Harmful Algae 62 (2017) 60–72

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Resolving the complex relationship between harmful algal blooms and environmental factors in the coastal waters adjacent to the Changjiang River estuary

Zheng-Xi Zhou[a,b], Ren-Cheng Yu[a,c,*], Ming-Jiang Zhou[a]

[a] Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] Laboratory of Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China

ARTICLE INFO

Article history:
Received 1 September 2016
Received in revised form 16 December 2016
Accepted 21 December 2016
Available online 4 January 2017

Keywords:
Harmful algal bloom
East China Sea
Principle component analysis
Path analysis

ABSTRACT

The sea area adjacent to the Changjiang River estuary is the most notable region for harmful algal blooms (HABs[1]) in China as both diatom and dinoflagellate blooms have been recorded in this region. Affected by the Changjiang diluted water (CDW[2]) and currents from the open ocean (i.e., Taiwan warm current, TWC[3]), the environmental conditions in the coastal waters adjacent to the Changjiang River estuary are quite complex. To obtain a better understanding of the mechanisms of HABs in this region, analyses based on field investigation data collected by the National Basic Research Priority Program (CEOHAB I[4]) were performed using principle component analysis (PCA[5]), multiple regression analysis (MRA[6]) and path analysis (PA[7]). The results suggested that phosphate and silicate are the major factors that directly affect the diatom bloom, while dissolved inorganic nitrogen (DIN[8]), temperature and turbidity are the factors that influence the dinoflagellate bloom. CDW and the TWC have different roles in affecting the two types of algal blooms. CDW, which has a high concentration of nitrate and silicate, is essential for the diatom bloom, while the intrusion of the TWC (mainly Kuroshio subsurface water that is rich in phosphate at the bottom) is critical for the maintenance of the dinoflagellate bloom. The results of this study offer a better understanding of the mechanisms of HABs in the East China Sea.

1. Introduction

The sea area adjacent to the Changjiang River estuary is the most notable region for harmful algal blooms (HABs) in China (Zhou and Zhu, 2006; He et al., 2013). A large number of HAB events have been reported in this region since the beginning of the 21st century. From 2000 to 2014, approximately 660 HAB events were recorded in the East China Sea (ECS[9]), and most of them occurred in the sea area adjacent to the Changjiang River estuary (data from the State Oceanic Administration of China, Wang and Wu, 2009). The HABs that recently appeared in the ECS were mainly formed by harmful dinoflagellates, such as *Prorocentrum donghaiense*,*Karenia mikimotoi* and *Alexandrium* spp. (Lu and Goebel, 2001; Tang et al., 2006; Zhou and Zhu, 2006). These extensive dinoflagellate blooms pose potent threats to marine ecosystems in the ECS and lead to serious impacts on marine fisheries and public health (Anderson et al., 1996, 2012; Zhou and Zhu, 2006).

Studies on harmful algal blooms over the last decade have indicated an apparent shift of major bloom-forming species from diatoms (such as *Skeletonema* spp.) to dinoflagellates in the ECS around the year 2000, and both diatom blooms and dinoflagellate blooms have been observed in spring (Guo et al., 2014; Zhou and Zhu, 2006). Diatom blooms generally occurred in March, followed

* Corresponding author at: Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China.
E-mail address: rcyu@qdio.ac.cn (R.-C. Yu).

[1] HABs: harmful algal blooms.
[2] CDW: Changjiang diluted water.
[3] TWC: Taiwan warm current.
[4] CEOHAB: A national basic research priority program "ecology and oceanography of harmful algal blooms in China".
[5] PCA: principle component analysis.
[6] MRA: multiple regression analysis.
[7] PA: path analysis.
[8] DIN: dissolved inorganic nitrogen.
[9] ECS: East China Sea.

http://dx.doi.org/10.1016/j.hal.2016.12.006
1568-9883/

by extensive dinoflagellate blooms lasting from May to June. Previous studies indicated that HABs were affected by many environmental factors and hydrodynamic processes (Chen et al., 2003; Acevedo-Trejos et al., 2013), and nutrient over-enrichment was considered to be the most important driver for large-scale blooms in highly eutrophic systems (Anderson et al., 2002). In addition, the formation and distribution of HABs were also affected by temperature, salinity, and photosynthetically active radiation (Gao and Song, 2005). To date, most studies have focused on the effects of a single factor or the combined effects of several factors on HABs (Zhu et al., 2009b). There is little knowledge concerning the effects of environmental factors on the two different types of microalgal blooms in the ECS.

The coastal waters adjacent to the Changjiang River estuary, which are influenced by both Changjiang diluted water (CDW) and the Taiwan warm current (TWC), are very complex in terms of their hydrological and hydrodynamic conditions (Qi et al., 2014). CDW is characterized by low-salinity (generally lower than 29), a high nutrient concentration and a high N/P ratio, and often imparts strong stratification and phosphorus stress on the phytoplankton community in spring (Zhang et al., 2007a; Liu et al., 2013). The TWC, which is a warm current flowing northward along the southeast coast of China, is composed of two different water masses during spring and summer. The surface water of the TWC is formed by the mixing of Taiwan Strait water and Kuroshio surface water, while the deep water of the TWC is mainly from the subsurface water of the Kuroshio current in the sea area northeast of Taiwan (Yang et al., 2012; Lian et al., 2016). The intrusion of Kuroshio subsurface water, as well as the prevailing monsoon during summer, was believed to be major factors driving the coastal upwelling in the sea area adjacent to the Changjiang River estuary (Zhang et al., 2007b). The upwelling can bring high-salinity seawater that is rich in phosphate to the surface during spring and summer time (Yang et al., 2013), which will affect hydrodynamic processes, such as stratification, and the distribution pattern of nutrients in this region (Chen et al., 2004). Therefore, both CDW and the TWC are important for controlling the physical, chemical and biological factors in the sea area adjacent to the Changjiang River estuary. To link these factors to the distribution and dynamics of algal blooms in this region, it is necessary to understand the formation mechanisms of HABs and predict the long-term changes of HABs in this region.

Thus, this study focus on: (1) determining the major factors regulating the distribution and dynamics of diatom and dinoflagellate blooms; (2) evaluating the effects of CDW and the TWC on the occurrence of HABs in the coastal waters adjacent to the Changjiang River estuary. To accomplish these goals, a set of statistical methods, including principal component analysis (PCA), multiple regression analysis (MRA) and path analysis (PA), were employed to analyze data collected during field surveys performed by the National Basic Research Priority Program (CEOHAB I). PCA was carried out to classify the environmental factors. MRA was applied to establish multiple regression equations. PA, which can separate direct and indirect effects of independent variables (Light and Marchetti, 2007; Wells et al., 2008; Seo et al., 2010), was performed to compare the roles of different environmental factors. Thus, PCA, MRA and PA were applied to resolve the complex relationships between the various environmental factors and HABs in the sea area adjacent to the Changjiang River estuary.

2. Materials and methods

2.1. Data sources

A data set including chlorophyll-*a*, nutrients, temperature, turbidity and salinity was compiled from cruises performed by CEOHAB I in 2005 (Fig. 1). Sampling sites were located in the sea area adjacent to the Changjiang River estuary (27°14′–30°32′N and 121°00′–123°23′E). The cruises were organized along seven transects (RA, RB, ZA, ZB, ZC, ZD and ZE) from March 27 (Julian Day 86) to June 17 (Julian Day 168) in the ECS.

The vertical profiles of temperature, salinity and turbidity were measured with a conductivity-temperature-depth recorder (SBE37-CTD[10]) and a multi parameter sonde (YSI6600) (Zhu et al., 2009a). Water samples were collected at different depths with a 20-L Niskin bottle at each sampling site. Phytoplankton cells in water were filtered onto glass fiber membranes (Whatman GF/F), and chlorophyll-*a* was extracted with acetone (90%) and measured using a fluorometer (Turner-Designs-Model 10) (Zhou et al., 2004). Water samples for nutrient analysis were filtered through glass fiber membranes and analyzed using colorimetric methods as described in Zhang et al. (2008). The results of the investigation regarding the nutrients and hydrological parameters were published in Zhang et al. (2008) and Zhu et al. (2009b).

