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Net-phytoplankton community structure and its environmental correlations in central Bohai Sea and the Bohai Strait

Yibo Wang,1,2,3,4 Yanyu Sun,1,2,3,4 Caixia Wang,1,2,4 Weiwei Chen,1,2,3,4 and Xiaoke Hu1,2,4*

1Key Laboratory of Coastal Biology and Bioresource Utilization, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, P. R. China
2Laboratory for Marine Biology and Biotechnology, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266237, P. R. China
3University of Chinese Academy of Sciences, Beijing 100049, P. R. China
4Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, P. R. China
*Corresponding author: xkhu@yic.ac.cn

Phytoplankton is an important indicator of, and responder to, environmental changes. This study aims to reveal the response of a phytoplankton community to environmental changes, especially the level of nutrients in the Bohai Sea. The distribution pattern of net-phytoplankton communities in the central Bohai Sea and the Bohai Strait in winter and summer were studied, and the relationship between the phytoplankton communities and environment was explored. The results showed that diatoms (e.g. A. octonarius, Paralia sulcata and Detonula pumila) dominated the phytoplankton communities in winter, while diatoms (e.g. Chaetoceros sp. and Thalassiosira frauenfeldii) and dinoflagellates (e.g. Ceratium fusus and Ceratium tripos) were both dominant in summer. By cluster analysis, the phytoplankton communities were divided into three clusters in winter and two in summer. The community that inhabited the waters around Qinhuangdao had higher abundance and distinct taxa composition in winter, related to the higher level of DIN and phosphate. Influenced by different water masses (the Yellow Sea Warm Current and the Bohai Sea Coastal Current), the phytoplankton community composition in the northern and southern parts of the Bohai Strait were also significantly different in winter. In summer, the difference in abundance and dominant species between the two phytoplankton communities was more closely linked to the N:P ratio in the environment. These results reflect that both nutrient level and hydrodynamic condition greatly influence the phytoplankton communities in the central Bohai Sea and the Bohai Strait. Our study will provide basic data for the eutrophication and environmental changes in the Bohai Sea.

Keywords: dominant species, N:P ratio, nutrient enrichment, hydrodynamics

Introduction

Marine phytoplankton is the most important primary producer of the marine food chain and plays a key role in element cycle and energy flow in marine ecosystem (Yang et al., 2016b). Phytoplankton is an important indicator of and responder to environmental changes (Luan et al., 2018).
Physical transport and dispersal have been recognized as an important mechanism structuring phytoplankton populations, and some species could be used to indicate specific water masses and water movements (Moita et al., 2016; Chen et al., 2018). Besides, phytoplankton communities are usually affected by temperature, light, nutrients, and predation by zooplankton and fish (Mette et al., 2011; Chen et al., 2018). The distribution and dynamics of marine phytoplankton in the ocean and its environmental mechanism are important parts of the study on the structure and function of marine ecosystem (Fu et al., 2009).

Bohai Sea is a semi-enclosed shallow coastal sea in northeastern China, affected by nutrient input from coastal rivers and has relatively high productivity (Liu et al., 2011). The Circum-Bohai Sea Economic Zone has been developing rapidly in recent decades, and the resulting eutrophication in the Bohai Sea has led to increased frequency and magnitude of harmful blooms in this area (Guo, Li et al., 2014). Due to a long-term increase of N:P ratio in the Bohai Sea, the phytoplankton community structure has changed greatly in recent decades and the proportion of dinoflagellates in phytoplankton communities increased notably (Sun et al., 2002; Xu, 2011; Luan et al., 2018).

Based on the phytoplankton and chlorophyll a data collected from the Bohai Sea and the Bohai Strait in winter and summer, we aim to reveal the distribution pattern of phytoplankton communities in this area and to illuminate its correlations and responses to environmental factors, especially the nutrient factors. Our study will provide basic data on the eutrophication and environmental changes in the Bohai Sea and will be instructive for marine pollution control.

