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Seasonal and spatial comparisons of phytoplankton growth and mortality rates due to microzooplankton grazing in the northern South China Sea

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9, 16005–16032, 2012

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Abstract

We conducted a comprehensive investigation on the microzooplankton herbivory effect on phytoplankton in the northern South China Sea (SCS) using the seawater dilution technique at surface and deep chlorophyll maximum (DCM) layers in two cruises (July–August of 2009 and January of 2010). We compared vertical (surface vs. DCM), spatial (onshore vs. offshore), and seasonal (summer vs. winter) differences of phytoplankton growth (μ_0) and microzooplankton grazing rates (m). During summer, both μ_0 and m were significantly higher at the surface than at the layer of DCM, which was below the mixed layer. During winter, surface μ_0 was significantly higher than at DCM, while m was not significantly different between the two layers, both of which were contained within the mixed layer. Surface μ_0 was, on average, significantly higher in summer than in winter; while average surface m was not different between the two seasons. There were no significant cross-shelf trends of μ_0 in summer or winter surface waters. In surface waters, μ_0 was not correlated with ambient nitrate concentrations and the effect of nutrient enrichment on phytoplankton growth was not pronounced. There was a decreasing trend of m from shelf to basin surface waters in summer, but not in winter. Microzooplankton grazing effect on phytoplankton (m/μ_0) did not increase with distance offshore, suggesting that the importance of microzooplankton as grazers of phytoplankton may not decrease in onshore waters. On average, microzooplankton grazed 73 % and 65 % of the daily primary production in summer and winter, respectively.

1 Introduction

Microzooplankton ($< 200\,\mu$m; including nanoflagellates, ciliates, dinoflagellates, sarcodines, and small metazoans) are the major grazers on phytoplankton, accounting for the loss of 60 % ∼ 80 % of daily primary production in the sea (Calbet and Landry, 2004). Owing to their fast reproduction rates (Banse, 1982), microzooplankton grazing is able to respond quickly to the increased phytoplankton growth rate

upon nutrient enrichment (Landry et al., 2000). Nutrients excreted by microzooplankton are particularly important for maintaining low phytoplankton biomass but relatively high growth rates of phytoplankton in some high-nitrate-low-chlorophyll (HNLC) regions (Frost and Franzen, 1992; Landry et al., 1997; Strom et al., 2000). Recently,
5 Landry et al. (2011a) have shown that the rate of phytoplankton biomass grazed by both microzooplankton and mesozooplankton can fully balance phytoplankton growth rate throughout the euphotic zone in the equatorial Pacific.

It is still unclear how the effect of microzooplankton grazing on primary production changes with environmental conditions such as temperature and nutrient supply. The
10 proportion of daily primary production consumed by microzooplankton (m/μ_0) is often believed to be greater in oligotrophic waters where phytoplankton with small size are more edible for microzooplankton (Liu et al., 2002a; Strom et al., 2007). It may also increase with increasing temperature because of different temperature coefficients for phytoplankton and microzooplankton growth (Rose and Caron, 2007).

15 Light also has the potential to decouple m from μ_0. From the surface of the ocean to the bottom of euphotic zone, light intensity decreases exponentially, which causes a substantial reduction of μ_0; while m may not be affected as much as μ_0 (Landry et al., 2011b). As such, microzooplankton should remove a greater proportion of primary production at depth compared with the light-saturated surface waters.

20 In spite of the above environmental effects, Calbet and Landry (2004) did not find any systematic trends of m/μ_0 along chlorophyll gradients in their analysis on a global dilution dataset. In another analysis using generalized additive models, Chen et al. (2012) found that the combination of temperature and chlorophyll only explains 4 % of the total variation of m/μ_0. Are there other parameters that were not taken into account in the
25 above analyses but are important in affecting m/μ_0? Or are the m/μ_0 ratios intrinsically not able to being predicted by external environmental parameters?

With these questions in mind, we conducted a series of microzooplankton grazing experiments in the northern SCS in two cruises, by taking advantage of the highly variable environments in this area. There are relatively few data on microzooplankton

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herbivory in this area compared with primary production data (Liu et al., 2002b; Chen and Chen, 2006). The northern SCS is affected by a number of physical forcings including the continental runoff from the north, China coastal current coming through the Taiwan Strait, and seasonal reversing monsoons. During summer, the southwest monsoon induces clockwise water current circulation in the northern SCS and coastal upwelling over the widened continental shelf (Wong et al., 2007; Gan et al., 2009), while the upper ocean layer forms a large-scale cyclonic circulation under the influence of the northeast monsoon in winter and the nutrient-rich East China Sea coastal water can flow into NSCS through the Taiwan Strait. The most salient seasonal pattern in offshore waters of SCS is the peak of phytoplankton biomass, primary production, and new production during wintertime when mixed layer deepens and nutrients are entrained into the euphotic zone (Liu et al., 2002b; Ning et al., 2004; Chen and Chen, 2006). In summer, the enhanced Pearl River discharge may also induce higher phytoplankton biomass and primary production in the plume area.