The major bloom-forming microalgal species were identified with light microscopes based on their morphological features (Xie et al., 2008). During the cruises, a diatom bloom occurred in early spring, lasting from March 27 to April 12 (Julian Day 86 to 102), and the major bloom-forming species were *Skeletonema* spp. and *Thalassiosira* spp. The dinoflagellate bloom occurred from May 29 to June 17 in early summer (Julian Day 148 to 168), and the major bloom-forming species were *K. mikimotoi* and *P. donghaiense*. Data collected at the surface layer (above 10 m depth) were selected to study the influence of different environmental factors on the diatom and dinoflagellate blooms, and the chlorophyll-*a* data of discrete water sample measured in the laboratory with a fluorometer was used in the statistical analysis.

2.2. Data analysis

Data of chlorophyll-*a* were log 10-transformed before analysis to meet the assumptions of normality, homogeneity of variance, and linearity of the analyses. Data of the environmental factors with different units were standardized to the range of 0–1, and a collinearity diagnosis was performed to filter out environmental factors that had significant collinearity with other independent variables.

PCA, MRA and PA were then applied to study the relationships between the blooms and different environmental factors. PCA was performed to determine the major factors affecting the distribution and dynamics of the blooms. MRA was then conducted to establish multiple regression equations, and the regression coefficients in the regression models were used to calculate the path coefficients.

2.2.1. Principal component analysis

PCA was used to classify the dominant environmental factors and define the effects of the hidden variables (major components) on the biomass of phytoplankton in the study area. The standardized environmental factor datas, including dissolved inorganic nitrogen (DIN), phosphate, silicate, temperature, turbidity and salinity, were used for PCA, and the covariance matrix and its eigenvectors were calculated. The eigenvectors were ordered by the eigenvalues from the highest to the lowest, which assigned the components an order of significance. Only the components whose accumulative contribution rate reached 85 percent were taken into account. Each component had its own characteristics according to the corresponding environmental factors.

[10] CTD: conductivity-temperature-depth recorder.

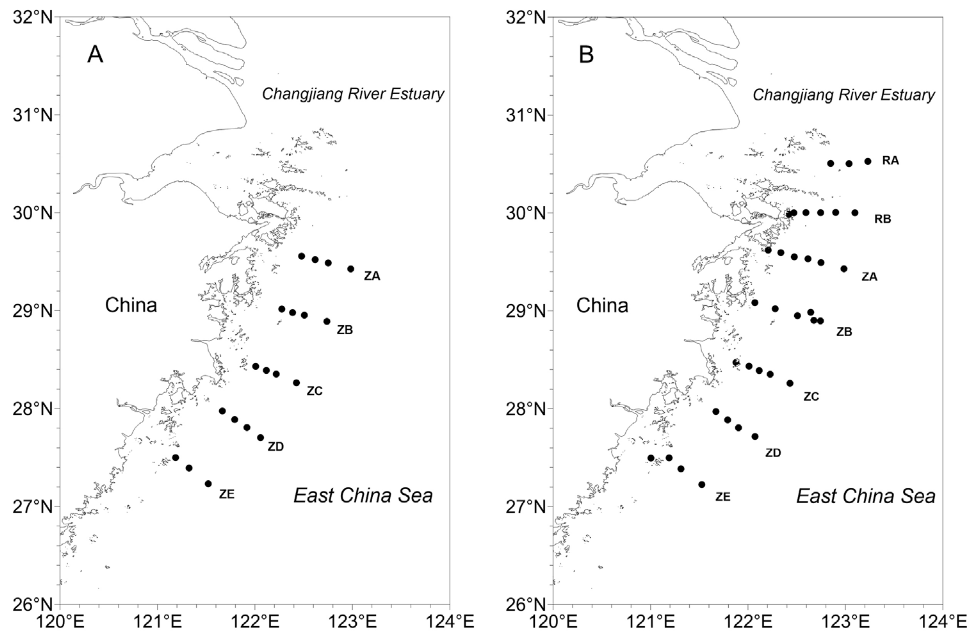

Fig. 1. Sampling sites in the sea area adjacent to the Changjiang River estuary during the diatom bloom (a) and dinoflagellate bloom (b).

2.2.2. Multiple regression analysis

Multiple regression analysis was performed to develop a regression model between the biomass of phytoplankton and different environmental factors. The chlorophyll-*a* concentration was set as the dependent variable for MRA. To avoid the influence of collinearity on the regression analysis, independent variables were selected by comparing the parameters (condition index, tolerance and variance inflation factor) of the collinearity diagnostics and coefficients of determination for each regression model.

A simple correlation analysis was performed to estimate the correlations between the dependent variable and hypothetical independent variables. Then, multiple regression analysis was performed using the least squares method. The basic function of the multiple regression analysis is listed below.

$$chla = \beta_0 + \beta_1 DIN + \beta_2 PO_4 + \beta_3 SiO_3 + \beta_4 T + \beta_5 Turbidity + \beta_6 Salinity$$

To verify whether the multiple regression results were statistically significant, an *F*-test was used to check the regression model and a *t*-test was used to check the partial regression coefficients. The Pearson correlation coefficients were then calculated, and the calculated *P* values were used as the index. If $P<0.10$, the regression model was considered significant and the regression coefficients could be used to estimate the relative contribution of each independent variable. All of the computational processes were performed with SPSS (16.0) software.

2.2.3. Path analysis

Path analysis, which allows for the separation of direct and indirect effects, was adopted to further resolve the effects of the different environmental factors. A conceptual model for path analysis was developed (Fig. 2A) first based on the effects of the different environmental factors on the biomass of phytoplankton, and six environmental factors were considered in this model. Since silicate cannot be used by dinoflagellates, it was not considered in resolving the effects of the environmental factors on the dinoflagellate bloom. The path coefficients, which were calculated by standardizing the partial regression coefficients, were used to describe the effects of each independent variable and sort their contributions (Petraitis et al., 1996). The path coefficients were divided into direct coefficients (P_i) and indirect coefficients (P_{ij}). The direct coefficients, which were equal to the standard regression coefficients, were calculated using the following formula.

$$P_i = \beta_i \frac{S_i}{S_{chla}}$$

where P_i is the direct coefficient, β_i is the regression coefficient calculated from the regression analysis, S_i is the standard deviation of each independent variable, and S_{chla} is the standard deviation of the dependent variable.

The indirect path coefficients defined as the arithmetic products of the direct path coefficients, were calculated using the following formula.

$$P_{ij} = P_i \times r_j$$

where P_{ij} is the indirect coefficient, P_i is the direct coefficient, and r_j is the correlation coefficient.

All analyses were performed with SPSS (16.0) software.

