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Chain response of microbial loop to the decay of a diatom bloom in the East China Sea

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ABSTRACT

Algal bloom has been regarded as one of the key causes for the summer hypoxia phenomena in the bottom water adjacent to the Yangtze River estuary in the East China Sea. Although a series of biological processes within microbial loop are involved in the development of oxygen depletion during the bloom decay, little has been known about the dynamics of microorganisms in response to the decaying process of the bloom through trophic interaction context. Here, we report some preliminary results of our observations about the response of microbial loop to the bloom decay, based on the onboard incubation experiments for 10 days during a diatom bloom near the Yangtze River estuary in August, 2011. Light and dark incubations were conducted to simulate the bloom decay inside and below the euphotic layer, respectively. In the first stage of bloom decay (Day 0 to Day 4), rapid response was found in heterotrophic bacteria (HB) and ciliate growth, which was in accordance with the decrease of total Chl *a*, indicating a "bottom-up" control at the early stage of bloom decay. However, the increase of heterotrophic nanoflagellates (HNF) abundance was rather inconspicuous, suggesting predation pressure on HNF from ciliate or other predator at this stage. In the second stage (Day 4 to Day 8), HB and ciliate decreased rapidly with the increase of HNF, revealing the release of HNF form ciliate predation, which suggested a "top-down" control. In the last stage of our experiment (Day 8 to Day 10), the trophic interactions were more complex, but it also implied a "top-down" control within the microbial loop. Meanwhile, virus had been monitored in the whole process of our incubations. It was found that virus lysed microalgae at the first stage, and lysed HB at the second stage. In addition, the bacterial mortality was principally caused by HNF grazing in the light-sufficient incubations and by viral lysis in the light-insufficient incubations. Our results suggest tight trophic interactions within the microbial loop in the decaying process of the algal bloom, which may assist our understanding of the role of microbial loop in hypoxia formation in coastal waters.

1. Introduction

The Yangtze River estuary is a seasonally hypoxic zone in the East China Sea (ECS) (Chen et al., 2007; Wei et al., 2007), where massive phytoplankton blooms have been observed almost every summer (Chen et al., 2003; Gao and Song, 2005). A vast amount of the primary production and nutrients fixed by phytoplankton were directed to the microbial loop (Kamiyama et al., 2000; Weisse et al., 1990), which is a key role in controlling carbon cycling and nutrient flow in the marine ecosystems (Azam, 1998; Gilbert et al., 1998; Jumars et al., 1989). Dissolved organic matter (DOM) released from phytoplankton through lysis or grazing is the major energy sources for heterotrophic bacteria (HB) in oceans and lakes, which may be responsible for microbial degradation processes (Arrigo, 2004; Azam, 1983; Brussaard et al., 1995). A large amount of studies about the changes of bacterial communities in phytoplankton blooms have been reported in most of aquatic ecosystems (Fandino et al., 2001; Larsen et al., 2004; Rink et al., 2007; Yager et al., 2001) and it has been confirmed that HB is a significant biotic factor in the process of biogeochemical cycling in aquatic ecosystems (Azam, 1983; Cole et al., 1988). As a major predator of HB, heterotrophic nanoflagellate (HNF) is an important

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link between HB and other higher trophic levels (such as ciliate) in microbial loop (Taylor, 1982). Through grazing on bacteria, HNF has a great influence on remineralization and plays a crucial role in carbon and nutrient recycling in pelagic ecosystems (Azam, 1983; Burns and Gilbert, 2006; Jürgens et al., 1999; Lim et al., 2005).

Besides prokaryotic and eukaryotic microorganisms, virus is considered to be a new component of the microbial loop (Bergh et al., 1989; Bratbak et al., 1990; Proctor and Fuhrman, 1990; Suttle et al., 1990). Over the years, numerous reviews have pointed out that virus acts as an important biological control on the mortality of phytoplankton (particularly during blooms) and bacteria (Brussaard et al., 1996; Gobler et al., 1997; Reisser, 1993; Short, 2012; Suttle, 1994). Although grazing by HNF seems responsible for the mortality of bacteria, viral lysis is also considered as a potential factor for bacterial loss (Proctor and Fuhrman, 1990; Suttle et al., 1990). Moreover, recent studies have also implicated that virus has an effect on the termination or control of various algal blooms (Brussaard et al., 1995; Castberg et al., 2001; Gastrich et al., 2004; Tomaru et al., 2007; Van Boekel et al., 1992).

In addition, light is one of the most important factors in determining the microbial communities in the aquatic ecosystems (Jiao et al., 2002). During bloom decay, when nutrients are depleted, phytoplankton cells will form aggregates, which will eventually sink out of the euphotic layer to the deep water. However, due to the wave action, a large portion of the aggregates may suspend and remain in the euphotic layer for quite a period of time. Till now, little is known about the difference in the responses of microbial loop to bloom decay inside and below the euphotic layer of the water column.

