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Size-fractionated mesozooplankton biomass and grazing impact on phytoplankton in northern South China Sea during four seasons

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ABSTRACT

Biomass and grazing impact of three size fractions of mesozooplankton were investigated across a wide range of trophic conditions in northern South China Sea (SCS) during four seasonal cruises from July 2009 to May 2011. The grazing impact of mesozooplankton was determined by measurements of gut fluorescence and experimentally-derived gut clearance coefficients. In the northern SCS, the variation in mesozooplankton biomass was influenced by bottom-up effects. Due to riverine runoff to the shelf and winter mixing in oceanic areas, an increase in mesozooplankton biomass was observed in late spring corresponding to an increase in Chl *a* concentrations. However, because a significant portion of the Chl *a* came from pico-sized phytoplankton cannot be directly consumed by most mesozooplankton, especially in the oceanic waters during autumn and spring, the bottom-up effect was rather weak. Mesozooplankton consumed 0.7–21.5% of phytoplankton Chl *a* standing stocks daily, and it was higher in shallow shelf waters than in oceanic waters during spring and summer due to combined effects of mesozooplankton feeding behavior (higher herbivory in shelf waters) and phytoplankton composition (higher contribution of pico-sized phytoplankton in oceanic waters). If only the >2 μm phytoplankton were considered, the grazing impact by mesozooplankton became substantial, reaching $\sim 31\%\ d^{-1}$. Among the three size fractions of mesozooplankton, large-sized mesozooplankton (>1000 μm) dominated the total biomass and contributed more than 50% of the herbivory.

1. Introduction

Mesozooplankton (0.2–20 mm) play a key role in marine ecosystems in many aspects. They serve as a link for energy transfer from phytoplankton to higher trophic levels such as fish. In turn, intensive grazing of mesozooplankton controls phytoplankton standing stocks and shapes the structure of prey community (Kiørboe, 1997; Calbet and Landry, 1999). By the processes of metabolism and evacuation, mesozooplankton help to regenerate nutrients in upper water column (Isla et al., 2004a; Hernández-León et al., 2008) and export biogenic matter to great depths (e.g. Landry et al., 1994a; Roy et al., 2000; Turner, 2002). However, the relative contribution of mesozooplankton in top-down control and carbon export varies among trophic gradients. Gasol et al. (1997) reported that a given phytoplankton biomass supported higher mesozooplankton biomass in the oligotrophic open ocean than in productive coastal waters and concluded that consumer control was relatively more important in oligotrophic conditions. The phenomenon of relatively high mesozooplankton biomass and low phytoplankton biomass could be simply due to the major contribution of microzooplankton in the diet of mesozooplankton in areas with low phytoplankton. Nevertheless, Calbet (2001) concluded that mesozooplankton grazing was relatively important in unproductive areas based on the fact that the slope of mesozooplankton ingestion rate versus primary production was significantly smaller than 1. In other words, the importance of the mesozooplankton grazing impact increases with decreasing productivity. Thus, intense mesozooplankton grazing may be one of the reasons (besides nutrient limitation) for the lack of large-sized diatoms in the oligotrophic oceanic gyres. Therefore, downward carbon flux in each system is characterized by different components, with a fecal pellet-based system in the open ocean and a diatom aggregate-based system in coastal waters (Wassmann, 1998).

Mesozooplankton of different sizes can have different magnitudes of grazing impact on phytoplankton due to their different feeding behaviors, and hence contribute differently to downward carbon flux, as small-sized, slow sinking fecal debris produced by small mesozooplankton may be re-utilized either through remineralization or coprophagy within the euphotic layer, while large, fast sinking fecal

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pellets produced by large copepods significantly contribute to vertical carbon export (Landry et al., 1994a). Thus, the size composition of mesozooplankton has important implications for the general role of mesozooplankton in consuming phytoplankton and in contributing to carbon exports. For example, the small-sized copepod *Oithona*, that usually dominates in both coastal areas and the open ocean is assumed to be more carnivorous preferring protozoan prey to diatoms and is also coprophagous (González and Smetacek, 1994; Nakamura and Turner, 1997). Thus, the grazing impact on phytoplankton by mesozooplankton communities dominated by such small-sized and omnivorous species will be relatively low.

In this paper, we investigated the biomass and grazing of three size fractions of mesozooplankton in northern South China Sea (SCS), extending from coastal-shelf waters to slope-oceanic waters in four separate seasons (2009–2011). The coastal and shelf region of the northern SCS is influenced by seasonal coastal upwelling, riverine discharge and coastal currents passing through Taiwan Strait, while the central part of the SCS is influenced by a basin-wide surface circulation gyre that effectively isolates the interior of the SCS from influences of the riverine discharge and coastal currents (Wong et al., 2007). The seasonality of nutrient supply in the upper layer of northern SCS is primarily influenced by Asian monsoonal winds (Wang et al., 1999), as well as internal waves and typhoons that could alter the depth of the mixed layer (Liu et al., 1998). During summer, the southwest monsoon induces coastal upwelling and offshore Ekman transport along the northern edge of the SCS, while freshwater discharge from Pearl River is at its maximum, injecting high nutrients into the northeast part of northern SCS shelf with the aid of southwest winds (Gan et al., 2010). During winter when the northeast monsoon prevails, a nutrient-rich coastal current passes through Taiwan Strait from the East China Sea, mixing with coastal waters. Northeast winds also bring cold air, cooling the surface seawater in the open gyre and deepening the mixed layer below the nitracline, resulting in higher phytoplankton productivity than in summer (Chen and Chen, 2006). Phytoplankton growth is nutrient-limited in the central gyre, especially during summer when water column stratification is at its peak (Chen et al., 2009b).

