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The impact of biotic and abiotic factors on the distribution of surface sediment dinoflagellate cyst assemblages on the Nanji Island in the East China Sea

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Abstract
The dinoflagellate cyst assemblages on the Nanji Island in the East China Sea, are documented at the first time to construct a quantitative overview of the cyst bank from 2014 to 2015. Thirty-four morphotypes from six groups are identified and quantified at eight sampling sites around the island, including a high proportion of potentially toxigenic species (14%). Autotrophic dinocysts constitute 74% of the total cyst counts, which is relatively low (two to thirty-three per millilitre sediment) compared with previous studies in adjacent areas. *Scrippsiella trochoidea* and *Protoperidinium avellana* are the most abundant autotrophic and heterotrophic species, respectively. A multivariate analysis is performed to assess associations between dinocysts and abiotic or biotic variables. Differentiation among seasons is evident in the detrended correspondence analysis (DCA) ordination plot, while a spatial pattern is not clearly revealed despite heterogeneity of the hydrodynamic conditions between sampling sites. Soluble reactive phosphate, the ratio of nitrogen to phosphorus concentrations and *Karenia mikimotoi* bloom are the three factors significantly ($P<0.05$) related to surface sediment cyst assemblage defined by the canonical correspondence analysis (CCA), highlighting the importance of nutrient regime to a dinocyst distribution in this area. Although attempts to address the origin of HAB events in recent years using seed banks have failed, knowledge can be valuable for further investigation of dinocyst dynamics and potential toxin threats on the Nanji Island.

Key words: dinoflagellate cyst, Nanji Island, nutrients, harmful algal blooms

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1 Introduction

Marine dinoflagellates constitute one of the most important components of phytoplankton. As a phase of sexual or asexual reproduction, cysts are produced by approximately 10% of dinoflagellates (Head, 1996), which play a noteworthy role in the dynamics and geographical distribution of the vegetative population (Bravo and Figueroa, 2014; Furio et al., 2012). The immobilized cysts may sink and finally accumulate in the sediments. After a mandatory dormancy period, the cysts could germinate under favourable conditions and potentially seed a planktonic population (Dale, 1983), sometimes leading to a bloom (Kremp and Anderson, 2000). Thus, seed banks on the sea floor can be crucial to the formation of phytoplankton blooms. The stability of sediments also makes them a valuable proxy for understanding environmental changes and paleoclimate (Dale and Fjellså, 1994; González et al., 2008). Owing to the ecological significance of cysts in an ecosystem, many studies have focused on morphology (Gu et al., 2015; Jansson et al., 2014), population dynamics (Krock et al., 2015), germination kinetics (Ishikawa et al., 2014) and the environmental indicator potential of this organism (Dale et al., 2002; Godhe and McQuoid, 2003), especially where water is considered to be anthropogenically polluted or eutrophicated (Dale, 2009; Pospelova et al., 2005).

Nanji Island locates in the southwestern Zhejiang coastal waters in the East China Sea. The hydrographical conditions in this region are complex. Upwelling influences the area throughout the year, and the coastal currents exhibit a strong seasonal variation. This area is well known for its high biodiversity and for being the first marine reserve to join the world biosphere protection network awarded by the UNESCO in 1999. In recent years, motivated by an increasing frequency of algal blooms (Xu et al., 2016; Zhou, 2010) and the presence of algal toxins in the local aquaculture region (Jiang et al., 2014a, b), increasing attention has been paid to investigating the effects and possible reasons for

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the degradation in the phytoplankton community (Jiang et al., 2014a; Li et al., 2010). *Prorocentrum donghaiense* and *Karenia mikimotoi* are two of the most common causative species for harmful algal blooms near Nanji Island. *Alexandrium tamarense* may also dominate a spring bloom in these areas (Li et al., 2010). However, little information is available about dinocyst communities (You et al., 2016). Benthic-pelagic interactions regarding environmental factors are so far absent in the coastal waters of Nanji Island.

Interplay between cysts in the sediments and an upper water column is well documented globally (Dale et al., 2002). Previous studies have shown that both abiotic (e.g., water chemistry, physical conditions, grain size of sediment) and biotic (e.g., phytoplankton community) parameters could alter the composition, assemblage and dynamics of a dinocyst community (Fertouna-Bellakhal et al., 2014; Prebble et al., 2013). At the unicellular level, morphology (Shin et al., 2013a) and chemical composition (Bogus et al., 2014) may also exhibit variation along environmental gradients. Mapping of the cysts provides a valuable reference to understand and interpret the environmental variation in confined regions (Fertouna-Bellakhal et al., 2014). In this context, we carried out a one-year investigation on both cyst assemblages and environmental factors in the coastal waters around Nanji Island. The aim of our study is to (1) provide the first record of the biogeographic distribution of dinocyst assemblages in the area around Nanji Island, (2) examine the extent to which measured abiotic and biotic drivers could be used to characterize cyst signals and (3) seek explanations for routinely harmful algal blooms and the possible origin of the causative species in this area. We expect that the information and conclusions given in our study will serve as a basis for further research and practice of local environmental management.

2 Materials and methods

2.1 *Study area and sampling sites*

The Nanji Island is located at the intersection of Zhejiang longshore currents and the Taiwan Warm Current (Fig. 1a). The direction of the longshore currents is different between summer (white arrow) and winter (grey arrow). In general, the southwestern current in summer is stronger than the northeastern current. High productivity in the region results from the prevailing upwelling. Eight sites were set around the Nanji Island, with four sites inside the fjord (N1 to N4) and the other four (N5 to N8) in a relatively open area (Fig. 1c). Water and sediment samples were collected with a seasonal frequency from April 2014 to January 2015.

2.2 *Water chemistry and phytoplankton data*

Water temperature, pH and salinity were recorded *in situ* with a thermometer, a pH meter and a salometer, respectively. Dissolved oxygen was measured by iodometry. Chlorophyll (Chl) data were obtained from ecobuoys. For nutrient analysis, water was pumped from 0.5 m below the surface and immediately filtered through 0.45 μm millipore filters. The filtrate was preserved at 4°C and then taken back to the laboratory in the dark until processing. The concentrations of NO_3-N, NO_2-N, NH_4-N and SRP (soluble reactive phosphate) were measured using a conventional spectrophotometry. Total dissolved inorganic nitrogen (DIN) concentration was calculated as the sum of NO_3-N, NO_2-N and NH_4-N concentrations.