3. Results

3.1. Characterization of variables

The statistics of the different environmental variables, including the mean, minimum, maximum, standard deviation (SD), coefficient of variation (CV) and sample numbers (N), measured during the two cruises are listed in Table 1. The maximum of chlorophyll-*a* during the diatom bloom (25.7 μg/L) was much lower compared to during the dinoflagellate bloom (70.3 μg/L), and the variability of chlorophyll-*a* during the diatom bloom (0.4–25.7 μg/L) was also smaller. Nutrient concentrations were higher during the diatom bloom (DIN 15.0 μmol/L; phosphate 0.7 μmol/L; silicate 17.5 μmol/L) than during the dinoflagellate bloom (DIN 8.3 μmol/L; phosphate 0.3 μmol/L; silicate 14.9 μmol/L). The seawater temperature during the diatom bloom (12.1 °C) was much lower than during the dinoflagellate bloom (21.0 °C). The salinity during the two different microalgal blooms was nearly the same. The turbidity during the diatom bloom (8.3 ntu) was higher than during the dinoflagellate bloom (4.1 ntu). Among the different environmental factors,

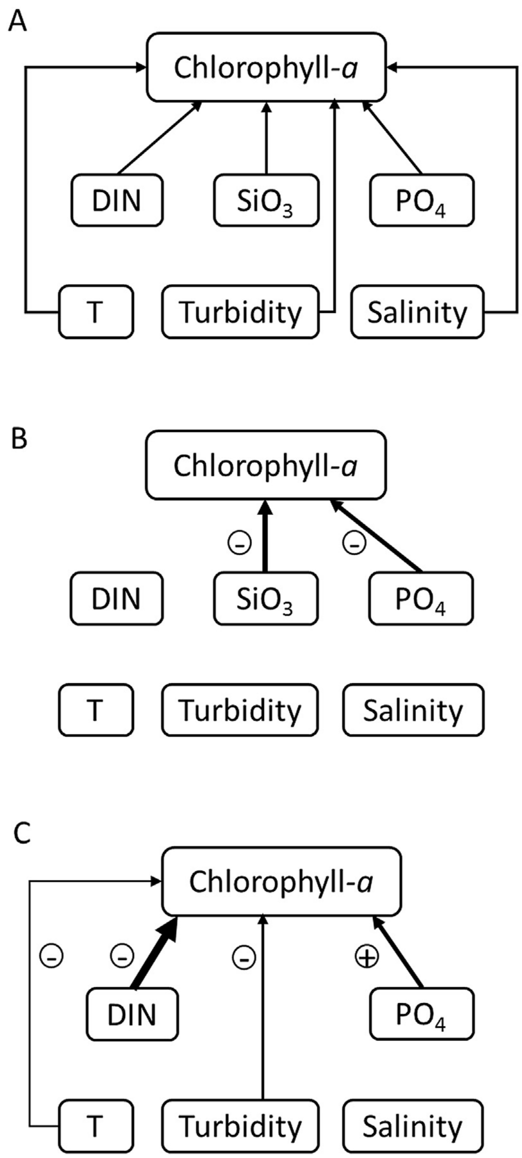

Fig. 2. The proposed conceptual path model (A) and significant direct paths ($P \leq 0.05$) between the environmental factors and diatom bloom (B) or dinoflagellate bloom (C). Only the signs of the significant path coefficients (values are given in Appendix F) are shown here. DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature. The bold arrows reflect the stronger effects.

temperature and salinity had relatively small variabilities, while nutrients and turbidity exhibited much greater variations.

The patterns of chlorophyll-*a*, DIN, phosphate, silicate, temperature, turbidity and salinity in the sea area adjacent to the Changjiang River estuary during the two blooms in 2005 are illustrated in Figs. 3–5 . The vertical profiles of these variables from a selected transect (ZA) are shown in Fig. 6.

The biomass, as indicated by the level of chlorophyll-*a*, was much lower during the diatom bloom than during the dinoflagellate bloom (Fig. 3, observe the different scales of the bars). The distributions of chlorophyll-*a* during the two blooms were both confined in the shallow waters along the coast. According to the vertical profiles of chlorophyll-*a* in section ZA during the diatom bloom and dinoflagellate bloom, the maximum values of chlorophyll-*a* appeared at the surface between depths of 0 m–20 m.

Nutrients (DIN, phosphate and silicate) exhibited similar distribution patterns at the surface during the diatom bloom (Fig. 4), the concentration of which decreased from inshore to offshore. The isolines of the nutrients were generally parallel to the shoreline. However, during the dinoflagellate bloom, this pattern was less evident for DIN and phosphate. Only silicate exhibited a similar distribution pattern. There were apparent decreases of both the DIN concentration and phosphate concentration from the diatom bloom to the dinoflagellate bloom, while the change of the silicate concentration was less obvious and the ranges of the silicate concentration were almost identical during the two stages of the different blooms. The vertical profiles of DIN and silicate were similar, and the concentration decreased with increasing depth and distance from the shoreline (Fig. 6). However, the vertical profile of phosphate was different from DIN and silicate, and the bottom water within the region from 122.5°E to 122.7°E was rich in phosphate.

The pattern of turbidity and nutrients were similar and decreased with the increasing distance from the shoreline, and maximum values were observed during the diatom bloom (Fig. 5). The vertical profile of turbidity showed a near-bottom maximum in the inshore coastal waters. Both temperature and salinity increased from inshore waters to offshore waters at the surface, and there was an apparent increase in temperature from the diatom bloom to the dinoflagellate bloom. The vertical profiles of temperature changed significantly during the two stages of blooms, which increased with depth during the diatom bloom, while it decreased with the depth during the dinoflagellate bloom (Fig. 6). The vertical profile of salinity remained relatively constant during the two blooms, but an apparent intrusion of high-salinity seawater was observed during the dinoflagellate bloom.

3.2. PCA analysis

Data processing was performed before statistical analysis, as shown in Table 2. The interferences of different units were removed from the variables through data standardization, and the normalized data of chlorophyll-*a* met the assumption of normality, homogeneity of variance and linearity of the analysis for MRA.

Processed data were partitioned into two stages (the diatom bloom and the dinoflagellate bloom), and the PCA results for the two different stages are shown in Appendix B. During the diatom

Table 1
Mean, range (min, max), standard deviation (SD), coefficient of variation (CV, %) and number (N) of chlorophyll-*a* and the associated environmental factors as observed during the diatom bloom and dinoflagellate bloom in 2005.

Variables	Diatom bloom						Dinoflagellate bloom					
	Mean	Min	Max	SD	CV (%)	N	Mean	Min	Max	SD	CV (%)	N
Chl *a* (μg/L)	3.5	0.4	25.7	5.0	142.6	158	6.1	0.0	70.3	10.3	168.6	165
DIN (μmol/L)	15.0	3.9	42.5	6.7	45.0	158	8.3	1.3	27.1	5.8	70.0	165
PO_4(μmol/L)	0.7	0.1	1.3	0.2	31.1	158	0.3	0.0	0.9	0.3	86.7	165
SiO_3 (μmol/L)	17.5	3.6	34.0	6.8	38.8	158	14.9	1.3	32.0	6.3	42.5	165
T (°C)	12.1	9.2	16.7	1.8	15.1	158	21.0	17.5	25.7	2.0	9.7	165
Turbidity (ntu)	8.3	0.4	45.2	9.4	113.6	158	4.1	0.1	31.0	5.1	125.8	165
Salinity	31.1	22.1	34.0	1.8	5.9	158	31.5	24.9	35.0	2.3	7.4	165

Chl *a*, chlorophyll-*a* concentration; DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

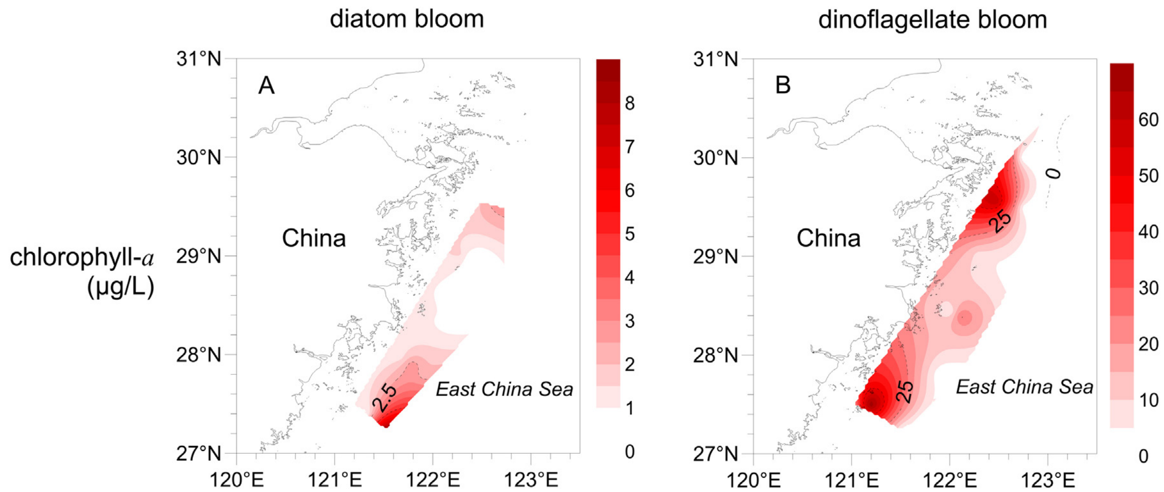

Fig. 3. The distribution of chlorophyll-*a* (μg/L) at the surface during the diatom bloom (A) in early spring from March 27 to April 12 and during the dinoflagellate bloom (B) in early summer from May 29 to June 17.

