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Does microzooplankton grazing contribute to the pico-phytoplankton dominance in subtropical and tropical oligotrophic waters?

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ABSTRACT

Microzooplankton grazing has been proposed as an important factor regulating the phytoplankton size composition, particularly in oligotrophic waters, but it has not been well examined. To examine the role of microzooplankton grazing in the pico-phytoplankton dominance in subtropical and tropical oligotrophic waters, dilution experiments with size-fractionated chl-*a* were conducted in the South China Sea (SCS) in August–September 2008 and May 2009. Total phytoplankton growth rate (μ) was 0.34–1.98 d^{-1}(0.96 ± 0.49 d^{-1}). The corresponding microzooplankton grazing rate (m) was 0.30–1.99 d^{-1} (0.83 ± 0.54 d^{-1}). The microzooplankton grazing impact (m/μ) on total phytoplankton was 83.5% ± 76.3%. The growth rates of pico-phytoplankton (<3 μm) (1.02 ± 0.55 d^{-1}) were higher than those of nano- (3–20 μm) (0.95 ± 0.58 d^{-1}) and micro-cells (20–200 μm) (0.60 ± 0.71 d^{-1}), while the microzooplankton grazing rates on pico-phytoplankton (0.77 ± 0.58 d^{-1}) were lower than those on nano-cells (1.00 ± 0.79 d^{-1}), resulting in the higher grazing impact on larger cells. Increase of the pico-cell proportion and decrease of the nano- and micro-cell proportions after the incubation coincided well with the varied grazing impacts. Our results indicate that the high microzooplankton grazing impact keeps the phytoplankton standing stock at a low level, and the selective grazing of microzooplankton on nano-phytoplnakton as well as the low growth rates of micro-phytoplankton contributes to the pico-phytoplankton dominance in subtropical and tropical oligotrophic waters of the SCS. Variation in the phytoplankton-size-dependent grazing impact in different studies has been discussed.

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1. Introduction

Phytoplankton size composition affects the fate of the synthesized organic matter in the planktonic ecosystem [1–3]. Most of the newly fixed carbon by small cells in oligotrophic waters is recycled within photic layer. By contrast, a significant fraction of primary production produced by large cells in nutrient-rich waters is exported into the ocean interior. Phytoplankton community in subtropical and tropical oligotrophic waters is usually dominated by small-sized pico-cells (<3 μm). Low concentration of dissolved inorganic nutrients is usually thought as the main reason for the dominance of pico-plankton [4,5]. Increase of temperature [6] and decrease of salinity [7] are also reported to account for the decrease of phytoplankton size. However, phytoplankton dynamics cannot be fully understood if only considering the abiotic environment and algal physiology [8], rather zooplankton grazing is another important factor for regulating phytoplankton communities [9,10]. Especially, microzooplankton is the major grazer of phytoplankton cells in marine ecosystems [11–14], and plays an important role in structuring phytoplankton communities [15–18]. Stronger gazing of microzooplankton on smaller cells has been reported as one of the reasons for the dominance of larger phytoplankton in nutrient-rich waters [19]. Grazing rather than cell division rate has been proposed as the main factor regulating the abundance and size composition of phytoplankton [8], particularly in oligotrophic oceans [20]. However, little has been examined on the role of microzooplankton grazing in the pico-phytoplankton dominance in subtropical and tropical oligotrophic waters.

The South China Sea (SCS) located in the subtropical and tropical Western Pacific is permanently stratified, and exhibits the characteristics typical of an oligotrophic ocean [21,22]. The phytoplankton community is dominated by pico-cells [23]. Previous studies showed that microzooplankton consumes most (even more than 100%) of the daily phytoplankton production in the SCS [24–27]. We hypothesize that microzooplankton grazing may contribute to the pico-phytoplankton dominance in the oligotrophic waters of the SCS.

To examine the effects of microzooplankton grazing on the phytoplankton size composition in subtropical and tropical oligotrophic waters, dilution experiments (n = 20) with size-fractionated chl-*a*

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were conducted in offshore waters of the SCS during the periods of August–September 2008 and May 2009. Our results indicates that higher grazing rates (m) on nano-phytoplankton and lower growth rates (μ) of micro-phytoplankton led to the higher grazing impact (m/μ) on larger-sized cells, and the higher grazing rates on nano-phytoplankton by microzooplankton indicate their contribution to the pico-cell dominant phytoplankton composition in the study waters.

2. Materials and methods

2.1. Experimental design

Seventeen dilution experiments were conducted on board *Shiyan 3* from August to September 2008 (Fig. 1); and the experimental stations were located in the offshore waters of the northern SCS. In addition, three other dilution experiments were conducted in the southern SCS in May 2009, with two experiments at a coral reef lagoon (YS) of the Nansha Islands, and one at an open-water station (kj35).