For phytoplankton determination, water samples of 500 mL were collected and fixed with 5 mL Lugol' s solution. After a 24 h settlement, each sample was concentrated to 10 mL, and 1 mL subsample was examined using a microscope under 100×. Both

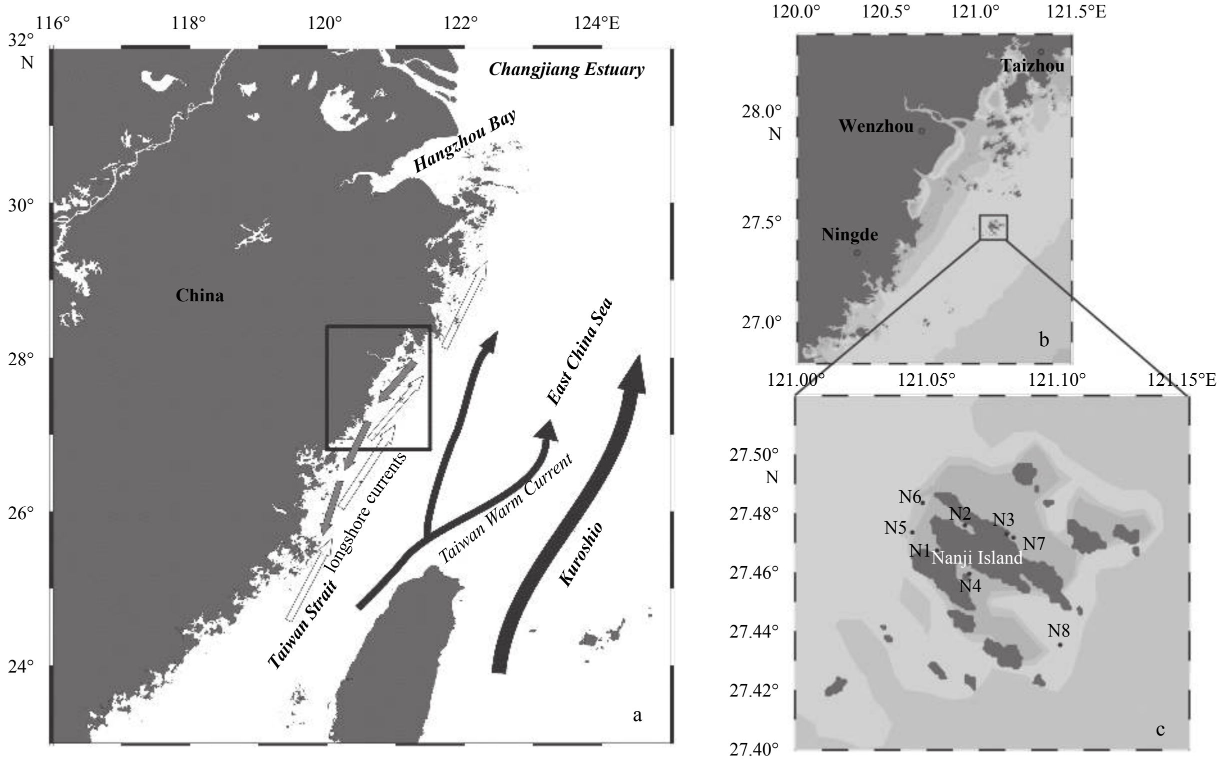

Fig. 1. Map of sampling sites on the Nanji Island in the East China Sea, with schematic plot of ocean current. Note that the seasonal longshore currents are indicated by the white (summer) and grey (winter) arrows, separately.

diatom and dinoflagellate cells were counted. Note that during the spring and summer samplings, samples were taken during *P. donghaiense* and *K. mikimotoi* blooms.

2.3 *Sediment sampling and palynological processing*

Surface sediment was taken with a gravity corer limited to the top 2–5 cm, which is considered mostly related to modern conditions. Samples were palynologically extracted for further cyst identification as described in Gu et al. (2015). Briefly, an aliquot of each sample was processed using 10% HCl (room temperature) to remove calcium carbonate particles. The slurry was rinsed twice with distilled water, sieved at 120 μm to eliminate coarse components and sequestered on 15 μm nylon mesh. Subsequently, 50% HF was added to remove siliceous particles. Finally, 10% hydrochloric acid was used to dissolve precipitated fluorosilicates. The residue was then rinsed with distilled water, ultrasonicated, and sieved again using the 15 μm nylon mesh. The identification and quantitative analysis of dinocysts were carried out using a light microscopy at 100×. The cyst concentration (calculated by individual per millilitre) was represented by cysts per millilitre sediment.

2.4 *Statistical analysis*

Multivariate analyses were performed year-round using the Canoco software version 5.0 for Windows system (Braak and Šmilauer, 2012) to examine relationships between environmental parameters and dinocysts on a quantitative basis. Taxa that represented less than 5% of the total abundance in each sample were defined as rare taxa and excluded from an ordination matrix (Leira and Sabater, 2005). In addition, phytoplankton community/bloom was introduced into the analysis as a descriptive variable. An analysis model was recommended by Canoco adviser based on the length of the first gradient, which is 3.42 (Table 1), indicating a characteristic of the unimodal response of cyst concentration to abiotic factors (Braak and Šmilauer, 2012). A detrended correspondence analysis (DCA) and a canonical correspondence analysis (CCA) were used eventually. In the DCA, detrending by segments was applied to eliminating the arch effect between the first and subsequent axes. In the CCA, only variables of significance (P<0.05) were chosen by forward selection and then plotted using arrows and symbols for quantitative and descriptive variables, separately.

Table 1. Results of DCA and CCA

	DCA			
Axis	1	2	3	4
Eigenvalues	0.451 9	0.258 2	0.152 6	0.123 6
Explained variation (cumulative)	16.20	25.46	30.93	35.36
Gradient length	3.42	2.81	3.07	1.84
	CCA			
Axis	1	2	3	4
Eigenvalues	0.392 4	0.216 1	0.106 5	0.292 7
Explained variation (cumulative)	14.07	21.81	25.63	36.12
Total variation	2.789 7			

3 Results

3.1 *Environmental factors and phytoplankton in upper waters*

The physicochemical parameters of the water column are summarized in Table 2. The matrix was also imported into the Canoco programme for analysis. The temperature (θ), salinity (S), pH and DO concentration (c_{do}) exhibited few spatial differences in separate sampling periods (Table 2). Seasonally, the water temperature (θ) varied from 10.2°C in winter to 29.6°C in autumn, while the salinity, pH and DO concentration remained constant year-round (Table 1). The depth of the water column was similar between Sites N1 and N2, which were located in the northern fjords of the main island (Figs 1 and 2). The other two inner sites (N3 and N4) were as deep as the relative open sites in the north (N5 and N6). Of all the sites, N3 and N7 were the most oceanward and showed the greatest seasonal variance (6–8 m). Inorganic nutrients between stations did not differ prominently, except during summer, when the largest variance in NO_3-N was detected (Fig. 3). In general, dissolved organic nitrogen, as well as soluble reactive phosphate (SRP), was higher in winter and autumn, when diatoms were dominant in the water column (Fig. 3, Table 2). The content and variance in DIN were mainly constituted by NO_3-N in all measurements. Chl *a* was relatively low during winter and autumn compared with spring and summer (Fig. 4). Dinoflagellate blooms were mainly observed in the spring and summer expeditions (Table 2, Fig. 5). *Karenia mikimotoi* was the causative species in the spring bloom of 2014, with the highest cell density of 984 mL^{-1}. The summer bloom was attributed to the simultaneous thriving of *P. donghaiense* and *K. mikimotoi*. This observation is consistent with the geographic distribution of Chl *a*. The highest Chl *a* content ($c_{\mathrm{Chl}\ a}$) was always detected around Sites N1 and N2, where the most concentrated bloom was observed (Figs 4 and 5).