bloom, the first two components calculated represented 72% of the total variation, and the first principle component alone explained 50% of the total variation. The correlation coefficient of each variable and its related component indicated that DIN, silicate, temperature and salinity had a higher capacity in the first principle component, while phosphate and turbidity had high capacity in the second component (Fig. 7A). According to the results of the principle component analysis performed during the dinoflagellate bloom, the first two components represented 77 percent of the total variation and the first principle component alone explained 50 percent of the total variation. The first principle component mainly represented the effects of DIN, phosphate, silicate, temperature and turbidity, and the second principle component represented the influence of salinity (Fig. 7B). In general, all of the environmental factors, including DIN, phosphate, silicate, temperature, turbidity and salinity, should be considered.

Salinity, as a dominant index reflecting the mixing process of freshwater and seawater, had intricate relationships with the other variables (the Pearson correlation coefficients are shown in Appendix C). During the diatom bloom, salinity had negative relationships with DIN and silicate, and a positive relationship with temperature. During the dinoflagellate bloom, salinity had a significant positive relationship with phosphate and negative relationships with silicate and temperature.

Table 2
Mean, range (min-max), standard deviation (SD), coefficient of variation (CV, %) and number (N) of standardized data of chlorophyll-*a* and different environmental factors during the diatom bloom and dinoflagellate bloom in 2005.

Variable	Diatom bloom						Dinoflagellate bloom					
	Mean	Min	Max	SD	CV (%)	N	Mean	Min	Max	SD	CV (%)	N
Chl *a* (μg/L)	0.0	−1.0	3.0	1.0	1.0	158	0.0	−4.0	2.0	1.0	1.0	165
DIN (μmol/L)	0.0	−1.6	4.1	1.0	1.0	158	0.0	−1.2	3.2	1.0	1.0	165
PO_4(μmol/L)	0.0	−2.6	2.4	1.0	1.0	158	0.0	−1.0	2.3	1.0	1.0	165
SiO_3 (μmol/L)	0.0	−2.0	2.4	1.0	1.0	158	0.0	−2.1	2.7	1.0	1.0	165
T (°C)	0.0	−1.6	2.5	1.0	1.0	158	0.0	−1.7	2.3	1.0	1.0	165
Turbidity (ntu)	0.0	−0.8	3.9	1.0	1.0	158	0.0	−0.8	5.3	1.0	1.0	165
Salinity	0.0	−4.9	1.6	1.0	1.0	158	0.0	−2.9	1.5	1.0	1.0	165

Chl *a*, chlorophyll-*a* concentration; DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Table 3
Covariance values between different environmental variables.

Bivariate relationships	Total covariance (A)	Correlation coefficient (B)	Total explained covariance (multiple regression) (C)	Residual covariance (D = A − B)	Covariance due to multi-collinearity (E = B − C)
DIN-dia	−0.09	−0.09	−0.05	0.00	−0.04
PO_4-dia	−0.30	−0.30	−0.29	0.00	−0.01
SiO_3-dia	−0.30	−0.30	−0.75	0.00	0.44
T-dia	−0.04	−0.04	−0.11	0.00	0.07
Turbidity-dia	−0.25	−0.25	0.03	0.00	−0.28
Salinity-dia	−0.14	−0.14	−0.60	0.00	0.45
DIN-dino	−0.24	−0.24	−0.20	0.00	−0.04
PO_4-dino	−0.69	−0.69	−0.66	0.00	−0.03
SiO_3-dino	0.05	0.05	0.39	0.00	−0.34
T-dino	0.49	0.49	−0.04	0.00	0.53
Turbidity-dino	−0.24	−0.24	−0.04	0.00	−0.21
Salinity-dino	−0.70	−0.70	−0.21	0.00	−0.49

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature; dia, diatom; dino, dinoflagellate.

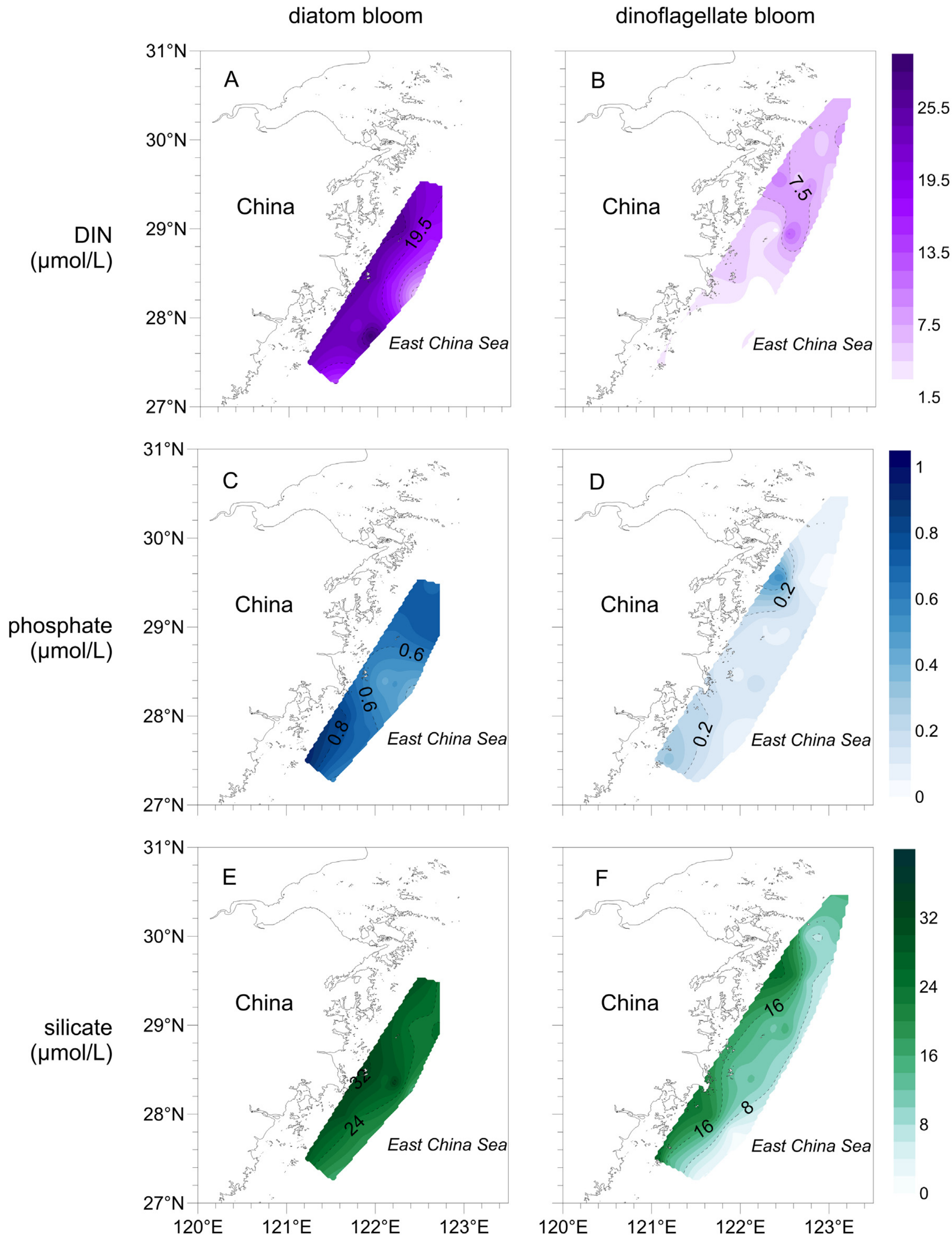

Fig. 4. The distribution of dissolved inorganic nitrogen (DIN, μmol/L), phosphate (μmol/L) and silicate (μmol/L) during the diatom bloom (A, C, E) from March 27 to April 12 and during the dinoflagellate bloom (B, D, F) from May 29 to June 17.