Materials and methods

Study area and sampling strategy

Two cruises took place in central Bohai Sea and Bohai Strait in December 2013 (winter) and August 2014 (summer) respectively, and sampling occurred at 27 sites in each season (Figure 1). Net-phytoplankton samples were collected with a 76-μm-mesh plankton net equipped with flowmeter, and a vertical haul was made from the bottom to the surface at each site. A total of 54 phytoplankton samples were obtained and fixed with neutral formaldehyde (final concentration: 5%) in plastic bottles. The samples were stored at room temperature in the dark until they were analyzed.

Surface and bottom chlorophyll a samples were collected from 40 and 42 sites in winter and summer, respectively (Figure 1) and a total of 164 chlorophyll a samples were obtained. For each sample, 500 ml of seawater was filtered through a 0.45 μm Whatman GF/F filter and the filters were stored in the dark at −20°C until they were analyzed. Water temperature and salinity in surface and bottom layers and depth of each site were measured by the CTD. Nutrient samples, including nitrate (NO3-N), nitrite (NO2-N), ammonium (NH4-N), phosphate (PO4-P), silicate (SiO3-Si), were collected from both surface and bottom layers at each site as previously described by Wang et al. (2018).

Sample analysis

Phytoplankton was enumerated and identified with a Leica DM2500 microscope at 400× or 200× magnification (Yang and Liu, 2009). Identification was based on morphological characteristics, as far as possible to the species level. It is noteworthy that net trawl method, compared with Utermöhl method (Utermöhl, 1958), can result in losses and underestimation of some small species, but its advantage is that the enriched net samples can contain some larger and more rare species, and therefore it is better for understanding the phytoplankton diversity in the studied area (Yang and Liu, 2009).
Chlorophyll a was extracted in the dark with 90% acetone for 24 h at −20°C and measured by a Turner-Designs fluorimeter (Welschmeyer, 1994). Nutrient samples were measured as previously described by Wang et al. (2018).

Data analysis

Microsoft Excel and Primer 5.0 were used for data statistics, and Surfer13 was used to plot locations of sites and phytoplankton distributions. Diversity indices for each sample were calculated according to the following equations.

Shannon-Wiener ($H'$) (Shannon and Weaver, 1949):

$$H' = - \sum_{i=1}^{S} P_i \log_2 P_i$$

Species richness ($D$) (Margalef, 1968):

$$D = (S - 1) / \log_2 N$$

Evenness ($J'$) (Pielou, 1969):

$$J' = H' / \log_2 S$$

Dominance ($Y$) of each species (Sun and Liu, 2005):

$$Y = \frac{n_i}{N} \times f_i$$

Where $S$ is the number of species; $P_i$ is the proportion of the $i$th species; $N$ is the total number of cells; $n_i$ is the cell number of the $i$th species; $f_i$ is the frequency that the $i$th species occurred at each site. Species with $Y > 0.2$ were considered as dominant species (Sun and Liu, 2005).

Cluster analysis was used to classify phytoplankton communities using the PRIMER v5.0 (PRIMER-E Ltd., Plymouth, UK) according to species composition and abundance. Bray-Curtis similarity matrix was computed on square root-transformed biotic data and Euclidean distance matrix was on ln(x + 1)-transformed abiotic data. Group average method was used to classify phytoplankton community into several clusters, each comprising samples with similar species and abundances. Variances between groups at different levels were tested using the submodule ANOSIM (analysis of similarities) in PRIMER v5. Species with a cumulative contribution of 90% to the average Bray-Curtis similarity within each group was analyzed using the submodule SIMPER (Similarity Percentage Analysis). To obtain a more detailed relationship between community composition and environmental factors, redundancy analysis (RDA) was conducted by using Canoco for Windows 4.5 package. Under forward selection, correlations between community composition and environmental variables were tested by Monte Carlo permutation test (999 permutations). RDA ordination plots were generated based on square root-transformed species-abundance data and ln(x + 1)-transformed environmental data. Spearman correlation analysis between biotic data and environmental variables was conducted by using SPSS v.18.0 (SPSS inc., Chicago, USA).