3.2 *Identification and distribution of dinocysts*

During the one-year survey, 34 morphotypes were identified in the surface sediment of the Nanji coastal area belonging to six groups: Caleoidinellid, Tuberculudinioid, Gonyaulacoid, Protoperidinioid, Diplopsalid and Gymndinioid (Table 3). According to the nutrient strategy of their vegetative cells, 17 species were assigned to autotrophs and the rest were considered heterotrophs. The abundance of dinocysts in the surface sediment ranged from 2 to 33 mL^{-1}. The cysts of autotrophs and heterotrophs constituted 76% and 24% of all counts, respectively. *Scrippsiella trochoidea* was the most abundant (28.89%) autotrophic cyst in the assemblage, followed by *Fragilidium mexicanum* (11.46%) and *Alexandrium affine* (8.34%). Toxic species, including *Alexandrium tamarense/affine*, *Gonyaulax spinifera*, and *Protoceratium reticulatum* were also detected, constituting a high proportion (14%) of cyst assemblages. Total cyst counts were higher during spring and autumn investigations. The spatial distribution of dinocysts was heterogeneous in the four seasons (Fig. 6). We found no sites that were always rich in dinocysts, indicating a quick transition of the surface sediment layer due to physiochemical factors in the upper water column. The cyst composition was also altered among seasons (Fig. 7). The Protoperidinioid group constituted a significant portion of all the sites in winter; however, this proportion decreased in spring. Otherwise, the spring exploration also witnessed an increase in the Caleoidinellid group. A consistent proportion was not observed in the cyst assemblage. No clear relationship was revealed between the inner and outer parts of the four fjords, except in the eastern fjord (N3 and N7), where similar cyst community structures were characterized.

3.3 *Results of DCA and CCA*

Analysis was carried out based on a unimodal model. The first and second DCA axes represent 16.2% and 9.26%, respectively, of the total variance in the dataset (Table 1).

Table 2. Geographic sample positions, date and environmental data used in the analysis

Sampling site	North latitude	East longitude	Sampling date	θ/°C	S	pH	c_{do} /mg·L^{-1}	Trans /m	Depth /m	c(NO$_2$-N) /mg·L^{-1}	c(NO$_3$-N) /mg·L^{-1}	c(NH$_4$-N) /mg·L^{-1}	c_{din} /mg·L^{-1}	c_{srp} /mg·L^{-1}	$c_{\text{Chl }a}$ /μg·L^{-1}	r_{NP}	Phytoplankton community
N1	27°28.045′	121°3.240′	2014–04–01	16.3	30.1	8.20	8.32	0.8	9.0	0.018	0.204	0.026	0.248	0.008	2.5	61.9	*K. mikimotoi* bloom
N2	27°28.559′	121°3.876′	2014–04–01	16.3	29.8	8.18	8.04	0.8	5.0	0.018	0.236	0.021	0.275	0.010	5.7	51.6	*K. mikimotoi* bloom
N3	27°28.383′	121°4.831′	2014–04–01	16.2	30.2	8.20	8.48	0.8	15.0	0.018	0.182	0.030	0.230	0.016	1.7	30.2	*K. mikimotoi* bloom
N4	27°27.570′	121°3.978′	2014–04–01	16.2	30.5	8.23	8.44	0.8	12.3	0.015	0.194	0.029	0.238	0.006	2.1	81.7	*K. mikimotoi* bloom
N5	27°28.413′	121°2.668′	2014–04–01	16.0	30.1	8.20	8.38	0.8	11.0	0.019	0.216	0.021	0.256	0.015	3.7	32.5	*K. mikimotoi* bloom
N6	27°29.016′	121°2.905′	2014–04–01	16.0	29.6	8.20	8.37	0.8	16.0	0.018	0.208	0.023	0.249	0.010	3.7	48.4	*K. mikimotoi* bloom
N7	27°28.308′	121°4.988′	2014–04–01	16.1	30.2	8.24	8.39	0.8	18.0	0.018	0.209	0.024	0.251	0.010	2.6	49.2	*K. mikimotoi* bloom
N8	27°26.123′	121°6.061′	2014–04–01	16.3	30.5	8.23	8.44	0.8	26.0	0.016	0.170	0.023	0.209	0.007	3.4	60.3	*K. mikimotoi* bloom
N1	27°28.045′	121°3.240′	2014–06–20	23.7	29.6	8.44	9.98	2.5	6.5	0.002	0.028	0.002	0.032	0.004	11.3	14.6	*K.* and *P.* bloom
N2	27°28.559′	121°3.876′	2014–06–20	23.6	29.9	8.52	10.01	3.8	5.0	0.001	0.030	0.003	0.034	0.004	11.1	16.2	*K.* and *P.* bloom
N3	27°28.383′	121°4.831′	2014–06–20	23.2	30.1	8.43	8.86	4.5	14.5	0.002	0.046	0.002	0.050	0.006	8.3	14.3	*K.* and *P.* bloom
N4	27°27.570′	121°3.978′	2014–06–20	24.1	29.5	8.53	8.83	4.0	11.5	0.002	0.024	0.003	0.029	0.007	6.3	8.2	*K.* and *P.* bloom
N5	27°28.413′	121°2.668′	2014–06–20	23.6	29.4	8.45	9.62	5.0	11.0	0.001	0.021	0.003	0.025	0.007	8.2	7.3	*K.* and *P.* bloom
N6	27°29.016′	121°2.905′	2014–06–20	23.4	29.6	8.55	9.35	4.5	12.5	0.002	0.035	0.003	0.040	0.007	4.9	10.7	*K.* and *P.* bloom
N7	27°28.308′	121°4.988′	2014–06–20	23.2	30.1	8.44	9.12	4.3	17.5	0.002	0.018	0.002	0.022	0.007	6.2	6.1	*K.* and *P.* bloom
N8	27°26.123′	121°6.061′	2014–06–20	23.5	30.4	8.54	9.10	4.0	21.0	0.001	0.027	0.002	0.030	0.007	8.8	7.8	*K.* and *P.* bloom
N1	27°28.045′	121°3.240′	2014–10–12	29.6	29.4	8.19	6.28	2.5	10.2	0.016	0.113	0.038	0.167	0.003	1.5	139.5	diatom
N2	27°28.559′	121°3.876′	2014–10–12	28.8	29.2	8.18	6.30	2.1	9.2	0.016	0.118	0.030	0.164	0.003	2.6	127.2	diatom
N3	27°28.383′	121°4.831′	2014–10–12	29.4	28.9	8.34	7.68	6.8	21.2	0.006	0.034	0.034	0.074	0.001	1.1	254.5	diatom
N4	27°27.570′	121°3.978′	2014–10–12	29.4	28.8	8.36	7.05	6.8	16.0	0.005	0.086	0.030	0.121	0.003	1.1	103.2	diatom
N5	27°28.413′	121°2.668′	2014–10–12	29.6	28.0	8.35	7.16	3.0	14.2	0.006	0.032	0.029	0.067	0.001	1.4	223.5	diatom
N6	27°29.016′	121°2.905′	2014–10–12	29.0	29.4	8.25	7.04	2.4	16.3	0.010	0.075	0.028	0.113	0.001	2.6	292.0	diatom
N7	27°28.308′	121°4.988′	2014–10–12	29.4	29.0	8.36	7.31	6.8	26.5	0.005	0.040	0.034	0.079	0.001	1.1	261.6	diatom
N8	27°26.123′	121°6.061′	2014–10–12	29.5	29.1	8.36	7.58	7.6	24.2	0.004	0.014	0.039	0.057	0.001	1.1	247.7	diatom
N1	27°28.045′	121°3.240′	2015–01–01	10.5	29.7	8.04	10.02	0.5	9.0	0.006	0.368	0.007	0.381	0.030	1.1	20.5	diatom
N2	27°28.559′	121°3.876′	2015–01–01	10.2	29.5	8.05	10.10	0.5	5.0	0.006	0.374	0.015	0.395	0.033	0.9	20.3	diatom
N3	27°28.383′	121°4.831′	2015–01–01	10.6	30.0	8.05	9.98	0.4	15.0	0.006	0.369	0.009	0.384	0.032	1.1	19.6	diatom
N4	27°27.570′	121°3.978′	2015–01–01	10.3	29.9	8.05	10.01	0.5	12.3	0.007	0.361	0.007	0.375	0.032	1.1	19.0	diatom
N5	27°28.413′	121°2.668′	2015–01–01	10.4	29.8	8.06	10.21	0.5	11.0	0.006	0.342	0.007	0.355	0.033	0.9	17.4	diatom
N6	27°29.016′	121°2.905′	2015–01–01	10.4	29.7	8.05	9.91	0.5	16.0	0.006	0.365	0.009	0.380	0.033	0.9	18.8	diatom
N7	27°28.308′	121°4.988′	2015–01–01	10.4	29.6	8.05	9.84	0.5	18.0	0.006	0.363	0.010	0.379	0.033	1.3	18.9	diatom
N8	27°26.123′	121°6.061′	2015–01–01	10.4	29.7	8.05	9.88	0.5	26.0	0.005	0.316	0.008	0.329	0.032	1.1	16.9	diatom