3.3. MRA analysis

The results of the variance analysis and multiple regression analysis are shown in Table 3. The values of residual covariance (equal to the deviation of the total covariance and the sum of the explained covariance) were close to zero, which means that the direct effects and indirect effects were acceptable in explaining the relationships between the environmental factors and chlorophyll-*a*.

The covariances due to multi-collinearity indicated that there were significant collinearities between the independent variables. A collinearity diagnosis was then performed to select the corresponding variables, and some variables were removed according to the determinant coefficients of each regression

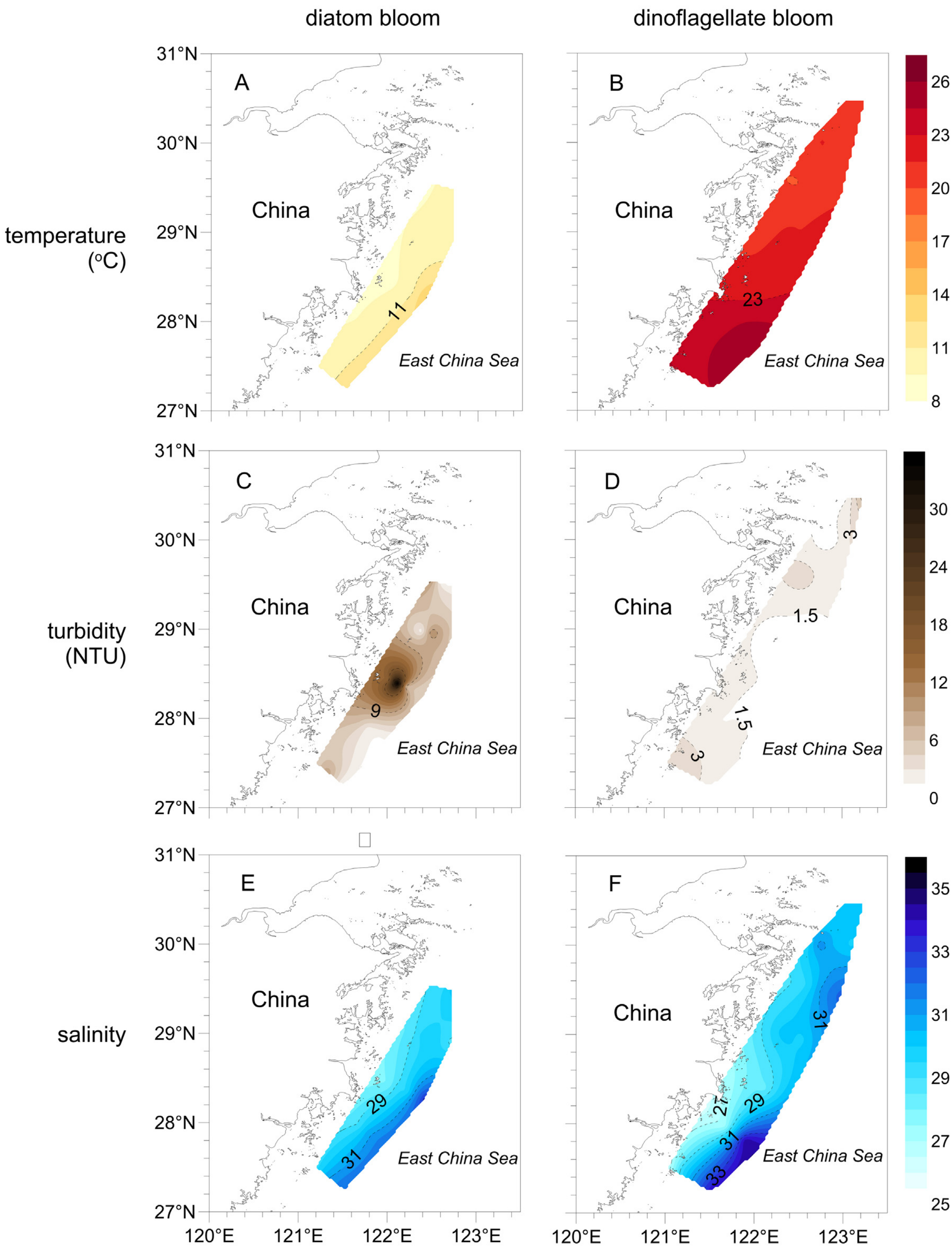

Fig. 5. Patterns of temperature (°C), turbidity (ntu) and salinity during the diatom bloom (A, C, E) from March 27 to April 12 and during the dinoflagellate bloom (B, D, F) lasting from May 29 to June 17.

model, which filtered out the causative variables in a stepwise manner. The results (shown in Appendix E) indicated that removing turbidity or salinity did not significantly change the determinant coefficient. Therefore both turbidity and salinity were removed from the independent variables during the diatom bloom. Using the same method, salinity was filtered out during the dinoflagellate bloom. The regression equations established for the diatom bloom and dinoflagellate bloom are shown in Appendix F.

3.4. Path analysis

The path coefficients for each environmental factor at the surface during the diatom bloom are illustrated in Fig. 2B (the values are shown in Appendix F). During the diatom bloom, only two variables exhibited significant direct effects on chlorophyll-*a* at the surface. Silicate is the most significant variable (−0.74, $P < 0.01$), which explained 57% of the total variation of