We test three hypotheses. First, in the oligotrophic basin waters, should microzooplankton grazing remove a greater proportion of primary production than in more eutrophic shelf waters? Second, in the warm summer, should m/μ_0 be greater than in winter? Third, should m/μ_0 be greater at depth than in surface waters?

2 Material and methods

Dilution experiments (Landry and Hassett, 1982) were conducted at a total of 46 stations during two cruises, one during the summer (18 July to 16 August 2009; 22 stations) and the other in winter (6 January to 30 January 2010; 24 stations) in the northern SCS (Fig. 1). At each station, seawater samples were collected from two depths (1 m and DCM layer) using an acid-washed Niskin bottle attached to a CTD rosette system. During the winter, a DCM layer did not exist at many stations (Tables S1, S2) and the so-called "DCM layer" was determined as roughly 5 % of surface irradiance. All incubation bottles, tubing and carboys were washed with 10 % HCl and rinsed thoroughly

with distilled water and ambient seawater before each experiment. Measured amounts of particle-free water, prepared by gravity filtering the seawater through a 0.2 µm filter capsule (Pall Corporation), were first added to 1.2 L polycarbonate bottles, and the bottles were then gently filled with whole seawater to capacity. The filter capsules were soaked in 10 % HCl for more than 2 h before the first use and were washed with diluted acid, distilled water and ambient seawater between each experiment to eliminate possible toxins associated with the capsules (Landry et al., 1995). Five dilution treatments of 15, 27, 50, 73 and 100 % natural seawater were prepared. All five bottles were enriched with inorganic nutrients (final concentrations of 0.5 mmol m^{-3} NH$_4$Cl, 0.03 mmol m^{-3} KH$_2$PO$_4$ 1 nmol L^{-1} FeCl$_3$, and 0.1 nmol L^{-1} MnCl$_2$) to promote constant phytoplankton growth. Another two bottles filled with unfiltered seawater without nutrient addition served as *no nutrient* controls. Two additional bottles filled with unfiltered seawater were sacrificed for initial samples for chlorophyll *a* (Chl *a*) and flow cytometric (FCM) analyses. All of the bottles were tightly capped and incubated for 24 h in a deck incubator cooled by running surface seawater and covered with neutral screens to simulate in situ light environment. Incubations were typically initiated within 1 h after water collection. After incubation, samples were taken from each bottle for Chl *a* and FCM analyses.

For Chl *a* analyses, 300 mL to 1.2 L seawater samples were filtered onto GF/F glass-fiber filters under low vacuum. The filters were extracted in 90 % acetone at 4 °C in the dark for 24 h and the Chl *a* concentrations were measured by the non-acidification method (Welschmeyer, 1994) on a Turner Designs fluorometer (Model No. Trilogy 040).

FCM samples were fixed with 0.5 % buffered paraformadehyde and frozen at −80 °C (Vaulot et al., 1989). Cell abundances of picophytoplankton were enumerated using a Becton-Dickson FACSCalibur cytometer, with different populations distinguished based on side-scattering (SS), orange and red fluorescence (Olson et al., 1993). Yellow-green fluorescent beads (1 µm, Polysciences) were added to the samples as an internal standard. For counting heterotrophic nanoflagellates, the samples were stained with 0.02 % SYBR Green I (Molecular Probes) in the dark under the presence of 30 mmol L^{-1}

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potassium citrate at 37 °C for 1 h before analysis (Zubkov et al., 2006). The exact flow rate was calibrated by weighing a tube filled with distilled water before and after running for certain time intervals and the flow rate was estimated as the slope of a linear regression curve between elapsed time and weight differences (Li and Dickie, 2001).

Ciliates and dinoflagellates were preserved by 5 % acidic Lugol's solution at room temperature until analysis. Upon return to the lab, the samples were observed with an inverted microscopy (Leica Dmirb). Cell length and width were sized using the software Simple PCI6. Cellular carbon content of ciliates was calculated from biovolumes using a conversion factor of $0.19 \, \mathrm{pg \, C \, \mu m^{-3}}$ (Putt and Stoecker, 1989). Biovolume of dinoflagellates was converted to cell carbon using the equation: $\mathrm{pg \, C \, cell^{-1}} = 0.76 \times \mathrm{volume} \, (\mu m^3)^{0.819}$, according to Mender-Deuer and Lessard (Menden-Deuer and Lessard, 2000). Only dinoflagellates known to have phagotrophic ability (such as *Gyrodinium*, *Protoperidium*) were included in the biomass of microzooplankton.

Assuming an exponential growth model, we calculated the net growth rate (k_i) of phytoplankton in each dilution treatment according to the formula $k_i = \ln[C_i/(D_i \cdot C_o)]$, where C_i is the Chl *a* concentration in the *i*-th treatment bottle at 24 h, D_i is the dilution factor (proportion of unfiltered seawater) of the *i*-th treatment, and C_o is the initial Chl *a* concentration. Estimates of phytoplankton growth rate with nutrient enrichment (μ_n) and mortality rate (m) were derived from Model I linear regressions of net growth rate against dilution factor (Landry and Hassett, 1982). In situ estimates of phytoplankton instantaneous growth rate (μ_0) were computed as the sum of m and net growth rate in control bottles without added nutrients. For a few cases of positive slope of the linear regression (negative grazing rates, but not significantly different from zero), we determined m to be zero and μ_n to be the average value of the net growth rates of all five dilution treatments with nutrient enrichment (Murrell et al., 2002).