Note: Trans is short for transparency; c content or concentration; r_{NP} the ratio of nitrogen to phosphorus concentrations; c_{srp} soluble reactive phosphate concentrations, and c_{din} dissolved inorganic nitrogen concentrations. *K.* represents *Karenia* spp. and *P. Prorocentrum* spp..

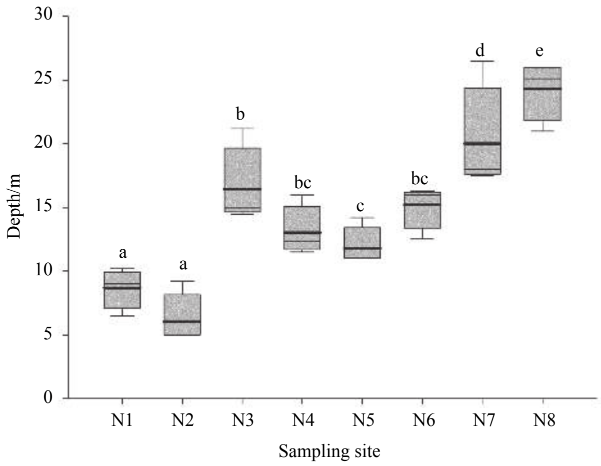

Fig. 2. Seasonal variation in the depth in the eight sampling sites depicted by boxplots. Lowercase letters above each box indicate significant difference.

Sampling sites from different seasons were well clustered in the plot of DCA results by visual classification (Fig. 8), except those from the spring, which generally overlapped with the summer and autumn samples. The winter and summer samples were ordinated separately on the left and right of the first axis, while the autumn samples were spread on the positive side of the second axis. Regarding variation within species distribution, autotrophic cysts (open circles) were mainly ordinated along the first axis, while heterotrophic cysts (solid circles) were randomly distributed (Fig. 8). The cysts of *Alexandrium andersonii* and *Scrippsiella donghaiense* were ordinated at the most positive side of the first axis, while *Protoperidinium pentagonum* and *P. latissimum* were on the negative side. Dinocysts belonging to Group Protoperidinioid conformed to the ordination of the winter samples, which was previously evidenced by the dominance of this group in winter (Fig. 7).

Fifteen parameters were introduced into the CCA, and only three were accepted through forward selection (Table 4). The SRP, the ratio of nitrogen to phosphorus concentrations and *K. mikimotoi* bloom significantly are related to surface cyst assemblage within the 95% confidence limit. The SRP and the ratio of nitrogen to phosphorus concentrations were correlated with variations along the first and second axes, respectively (Fig. 9a), which contributed 21.8% of the explained variance (Table 1). However, to a certain extent, the SRP was negatively correlated with the ratio of nitrogen to phosphorus concentrations because this ratio was calculated using DIN and the SRP described above. *K. mikimotoi* bloom was located on the negative side of both the ratio of nitrogen to phosphorus concentrations and SRP, suggesting a potential influence of phytoplankton bloom on nutrient regime. *Gymnodinium impudicum* and *Lingulodinium polyedrum* were ordinated on the most positive side of the ratio gradients. The cysts of the Protoperidinioid group spread mainly on the

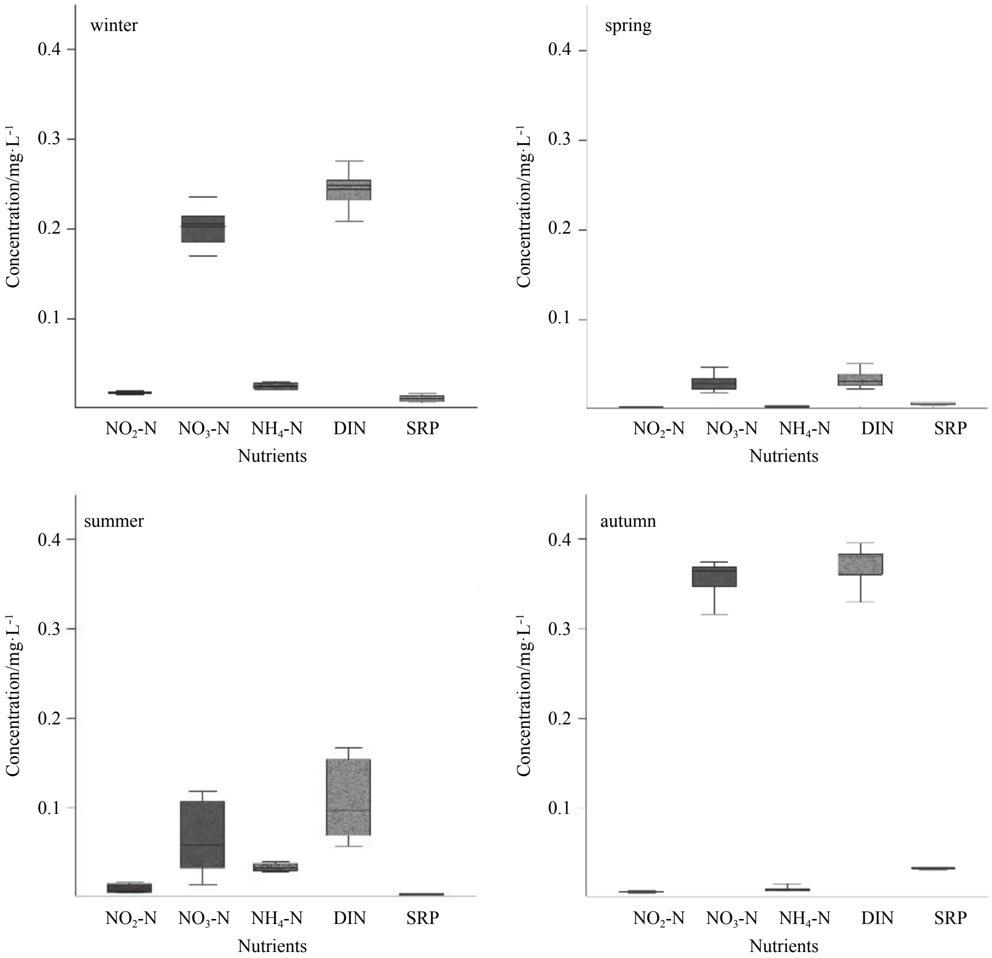

Fig. 3. Variation in nutrients among eight sites in separate seasons.