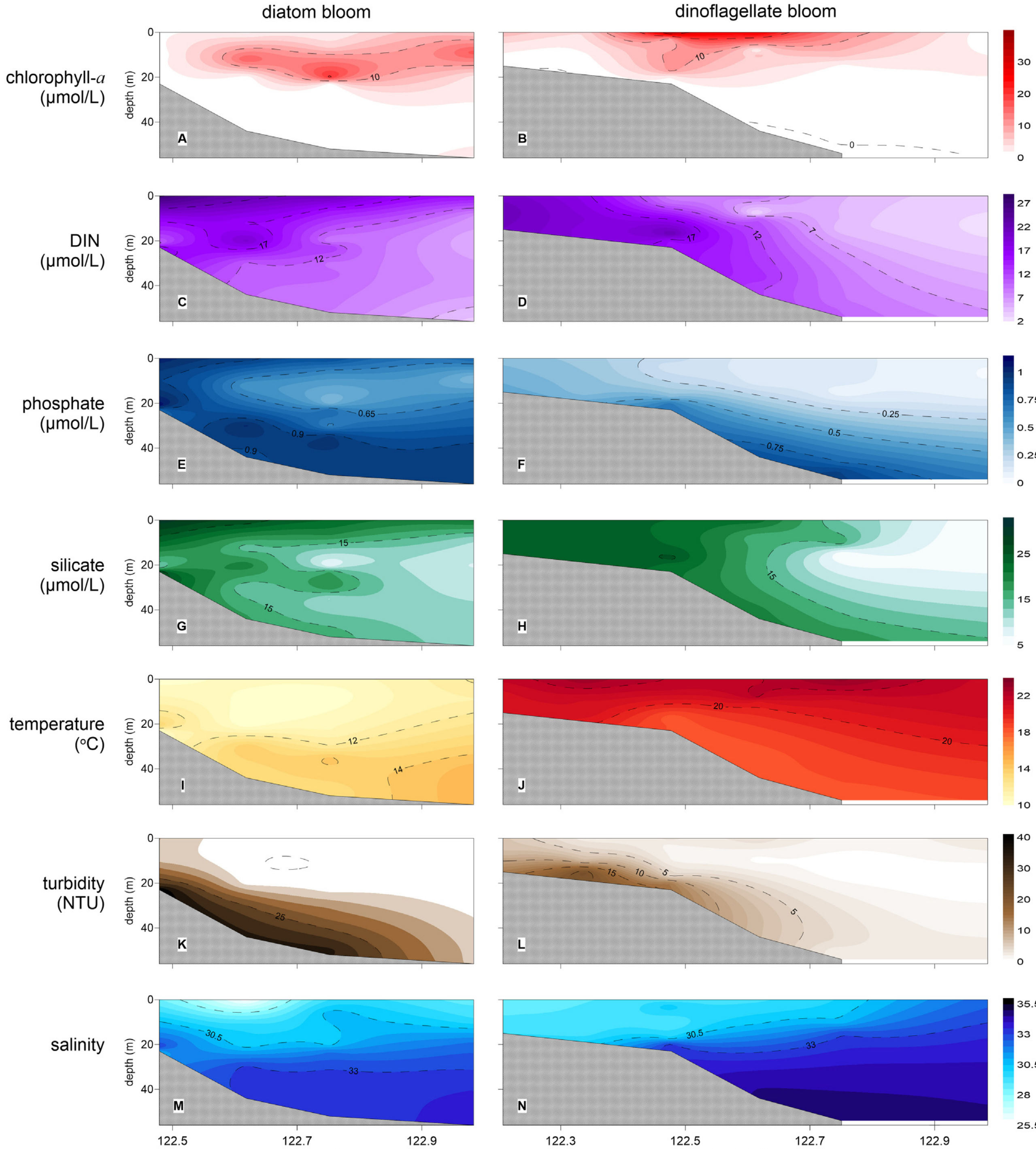

Fig. 6. Vertical profiles of chlorophyll-*a* (μg/L), DIN (μmol/L), phosphate (μmol/L), silicate (μmol/L), temperature (°C), turbidity (ntu) and salinity at transects ZA during the diatom bloom (A, C, E, G, I, K, M) from March 27 to April 12 and during the dinoflagellate bloom (B, D, F, H, J, L, N) from May 29 to June 17.

chlorophyll-*a*. Phosphate also directly influenced chlorophyll-*a* (−0.18, $P < 0.01$), but the effect was less significant. Temperature ($r = -0.48$, $P < 0.001$), DIN ($r = -0.41$, $P < 0.001$) and salinity ($r = -0.38$, $P < 0.001$) showed no significant direct influences but notable indirect influences through silicate and phosphate.

The path coefficients for each factor during the dinoflagellate bloom are illustrated in Fig. 2C (the values are shown in Appendix F). According to the results of the PA, the direct and indirect influences of each environmental factor were sorted. At the surface layer, four variables showed significant direct effects. DIN had the most significant direct effects on chlorophyll-*a* followed by phosphate (0.21, $P < 0.05$), turbidity (−0.20, $P < 0.01$) and temperature (−0.18, $P < 0.01$). DIN alone could explain 54 percent of the chlorophyll-*a* variability during the dinoflagellate bloom (0.70, $P < 0.01$).

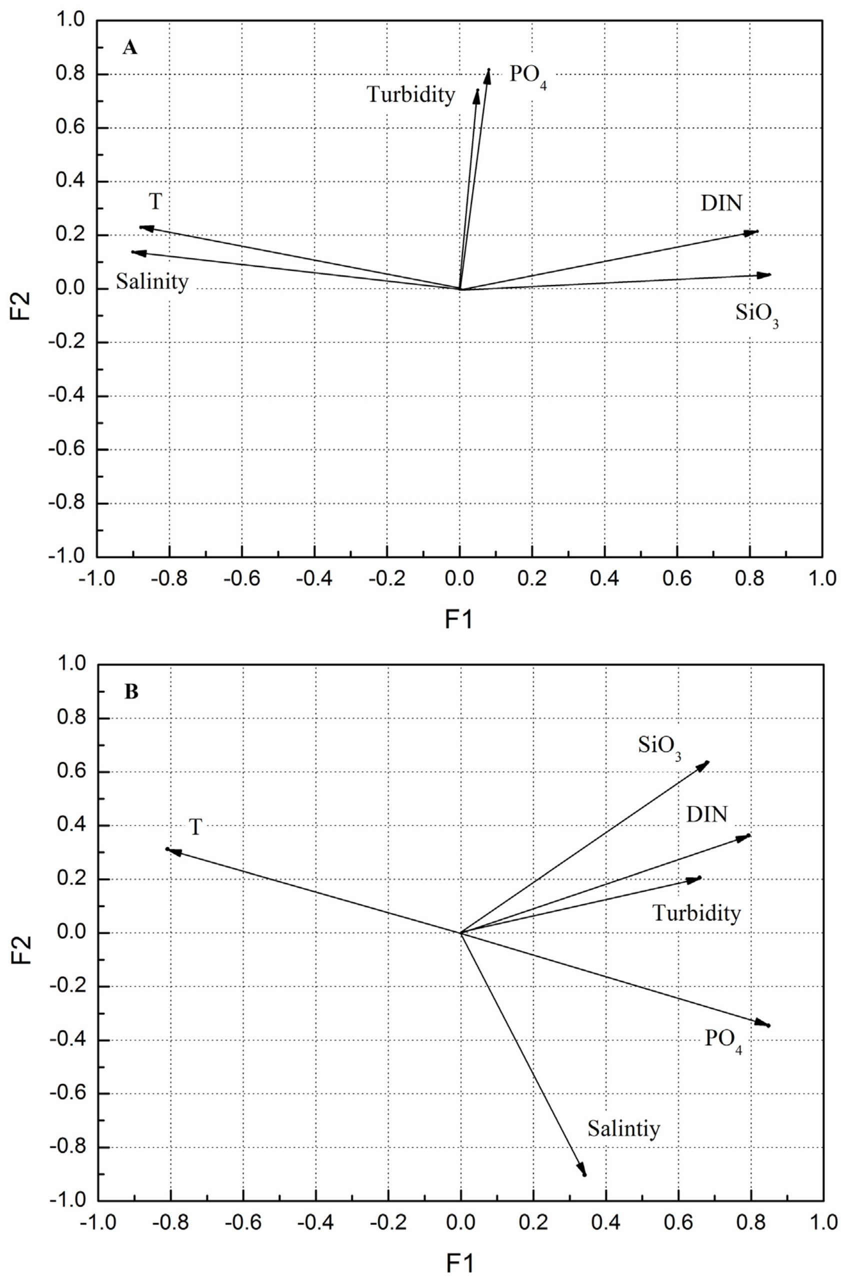

Fig. 7. Plot of principle component analysis during the diatom bloom (A) and dinoflagellate bloom (B). F1, the first component; F2, the second component.

4. Discussion

4.1. Factors controlling different blooms in the coastal waters adjacent to the Changjiang River estuary

In the sea area adjacent to the Changjiang River estuary, environmental factors, such as nutrients, temperature, salinity and turbidity, have various effects on the distribution and dynamics of algal blooms. According to the results of MRA and PA, the roles of the different environmental factors were evaluated during both the diatom bloom and dinoflagellate bloom.

DIN exhibited no direct effects on chlorophyll-*a* during the diatom bloom, but it became the major factor determining chlorophyll-*a* during the dinoflagellate bloom. Although DIN is critical for the growth of diatoms, the concentration of DIN was high enough to support the diatom bloom (Zhang et al., 2008). Therefore, DIN showed no direct effects on chlorophyll-*a* during the diatom bloom. Along with the development of the dinoflagellate bloom, the DIN concentration gradually decreased and became an important factor affecting the growth of dinoflagellates. During the dinoflagellate bloom, DIN alone explained 70 percent of the chlorophyll-*a* variation. The negative correlation between DIN and chlorophyll-*a* probably reflects a large amount of DIN consumed in the area where dinoflagellates bloomed. The rapid decrease of the DIN concentration would limit the growth of dinoflagellates and finally lead to the decline of the dinoflagellate bloom in this region.