We used FCM-derived estimates of cellular biovolume and fluorescence to correct Chl *a* estimates of phytoplankton growth rate for pigment photoacclimation. For each experiment, the ratios (R) of cellular red fluorescence to biovolume were calculated for initial and final FCM samples. Corrected phytoplankton growth rates (μ_0' and μ_n') were

calculated as $\mu' = \mu - \ln(R_f/R_i)$, where R_i and R_f are the initial and final R estimates (Landry et al., 2003; Chen et al., 2009b). m was not affected by changes in cellular pigment contents.

Corresponding seawater temperature, salinity, pressure, nutrient, and Chl a concentrations were also measured. Temperature, salinity, and pressure were determined by Conductivity-Temperature-Depth (CTD) probes. Mixed layer depth (MLD) was defined as the first depth where temperature was 0.2 °C lower than at surface (5 m). Nutrients were measured following standard methods (Parsons et al., 1984).

3 Results

For identifying spatial patterns, we classify the stations into three groups according to bathymetry: shelf (bottom depth ≤ 100 m), slope (100 m < bottom depth ≤ 2000 m), and basin (bottom depth > 2000 m). Note that although this crude approach neglects the variations of mesoscale features such as river plume and eddies, it provides a straightforward way to show the major cross-shelf gradients.

3.1 Temperature, nutrients, and mixed layer depth (MLD)

The background information of physical and chemical parameters is shown in Table 1. Most summer stations were warm, oligotrophic, and stratified, while winter stations were relatively cool, mesotrophic, and well-mixed. Except for a few stations, there were no evident cross-shelf gradients of temperature and nutrient concentration in summer; while in winter, shelf waters were cooler and richer than slope and basin waters. The depth of DCM layer was usually below MLD in summer but shallower than MLD in winter.

3.2 Chl *a* and microzooplankton biomass (B_z)

In summer, surface Chl *a* concentrations (mean = 0.12 and 0.15 mg m^{-3}, for slope and basin waters, respectively) were significantly lower than those at DCM layers (mean = 0.62 and 0.57 mg m^{-3}, respectively) in slope and basin waters (paired Wilcoxon-tests, $p < 0.05$); while this vertical difference was not observed in winter due to more vigorous mixing (median stratification index = 0.041 and 0.012 kg m^{-4}, in summer and winter, respectively) (Fig. 2). In shelf waters, Chl *a* concentrations were insignificantly different between surface and DCM waters in both summer and winter (paired Wilcoxon-tests, $p < 0.05$; Fig. 2a, b). Comparing seasonal differences, in slope and basin waters, surface Chl *a* concentrations were significantly lower in summer than in winter (mean = 0.55 and 0.61 mg m^{-3}, for winter slope and basin waters, respectively; Wilcoxon-tests, $p < 0.01$); while surface Chl *a* concentrations were insignificantly different between summer in winter in shelf waters ($p > 0.05$). In both seasons, spatially, there is a decreasing trend of both surface and DCM Chl *a* concentrations from shelf to deeper stations (Fig. 2).

In spite of the large differences of Chl *a* concentrations between surface and DCM in summer slope and basin waters, B*z* did not differ significantly between the two depths in summer ($p > 0.05$; Fig. 3). Within each region, B_z did not differ significantly between summer and winter, either ($p > 0.05$). There is a decreasing trend of surface B*z* from shelf to basin waters in summer (Wilcoxon-tests, $p < 0.01$), but not in winter (Fig. 3). During summer, B_z was positively correlated with Chl *a* in surface waters (Spearman $r = 0.46$, $p < 0.05$), but not in DCM waters ($p > 0.05$). There was no such positive correlation in the winter. The ratio of B_z over Chl *a* was significantly greater in surface waters than in DCM in the summer (paired Wilcoxon-test, df = 15, $p < 0.001$), but not in winter. In surface waters, the ratio of B_z : Chl *a* was also significantly higher in the summer than in the winter (Wilcoxon test, $p < 0.001$), which might be related with both carbon-to-chlorophyll ratios and microzooplankton-to-phytoplankton biomass ratios.

3.3 Phytoplankton growth and mortality rates due to microzooplankton grazing

The detailed results for each experiment are shown in data appendices Tables S1 and S2. In both seasons, surface μ_0 (mean ± sd: $0.89 \pm 0.45\,\mathrm{d}^{-1}$ and $0.61 \pm 0.32\,\mathrm{d}^{-1}$, for summer and winter, respectively) were significantly higher than that in DCM layers (mean ± sd: $0.29 \pm 0.34\,\mathrm{d}^{-1}$ and $0.45 \pm 0.21\,\mathrm{d}^{-1}$, for summer and winter, respectively) (paired Wilcoxon tests, $p < 0.01$) (Fig. 4). Spatially, there were no significant cross-shelf trends of μ_0 in summer or winter surface waters. On average, surface μ_0 were significantly higher in summer than in winter in shelf waters (Wilcoxon test, $p < 0.05$), but were similar in slope and basin waters (Fig. 4).

