceratium reticulatum*, *Prorocentrum micans*, *Alexandrium tamiyavanichii*, *Prorocentrum* sp., *Alexandrium* leei, *Dinophysis* sp.,
Dec. 2021	Q7	*Prorocentrum* sp., *Alexandrium leei*, *Gonyaulax spinifera*, *Karenia selliformis*, *Prorocentrum micans*, *Protoceratium reticulatum*, *Alexandrium affine*
May 2022	Q4	*Alexandrium leei*, *Alexandrium tamiyavanichii*, *Prorocentrum micans*, *Dinophysis* sp., *Lingulodinium polyedra*, *Gonyaulax spinifera*