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Nutrients structure changes impact the competition and succession between diatom and dinoflagellate in the East China Sea

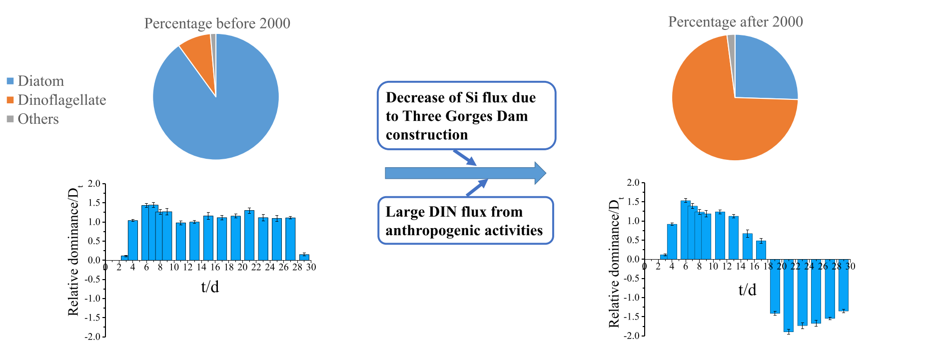
Yuping Zhou [a,b], Yanmin Zhang [b], Fangfang Li [b], Liju Tan [b], Jiangtao Wang [a,b,*]

[a] Laboratory of Marine Chemistry Theory and Technology, Ministry of Education, Ocean University of China, 266100, PR China
[b] College of Chemistry and Chemical Engineering, Ocean University of China, 266100, PR China

HIGHLIGHTS

- The competition between diatom and dinoflagellate were evaluated through field and indoors experiments in the ECS.
- Low Si/N caused by Three Gorges Dam construction could reduce relative abundance of diatom and benefit dinoflagellate.
- Large DIN flux from anthropogenic activities and induced high N/Si and N/P impel the eruption of dinoflagellate.
- D_t is a preferable parameter to represent the relative superiority of two algae.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrients variations caused by anthropogenic activities alter phytoplankton community interactions, especially competition and succession between two algal species. East China Sea experiences annual successions of *Skeletonema costatum* and *Prorocentrum donghaiense* and large-scale blooms of *P. donghaiense*. In this study, the growth and competition responses of *S. costatum* and *P. donghaiense* to different inorganic nutrients structure were evaluated through field and indoors experiments to further understand the nutrients mechanism of these events. Results showed that low Si/N ratio (Si/N < 1) and high N/P (>50) possibly accelerated P. donghaiense outbreak and decreased Si/N caused by low Si concentration could speed up *S. costatum* decay. Excessive DIN also accelerated blooms dominated by *P. donghaiense* (D_t up to −3) when *S. costatum* perished. Increased DIN loads from anthropogenic activities were possibly responsible for the changes in phytoplankton communities and dinoflagellate outbreak when Si concentration decreased as a result of governmental control efforts. With effective management practices for Si and P reductions worldwide, managers should be aware of the negative implications of unsuccessful management of system N loading because N may significantly alter the composition and ecosystem of phytoplankton communities.

* Corresponding author at: College of Chemistry and Chemical Engineering, Ocean University of China, No.238 Songling Road, Qiangdao ZIP 266100, China.
E-mail address: jtwang@ouc.edu.cn (J. Wang).