Phytoplankton mortality rates due to microzooplankton grazing (m) averaged $0.49 \pm 0.47\,\mathrm{d}^{-1}$ and $0.35 \pm 0.21\,\mathrm{d}^{-1}$ (mean ± sd) for summer and winter, respectively, in surface waters and averaged $0.21 \pm 0.13\,\mathrm{d}^{-1}$ and $0.34 \pm 0.11\,\mathrm{d}^{-1}$ (mean ± sd) for summer and winter, respectively, in DCM waters. m were significantly higher in surface than in DCM layers (Wilcoxon tests, $p < 0.05$) in summer shelf and slope waters, but not so in basin or during winter ($p > 0.05$; Fig. 5). There was a decreasing trend of m from shelf to basin waters ($p < 0.05$) in summer, but not in winter. No differences of surface m could be found between summer and winter; while m at DCM were significantly lower in summer than in winter (Wilcoxon test, $p < 0.01$).

The percentage of daily primary production consumed by microzooplankton (m/μ_0) did not differ significantly between surface (mean ± sd: 62 % ± 44 %) and DCM layers (mean ± sd: 86% ± 89 %) in summer, but was significantly higher at DCM (mean ± sd: 102 % ± 110 %) than in surface waters (mean ± sd: 58 % ± 33 %) in winter (paired Wilcoxon test, $p < 0.05$; Fig. 6). There was a decreasing trend of surface m/μ_0 from shelf to basin waters in summer ($p < 0.05$) as μ_0 did not but m did decrease offshore. This trend did not exist in winter.

The high growth rate of phytoplankton in the summer surface waters was consistent with the relative high nutrient limitation index (μ_0/μ_n) (median = 85.3 % and 94.4 % in

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summer and winter, respectively; Fig. 7). Surface nitrate concentration was not correlated with μ_0 or μ_0/μ_n in surface waters in either season ($p > 0.05$).

The relatively high μ_0 in the summer surface waters was partially related with high temperature given the positive correlation between temperature and μ_0 in the pooled dataset (Spearman $r_s = 0.30$, $p < 0.05$). m was positively correlated with temperature during the winter after excluding a lowest value ($r_s = 0.46$, $p < 0.05$), but were positively correlated with B_z ($r_s = 0.49$, $p < 0.05$) and Chl a ($r_s = 0.53$, $p < 0.05$) in summer.

4 Discussion

4.1 Comparisons of rate estimates with previous studies in the northern SCS and in other areas with similar latitude

Before discussing environmental effects on microzooplankton grazing effects on phytoplankton, it is prudent to compare our data with other studies in the same area or similar environments. There are not many studies on microzooplankton grazing in the northern SCS and, if any, the estimates on phytoplankton growth and microzooplankton grazing rates are concentrated in surface waters. One impression arising from browsing the available data is that the rate estimates are quite variable as responding to the complex coastal hydrographic dynamics such as upwelling, typhoons, coastal current and river plume etc. For example, Huang et al. (2011) reported an average phytoplankton growth rate of $1.02 \pm 0.27\,\mathrm{d}^{-1}$ and an average microzooplankton grazing rate of $0.85 \pm 0.37\,\mathrm{d}^{-1}$ in upwelling regions of northeastern SCS during summertime. While in non-upwelling regions, the rate estimates lowered to $0.51 \pm 0.05\,\mathrm{d}^{-1}$ and $0.50 \pm 0.17\,\mathrm{d}^{-1}$ for phytoplankton growth and microzooplankton grazing, respectively. Zhou et al. (2011) also estimated phytoplankton growth and microzooplankton grazing rates in the northeastern SCS after passage of a typhoon. They seemed had sampled a post-bloom phase as many of their experiments demonstrated negative phytoplankton growth rates and the microzooplankton grazing rates were highly variable. Chen et al. (2009a) and Lie

and Wong (2010) have reported high phytoplankton growth ($> 1.5\,\mathrm{d}^{-1}$) and microzooplankton grazing rates ($> 1\,\mathrm{d}^{-1}$) in Hong Kong nearshore waters during summertime, which are more eutrophic than most of our sampling stations. Su et al. (2007) also reported high phytoplankton growth and microzooplankton grazing rates at a coastal station near Hong Kong. Their estimates ($\sim 0.1\,\mathrm{d}^{-1}$) at 75 m of other 4 basin stations are similar to our estimates at DCM layers of basin waters in summer.