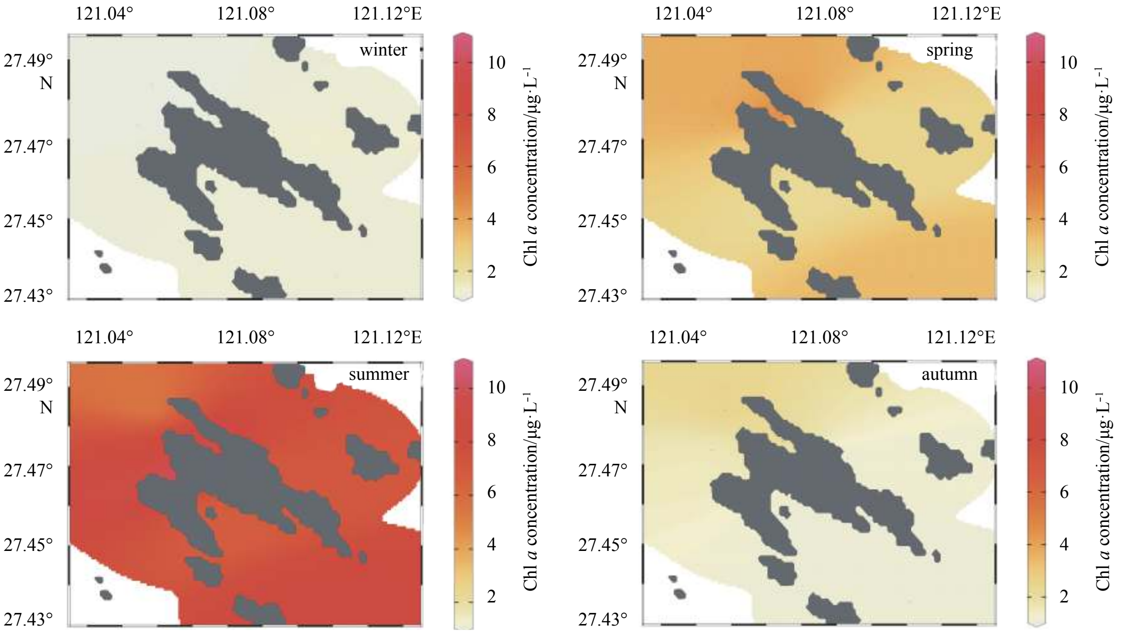

Fig. 4. Geographic distribution of Chl *a* content on the Nanji Island.

negative side or centre of the ratio of nitrogen to phosphorus concentrations. The SRP gradients showed a significant relationship with *Protoperidinium latissimum*, *Protoperidinium pentagonum*, *Gonyaulax verior*, *Polykrikos hartmannii* and *Scrippsiella enormis* at the positive end. Species near the symbol of *K. mikimotoi* bloom were also characterized as having a high proportion in the cyst assemblage, for example, *Scrippsiella trochoidea* (29%), *Scrippsiella donghaiense* (6.95%) and *Alexandrium tamarense* (2.9%). All the samples from winter were ordinated in the positive direction of the SRP gradients (Fig. 9b). The autumn samples were distributed along the ratio of nitrogen to phosphorus concentrations, while the spring and summer samples were clustered near *K. mikimotoi* bloom. Samples of the two seasons were also spread at the centre or negative side of the ratio of nitrogen to phosphorus concentrations and the SRP gradients, consistent with the fact that low nutrient levels were present during spring and summer.

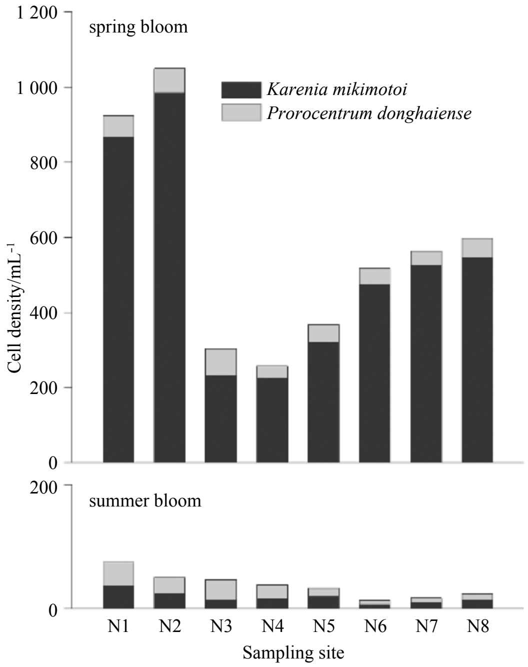

Fig. 5. Cell density of the dominant species in the spring and summer blooms in 2014.

4 Discussion

This study constructed a quantitative portrayal of the composition and distribution of dinoflagellate cysts, including species defined as toxic (*Alexandrium tamarense*/*affine*, *Gonyaulax spinifera*, *Protoceratium reticulatum*) in surface sediment on Nanji Island in the East China Sea. Additionally, we employed multivariate ordination technologies to obtain insight into associations between the critical factors and the cyst community.

4.1 *Spatiotemporal distribution of dinocyst communities*

The ordination results revealed the seasonal variation in the surface sediment dinocyst composition and abundance (Figs 8 and 9), which has been reported in numerous studies (Fujii and Matsuoka, 2006; Morquecho and Lechuga-Devéze, 2004; Price and Pospelova, 2011). Dinocyst samples from the Changjiang Estuary show no obvious differences in composition and abundance among seasons. Hydrographic conditions and suspended matters are considered essential in the geographic distribution of dinocysts in the estuary (Wang et al., 2004). Compared with an estuary with massive outflow, the coastal waters around Nanji Island are relatively stable. The seasonal pattern revealed here is more likely due to seasonal fluctuations in local biotic and abiotic factors. However, the surface sediment samples could represent cyst communities over several years, making a conventional sediment sampling method used in our study insensitive to an upper water variation on a seasonal scale. Particle-intercepting traps (Ishikawa and Taniguchi, 1996) shed light on the problem with the ability to collect sinking particles during deployment. Fujii and Matsuoka (2006) found the presence of certain groups of cysts during different seasons. Not all the species appeared throughout the year in the sediment trap. The heterotrophic protoperidinioid cysts showed a seasonal variance and probably res-

Table 3. Groups, biological and paleontological names of dinocysts identified in surface sediment

