



Distribution of picoplankton in the northeastern South China Sea with special reference to the effects of the Kuroshio intrusion and the associated mesoscale eddies

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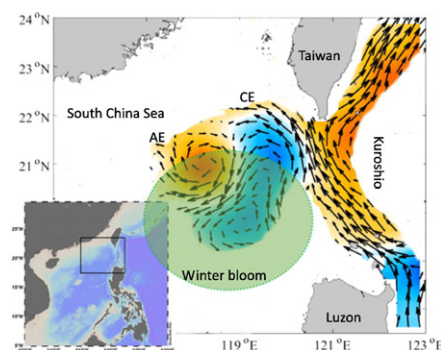
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HIGHLIGHTS

- Picoplankton groups were studied in the northeastern South China Sea during the winter phytoplankton bloom
- The Kuroshio intruded into the SCS in a form of leaking current and associated with an eddy pair
- The picoplankton distributions pattern were influenced significantly by the perturbations of the complex physical processes

GRAPHICAL ABSTRACT



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ABSTRACT

We investigated picoplankton distribution patterns and environmental variables along an east-to-west transect in the northeastern South China Sea (SCS) during late winter 2016, giving us the opportunity to examine the impacts of the Kuroshio intrusion and the associated eddies. The results indicated that the subsurface (50–75 m) phytoplankton biomass chlorophyll (Chl *a*) maximum (SCM) disappeared and was replaced by higher Chl *a* in the middle part of the transect due to the impacts of the Kuroshio intrusion and mesoscale eddies. Both flow cytometry and pyrosequencing data revealed that picoplankton abundance and community structure were significantly influenced by perturbations in complex physical processes. Picoeukaryotes represented most of the total phytoplankton biomass, and their maximum abundance ($> 10^4$ cells mL⁻¹) occurred within cyclonic eddy-affected regions (Stations 11 and 12), whereas the abundance of *Prochlorococcus* was the lowest in these regions. *Prochlorococcus* showed a higher abundance in the Kuroshio-affected area, while *Synechococcus* was mostly distributed at the upper well-lit depths, with its maximum abundance observed in surface waters (0–30 m) adjacent to the cyclonic eddy center. Heterotrophic bacteria (HBA) displayed high abundance along the transect, consistent with the total phytoplankton biomass. Phylogenetic analysis revealed 26 bacterial phyla, with major components belonging to *Proteobacteria*, *Cyanobacteria*, *Actinobacteria*, and *Bacteroidetes*, as well as SAR406. Notably, relatively more *Rhodobacterales*, *Flavobacteriales*, *Alteromonadales*, and *Vibrionales* that were distributed in surface waters of the cyclonic eddy center were specifically associated with the phytoplankton (mainly

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picoeukaryotes) bloom. Our study highlights the impacts of the Kuroshio intrusion in regulating the microbial ecology of the northeastern SCS and the potential coupling between phytoplankton and bacteria.

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1. Introduction

Picoplankton groups, including picophytoplankton and heterotrophic bacteria (HBA), are the major microbial components of plankton communities in oceans. They also play a fundamental role in biogeochemistry and food web dynamics in marine ecosystems (Azam and Malfatti, 2007; Ducklow, 1999). As a component of picoplankton, picophytoplankton communities (*Synechococcus*, *Prochlorococcus* and picoeukaryotes) are the most important components of photoautotrophic plankton, usually contributing to 50%–90% of the total chlorophyll (Chl *a*) in oligotrophic waters (Agawin et al., 2000; Zubkov et al., 1998). Another major component of picoplankton, HBA, are the main consumers of dissolved organic matter (DOM) and contribute significantly to carbon and nutrient cycling (Ducklow, 1999). Different phylogenetic compositions of HBA have unique ecological functions that are crucial for biogeochemical cycles in the ocean. Open oceans are isolated from terrestrial sources of organic matter, and DOM mainly comes from primary producers. Moreover, picophytoplankton and HBA interact with each other in many respects (Amin et al., 2015; Amin et al., 2012). Thus, the identification of factors that regulate the abundance and community composition of picoplankton is one of the central challenges in marine microbial ecology today. Picoplankton changes along well-characterized environmental gradients provide opportunities not only to study the ways in which picoplankton shift in response to

surrounding environmental changes but also to enhance our understanding of the biogeochemical effects of universally occurring physical processes that can cause environmental gradients in oceans (Lee et al., 2014; Linacre et al., 2015; Nelson et al., 2014). Target observations (e.g., the EDDIES project, Sargasso Sea and the *E-FLUX* project, Hawaii) have analyzed the responses of picoplankton to complex physical processes (Baltar et al., 2010; Benitez-Nelson and McGillicuddy, 2008; Huang et al., 2010; Nelson et al., 2014); examples will be detailed in the discussion section. However, physical and biological processes differ according to region, and we are still far from understanding the relationships between picoplankton and ocean environments.