Globally, although hundreds of papers have been published estimating microzooplankton grazing rates using the dilution technique (Calbet and Landry, 2004; Chen et al., 2012), there are relatively few studies at similar latitudes ($\sim 20°\,\mathrm{N}$) in open ocean waters. The μ_0 and m estimated by Landry et al. (1998) in the Arabian Sea, which is at similar latitudes with ours, are similar with our estimates both in summer (mean growth rate $= 0.85\,\mathrm{d}^{-1}$ and mean grazing rate $= 0.68\,\mathrm{d}^{-1}$ at surface) and winter (mean growth rate $= 0.62\,\mathrm{d}^{-1}$ and mean grazing rate $= 0.65\,\mathrm{d}^{-1}$ at surface) (see their Fig. 3). Their rate estimates at low light (5 % surface irradiance) were also similar to ours. Also in the Arabian Sea, the estimates of Edwards et al. (1999) were slightly lower (growth rate ranged from $0.25\,\mathrm{d}^{-1}$ to $1.77\,\mathrm{d}^{-1}$ and grazing rate from $0.15\,\mathrm{d}^{-1}$ to $0.68\,\mathrm{d}^{-1}$) but still lied within the normal range. For the Pacific and Atlantic Ocean at similar latitudes, we are not aware of any comprehensive studies on microzooplankton herbivory.

It is still difficult to reliably predict m, not even mentioning m/μ_0, using remotely sensed variables such as temperature and Chl a concentrations. Using a global dataset we compiled previously (Chen et al., 2012), we found that temperature and Chl a concentrations together explained less than 20 % of total variance of m even using the flexible generalized additive modeling (the authors' unpublished data). Predator-prey interactions within the plankton consortium are complex (Peters, 1994; Poulin and Franks, 2010) and it remains to be investigated whether we should strive to develop a better model or whether it is impossible to predict microzooplankton biomass and grazing activity only relying on remotely sensed variables and we should be conservative on the applications of remote sensing on the heterotrophic processes in the ocean (Banse, 2013).

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4.2 Vertical variation of phytoplankton growth and microzooplankton grazing rate

Comparison of μ_0 between surface and DCM waters confirms our original hypothesis that light extinction greatly diminishes phytoplankton growth rate at DCM layers. Also consistent with the findings by Landry et al. (2011b), we find similar m between surface and DCM layer in winter and therefore microzooplankton grazed a higher proportion of primary production at DCM layer in winter. As the two sampling depths in winter lied within the surface mixed layer at many stations, it is not surprising to find similar microzooplankton community structure and biomass at the two depths in winter (Fig. 3). Although light has been reported to stimulate the grazing activity of some protists (Strom, 2001), this stimulation effect should not be as strong as the light effect on phytoplankton growth rate.

In contrast, the mean m at DCM layer was also lower than at surface in summer shelf and slope waters and m/μ_0 was not different between the two depths. The similar microzooplankton biomass at the two depths suggests that the difference was mainly due to the grazing activity per capita microzooplankton biomass (m/B_z).

The reason for the reduced m/B_z at DCM in summer is unclear. As all the experiments were incubated at surface temperatures, it should not be the temperature effect that caused the reduced m/B_z at DCM layers. The level of light screening was similarly used in the two cruises so that it is unlikely that the light differences between the two depths caused the lower m/B_z at DCM in summer, but not in winter. Our resolution of identifying microzooplankton species is inadequate to address whether microzooplankton community composition differed significantly between surface and DCM in summer. There was no significant difference of the biomass ratio of ciliates and dinoflagellates between the two depths in summer (data not shown). Either, there was no significant difference of average microzooplankton cell size between the two depths in summer. Phytoplankton biomass and average cell size should not cause the reduced m/B_z at DCM in summer because phytoplankton biomass and average cell size was similar

between summer and winter at DCM. This problem should be further tested in future studies. It also calls for the attention against extrapolating surface rate estimates to deep depths.

4.3 Spatial variations of phytoplankton growth and microzooplankton grazing rates

Contrary to our original hypothesis, we observed a decreasing trend of m/μ_0 from the eutrophic shelf waters to the oligotrophic basin waters in summer surface waters, which is partially related with increasing microzooplankton biomass with increasing Chl a concentration. This suggests that microzooplankton biomass instead of phytoplankton size structure is the principle factor determining m. Sherr and Sherr (2007) pointed out that heterotrophic dinoflagellates, which have a variety of feeding mechanisms (Jeong, 1999) and can feed on prey equal or larger than their own size (Hansen et al., 1994), tend to dominate in high Chl waters.

One difference of our study to the high latitude study by Liu et al. (2002a) is that we did not observe a positive correlation between Chl a concentration and phytoplankton growth rate (i.e., μ_0 was not lower in oligotrophic waters), which may cause the decreasing trend of m/μ_0 from shelf to basin waters. Similar to observations in subtropical and equatorial Pacific (Laws et al., 1987; Landry et al., 2011b), we find high phytoplankton growth rates ($> 0.5\,\mathrm{d}^{-1}$) in the basin surface waters of the SCS especially in the oligotrophic summer, which are probably sustained by grazer nutrient excretion and nitrogen fixation. SCS is well known for the occurrences of internal waves and typhoons (Chen et al., 2009c), which can disturb the stratified water column and periodically inject the nutrients into the euphotic zone from below. The effect of nutrient enrichment on μ_0 is small, suggesting that phytoplankton were not experiencing severe nutrient limitation at this time.