Phosphate had notable effects on chlorophyll-*a* during the diatom bloom, although not as significant as silicate. The negative correlation between phosphate and chlorophyll-*a* at the surface suggested that much phosphate had been consumed to support the diatom bloom. Due to the relatively low concentration of phosphate and the high N/P ratio in seawater, phosphate often becomes a limiting factor for the growth of diatoms since bloom-forming diatoms, such as *Skeletonema costatum* and *Thalassiosira* spp., are susceptible to nutrient stress (Li and Wang, 2012; Tiselius and Kuylenstierna, 1996). It has been suggested that phosphate limitation and a high N/P ratio have played a dominant role in the decline of diatom blooms and the succession of different blooms (Huang et al., 2013). However, during the dinoflagellate bloom, phosphate had notable positive correlation with chlorophyll-*a* at the surface. Previous studies have indicated that coastal upwelling, which could bring phosphate-rich bottom water to the surface, nearly co-occurs with dinoflagellate blooms in early summer (Liu et al., 2013). The vertical distribution of phosphate also indicated the presence of phosphate-rich seawater at the bottom during the dinoflagellate bloom. Therefore, supply of "new" phosphate into seawater would promote the growth of dinoflagellates and have positive effects on chlorophyll-*a* during the dinoflagellate bloom.

Silicate is necessary for the growth of diatoms, but not for dinoflagellates. Thus, the effects of silicate on chlorophyll-*a* during the dinoflagellate bloom were not considered. Silicate had a negative correlation with chlorophyll-*a* during the diatom bloom, probably due to the consumption of silicate by diatoms. This negative correlation resulted in a low concentration of silicate in the area with high level of chlorophyll-*a*. Due to the supply of silicate from the CDW in the coastal waters adjacent to the Changjiang River estuary, the distribution and concentration of silicate did not change much during the two different types of algal blooms.

Temperature is probably the most widely recognized physical factor affecting microalgae growth, but the relationship between temperature and algal blooms is not always straightforward (Fu et al., 2012). According to the analysis in this study, temperature had no effects on chlorophyll-*a* during the diatom bloom, but it had a notable negative correlation with the dinoflagellate bloom. During the investigations, the water temperature at the surface continued to increase beyond the range of the optimal temperature for the growth of dinoflagellates in early summer (Xu et al., 2010). The increase in temperature could be another important reason accounting for the decline of the dinoflagellate bloom.

Light is a key factor affecting the growth of phytoplankton (Oguz and Merico, 2006). The shading effects of suspended materials in seawater (measured as turbidity) inhibit the growth of phytoplankton by limiting the photosynthetically active radiation (Li et al., 2005). In this study, turbidity showed a slight negative correlation with chlorophyll-*a* during the dinoflagellate bloom, which reflects the potential role of turbidity on the growth of algae.

Salinity showed no significant direct effects on either the diatom bloom or dinoflagellate bloom in this study. However, salinity exhibited strong indirect effects on the two blooms through other environmental factors. The strong correlations between salinity and other environmental factors (Appendix C) suggested that these factors co-vary with salinity. During the diatom bloom, salinity had notable indirect effects on chlorophyll-*a* via silicate at the surface. The negative correlation between silicate and salinity suggested that freshwater discharge from the Changjiang River supports silicate for diatom bloom. During the dinoflagellate bloom, salinity had indirect effects through phosphate. The significant positive correlation between phosphate and salinity suggested that TWC characterized by high-salinity seawater is a major source for phosphate during the bloom of dinoflagellates.

4.2. Influences of CDW and TWC on the diatom bloom and dinoflagellate bloom

The sea area adjacent to the Changjiang River estuary, a notable region for harmful algal blooms in China, has complex environmental conditions affected by both CDW and the TWC (Zhang et al., 2007a; Jiang et al., 2014). The CDW at the surface, characterized by low-salinity, nitrate-rich and silicate-rich water, is affected by the Changjiang River (Zhang et al., 2007b) which transports an enormous amount of freshwater and nutrients into the target area. The TWC, characterized by high-salinity and phosphate-rich seawater from the offshore area, is significantly influenced by the intrusion of Kuroshio branches (Lian et al., 2016). CDW and the TWC could affect the development of algal blooms through their influences on the environmental factors.

4.2.1. Roles of CDW and TWC during the diatom bloom

According to the results of the PCA, the two selected principle components could explain a majority of the biomass variation during the diatom bloom. The first principle component had positive relationships with DIN and silicate, and negative relationships with temperature and salinity, which represented the characteristics of CDW in early spring. The second principle component, which had positive relationships with phosphate and turbidity, was more likely to reflect the effects of the TWC at the bottom. Thus, the role of CDW was more important than the role of the TWC in controlling the diatom bloom.

The bloom-forming diatoms (*S. costatum*), in contrast to the bloom-forming dinoflagellates (*P. donghaiense* and *K. mikimotoi*), had a stronger capacity for nutrient absorption and assimilation to support a high growth rate (Philippart et al., 2000). The Changjiang River transported a large amount of nutrients, particularly DIN and silicate, into the coastal waters adjacent to the Changjiang River estuary (Chen et al., 2003, 2010), and made this region highly eutrophic and suitable for the growth of diatoms. In addition, the strong stratification associated with CDW, which leads to the accumulation of diatoms, was another important factor accounting for the formation of diatom blooms in early spring. Therefore, the important role of low salinity, nutrient-rich CDW on the occurrence of diatom blooms is clear.

Due to the important role of CDW on the diatom bloom, it can be expected that the long-term changes of nutrient flux transported by the Changjiang River would significantly affect diatom blooms in this region. From the 1950s until now, a rapid increase of the DIN concentration in the Changjiang River has been recorded, with a slight increase in phosphate flux and an apparent decrease in silicate (Li et al., 2009, 2011a). This led to an extraordinarily high N/P ratio and N/Si ratio in the sea area affected by CDW. As indicated by the PA in this study and many previous studies, both silicate and phosphate could become limiting factors for the growth of diatoms in spring (Zhu et al., 2009b; Liu et al., 2013). This will lead to the decline of diatom blooms and leave excess nitrogen for the growth of dinoflagellates. The flux of riverine phosphate and silicate from the Changjiang River are expected to decline in the future (Chen et al., 2010) due to the control of P-containing detergent and the construction of reservoirs and dams in the drainage basin of the Changjiang River. This could further intensify the stress on diatom growth caused by phosphate or silicate limitation, and lead to the decrease of diatom blooms and increase in excess nitrogen for the growth of dinoflagellates in the long run.

4.2.2. Roles of CDW and TWC during the dinoflagellate bloom

According to the PCA results conducted during the dinoflagellate bloom, the first principle component had strong positive correlations with phosphate and salinity, but a negative relationship with temperature, reflecting the effects of the TWC (particularly intrusion of Kuroshio subsurface water at the bottom of the study area) in early summer. The second principle component, which had a strong positive correlation with silicate but a negative correlation with salinity, matched the features of CDW. Thus, it was proposed that the TWC had more significant contributions to the dinoflagellate bloom compared to CDW.

During the dinoflagellate bloom in early summer, the intrusion of the Kuroshio subsurface water intensified, which is associated with stronger upwelling in the coastal waters adjacent to the Changjiang River estuary. Meanwhile, the impacts of CDW on this region become weaker due to the northward extension of CDW beginning in May (Lie et al., 2003). Along with the diversion of CDW, the nutrient supply from CDW decreases significantly (Chen et al., 2010), and phosphate becomes a limiting factor for the growth of microalgae. During this stage, dinoflagellates dominate the phytoplankton community due to their adaptability to oligotrophic conditions (Ou et al., 2008, Li et al., 2011b). The strong upwelling associated with intensified intrusion of Kuroshio subsurface water at the bottom brings phosphate-rich seawater to the surface to remediate phosphate stress (Yang et al., 2012, 2013; Liu et al., 2013) and maintains the large-scale bloom of dinoflagellates. Thus, the intrusion of Kuroshio subsurface water is important to the occurrence of dinoflagellate blooms. However, the exact role of Kuroshio subsurface water on the occurrence of dinoflagellate blooms still needs to be studied in detail.