The dilution technique [28] was adopted following Landry et al. (1995) [29] and Liu et al. (2002) [30]. All incubation bottles, tubes and other containers were acid-cleaned before each experiment. Surface seawater was collected at each station, and pre-screened with a 200-μm aperture nylon net to remove meso-plankton. Part of the pre-screened water was gently filtered to generate particle-free water. Measured amounts of particle-free and natural seawater were added successively to fill the 2.4-L polycarbonate bottles. Duplicates of four dilution treatments with 100%, 75%, 50% and 25% of natural seawater were prepared. Two additional bottles were filled with natural seawater and sacrificed for size-fractionated chlorophyll *a* (chl-*a*) and dissolved nutrients. For the August–September experiments, additional bottles were filled according to the four dilution treatments and sacrificed for measuring the actual dilution factor (the proportion of natural seawater) of each treatment. For the May experiments, nutrients (0.5 μM NH_4Cl, 0.03 μM KH_2PO_4 and 1.0 nM $FeSO_4$) were added to each bottle except that two control bottles were filled with only undiluted seawater. To detect the effects of nutrient amendment on phytoplankton growth and microzooplankton grazing, a dilution experiment without nutrient amendment was conducted synchronously at YS as a control.

All the prepared incubation bottles were tightly capped and incubated for 24 hours on deck in perspex incubators covered with a neutral-density screen to simulate the natural light regime. The temperature was controlled by the continuous running-through of seawater pumped from the sea surface.

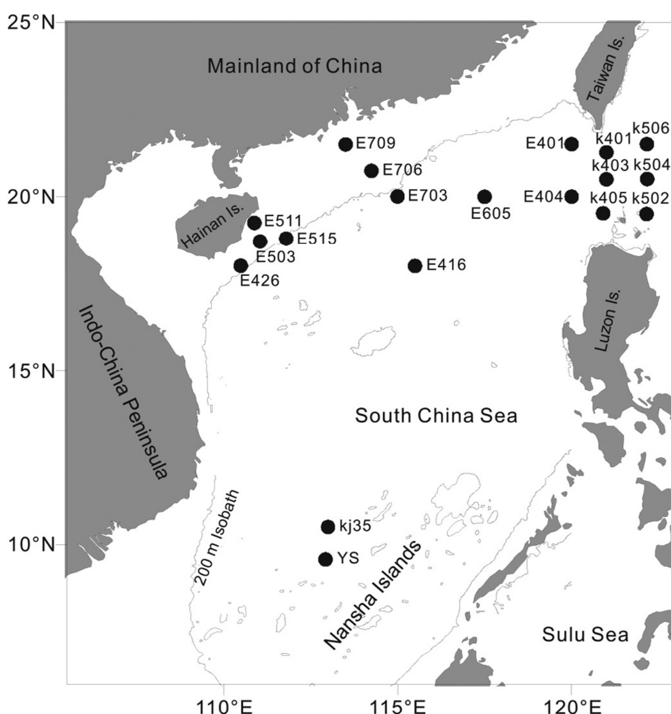

Fig. 1. Experimental stations in the South China Sea in August–September 2008 and May 2009.

2.2. Chl-a sampling and measurement

Half to 1 L seawater was filtered through a sequence of 20- and 3-μm pore size polycarbonate filters and GF/F filter for size-fractionated chl-*a* of micro- (20–200 μm), nano- (3–20 μm) and pico-phytoplankton (<3 μm) before and after incubation. Total chl-*a* was calculated as the sum of the three size fractions. These filters were dipped into 90% acetone for 24 hours at −20 °C in the dark. Chl-*a* was analyzed by fluorometry using a Turner Designs Model 10 Fluorometer [31].

2.3. Nutrient sampling and determination

For nutrient measurement, the water sample was pre-filtrated through a filter with 0.45-μm pore size and dispensed into an 80-mL polyethylene bottle, which was immediately frozen and stored at −20 °C for later analysis. The undiluted treatments were sampled before and after incubation for detecting potential nutrient change during incubation. The frozen sample was then thawed and the concentrations of nitrate (NO_3^-) and silicate (SiO_3^{2-}) were analyzed with a nutrients-autoanalyzer (Quickchem 8500, Lachat Instruments, USA) according to the standard manual.

2.4. Estimates of chlorophyll content per cell

To examine changes of chl-*a* content per cell during the incubation, 2 mL seawater from the undiluted treatments was sampled before and after the incubation. The samples were fixed with paraformaldehyde (final concentration of 1%), quick-frozen in liquid nitrogen and stored at −80 °C before analysis. Cellular red fluorescence of *Synechococcus* and autotrophic eukaryotes were measured using a Becton-Dickson FACSCalibur Flow Cytometer. The values of red fluorescence were used as the proxy of cellular chl-*a* [32].

2.5. Ciliate sampling and enumeration

For ciliate quantification, 3–5 L seawater was fixed with formaldehyde (final concentration ~2%) and kept in the dark. The sample was concentrated into 15 mL by gently siphoning the supernatant after at least a 24-hour settling period in the laboratory. The concentrate was used to determine the ciliate abundance under an inverted microscope.

2.6. Data analysis

Phytoplankton growth and microzooplankton grazing rates were estimated by least squares regression between apparent growth rates (AGR) and dilution factors according to Landry and Hasset (1982) [28] as follows:

$$k = \mathrm{AGR} = 1/t \ln(P_t/P_0) = \mu - d \times m$$

where t = the incubation time, P_0 = the initial phytoplankton biomass in terms of chl-*a* before incubation, P_t = the phytoplankton biomass

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