Marra and Barber (2005) and Behrenfeld (2010) suggested that the key factor regulating the variations of phytoplankton biomass in the Arabian Sea and the North Atlantic is likely the changing grazing effect induced by the mixing process, instead of

bottom-up factors such as nutrients or light. When vertical mixing occurs induced either by upwelling or winter surface cooling, the particle-poor subsurface waters dilute the surface water within the euphotic zone, acting as a natural "dilution" experiment. The grazer biomass and grazing impact on phytoplankton decreases and, as a consequence, net growth rate of phytoplankton becomes positive and phytoplankton biomass accumulates. Whether phytoplankton growth rate (μ_0) increases or not after the mixing event is not a key issue here. Our data partially support this hypothesis. The similar μ_0 between summer and winter in basin waters suggests that the elevated nutrient levels induced by winter mixing do not substantially increase phytoplankton growth rate. It should be the relaxed grazing pressure induced by natural mixing event that leads to net positive growth of phytoplankton during the progression from summer to winter. However, at present, we do not have sufficient time-series data of phytoplankton biomass, μ_0 and m to fully validate this hypothesis.

4.4 Temperature effects on microzooplankton grazing effect

While it is well founded in theory that the growth rate of phytoplankton should increase more slowly with temperature than microzooplankton growth and grazing rates (Lopez-Urrutia et al., 2006; Rose and Caron, 2007; Lopez-Urrutia, 2008), it is difficult to disentangle the individual effect of temperature in the overall grazing impact. For example, comparing the surface basin waters between summer and winter, m/μ_0 was lower in the warmer summer than the colder winter (Fig. 7) due to the negative correlation between temperature and grazer biomass.

The temperature effect is supposed to be more pronounced in eutrophic shelf waters because seasonal variations of temperature are greater than in basin waters and also because the negative correlation between temperature and grazer biomass is weaker. When we calculate the temperature coefficient of m only for shelf surface waters by linearly regressing $\ln m$ against $1/kT$, the mean activation energy is 0.70 eV, close to the global average 0.65 eV (Chen et al., 2012). In comparison, the mean activation

energy of m for all the data is only 0.28 eV. These calculations suggest that temperature effects on microzooplankton grazing are more salient in shelf waters.

In summary, we have conducted a comprehensive study on microzooplankton herbivory in the northern SCS. Although microzooplankton herbivory is an important loss pathway of primary production, we still do not have sufficient measurements in the ocean particularly in the lower part of the euphotic zone (Landry et al., 2011b). As a consequence, there is still no widely accepted theory on microzooplankton grazing that can easily fit to field data. Although the global average proportion of primary production grazed by microzooplankton is estimated as from 60 % to 80 %, the real ratio of m/μ_0 can range from 0 to 100 % with little predictability (Calbet and Landry, 2004; Chen et al., 2012). While primary production has been mapped at global scales using remote sensing techniques, the estimates of microzooplankton grazing rate are largely scattered. But these estimates are essential for understanding the dynamics of phytoplankton biomass in the ocean (Banse, 2013). Clearly, plankton ecologists need more accurate measurements in the ocean and also need to develop sophisticated theories that can capture the essence of microzooplankton grazing and can do relatively well in prediction.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/16005/2012/ bgd-9-16005-2012-supplement.pdf.

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Table 1. Background information of physical and chemical parameters of experimental stations. The stations are grouped ba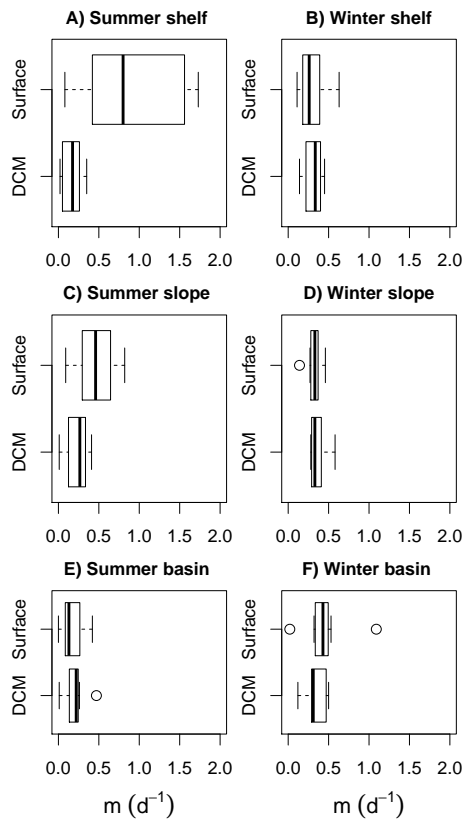sed on bathymetry (see text for details). SST: sea surface temperature ($^\circ$C). [NO_3]: nitrate concentration (mmol m^{-3}). MLD: mixed layer depth (m). DCM: Depth of deep chlorophyll maximum (m). The numbers in parentheses indicate ranges of the variables.