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1. Introduction

Harmful Algal Blooms (HABs) have emerged as a global phenomenon affecting coastal areas (Granéli et al., 2008). Large-scale of dinoflagellate blooms, which increasingly erupted in recent years (Park et al., 2013; Lim et al., 2014; Giussani et al., 2015; Menden-Deuer and Montalbano, 2015), have progressively replaced diatom as dominant harmful algae and severely threatened global coastal ecosystem and economies (García-Camacho et al., 2007; Fuentes-Grünewald et al., 2015; Gutierrez- Lopez-Rosales et al., 2015; Gutierrez-Mejia et al., 2016). This phenomenon was traditionally thought to occur as a result of interspecific competition ascribed to changes in environmental factors, such as temperature, salinity, irradiance, DO, and disruption of chemical release (Hong and Xu, 2014; Van der Lingen et al., 2016). For example, increased CO_2 alone or increased CO_2 and temperature stimulate *Heterosigma akashiwo* to become more dominant than *Prorocentrum minimum* (Fu et al., 2008). Low illumination intensity reduces the dominance of *Heterosigma akashiwo* with respect to *Skeletonema costatum* (Xu et al., 2010). Algal dominance is maintained by releasing allelochemicals, for instance, *Chaetoceros curvisetus* inhibits *S. costatum* growth through allelopathy (Zhang et al., 2014). Coastal dinoflagellate blooms are also restricted by warm waters (Ryan et al., 2008; Pitcher et al., 2010; Kibler et al., 2015; Van der Lingen et al., 2016). Nutrient-rich waters can stimulate dinoflagellate blooms, although dinoflagellate can endure low nutrient concentrations (Charles et al., 2005). Sea water composition influences the relative abundance of *Prorocentrum* and *Skeletonema* sp. because of competition for resources (Hong and Xu, 2014). Under different nutrients conditions, these algae employ different selected adaptive strategies. For instance, *Skeletonema* sp. yields a higher nutrient uptake rate than *Prorocentrum* sp. do, and *Prorocentrum* sp. are K-selected, that is, it has adapted to low trophic conditions (Zhao et al., 2009; Liang et al., 2014). The two kinds of algae also assimilate nutrients in different proportions. In general, cultures with low N/P ratios benefit the growth of diatoms and cultures with low Si/N ratios favor the growth of dinoflagellates (Papush and Danielsson, 2006; Gieskes et al., 2007). Considering these phenomena, we hypothesized that changes in nutrient compositions likely influence the relative abundance of algae. Hence, the effects of nutrient structural changes on the competition and succession between diatom and dinoflagellate were evaluated in the East China Sea (ECS).

In ECS, *P. donghaiense* blooms occurred in late spring and summer (May and June) from 2002 to 2013 (Lin et al., 2008; Ma et al., 2013). These blooms are associated with changes in environmental factors, such as temperature increase (Wang et al., 2008; Liu et al., 2013) and eutrophication caused by anthropogenic perturbations along the Changjiang (Yangtze) River, which resulted in increasing of N concentration and P concentration (Zhang et al., 2006a, b, 2007; Li et al., 2014). SiO_3-Si flux was mainly influenced by the construction of the Three Gorges Dam, and the mean SiO_3-Si concentration decreased from 35 $\mu mol\cdot L^{-1}$ in 1959 to 18 $\mu mol\cdot L^{-1}$ in 2010 (Li et al., 2007). Phosphate supplied by Taiwan Warm Current is also an important factor that stimulates the *P. donghaiense* outbreak (Zhou et al., 2001, 2003). Anomalous nutrient variation during *P. donghaiense* and *S. costatum* blooms has also been extensively explored through field investigations since the 1980s. Results revealed that DIN/Si and DIN/P abruptly increase because of increased DIN flux and decreased Si flux (Harrison et al., 2010; Jin et al., 2010) in ECS areas where HABs frequently occur. This observation suggests that excessive DIN and increasing N/P may be responsible for the changes in phytoplankton community structures in ECS (Wang, 2006). Nutrient compositions also significantly differ during the outbreak and eradication of different phytoplankton species (Li et al., 2014). In terms of individual algal behaviors related to nutrient changes, *P. donghaiense* is more adaptable to low phosphate conditions than *S. costatum* significantly (Zhao et al., 2009).

Field nutrient changes during blooms and individual algal responses to nutrients have been widely explored, however, the effects of anthropogenic activities, especially induced nutrients structural variations, on the competition between *P. donghaiense* and *S. costatum* have been rarely investigated. With an enhanced understanding of competition, ecological factors influencing the gradual domination of dinoflagellates might be fully elucidated. Therefore, our study aimed to evaluate the effects of anthropogenic activities on phytoplankton community. Changes in the competitive response of *P. donghaiense* and *S. costatum* to increase inorganic N and decrease inorganic Si throughout the growing season were examined through mixed culture biotechnology under field and indoor conditions.