Groups	Biological names	Paleontological names
Caleoidinellid	*Scrippsiella donghaiense*	–
	Scrippsiella trochoidea	cyst of *Scrippsiella trochoidea complex*
	Scrippsiella rotunda	–
	Scrippsiella enormis	–
	Scrippsiella sp.	cysts of *Scrippsiella* sp.
Tuberculudinioid	*Pyrophacus steinii*	*Tuberculodinium vancampoae*
Gonyaulacoid	*Fragilidium mexicanum*	–
	Alexandrium tamarense	cyst of *Alexandrium tamarense*
	Alexandrium pacificum	–
	Alexandrium andersonii	–
	Alexandrium affine	cyst of *Alexandrium affine*
	Gonyaulax verior	–
	Gonyaulax spinifera	*Spiniferites mirabilis*
	Protoceratium reticulatum	*Operculodinium centrocarpum*
	Lingulodinium polyedrum	*Lingulodinium machaerophorum*
	Gonyaulax membranous	*Spiniferites membranaceus*
	Alexandrium pseudogoniaulax	cyst of *Alexandrium pseudogoniaulax*
Protoperidinioid	*Protoperidinium quadrioblongum*	–
	Protoperidinium avellana	*Brigantedinium cariacoense*
	Protoperidinium parthenopes	–
	Protoperidinium sp.	*Brigantedinium* sp.
	Protoperidinium leonis	*Quinquecuspis concreta*
	Protoperidinium americanum	cyst of *Protoperidinium americanum*
	Protoperidinium shanghaiense	–
	Protoperidinium claudicans	*Votadinium spinosum*
	Protoperidinium oblongum	*Votadinium clavum*
	Protoperidinium conicum	*Selenopemphix quanta*
	Protoperidinium minutum	cyst of *Protoperidinium* cf. *minutum*
	Protoperidinium pentagonum	*Trinovantedinium applanatum*
	Protoperidinium latissimum	cyst of *Protoperidinium latissimum*
Diplopsalid	*Diplopsalis lenticular*	cyst of *Diplopsalis lenticulata*
Gymndinioid	*Gymnodinium impudicum*	–
	Polykrikos kofoidii	cyst of *Polykrikos kofoidii*
	Polykrikos hartmannii	cyst of *Polykrikos hartmannii*

ulted from food availability of their vegetative stages during different seasons. The constant presence of autotrophic species is due to their survival strategy under ambient conditions (Fujii and Matsuoka, 2006). In addition, the germination rate and deposition rate of dinocysts could also be variable (Ishikawa and Taniguchi, 1996), leading to a seasonal pattern observed in the sediment traps. The depth of the water column at our sampling sites ranged from 5 to 26 m and exhibited strong seasonal fluctuations (Fig. 2). The availability of sediment trap methods in Nanji coastal waters still needs to be further tested concerning the potential contamination by sedimentary resuspension in shallow areas (de Jorge and van Beusekom, 1995).

Other than seasonal distribution, which is clearly clustered in ordination (Fig. 8), the spatial variation pattern of the dinocyst community around Nanji Island has not been clearly revealed. In general, the spatial distribution of dinocysts in marine environment is primarily influenced by hydrological parameters such as sea-surface temperature (SST), sea-surface salinity (SSS) and the availability of nutrients or prey organisms (Dale et al., 2002; Pospelova et al., 2008; Sherr and Sherr, 2007; Verleye and Louwye, 2010). Certain benthic conditions, such as anoxia and hypoxia, could provide better preservation for the dinocyst, leading to the higher cyst abundance observed in the sediment (Persson et al., 2000). In our study, although the four fjords are different in hydrodynamic conditions and interact separately with the open regions, the dinocyst community is expected to respond to a broader ecological span (Dale et al., 2002). Regarding to the dinocyst distribution in a larger area, the concentration gradient was detected in the estuary of the Changjiang River, where the characteristics of suspended matter, the depth of the water column and dilution as a result of high sedimentation rate were the fundamental factors driven by the gradient (Wang et al., 2004). In addition, some of the species were rarely observed and only detected in one sediment sample with low concentration, e.g., *Diplopsalis lenticular*, which was identified only in the spring samples from N2, near one of the busiest wharfs of Nanji Island. These individuals are likely to be non-indigenous species introduced randomly by ballast water (Hallegraeff and Bolch, 1992) or currents (Sætre et al., 1997).

4.2 *Relationships between nutrients and dinocysts*

Of all the parameters introduced into the CCA analysis, only SRP, ratio of nitrogen to phosphorus concentrations and *K. mikimotoi* bloom were significantly related to the surface sediment cyst assemblage. Interestingly, the three factors around Nanji coastal waters are directly or indirectly related to nutrient,

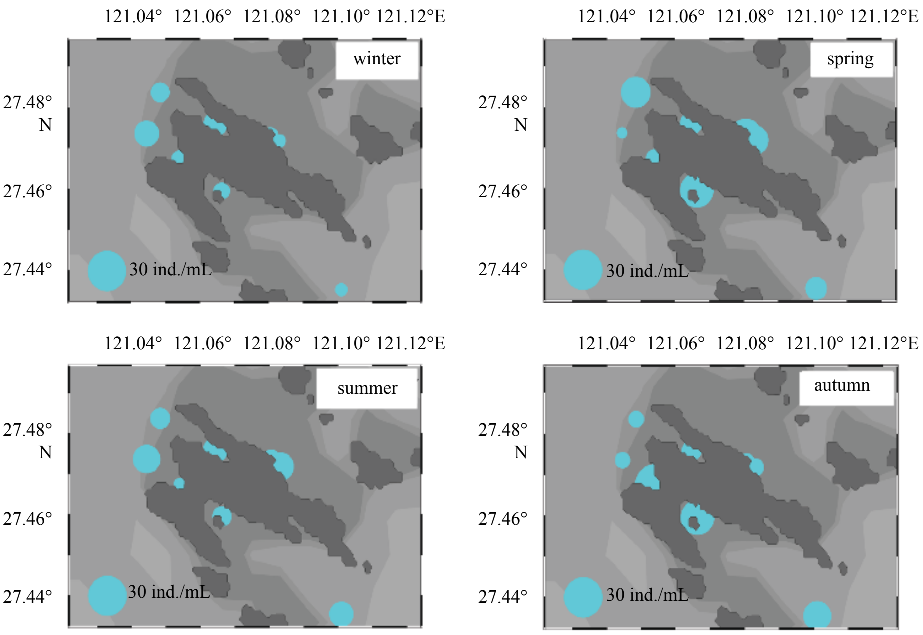

Fig. 6. Seasonal distribution of dinoflagellate cysts (ind./mL) on the Nanji Island.