Results

Net-phytoplankton community structure

The net-phytoplankton (or phytoplankton) community composition in the studied area consisted of a total of 48 phytoplankton species...
affiliated with 25 genera in winter, including 40 diatom species, 7 dinoflagellate species, and 1 chrysophyte species. The abundance of phytoplankton in the study area ranged from $17.0 \times 10^4$ cells m$^{-3}$ to $882.4 \times 10^4$ cells m$^{-3}$, with mean abundance of $126.1 \times 10^4$ cells m$^{-3}$. The highest abundance was found in the waters around Qinhuangdao, followed by the waters at the mouth of the Bohai Bay and near the city of Weihai (Figure 2A). The dominant phytoplankton species in the study area in winter were *Actinocyclus octonarius* and *Paralia sulcata* (Table 1). The most abundant genera were *Paralia*, *Actinocyclus* and *Coscinodiscus* (Figure 3A).

In summer, 33 genera and 60 species of phytoplankton were identified, including 46 diatom species, 13 dinoflagellate species, and 1 chrysophyte species. The abundance of phytoplankton ranged from $9.3 \times 10^4$ cells m$^{-3}$ to $1,423.5 \times 10^4$ cells m$^{-3}$, with an average abundance of $311.9 \times 10^4$ cells m$^{-3}$. The phytoplankton abundance in the southern part of the study area was greater than in the northern part, and the greatest value was observed in the waters near the mouth of Laizhou Bay and Penglai (Figure 2B). The most dominant species in the whole study area was *Chaetoceros* sp., followed by *Ceratium fusus* and *Ceratium tripos* (Table 1). The most abundant genera were *Chaetoceros* and *Ceratium* (Figure 3B). In summer, dinoflagellates accounted for a much larger proportion of the phytoplankton abundance (55.3%) than in winter (4.4%).

Cluster analysis identified three phytoplankton groups in winter at the similarity of 15%. The sample from the site N1 (Group 1) was separated from the other samples at the similarity of only 15% (Figure 4A). And the samples of sites M3, L5, E4, K7, K8 (Group 2), which were along the Bohai Strait and between the northern and southern Bohai Strait, were separated from the rest samples (Group 3) at the similarity of 35%. ANOSIM indicated the difference in community composition among groups was significant ($R = 0.737, P = 0.001$, permutations = 999). SIMPER determined the most contributive species to the dissimilarity among groups. *Detonula pumila*, *Pseudo-nitzschia pungens* and C. sp. were much more abundant in Group 1 than in the other groups, while *A. octonarius* and *P. sulcata* were more abundant in Group 2 and Group 3, respectively. The average abundance of phytoplankton varied considerably among groups. Group 1 had the greatest abundance ($882.4 \times 10^4$ cells m$^{-3}$), followed by Group 2 ($251.6 \times 10^4$ cells m$^{-3}$), and the abundance of Group 3 ($60.2 \times 10^4$ cells m$^{-3}$) was the least. The diversity indices of the phytoplankton communities were compared among groups. Group 1 had the least species richness but relatively high Shannon-Wiener diversity and evenness, and

### Table 1. Dominant phytoplankton species in the central Bohai Sea and the Bohai Strait.

| Dominant species                  | Winter          | Dominant species                  | Summer           |
|-----------------------------------|-----------------|-----------------------------------|------------------|
| Dominance ($Y$)                   | Average abundance ($\times 10^4$ cells m$^{-3}$) | Dominance ($Y$) | Average abundance ($\times 10^4$ cells m$^{-3}$) |
| *Actinocyclus octonarius*         | 0.324           | 408.0                             | *Chaetoceros sp.* | 0.333           | 117.0              |
| *Paralia sulcata*                 | 0.168           | 248.0                             | *Ceratium fusus*  | 0.133           | 41.5               |
| *Coscinodiscus*                   | 0.059           | 73.9                              | *Ceratium tripos* | 0.074           | 23.1               |
| *Pseudo-nitzschia pungens*        | 0.027           | 90.9                              | *Thalassiothrix  frauenfeldii* | 0.046 | 21.6               |
| *Detonula pumila*                 | 0.025           | 170.1                             | *Ceratium furca*  | 0.043           | 24.0               |
|                                   |                 |                                   | *Pyrophacus steinii* | 0.031 | 10.8               |
|                                   |                 |                                   | *Chaetoceros curvisetus* | 0.027 | 20.5               |
|                                   |                 |                                   | *Coscinodiscus sp.* | 0.026 | 8.1                |
|                                   |                 |                                   | *Paralia sulcata*  | 0.025 | 14.4               |
Group 2 had the least Shannon-Wiener diversity and evenness (Table 2).