Previous studies of mesozooplankton in northern SCS are rare, with most studies focusing on species composition, but with limited spatial or temporal coverage (e.g. Hwang and Wong, 2005; Tan et al., 2004; Li et al., 2006; Zhang et al., 2009; Guo et al., 2011). Zhang et al. (2009) reported that mesozooplankton were overall more abundant in onshore water, but more diverse in offshore water. Studies on grazing impact of mesozooplankton are limited to only a few copepod species and in the Pearl River estuary (Wong et al., 1991; Tan et al., 2004). Tan et al. (2004) found that the daily grazing impact by the copepod community was higher during the warm wet season than during the cold dry season in the Pearl River estuary. In this study, we investigated mesozooplankton biomass and gut contents across a wide range of trophic conditions in the northern SCS. Our goal was to compare the mesozooplankton ingestion rates and daily consumption on phytoplankton in different regions and different seasons, in order to examine how the impact of mesozooplankton grazing on phytoplankton change under different chlorophyll *a* concentrations.

2. Materials and methods

2.1. Sampling stations and water properties

Field investigations were conducted during 4 seasonal cruises in the northern SCS from July 2009 to May 2011. A total of 45 stations were sampled, including 17 stations for shelf waters and 28 stations for oceanic waters (Fig. 1). Seawater temperature profiles were measured with a CTD probe (SBE911). Water samples for chlorophyll a (chl *a*) determination were collected from 4 to 9 depths in upper 200 m water column (or the whole water column if it was shallower than 200 m) using Niskin bottles attached to a CTD rosette system. About 0.5–2 L of seawater was immediately filtered onto 25 mm Whatman GF/F glass–fiber filters that were extracted with 90% acetone at 4 °C overnight, and the chl *a* fluorescence was determined by a Turner Designs fluorometer (Strickland and Parsons, 1972).

2.2. Mesozooplankton dry weight and gut fluorescence

Mesozooplankton biomass and grazing rate were estimated by measuring dry weight and gut fluorescence, respectively. We followed the procedures described by Mackas and Coyle (2005) and Båmstedt et al. (2000) for gut fluorescence analysis. Briefly, mesozooplankton samples were towed vertically from 200 m (or near the bottom for shallow stations) to the surface at a speed of about 0.5 m s^{-1}, using a plankton net (0.5 m diameter, 200 μm mesh) equipped with a digital flowmeter (HYDRO-BIOS, Kiel). The contents of the cod-end were immediately transferred to a plastic beaker containing a soda solution at a final concentration of about 10% (soda:seawater, v-v), which was added to anaesthetize the animals to avoid gut pigment loss during further lab processing (Head et al., 1999). The samples were mixed in a beaker and divided into two equal aliquots, one for dry weight measurement and one for gut fluorescence measurement. We separated different size fractions of mesozooplankton by sequentially sieving the subsamples through mesh of different pore-sizes (1000, 500 and 200 μm) attached to bottom-cut beakers. Large gelatinous animals were removed from the samples if present to avoid entanglement in the mucus during size-fractionation (Landry et al., 1994a). Mesozooplankton on each size of mesh were then washed carefully with filtered seawater to avoid any contamination by large-celled phytoplankton. Stations with a phytoplankton bloom (e.g. *Phaeocystis*) that made it hard to separate mesozooplankton from phytoplankton contamination were abandoned, based on an abnormally high value of Chl/phaeopigment ratio (>5). For dry weight measurements, the size-fractionated mesozooplankton were gently washed off the mesh and filtered onto a pre-weighed 20 μm PC membrane (47 mm diameter), dried at 60 °Coven for 24 h and weighed using a precise electronic balance in the laboratory. For gut fluorescence determination, the size-fractionated mesozooplankton were also gently washed off the mesh and onto a 20 μm PC membrane. The membranes were then wrapped with foil and quick frozen at −80 °C for later processing. The frozen samples were thawed in the laboratory and placed into 15 ml centrifuge tubes. Gut pigments of the samples were then extracted by sonication (15 min) in 90% acetone and kept in the dark at 4 °C for about 24 h. After centrifugation, the fluorescence of the supernatants were measured by a Turner Design fluorometer using the method of acidification and the amount of gut pigments in the mesozooplankton guts was calculated as

$$\text{Chl } a \ (\mu g \text{ mg DW}^{-1}) = C \times (F_0 - F_a)/\text{DW}$$

$$\text{Phaeopigment } (\mu g \text{ mg DW}^{-1} = C \times (A \times F_a - F_0)/\text{DW}$$

where C is the fluorometer calibration constant; F_0 and F_a are the fluorescence readings of mesozooplankton samples before and after acidification, respectively; A is the acidification ratio; DW is the dry weight of mesozooplankton (mg DW m^{-3}). A correction factor was applied to convert measured phaeopigment to chlorophyll equivalents for total gut contents (Båmstedt et al., 2000). Thus, the total gut contents were calculated as

$$\text{Gut contents } (G, \ \mu g \text{ chl mg DW}^{-1}) = \text{Chl } a + 1.51 \times \text{Phaeopigments}.$$

2.3. Gut clearance coefficient and ingestion rate

The gut clearance coefficients (k), were acquired from time-series experiments of gut disappearance, and were applied to calculate the