The continuous supply of phosphate through upwelling will benefit the growth of dinoflagellates until the excess nitrogen is depleted. This finding was supported by the PA results of this study, which indicated a negative correlation between chlorophyll-*a* and DIN during the dinoflagellate bloom. Over the last several decades, the continuous increase of DIN flux from the Changjiang River is believed to be the major factor accounting for the occurrence of large-scale dinoflagellate blooms in the sea area adjacent to the Changjiang River estuary (Li et al., 2007; Zhou et al., 2008, Li et al., 2009, 2014). Thus, the reduction of the riverine DIN flux should be an important measure to control the scale of dinoflagellate blooms and restore the structure and function of the phytoplankton community.

5. Conclusions

HAB events have frequently been reported in the coastal waters adjacent to the Changjiang River estuary from the beginning of the 21st century. Determining the major factors controlling the distribution and dynamics of HABs is critical for elucidating the mechanisms of HABs and predicting the trend of HABs in this region. In this study, statistical tools were applied to interpret the effects of different environmental factors as well as the roles of CDW and the TWC on the occurrence of algal blooms in this region.

Based on statistical analyses, it was found that silicate and phosphate are two major factors that directly affected the diatom blooms, and there were negative correlations between chlorophyll-*a* and those two types of nutrients.Nitrate, phosphate, temperature and turbidity are major factors that directly affect the dinoflagellate blooms. There was positive correlation between chlorophyll-*a* and phosphate, and negative correlations between chlorophyll-*a* and DIN, temperature and turbidity. It's suggested that enrichment of phosphate during this stage is critical for the maintenance of dinoflagellate blooms, and DIN limitation and temperature increases may account for the decline of dinoflagellate blooms.

CDW and the TWC are two major driving forces affecting the variation of environmental factors and consequently the occurrence of algal blooms. These two water masses play different roles during the diatom and dinoflagellate blooms. CDW brings abundant DIN and silicate into the sea area adjacent to the Changjiang River estuary and is more important for diatom blooms, and the decrease in silicate and phosphate supply from the Changjiang River might lead to the decrease of diatom blooms in the future. The TWC, however, supplies phosphate to the blooming region and is more important for dinoflagellate blooms. However, the role of CDW, particularly Kuroshio subsurface water, on dinoflagellate blooms still needs to be further examined in detail.

Acknowledgements

This study was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (CAS) [grant number XDA11020304]; the project jointly supported by Shandong province and the National Natural Science Foundation of China (NSFC) [grant number U1606404]; the National Basic Research Priority Program of the Ministry of Science and Technology of China [grant number 2010CB428705], and the Programs of the Qingdao National Laboratory for Marine Science and Technology [grant numbers 2016ASKJ02 and 2015ASKJ02]. The data used in this study was from the project "Ecology and Oceanography of Harmful Algal Blooms in China (CEOHAB)", and we are indebted to the colleagues of CEOHAB-I who took part in the sample collection and analysis during the cruises in 2005.

Appendix A. Total variance explained by the principle components during the diatom bloom and dinoflagellate bloom in 2005 and the component matrix of different variables

	components					
	diatom bloom			dinoflagellate bloom		
	1	2	3	1	2	3
Zscore (DIN)	0.821	0.214	−0.28	0.793	0.363	−0.090
Zscore (PO_4)	0.081	0.817	−0.513	0.848	−0.346	−0.081
Zscore (SiO_3)	0.854	0.053	0.28	0.678	0.635	−0.203
Zscore (T)	−0.879	0.228	−0.143	−0.809	0.312	0.284
Zscore (Turbidity)	0.05	0.741	0.645	0.658	0.206	0.713
Zscore (Salinity)	−0.901	0.137	0.14	0.341	−0.903	0.113
Eigenvalues	2.997	1.335	0.876	3.013	1.609	0.658
% of Variance	49.952	22.248	14.608	50.218	26.824	10.962
Cumulative%	49.952	72.199	86.807	50.218	77.042	88.004

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Appendix B. Pearson correlation coefficients (*r*) between salinity and other factors

Factors	Salinity			
	diatom bloom		dinoflagellate bloom	
	Correlation coefficient	*P*	Correlation coefficient	*P*
DIN	−0.689***	0.000	−0.012	0.879
PO_4	−0.031	0.699	0.571***	0.000
SiO_3	−0.656***	0.000	−0.347***	0.000
T	0.769***	0.000	−0.471***	0.000
Turbidity	0.105	0.189	0.099	0.207

The significance of the correlation coefficient is: $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$.

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Appendix C. Correlation coefficients between each environmental factor and chlorophyll-*a* during the diatom bloom and dinoflagellate bloom in 2005

Factors	Chlorophyll-*a*			
	diatom bloom		dinoflagellate bloom	
	Correlation coefficient	*P*	Correlation coefficient	*P*
DIN	−0.414**	0.005	−0.093	0.223
PO_4	−0.278	0.067	0.223	0.027
SiO_3	−0.610***	0.000		
T	0.483***	0.001	−0.107	0.249
Turbidity	−0.175	0255	0.027	0.216
Salinity	0.382**	0.011	−0.598***	0.000

The significance of the correlation coefficient is: *** $P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$.

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Appendix D. Determination coefficients of each regression equations which removed the corresponding variables

Factors removed	Determination coefficients	
	Diatom bloom	Dinoflagellate bloom
None	0.405	0.639
DIN	0.399	0.464
PO_4	0.380	0.619
SiO_3	0.297	
T	0.399	0.619
Turbidity	0.403	0.614
Salinity	0.403	0.639

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Appendix E. Regression equations established for the diatom bloom and the dinoflagellate bloom in 2005

Sampling depth	Regression equation	R	*F*	*P*
Diatom bloom	$chla = 0.13(DIN) - 0.18(PO_4) - 0.57(SiO_3) + 0.11(T)$	0.40	5.52	0.00
Dinoflagellate bloom	$chla = -0.58DIN + 0.54PO_4 - 0.30T - 0.02Turbidity$	0.46	3.26	0.02

DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.

Appendix F. Direct and indirect influence of each environmental factor on chlorophyll-*a* at the surface layer during the diatom bloom and the dinoflagellate bloom in 2005

Sampling period	Factors	Direct influence			Indirect influence (Pij)					
		Pi	contribution	sorting	Via DIN	Via PO_4	Via SiO_3	Via T	Via Turbidity	Via Salinity
Diatom bloom	DIN	0.13	13%	3		-0.10	-0.40	-0.05		
	PO_4	-0.18*	18%	2	0.07		-0.15	-0.02		
	SiO_3	-0.57**	57%	1	0.09	-0.05		-0.08		
	T	0.11	11%	4	-0.06	0.03	0.40			
	Turbidity				0.03	-0.01	-0.12	-0.02		
	Salinity				-0.08	0.09	0.35	0.05		
Dinoflagellate bloom	DIN	-0.70**	54%	1		0.34		0.15	-0.01	
	PO_4	0.21**	16%	2	-0.36			0.05	-0.01	
	T	-0.18*	14%	4	0.28	-0.09			0.00	
	Turbidity	-0.20**	15%	3	-0.27	0.24		0.08		
	Salinity				0.13	-0.21		-0.08	0.00	

The significance of the correlation coefficient is: **$P \leq 0.01$, *$P \leq 0.05$.
DIN, dissolved inorganic nitrogen; PO_4, dissolved phosphate; SiO_3, dissolved silicate; T, temperature.
The values in grey means the indirect effects were negligible because the direct effects of the intermediate variables were not significant statistically.

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