In summer, two distinct phytoplankton groups were identified at the similarity of 28% (Figure 4B). The samples of the sites P1, P3, B10, R7, L7, which were located near the Laizhou Bay and the city of Penglai, were classified as Group 1, and the rest samples were classified as Group 2. ANOSIM indicated the community composition between groups was significantly different ($R = 0.795$, $P = 0.001$, permutations = 999). SIMPER analysis indicated that C. sp., Ceratium furca, Thalassiothrix frauenfeldii, and Chaetoceros curvisetus were much more abundant in Group 1 than in Group 2, cumulatively contributing to 79% of the dissimilarity between two groups. The mean abundance of phytoplankton in Group 1 ($1.118.6 \times 10^4$ cells m$^{-3}$) was almost 9 times that in Group 2 ($128.6 \times 10^4$ cells m$^{-3}$). In Group 2, although $C. fuscus$, $C. tripos$ and Pyrophacus steinii did not have obvious advantage in absolute abundance compared to Group 1, their contribution to the total abundance in Group 2 (74.12%) was much higher. Therefore they were the most contributive species to the specificity of Group 2. In addition, the community represented by Group 1 had lower species richness, Shannon-Wiener diversity and evenness than Group 2 (Table 2).

Phytoplankton community composition and abundance were not only different between winter and summer in the whole studied area, but also significantly different between the north and south parts of the Bohai Strait in winter. The highest phytoplankton abundance in the strait was observed in the southeastern part of the strait in winter. The dominant phytoplankton species in the strait were A. octonarius and P. sulcata, and the most dominant genera were Actinocyclos and Paralia. The genus Paralia
dominated the phytoplankton community in the northern Bohai Strait, while the genus *Actinocyclus* had a higher dominance in the southern part (Figure 3A).

### Chlorophyll a and physicochemical factors

Environmental parameters were compared between the areas inhabited by different phytoplankton communities. In winter, the area inhabited by Group 1 had lower temperature and higher level of NO$_2$-N, NO$_3$-N and PO$_4$-P than the other areas (Table 3). Group 2 was in the area with the lowest level of dissolved inorganic nitrogen (DIN, including NO$_3$-N, NO$_2$-N and NH$_4$-N) and a slightly higher level of chlorophyll a (Table 3). In general, the level of DIN in summer was lower than winter (Table 3). In summer, the area inhabited by Group 1 was with greater water temperature and chlorophyll a concentration but generally lower nutrient level than where Group 2 inhabited (Table 3).

### Correlations between phytoplankton and environmental factors

The relationship between the phytoplankton communities and environmental factors was investigated using redundancy analysis (RDA). In winter, the most influential environmental factors on phytoplankton communities were NO$_2$-N, PO$_4$-P and SiO$_3$-Si (Figure 5A). A strong and positive correlation was shown between Group 1 and concentrations of NO$_2$-N and PO$_4$-P (Figure 5A). Group 2 was positively correlated with chlorophyll a concentration and negatively correlated with DIN and SiO$_3$-Si concentrations (Figure 5A). In contrast, there was no obvious correlation between Group 3 and the measured environmental factors (Figure 5A). The Spearman correlation between the phytoplankton abundance/chlorophyll a concentration and environmental factors was tested and the correlation between them in winter was weak, but a positive correlation was found between the total phytoplankton abundance and the chlorophyll a concentration in surface waters (Table 4). In summer, the main environmental factors influencing phytoplankton communities were salinity, NO$_3$-N and PO$_4$-P (Figure 5B). Group 1 was negatively correlated with salinity and PO$_4$-P concentration, but was positively correlated with DIN concentration. Group 2, in contrast, was positively correlated with salinity and PO$_4$-P concentration, but was negatively correlated with DIN concentration (Figure 5B). The total phytoplankton abundance in summer was positively correlated with NO$_3$-N and bottom water temperature and was negatively correlated with PO$_4$-P in both surface and bottom layers (Table 4). Also, the total abundance had a positive correlation with the chlorophyll a concentration in bottom waters (Table 4).