It can be expected that most of the organic carbon accumulated in algal blooms will be combusted within microbial loop, accompanying with a significant reduction of oxygen concentration in the water column, which in turn may affect the composition of microbial loop (Dagg et al., 2007, 2008). Thus, algal bloom has been suggested as one of the key causes for the summer hypoxia phenomena in the bottom water adjacent to the Yangtze River estuary in the ECS (Li et al., 2002; Rabouille et al., 2008; Zhu et al., 2011), where microbial organisms (including prokaryote, eukaryote and virus) are active and have a fluctuation in their abundance during the oxygen depletion process (Baird et al., 2004; Bręk-Laitinen et al., 2012; Park and Cho, 2002). During the last decades, the microbial loop have been widely investigated in fresh water and marine ecosystems (Chen et al., 2008, 2009, 2010; Lefranc et al., 2005; Moon-van Der Staay et al., 2001). However, little attention has been paid on the trophic interactions within microbial loop during the bloom decay, especially the "top-down" control, and thus the role of microbial loop (from HB to ciliate and virus as well) in the fate of algal bloom is still poorly understood.

In the current study, our aims were to investigate the response of microbial loop to the decay of algal bloom (as well as the process of oxygen depletion), and figure out the different role of virus in different stage of the bloom decay. Meanwhile, we also try to identify the difference of the above response between inside and below the euphotic layer. For this purpose, the incubation experiments accompanied with multiple measures were adopted allowing for a detailed description of changes in the microorganisms (i.e. phytoplankton, heterotrophic bacteria, nanoflagellate, ciliate and virus) and the associate parameters (i.e. nutrients, dissolved organic matter and dissolved oxygen).

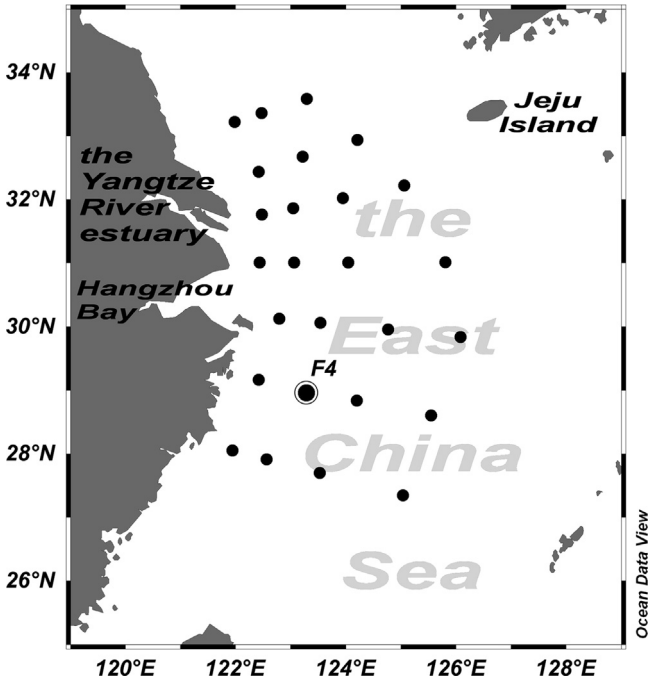

Fig. 1. The investigation area and the location of Stn.F4 in the ECS. Stn.F4 was about 150 km to the south of Hangzhou bay and at the edge of a bottom water hypoxia area in the East China Sea which reported by Chen et al. (2007) and Wei et al. (2007). The water depth of the station was 72.4 m.

2. Materials and methods

A multidisciplinary investigation, aboard *R.V.* Beidou, on the bottom water oxygen depletion phenomenon around the ESC coastal waters, was carried out from August 10 to 31, 2011. The scope of survey area (27.3–33.4°N, 121.9–126.1°E) is shown in Fig. 1. High concentration (~8 mg/m^3) of Chl *a* in the surface water was detected at Stn.F4 (29.0°N, 123.2°E) on August 19. The microscopic examination revealed that it was a diatom bloom at the beginning of declining phase. In order to track the succession of microbial loop along with the process of bloom decay in the water, the incubation experiments were conducted from August 19 to 29. The surface seawater at Stn.F4 was collected by 10 L Niskin bottles on a "Sea Bird" CTD, then transferred into 14 polycarbonate carboys (20 L) and incubated in a tank on the forecastle of the vessel. Six of the incubation carboys were wrapped in thick black plastic bags to simulate light-insufficient condition in the water below the euphotic layer (D-group). The others were directly exposed to sun light to simulate light-sufficient condition in the euphotic layer (L-group). Water bath was achieved by pumping seawater continuously from the sea surface to the incubation tank. Sampling was conducted at 10.00–11.00 a.m. on Days 0, 4, 8 and 10 from the start of incubation (Day 0). Samples were duplicated, and each carboy served as a sample.

Dissolved oxygen (DO) was measured with Winkler method as described in Zhu et al. (2011). Water samples (500 mL) for chromophoric dissolved organic matter (CDOM) detection were filtered with Waterman GF/F filters and the absorption spectra measurement was performed following the protocol of Guo et al. (2011). The absorption coefficient at 280 nm (a_{280}) was chosen as an index of CDOM concentration. Samples (300 mL) for Chl *a* analyses were filtered on to 0.2 μm Millipore polycarbonate membranes filters and extracted with 90% acetone and determined fluorometrically (Parsons et al., 1977). Samples (100 mL) for nutrients determination were filtered through Whatman GF/F filters and analyzed using an Auto-Analyzer Skalar SAN^{plus} (Liu et al., 2010).

Samples (250 mL) for phytoplankton identification and cell counting were fixed with formaldehyde (1%, final conc.) and analyzed in the laboratory with inverted microscope as described by Utermöhl (1958). Samples (1 L) for ciliate identification and