The South China Sea (SCS), the largest marginal sea of the western Pacific Ocean, is under the strong influence of the East Asian monsoon. Therefore, cyclonic and anticyclonic basin-scale circulations often occur around the SCS continental margin due to monsoon-induced flows in winter and summer, respectively (Fang et al., 2002; Gan et al., 2006). This area is also influenced year-round by the western boundary current of the North Pacific subtropical gyre (Kuroshio) (Fang et al., 2002; Gan et al., 2006; Nan et al., 2015; Qu, 2000). The Luzon Strait (LS) is the deepest passage connecting the SCS to the Pacific Ocean, (Fig. 1a), through which the Kuroshio affects the SCS with seasonal and short temporal intrusions (Metzger and Hurlburt, 2001). This is an important issue and has been investigated for years by multidisciplinary researchers. The Kuroshio carries the northwestern Pacific

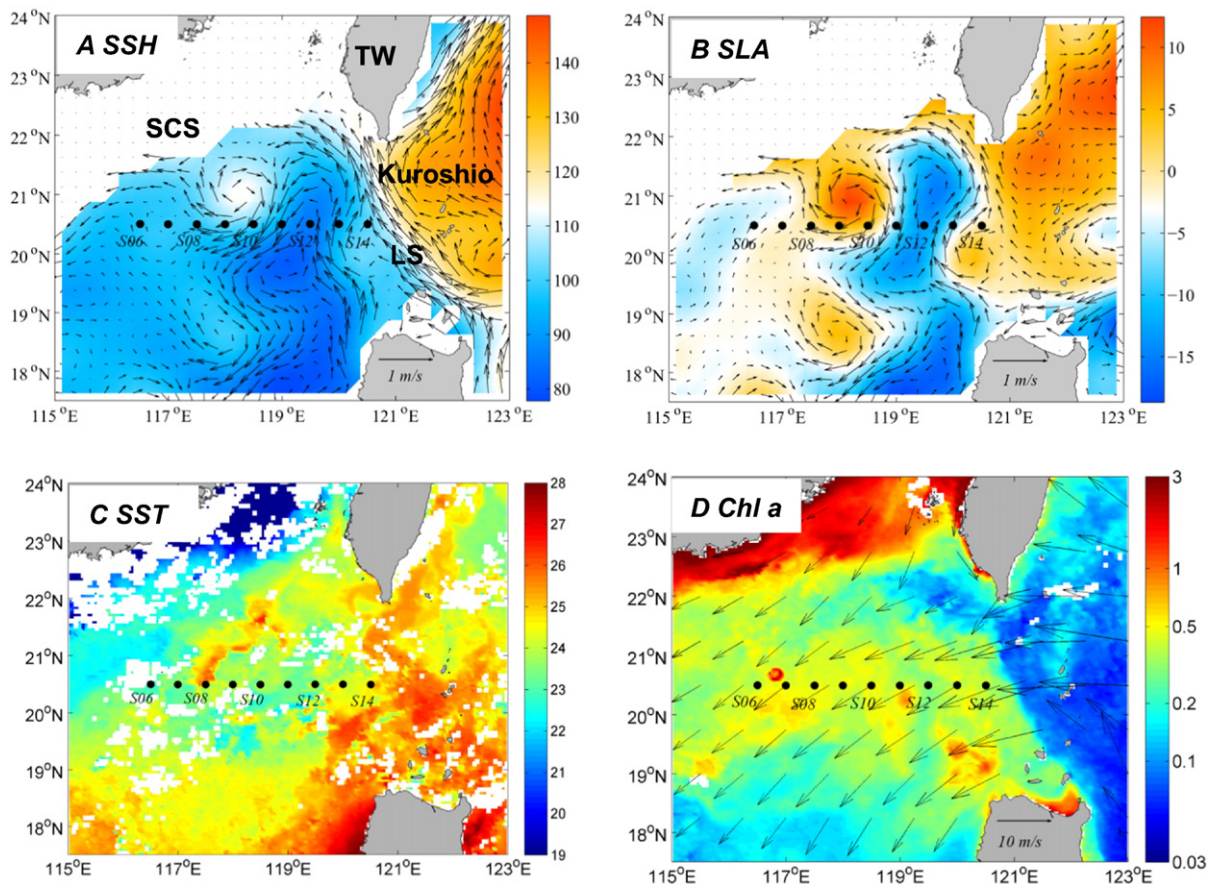


Fig. 1. Maps of (A) sea surface height (SSH, cm) with geostrophic currents (black vectors in m s^{-1}), (B) sea level height anomaly (SLA, cm), (C) satellite surface temperature (SST, $^{\circ}\text{C}$), and (D) sea surface Chl *a* (mg m^{-3}) with sea surface winds (vectors in m s^{-1}) in the northeastern SCS during the cruise. Regions shallower than 200 m are masked in the maps of SSH and SLA.

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