The correlation between specific species and environmental variables was also studied. A strong and positive correlation was shown between the abundance of *D. pumila*, *P. pungens* and *C. sp.* and the level of NO$_2$-N according to the RDA result (Figure 5C). *D. pumila* (444.9 $\times$ $10^4$ cells m$^{-3}$), *N. pungens* (185.8 $\times$ $10^4$ cells m$^{-3}$) and *C. sp.* (158.9 $\times$ $10^4$ cells m$^{-3}$) were particularly abundant at site N1 off the coast of Qinhuangdao in winter, contributing significantly to the total abundance (882.4 $\times$ $10^4$ cells m$^{-3}$) in this area. Meanwhile, an extremely high level of NO$_2$-N (105.8 $\mu$g/L) was detected at site N1, exactly matching with the area with the maximum phytoplankton abundance (Figure 6). Besides, *A. octonarius* showed

### Table 2. Diversity indices of the phytoplankton communities in the central Bohai Sea and the Bohai Strait.

|          | Group | Species richness ($D$) | Evenness ($J'$) | Shannon-Wiener ($H'$) |
|----------|-------|------------------------|----------------|-----------------------|
| Winter   | Group 1 | 1.327                  | 0.609          | 2.023                 |
|          | Group 2 | 2.351 ± 0.180          | 0.442 ± 0.050  | 1.668 ± 0.200         |
|          | Group 3 | 3.759 ± 0.176          | 0.549 ± 0.038  | 2.170 ± 0.159         |
| Summer   | Group 1 | 2.971 ± 0.208          | 0.419 ± 0.068  | 1.848 ± 0.280         |
|          | Group 2 | 3.807 ± 0.262          | 0.607 ± 0.026  | 2.467 ± 0.114         |

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a positive correlation with chlorophyll $a$ and PO$_4$-P concentrations, while $P. sulcata$ showed a positive correlation with water temperature in the surface and bottom layers but a negative correlation with DIN and PO$_4$-P concentrations (Figure 5C). In summer, the diatoms $C. sp., T. frauenfeldii$ and $C. curvisetus$ were positively correlated with the NO$_3$-N concentration in surface layer and were negatively correlated with PO$_4$-P concentration, while the dinoflagellates $C. fusus, C. tripus$ and $P. steinii$ were negatively correlated with the PO$_4$-P concentration in surface layer and were positively correlated with the NH$_4$-N concentration in bottom layer (Figure 5D).

**Discussion**

In winter, the phytoplankton community represented by Group 1 contained an abundance of $D. pumila, P. pungens$ and $C. sp.$ Among them, $D. pumila$ and $P. pungens$ were dominant species in the whole study area and peaked in Group 1. In contrast, $C. sp.$ was less dominant within the whole study area but was particularly abundant in Group 1. We detected that in winter, the NO$_2$-N and NO$_3$-P concentrations peaked at site N1, where the maximum phytoplankton abundance occurred. Meanwhile, a significant correlation was found between the abundance of these dominant species and NO$_2$-N concentration, followed by NO$_3$-N and PO$_4$-P concentrations. NO$_2$-N is a dynamic component of the marine nitrogen cycle that is produced and consumed by a variety of processes. Release by phytoplankton is a major source of nitrite in the waters where there are sufficient nitrate concentrations, high phytoplankton standing stock and suitable light conditions (Carlucci et al., 1970). The formation of primary nitrite maxima in the ocean has been attributed to the release of nitrite owing to an uncoupling of assimilatory nitrate and nitrite reduction in phytoplankton (Kuyper et al., 2018). Thus, the particularly high concentration of NO$_2$-N in the waters near Qinhuangdao could be attributed to the phytoplankton bloom, and the enrichment of N and P nutrients might be responsible for the phytoplankton bloom.

