Marine Pollution Bulletin 135 (2018) 239–248

Contents lists available at ScienceDirect

Marine Pollution Bulletin

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

Effects of increasing nutrient disturbances on phytoplankton community structure and biodiversity in two tropical seas

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ARTICLE INFO

Keywords:
Atmospheric deposition
Phytoplankton community
Biological diversity
South China Sea
Eastern Indian Ocean

ABSTRACT

Statistical analysis of rainfall data from 2005 to 2015 showed that atmospheric deposition supplied large amount of dissolved inorganic nitrogen (38–155 mg·m^{-2}·month^{-1}) in N-deficient South China Sea and Eastern Indian Ocean. To understand marine ecosystem responses to increasing nutrient disturbances, we implemented field mesocosm experiments to study phytoplankton community structure and biodiversity responses to nutrient treatments with nitrate, phosphate and iron across tropical seas. Our results showed that DIN supply would change phytoplankton community structure and stimulated the regime shift from cyanobacteria to diatoms (relative dominance $R > 0$). Phytoplankton communities were dominated by diatoms (relative abundance > 50%) accompanied by high chlorophyll *a* content with 1.58–39.27 μg·L^{-1} in DIN-added cultures, whereas cyanobacteria dominated communities (relative abundance > 60%) with low biomass of 0.12–0.18 μg·L^{-1} in undisturbed cultures. Simultaneously increased DIN loading from atmospheric deposition would decrease ecological diversity of tropical seas owing to species competition and succession (Shannon diversity H' decreased to < 1).

1. Introduction

Increased nutrients due to anthropogenic activities and climate change have profound effects on most aquatic ecosystems (Inoue and Berg, 2017; Yeh et al., 2017). Marine phytoplankton account for a majority of global primary productivity, whose relationship with global change is of considerable interest and concern worldwide (Martin et al., 2011). In temperate marine ecosystems, spatially nutrient structure has a homogenous trend affected by terrestrial run-off (Liang et al., 2013), where frequent eruptions and high productivity of mono-species (specific diatoms or dinoflagellates) responded to increased nutrients (Lopez-Rosales et al., 2007; Zhou et al., 2017). However, in tropical zones, influences of increased nutrients on ecosystems were poorly understood because of the complexity of nutrient resources and biological diversity (Gowen and Stewart, 2005). Tropical seas experienced complex phytoplankton communities as a result of their latitudinal and longitudinal variation coupled with characteristic climate and topography (Graham and Duda, 2011; Vallina et al., 2014), which could have apparent vulnerability and complex responses to natural and anthropogenic disturbances. It is therefore essential to implement studies about influences of nutrient variations on tropical ecosystems in order to comprehensively understand the effects of anthropogenic activities and climate change on marine ecosystems.

Phytoplankton communities are key indicators of ecosystem stability and their studies would provide an insight of marine biological responses to exogenous disturbances (Yang et al., 2017). Phytoplankton assemblages are the joint result of expression of species' niches and stochastic processes related to colonization, extinction and speciation (Stokes and Archer, 2010; Larsen and Ormerod, 2014). Empirical evidences revealed that phytoplankton community structure is influenced by habitat condition, spatial scale and ecological succession (Ellwood et al., 2009; Farjalla et al., 2012). External stressors such as temperature change and natural disturbances frequently alter phytoplankton community structure (Sanders et al., 2003) through disrupting biotic interactions and biological processes (Folke et al., 2004; Brothers et al., 2016). Furthermore, investigating size distribution and biodiversity of phytoplankton communities is helpful to evaluate the effects of increased nutrients on the stability of marine ecosystems (Vallina et al., 2014). Previous studies showed communities prospering in initial tropical ecosystems were with small body size and more likely to resist

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https://doi.org/10.1016/j.marpolbul.2018.07.033
Received 28 March 2018; Received in revised form 6 July 2018; Accepted 11 July 2018