	Regions	No. of stations	SST	Surface [NO_3]	MLD	DCM
Summer	Shelf	6	29.1 (28.0–30.1)	0.14 (0.08–0.16)	11 (8–20)	50 (25–50)
	Slope	8	29.7 (29.3–29.7)	0.11 (0.04–0.14)	23 (4–37)	52 (50–75)
	Basin	8	29.4 (28.6–29.8)	0.10 (0.08–0.15)	22 (3–31)	70 (50–75)
Winter	Shelf	9	21.3 (16.8–22.7)	0.90 (0.14–11.7)	42 (28–82)	20 (15–25)
	Slope	9	23.9 (22.7–24.6)	0.23 (0.10–0.62)	66 (21–155)	50 (30–75)
	Basin	7	24.5 (23.8–25.9)	0.25 (0.10–1.21)	54 (26–68)	50 (50–75)
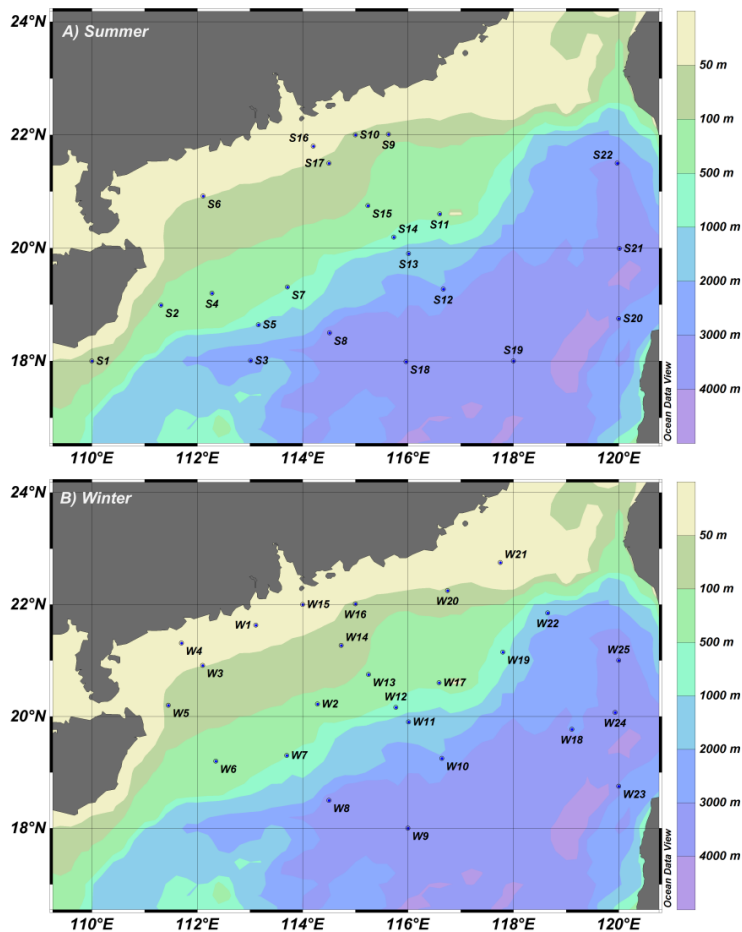
Fig. 1. Experimental locations.
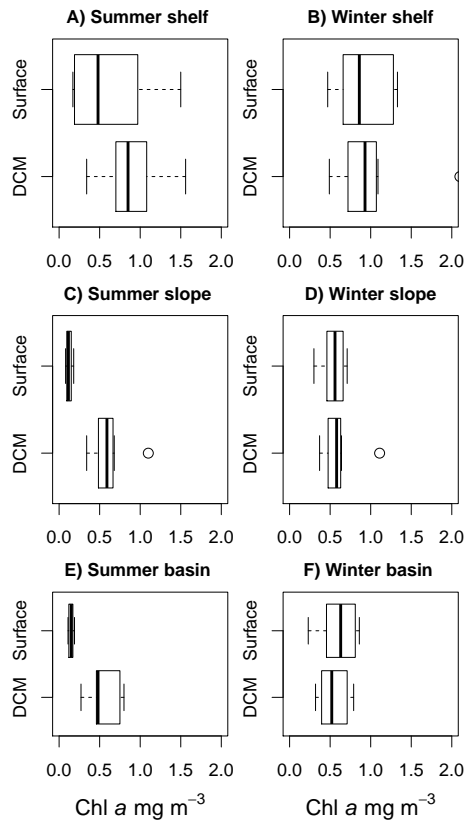
Fig. 2. Boxplots of Chl *a* ($\mathrm{mg\,m^{-3}}$) in surface and DCM waters. The line through the middle of the box shows the median. The outer edges of the box correspond to the 25th and 75th percentiles, and the "whiskers" to the 10th and 90th percentiles. The dots represent extreme values.