Since Bohai Sea is strongly affected by human activities in recent decades, severe eutrophication has been appearing more frequently in the Bohai Sea and the affected area has been expanding.
However, eutrophication used to occur in the three bays (Liaodong Bay, Bohai Bay, and Laizhou Bay) in the Bohai Sea but rarely in the central Bohai Sea and the Bohai Strait (Yu et al., 2013; Yu et al., 2015). It is important to study and monitor the changes of phytoplankton communities in the central Bohai Sea and the Bohai Strait, since phytoplankton is an important indicator of and responder to environmental changes (Luan et al., 2007). A few studies have reported a close relationship between *D. pumila* and nutrient levels. Yuan et al. (2014) found that *D. pumila* was one of the dominant phytoplankton species in spring in three bays at the coast of the Yellow Sea, China, and suggested its abundance was strongly related to silicate level (Yuan et al., 2014). Huo et al. (2018) reported that *D. pumila* dominated the phytoplankton communities in autumn in an eutrophic bay in the East China Sea, also showing a positive correlation to silicate concentration. *D. pumila* was also reported as a dominant species in summer in the East China Sea (Guo et al., 2011) and in winter in the Jiaozhou Bay, China (Guo et al., 2019), but it positively correlated with phosphate (Guo et al., 2011) and with phosphate.
temperature, transparency and stratification index (Guo et al., 2019), respectively. Our results showed that *D. pumila* bloomed in winter, closely related with the higher levels of DIN and phosphate, especially NO$_2$-N. *D. pumila* was also reported as common species causing spring and summer blooms in the Tagus estuary on the west coast of Europe (Gameiro et al., 2004; Brito et al., 2015). It seems that this species could bloom in different seasons and is very sensitive to nutrient concentration in the water column. Since *D. pumila* can potentially play a role in indicating the changes of nutrient level and eutrophication, its relationship with different nutrients deserves further research.

We noticed that the phytoplankton community composition and abundance were significantly different between the northern and southern parts of the Bohai Strait in winter. *P. sulcata*, which was more abundant in Group 3, dominated the phytoplankton community in the northern part of the strait, while *A. octonarius* was more dominant in Group 2 in the southern part of the strait, the same as in most of the study area. *P. sulcata* showed a positive correlation with water temperature in the surface and bottom layers but a negative correlation with DIN and PO$_4$-P concentrations (Figure 5C). The Bohai Strait is the only pathway connecting the Bohai Sea and the Yellow Sea and is crucial for water exchange between them (Wang et al., 2018). In winter, the Yellow Sea Warm Current (YSWC), which is characterized by high temperature and salinity, intrudes into the Bohai Sea through the northern strait and joins with the Bohai circulation. When the circulation reaches the Bohai Bay, it makes a counterclockwise turn and joins with the terrestrial fresh water, forming the Bohai Sea Coastal Current which flows out of the Bohai Sea through the southern strait (Guan, 1994; Fang et al., 2000; Wang et al., 2018). Thus, different water masses occupied the northern and southern Bohai Strait in winter, making the hydrodynamic condition differ greatly between the northern and the southern strait. *P. sulcata* is a benthic diatom that prefers the environment with lower light intensity and higher nutrient content, but can be transported to the upper layer of water column in autumn and winter due to the vertical mixing caused by winds (McQuoid and Nordberg, 2003; Guo, Li et al., 2014). According to Guo, Li et al. (2014), *P. sulcata* is not a species that can cause red tide. Our results showed that the region with higher abundance of *P. sulcata* was almost consistent with the region influenced by the YSWC. Meanwhile, the abundance of *P. sulcata* was closely related to higher water temperature, which was the primary feature of YSWC, suggesting that the predominance of *P. sulcata* in the northern strait might be closely related to the YSWC.