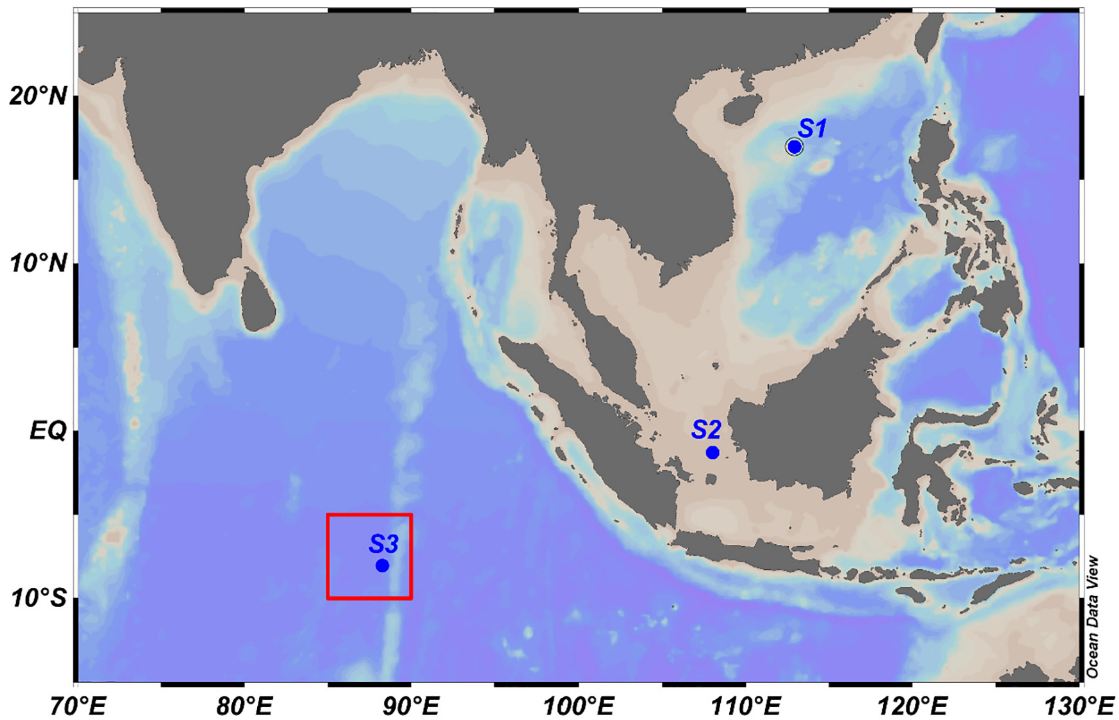

Fig. 1. The field experiment stations (S1, S2) of South China Sea and station S3 of Eastern Indian Ocean, and coverage area of collected rainfall data at station S3 (red rectangle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

oligotrophic environments, because they have high affinity with nutrients (Zander et al., 2017). However, larger species in body size with high growth rates could outcompete initial pioneer species and survive in disturbed environments with increased nutrient supply (Hunter-Cevera et al., 2016). The interspecific competition would impact size distribution of phytoplankton (Vallina et al., 2014) and biodiversity of tropical ecosystems. Previous investigations on bulk chlorophyll *a* (chl *a*) content only presented a total productivity of composite phytoplankton, which would obscure community dynamics mechanisms (Long et al., 2006; Hunter-Cevera et al., 2016). Moreover, the relative changes of community structure probably vary over a continuum (Larsen and Ormerod, 2014), which have different responses to nutrient increase.

To adequately capture how increased nutrients influence tropical marine ecosystems at a large scale, we conducted mesocosm experiments in South China Sea (SCS) and Eastern Indian Ocean (EIO). The two tropical seas have high biodiversity and plenty of nutrient supply (Graham and Duda, 2011; Vallina et al., 2014). Nutrient loading along the coastal areas has dramatically increased under the disturbances of anthropogenic activities in the past several decades (Hodgkiss and Lu, 2004). Previous investigations have indicated that these changes in nutrient structure, especially high DIN/DIP (dissolved inorganic nitrogen and dissolved inorganic phosphorous) ratio (Shen, 2001; Pastres et al., 2004), altered primary productivity and stimulated frequent eruptions of diatoms or dinoflagellates (Schiewer, 1998; Pastres et al., 2004). However, in the open zones atmospheric deposition is one of most important sources of nutrients due to the increase in rainfall and atmospheric nutrients loading driven by climate changes and human activities (Reichwaldt and Ghadouani, 2012; Yeh et al., 2017). Increased nutrient supply and altered nutrient structure would favor some inferior competitors while impact total productivity of marine ecosystems (Dudgeon et al., 2006). These effects could disproportionately impact the abundance and composition of species through directly disrupting the interspecific competition and growth rates of species (Davis et al., 2006), which would drive regime shifts of phytoplankton communities associated with nutrient structure (Vörösmarty et al., 2010).

Given previous studies mainly focused on the temporal and spatial variations of chl *a* concentration in two tropical seas (Li et al., 2017; Wu et al., 2017), this study implemented field mesocosm experiments to investigate the influences of inorganic nutrient supply on phytoplankton community structure and diversity in SCS and EIO. The size-structure relative abundance and biodiversity responses to increased nutrients were both evaluated to get a comprehensive understanding of community dynamics. To address the importance of the atmospheric deposition on community dynamics, the study statistically analyzed inorganic nutrient flux from atmospheric deposition at the spatio-temporal scale, which was expected to show their effects on community structure and diversity. These results would identify potential influences of increased nutrient disturbances on community structure and biological diversity of marine phytoplankton in response to future atmospheric deposition and nutrient enrichment in tropical seas.

2. Materials and methods

SCS and EIO are typical tropical areas with abundant phytoplankton, and connected by the Strait of Malacca. Surface seawater temperature (23–29 °C), salinity and pH (mean: SCS, 33.0 ± 0.4 and 8.2 ± 0.1; EIO, 34.5 ± 0.3 and 8.4 ± 0.2, respectively) of the two tropical seas were stable throughout the entire year. Three characteristic stations (Fig. 1) were chosen to study effects of exogenous nutrients on phytoplankton community structure in different regions. From December 2013 to January 2014, short-term mesocosm experiments were conducted on board "*Dong Fang Hong 2*" at two SCS stations crossing a latitudinal range from 25°N to 5°S (S1, S2; Fig. 1), and station S3 in the South Equatorial Current area of EIO (Fig. 1) was accessible on board "*Hai Ce 3301*" in August 2016 due to expedition schedule. Three experimental sites are of oligotrophic state (SCS, DIN 1.56 ± 0.2 μM, DIP 0.11 ± 0.02 μM; EIO, DIN 0.58 ± 0.2 μM, DIP 0.18 ± 0.02 μM) and low chl *a* concentration (SCS, 0.21 ± 0.03 $\mu g \cdot L^{-1}$; EIO, 0.39 ± 0.03 $\mu g \cdot L^{-1}$). Precipitation is the main nutrient source of three stations, which would impact primary productivity and phytoplankton community structure of the two tropical seas.