2. Materials and methods

2.1. Nutrient enrichment experiments

Blooms in ECS persist from April to July every year. *S. costatum* dominates the phytoplankton community biomass in April and early May, comprising approximately 90% of the biomass. *P. donghaiense* bloom is dominant in mid-to-late May. Station Za1 is a typical representative of HABs in ECS as shown in Fig. 1. Upon sampling on May 12, 2011 in Za1 (29°33′N, 122°28.5′E), the phytoplankton community was co-dominated by *S. costatum* and *P. donghaiense*. The water samples were used for short-dated field mesocosm experiments. Throughout the whole period of culturing in station A, surface water temperature ranged from 16.5 to 23.1 °C, and salinity and pH were roughly constant (mean: 33.4 ± 0.2 and 8.46 ± 0.04, respectively). DIN average concentration ranged from 5–25 $\mu mol\cdot L^{-1}$ (Cheng and Li, 1992; Li et al., 2013) and the average PO_4-P concentration was approximately 0.8 $\mu mol\cdot L^{-1}$ (Chen et al., 2004; Wang, 2006), and the mean SiO_3-Si concentration in ECS ranged from 18–35 $\mu mol\cdot L^{-1}$ (Li et al., 2007). The following field and lab experiments were conducted based on these concentrations. The environmental conditions and culturing media parameters of indoor experiments were similar to field surroundings (temperatures 20.0 ± 0.2 °C, light levels 70 $\mu mol m^{-2} s^{-1}$, photoperiods 14:10 h).

2.1.1. Field experiment

Short-dated field mesocosm experiments were conducted to evaluate the impact of increased inorganic N concentration on the competition and succession between *S. costatum* and *P. donghaiense* in the ECS. From May 13 to 30, 2011, a total of 12 mesocosm experiments were conducted on the coastal station A (Fig. 1). A total of 1000 L clear PE enclosure containers ($n = 12$) were filled with 750 L original surface seawater containing the natural phytoplankton community from the station Za1 on May 12, 2011. Four nutrient treatments, in sets of triplicate, were tested as follows: the control contained original surface water (Control, 10 $\mu mol\cdot L^{-1}$ DIN, 1.0 $\mu mol\cdot L^{-1}$ P and 7.1 $\mu mol\cdot L^{-1}$ Si), and the experimental cultures were added to a final stationary concentration of Si (15 $\mu mol\cdot L^{-1}$) with exponential N concentration 10 $\mu mol\cdot L^{-1}$ (A1), 20 $\mu mol\cdot L^{-1}$ (A2) and 30 $\mu mol\cdot L^{-1}$ (A3). When *S. costatum* blooms were about to disappear (approximately day 13), N and Si treatments were all resupplied with the initial content whereas P was resupplied with a fixed concentration (0.8 $\mu mol\cdot L^{-1}$) in all experimental cultures.

2.1.2. Lab experiment

To make a comprehensive exploration about the effects of inorganic nutrients on the competition and succession between *S. costatum* and *P. donghaiense*, two series of experiments similar to field experiments were conducted in the laboratory. A series of four experimental cultures (group M) were conducted to evaluate the impacts of increased N loading, decreased Si loading and N/Si, which were designed as follows: all P treatments were amended to 0.8 $\mu mol\cdot L^{-1}$, and three experimental cultures were amended to a final N concentration of 22.0 $\mu mol\cdot L^{-1}$ with exponential Si concentration of 15.0 $\mu mol\cdot L^{-1}$ (M1), 30.0 $\mu mol\cdot L^{-1}$ (M2) and 45.0 $\mu mol\cdot L^{-1}$ (M3), and the last experimental culture was supplied to a final N concentration of 44.0 $\mu mol\cdot L^{-1}$ (M4) with Si