Furthermore, several studies suggested that *Coscinodiscus* spp., *P. sulcata* and dinoflagellates (mainly *N. miliaris* and *Ceratium* spp.) have gradually become more dominant in the phytoplankton communities in the Bohai Sea since 2000s (Yang et al., 2016a). We compared our data with historical data (Kang, 1991; Wang and Kang, 1998; Sun et al., 2002; Sun et al., 2004; Sun and Liu, 2005; Sun et al., 2008; Guo, Li et al., 2014; Yang et al., 2016a; Sun et al., 2016; Luan et al., 2018), and found that in recent years, the abundance of *Coscinodiscus* spp. in the Bohai Sea had not increased significantly compared with in 1980s (Figure 7C), but the abundance of *P. sulcata* in winter (Figure 7A) and dinoflagellates in summer (Figure 7A) had increased remarkably. Although the spatial variation of *P. sulcata* in winter 2013 in the Bohai Sea was significantly influenced by the hydrodynamic condition, the driver that caused the long-term increase of *P. sulcata* populations remains unknown and needs to be further studied.

In summer, the highest phytoplankton abundance occurred in the coastal area near Penglai and in the southern Bohai Strait, coinciding with the area inhabited by Group 1. The lower richness, Shannon-Wiener diversity and evenness were observed for Group 1 (Table 2), suggesting a less balanced distribution of abundance among species. According to Gharib et al. (2011), lower diversity and evenness of phytoplankton community are indicative of a less healthy ecosystem (more pollution). In such a community, only one or a few species grow rapidly in response to environmental changes such as nutrient enrichment, whereas most species stay in relatively low abundance. *C. sp.*, *T. frauenfeldii* and *C. curvisetus*, which contributed significantly to Group 1, had a positive correlation with the DIN concentration and the chlorophyll *a* concentration in bottom layer. In contrast, the dinoflagellates *C.*
|                | sNO$_2$-N | sNO$_3$-N | sNH$_4$-N | sPO$_4$-P | sSiO$_3$-Si | sT | sSal | sChl  | bNO$_2$-N | bNO$_3$-N | bNH$_4$-N | bPO$_4$-P | bSiO$_3$-Si | bT | bSal | bChl  |
|----------------|------------|------------|------------|------------|-------------|----|------|-------|------------|------------|------------|------------|-------------|----|------|-------|
| **Winter Abundance** |            |            |            |            |              |    |      |       |            |            |            |            |              |    |      |       |
| $R$            | -0.004     | -0.002     | -0.041     | 0.098      | -0.202      | -0.185 | -0.210 | 0.422* | 0.001      | -0.019     | 0.022      | 0.084      | -0.299      | -0.236 | -0.288 | 0.396  |
| $P$            | 0.985      | 0.993      | 0.841      | 0.635      | 0.322       | 0.375  | 0.314  | 0.040  | 0.996      | 0.927      | 0.917      | 0.685      | 0.138       | 0.256  | 0.162  | 0.056  |
| sChl $a$       |            |            |            |            |              |      |       |       |            |            |            |            |              |      |      |       |
| $R$            | 0.106      | 0.060      | 0.189      | -0.271     | -0.097      | -0.057 | -0.212 |        |            |            |            |            |              |      |      |       |
| $P$            | 0.623      | 0.780      | 0.376      | 0.199      | 0.653       | 0.791  | 0.321  |        |            |            |            |            |              |      |      |       |
| bChl $a$       |            |            |            |            |              |      |       |       |            |            |            |            |              |      |      |       |
| $R$            | —          | —          | —          | —          | —           | —     | —     | —     | —          | —          | —          | —          | —             | —    |      | —     |
| $P$            | —          | —          | —          | —          | —           | —     | —     | —     | —          | —          | —          | —          | —             | —    |      | —     |
| **Summer Abundance** |            |            |            |            |              |    |      |       |            |            |            |            |              |    |      |       |
| $R$            | 0.184      | 0.558**    | 0.153      | -0.481*    | 0.214       | 0.104  | -0.451* | 0.156  | 0.319      | -0.070     | 0.237      | -0.571**   | -0.264      | 0.503** | -0.475* | 0.404* |
| $P$            | 0.359      | 0.003      | 0.445      | 0.011      | 0.284       | 0.607  | 0.018  | 0.438  | 0.105      | 0.728      | 0.234      | 0.002      | 0.183       | 0.007  | 0.012  | 0.037  |
| sChl $a$       |            |            |            |            |              |      |       |       |            |            |            |            |              |      |      |       |
| $R$            | 0.398*     | -0.353     | 0.109      | 0.263      | 0.151       | -0.410* | -0.340  |        |            |            |            |            |              |      |      |       |
| $P$            | 0.040      | 0.071      | 0.588      | 0.186      | 0.453       | 0.034  | 0.083  |        |            |            |            |            |              |      |      |       |
| bChl $a$       |            |            |            |            |              |      |       |       |            |            |            |            |              |      |      |       |
| $R$            | —          | —          | —          | —          | —           | —     | —     | —     | —          | —          | —          | —          | —             | —    |      | —     |
| $P$            | —          | —          | —          | —          | —           | —     | —     | —     | —          | —          | —          | —          | —             | —    |      | —     |