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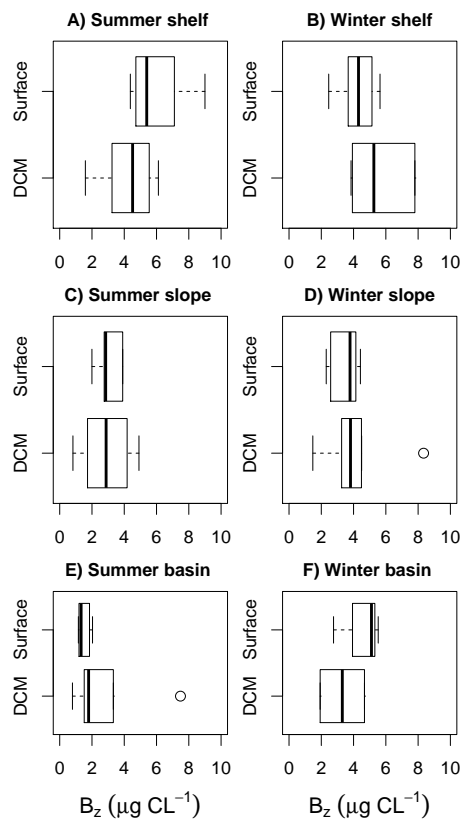
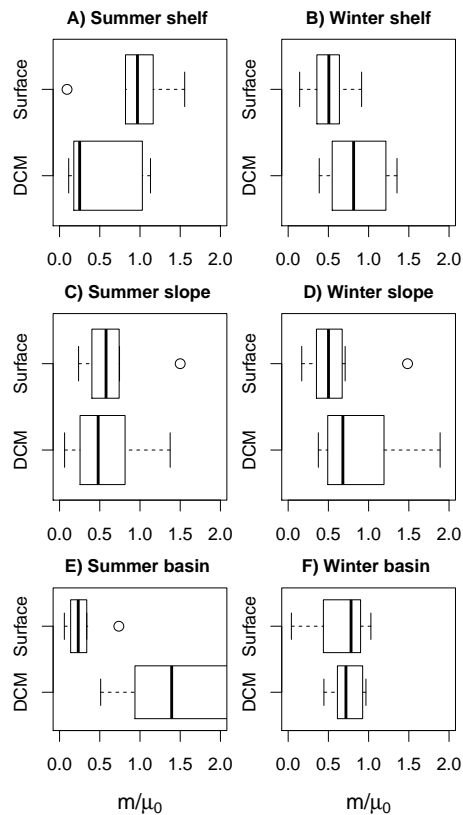Back | Close

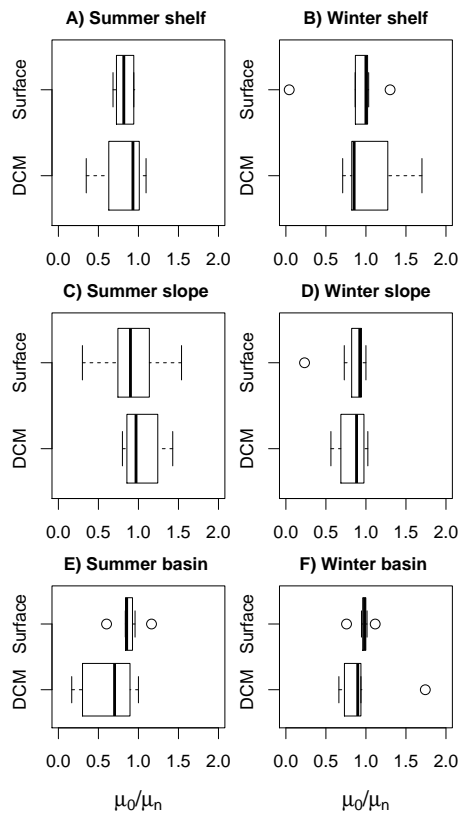Full Screen / Esc

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Fig. 3. Boxplots of microzooplankton biomass (B_z).
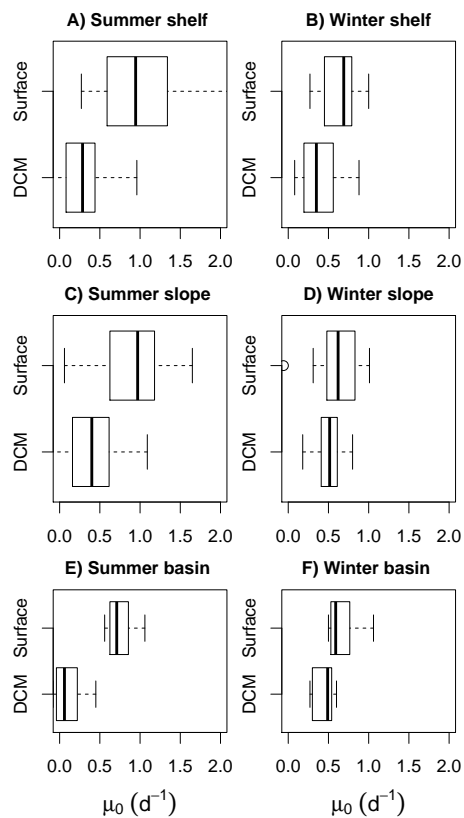
Fig. 4. Boxplots of phytoplankton instantaneous growth rate (μ_0).

Fig. 5. Boxplots of microzooplankton grazing rate (m).

Fig. 6. Boxplots of $m : \mu_0$.

Fig. 7. Boxplots of $\mu_0 : \mu_n$. μ_n: nutrient enriched phytoplankton growth rate.