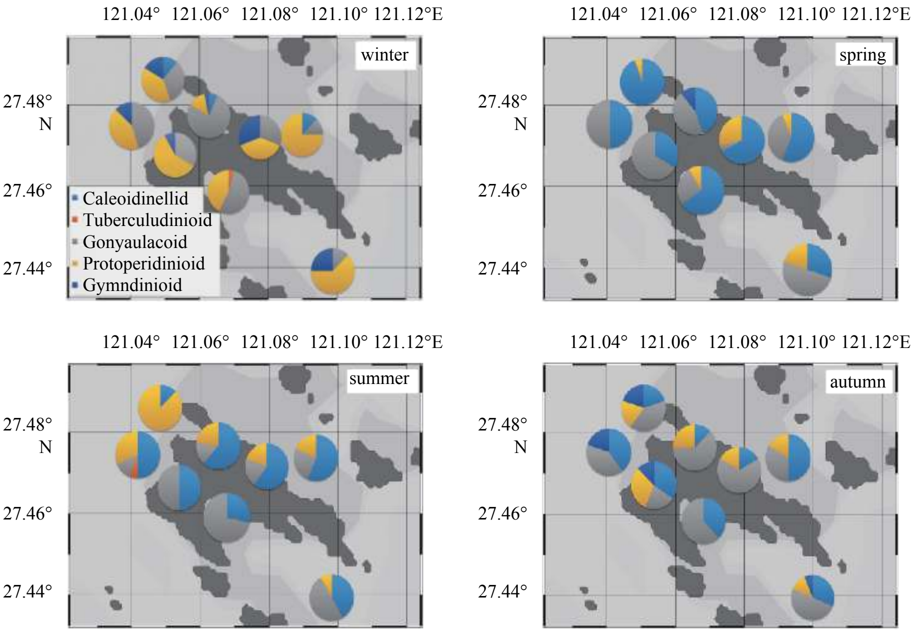

Fig. 7. Seasonal distribution of dinocysts at the group level on the Nanji Island. Dinocysts belonging to the group Diplopsalid were only detected in one sample and are not plotted here.

highlighting the importance of nutrient regime to planktonic and benthic coupling in this area.

The distribution of dinocysts is generally accepted to be controlled by the trophic characteristic of the original upper water column (Devillers and De Vernal, 2000; Nagai et al., 2004). Dinocysts have also been considered indicators of eutrophication and are deeply reviewed by Dale in 2009 (Dale, 2009; Matsuoka, 1999; Matsuoka et al., 2003). Species richness, total cyst concentrations and fluxes, proportions of some heterotrophic species, and abundance of indicator species could respond to eutrophic signals (Pospelova et al., 2002; Shin et al., 2013b), particularly *Brigantedinium* spp., *Lingulodinium polyedrum* and species belonging to Protoperidinioid, Polykrikaceae and Diplopsalidaceae (Dale, 2009; Harland et al., 2004; Matsuoka et al., 2003; Radi et al., 2007). The cyst abundance might show a significant positive correlation with the nutrient gradients (Liu et al., 2012); however, this may not be true for highly eutrophic and polluted regions where the dinocyst diversity may be adversely influenced (Pospelova et al., 2005). The Nanji sea area exhibited a seasonal eutrophication characteristic, which stated from a slight to moderate level, due to the effect by anthropogenic pollutants expanded from the Aojiang River. The eutrophic conditions were only detected in early spring and autumn around the study area (Table 2 and Fig. 3). In the winter samples, Nanji coastal waters exhibited substantially significant heterotrophic morphotypes, with a proportion of 51% mainly belonging to the group of *Protoperidinium*.

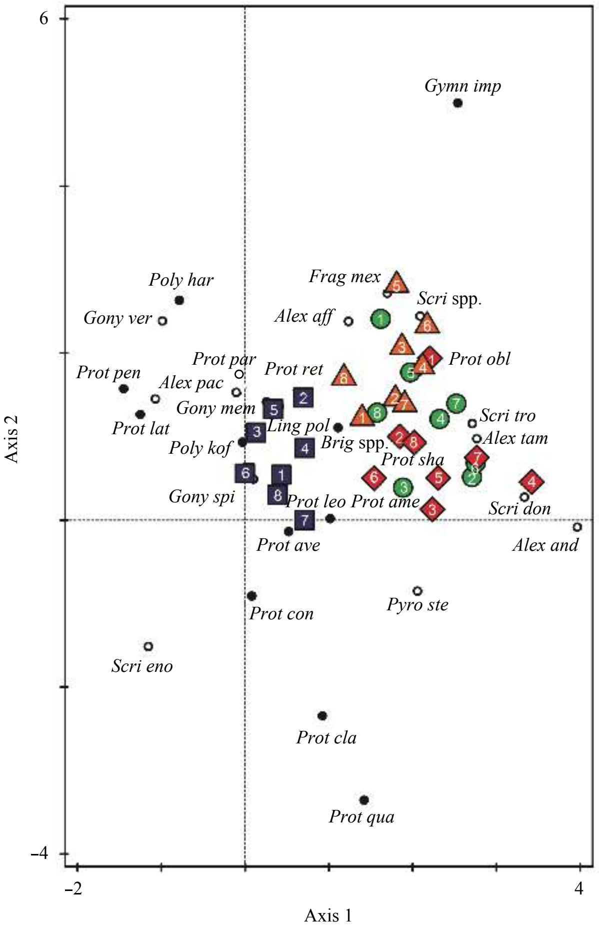

Fig. 8. DCA plot of the variation between sampling sites and species distribution. Values along the axes are given in standard deviations. Solid and open circles indicate heterotrophic cysts and autotrophic cysts, respectively. *Scri don* represents *Scrippsiella donghaiense; Scri tro S. trochoidea; Scri eno S. enormis; Scri spp Scrippsiella* spp.; *Pyro ste Pyrophacus stenii; Frag mex Fragilidium mexicanum; Alex tam Alexandrium tamarense; Alex pac A. pacificum; Alex and A. andersonii; Alex aff A. affine; Gony ver Gonyaulax verior; Gony spi G. spinifera; Prot ret Protoceratium reticulatum; Ling pol Lingulodinium polyedrum; Gony mem Gonyaulax membranous; Prot qua Protoperidinium quadrioblongum; Prot ave P. avellana; Prot par P. parthenopes; Brig spp Brigantedinium* spp.; *Prot leo P. leonis; Prot ame P. americanum; Prot sha P. shanghaiense; Prot cla P. claudicans; Prot obl P. oblongum; Prot con P. conicum; Prot pen P. pentagonum; Prot lat P. latissimum; Gymn imp Gymnodinium impudicum; Poly kof Polykrikos kofoidii; Poly har P. hartmannii.*

In the other eutrophic sample assemblage (autumn), autotrophic cysts constituted 76% of all cell counts, characterizing a distinguishing eutrophic signal with elevated phytoplankton productivity (Dai et al., 2012; Dale, 2009). In addition, many *Protoperidinium* species are proved to preferentially feed on large diatoms (Sherr and Sherr, 2007). The high proportion of heterotrophic dinocysts in the winter sediment samples is consistent with the diatom-dominated planktonic community during that period.

Investigations on the interaction between certain forms of nutrients and dinocysts were carried out in detail based on cultural experiments. Figueroa and Bravo (2005) reported that phosphate-depleted medium favoured the formation of resting cysts of *Lingulodinium polyedrum*, whereas replete conditions prevented their encystment process. Nutrient levels could also regulate encystment and excystment, as evidenced by the extended duration of the *Alexandrium catenella* cyst formation process under replete nitrogen and phosphorus medium as well as accelerated germination under depleted external conditions (Figueroa et al., 2005). The chemical composition of the dinocyst wall was examined in a recent study. Because the nutritional strategy of the vegetative cells was more important for predicting the chemical composition of the cyst wall than phylogeny, the authors proposed the potential for reconstruction past nutritional strategies using cyst wall chemistry (Bogus et al., 2014). The implication here is that rather than simply relying on the dinocyst community structure and composition as indicators of environmental conditions, particular characteristics should also be taken into account (Shin et al., 2013a). A more comprehensive image of the interaction between nutrients and dinocysts in this region still requires integrated research.