**Note:**
*Correlation is significant at the 0.05 level,
**Correlation is significant at the 0.01 level. The initials “s” and “b” of the labels represent surface and bottom, respectively.
fusus, C. tripos, and P. steinii, which contributed significantly to Group 2, showed a negative correlation with the PO4-P concentration in surface layer and a positive correlation with the NH4-N concentration in bottom layer. Meanwhile, the area inhabited by Group 2 had a higher N:P ratio compared to the other area, suggesting that C. sp., T. frauenfeldii and C. curvisetus could have an advantage over other species in growing in the environment with a higher N:P ratio.

Dinoflagellates made up more than a half of the total phytoplankton abundance in summer, and species affiliated with genus Ceratium, especially C. fusus, C. tripos and C. furca) contributed the most to the total abundance. Consistent with the findings in other studies (Sun et al., 2002; Guo, Li et al., 2014; Luan et al., 2018), our data reflected that the abundance of dinoflagellates in summer in the Bohai Sea had been increasing dramatically (Figure 7B). In fact, a number of studies have already revealed that in recent decades, dinoflagellates, especially Ceratium spp., were frequently among the dominant species in summer in the Bohai Sea resulted from the greatly increased N:P ratio of the water column (Sun et al., 2002; Sun and Liu, 2005; Xu, 2011; Guo, Feng et al., 2014; Luan et al., 2018). Previous studies have revealed that diatoms preferred lower temperature and higher nutrient concentrations, while dinoflagellates were less sensitive to temperature and nutrient concentrations, but tended to prevail at low phosphorus and high N:P ratio conditions (Guo, Feng et al., 2014; Xiao et al., 2018). Particularly, the growth rates of two common dinoflagellate species in coastal waters, Ceratium furca and Ceratium fusus, were found increased readily under P-limited and high N:P ratio conditions through both field monitoring and laboratory culture experiments, indicating an advantage over other algal species in phosphorus-limited environments (Baek et al., 2008). Since the harmful blooms caused by dinoflagellates have more chances of occurrence during summer, it is suggested that summer was the best time to take measures to control the harmful blooms caused by dinoflagellates (Sun et al., 2002). And it is more important
to keep the N:P ratio of the Bohai Sea ecosystem more appropriate to prevent this type of harmful blooms.

Conclusions

This study revealed that the phytoplankton community composition and the dominant species in the central Bohai Sea and the Bohai Strait were significantly different between winter and summer. Diatoms dominated the phytoplankton communities in winter while diatoms and dinoflagellates were both dominant in summer. The community inhabited in the waters off the coast of Qinhuangdao city had a distinct community composition and extremely high abundance in winter related to the high level of DIN and phosphate. Influenced by different water masses, the phytoplankton community composition was also significantly different between the northern and southern parts of the Bohai Strait in winter. The phytoplankton communities with significant different abundances and dominant species in summer were more closely linked to the different N:P ratios in the environment. In summary, our results reflect that nutrient levels and hydrodynamic conditions together greatly influence the phytoplankton communities in the central Bohai Sea and the Bohai Strait.

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