Table 4. Percentage of variance explained by the environmental variables used in CCA

	Explanation/%	Contribution/%	Pseudo-F	P
SRP	**12.4**	**22.3**	**4.2**	**0.002**
r_{NP}	**8.3**	**14.9**	**3.0**	**0.002**
***K. mikimotoi* bloom**	**5.0**	**9.0**	**1.9**	**0.006**
K and *P* bloom	3.0	5.4	1.1	0.316
c_{dia}	3.0	5.4	1.1	0.352
c_{do}	3.6	6.5	1.4	0.134
$c(NH_4\text{-}N)$	2.8	5.0	1.1	0.374
Trans.	2.8	5.0	1.1	0.396
pH	3.0	5.5	1.2	0.274
$c(NO_2\text{-}N)$	2.7	4.9	1.1	0.362
$C_{Chl\ a}$	2.9	5.2	1.1	0.330
Depth	2.5	4.5	1.0	0.472
θ	2.2	4.0	0.9	0.616
c_{din}	2.8	5.1	1.1	0.312
S	1.8	3.2	0.7	0.814

Note: Bold variables are significant at the 5% significance level ($P \leqslant 0.05$). c_{dia} represents the diatom concentration.

4.3 *Cyst formation and phytoplankton bloom in upper waters*

The frequent presence of dinocysts seems to mostly coincide with a high dinoflagellate biomass in the surface waters as well as encystment efficiency (Dale, 1976; Fertouna-Bellakhal et al., 2014; Joyce et al., 2005). We suggest that there may be two explanations for this phenomenon. (1) The formation of the cyst community is a result of sexual reproduction of vegetative cells in the upper water column, generally accompanied by nutrient depletion and environmental degradation. In this context, planktonic and benthic coupling plays an important role in encystment and excystment (Ishikawa et al., 2014). Valid evidence of those couplings could provide a better understanding of the bloom formation process. (2) Encysted species are not the dominant planktonic species but are those who become dormant cysts for survival under adverse conditions. Therefore, cysts and phytoplankton communities exhibit less overlap, and the possibility of using cysts as inocula for bloom initiation is small (Díaz et al., 2014). Regarding to our results (Fig. 5 and Table 3), the second scenario is more likely the case on Nanji Island. Accord-

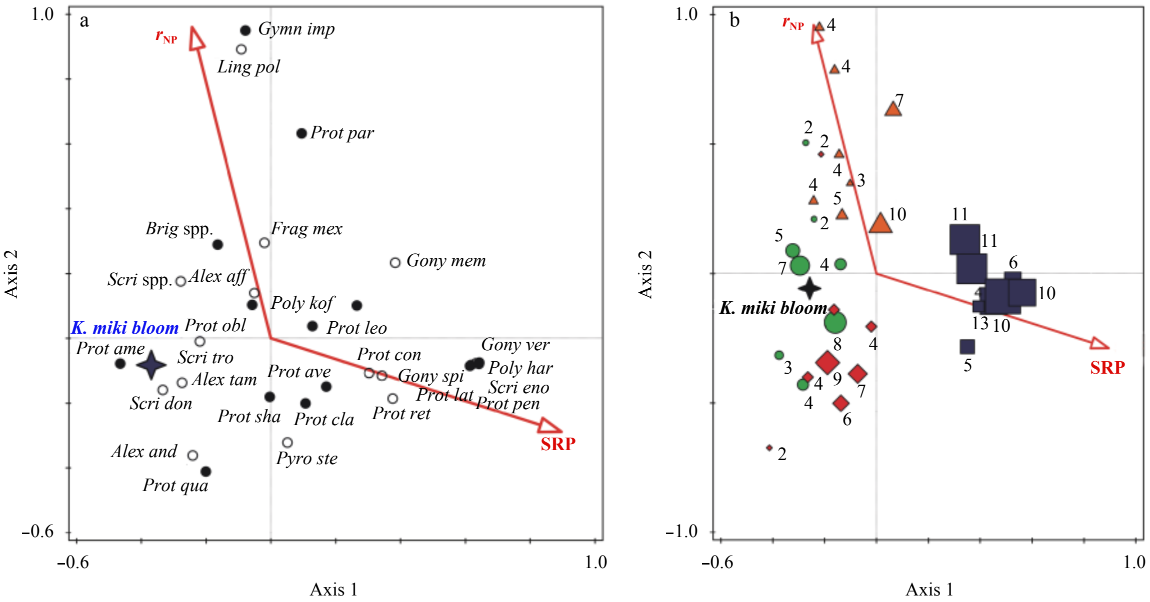

Fig. 9. Results of the CCA illustrating dinoflagellate cyst species (a) and samples (b) in relation to environmental variables (only significant parameters are plotted). *K. miki* bloom stands for *Karenia mikimotoi* bloom. Numbers above the symbol stand for cyst concentration (mL^{-1}) in that sample. The abbreriaions are same as Fig. 8.

ing to the 2014 to 2015 Marine Environment Quality Bulletin of Pingyang County, *Gonyaulax polygramma*, *P. donghaiense* and *K. mikimotoi* are the causative species for massive algal blooms and are considered to be obnoxious due to either haemolytic and cytotoxic effects (Neely and Campbell, 2006) or accompanying fish mortality (Jeong et al., 2005; Zhou et al., 2006). Fistarol et al. (2004) found that *Scrippsiella trochoidea* forms a temporary cyst as a defence mechanism when exposed to cell-free filtrate of *Karenia mikimotoi* as well as two other toxic species cultures. Wang and Tang (2008) reported that a high density of *P. donghaiense* depressed the growth of *S. trochoidea* and that the effect was mutual and dose dependent. Wang et al. (2004) examined the cyst assemblage in the Changjiang Estuary and found that the highest cyst density was obtained immediately after the proliferation of small diatoms and *P. donghaiense*. In the present study, we also found a close relationship between *K. mikimotoi* bloom and *S. trochoidea* cysts revealed by the CCA analysis (Fig. 9a). We assume that of all the abiotic and biotic factors, toxic algal blooms that frequently occurred are partially responsible for encystment in this area. The relationship between algal blooms and benthic communities may involve a variety of factors, such as sensitivity of the target species to the bloom-forming species, the concentration of potential allelopathic compounds and competition for nutrients or prey organisms (Accoroni et al., 2016; Fistarol et al., 2004; Uchida et al., 1999). However, the hypothesis may be more robust if tested using the sediment trap method during algal blooms or controlled experiments in mesocosm systems.

The dinocyst distribution in marine ecosystem is involved in a multi-step process and is probably driven by various factors. Although dinocysts in the sediment were not responsible for HAB events in recent years, priority should be given to research on their distribution and dynamics on Nanji Island because this knowledge could be indicative of harmful bloom recurrence and dispersal in the area. Moreover, a combination of morphological studies, germination trials and molecular identification is needed to investigate the dinocysts in Coastal area of China (Gu et al., 2011). The presence of cysts belonging to toxin-producing species also stresses the need for routine monitoring as a precaution for new toxicity threats.

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