

Bottom-up and top-down controls on picoplankton

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Bottom-up and top-down controls on picoplankton in the East China Sea

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Abstract

Dynamics of picoplankton population distribution in the East China Sea (ECS), a marginal sea in the western North Pacific Ocean, were studied during two “CHOICE-C” cruises in August 2009 (summer) and January 2010 (winter). Dilution experiments were conducted during the two cruises to investigate the growth and grazing among picophytoplankton populations. Picoplankton accounted for an average of $\sim 29\%$ (2% to 88%) of community carbon biomass in the ECS on average, with lower percentages in plume region than in shelf and kuroshio regions. Averaged growth rates (μ) for *Prochlorococcus* (Pro), *Synechococcus* (Syn) and picoeukaryotes (peuk) were 0.36 , 0.89 , 0.90 d^{-1} , respectively, in summer, and 0.46 , 0.58 , 0.56 d^{-1} , respectively, in winter. Seawater salinity and nutrient availability exerted significant controls on picoplankton growth rate. Averaged grazing mortality (m) were 0.46 , 0.63 , 0.68 d^{-1} in summer, and 0.22 , 0.32 , 0.22 d^{-1} in winter for Pro, Syn and peuk respectively. The three populations demonstrated very different distribution patterns regionally and seasonally affected by both bottom-up and top-down controls. In summer, Pro, Syn and peuk were dominant in Kuroshio, transitional and plume regions respectively. Protist grazing consumed 84% , 78% , 73% and 45% , 47% , 57% of production for Pro, Syn and peuk in summer and winter respectively, suggesting more significant top-down controls in summer. In winter, all three populations tended to distribute in offshore regions, although the area of coverage was different (peuk > Syn > Pro). Bottom-up factors can explain as much as 91.5% , 82% and 81.2% of Pro, Syn and peuk abundance variance in winter, while only 59.1% and 43.7% for Pro and peuk in summer. Regionally, Yangtze River discharge plays a significant role in affecting the intensity of top-down control, indicated by significant and negative association between salinity and grazing mortality of all three populations and higher grazing mortality to growth rate ratio (m/μ) in plume region than Kuroshio region in summer. The gradient of bottom-up factors caused by Yangtze River input and Kuroshio warm current intrusion also exerted important influence on picoplankton abundance evidenced by the significant correlations. Vertically,

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picoplankton exhibited highest abundance at subsurface layer around 20 m thick in summer, while at surface in winter. Both growth rate and grazing mortality were higher at surface than at the deep chlorophyll maximum (DCM) layer. Our study first systematically described the bottom-up and top-down regulations of different picoplankton populations between contrasting seasons, different depths, and among different regions in the ECS, which provide insights for better understanding the population dynamics of picoplankton and trophic transfer in microbial food web in highly dynamic shelf ecosystems and in general.

1 Introduction

Pico-phytoplankton groups ($< 5 \mu\text{m}$), including *Prochlorococcus* (Pro), *Synchococcus* (Syn), and pico-sized eukaryotes (peuk), are the dominant components of primary producers in the oligotrophic oceanic waters mainly due to their small size that enables them a high ability of nutrient utilization and carbon fixation (Raven, 1998). They are also essential participants of the microbial food web, playing important roles in nutrient and carbon cycling (Azam et al., 1983; Raven, 1998). Many efforts are made on studying the ecological, physiological and genetic characters of picoplankton in order to get a better understanding of their global distribution and biogeochemical significance (Partensky et al., 1999; Rocap et al., 2003; Zwirgmaier et al., 2008), which is especially important under the current circumstance of the changing climate. It has been documented that environmental factors, such as temperature, salinity, light and nutrient availability are closely related to picoplankton distribution patterns. Seasonal and spatial shifts of different picoplankton populations that are adapted to different ecological niches have been reported in different oceanic regions (Olson et al., 1990; Li, 1995; Campbell et al., 1997; Agawin et al., 1998; Chen et al., 2011; Liu et al., 2002a).

The small size of picoplankton also determines that the majority of their fixed carbon is respired back to CO_2 , although part of them could be packed by protist grazers via microbial food chain to reach higher trophic levels (Michaels and Silver, 1988;

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Legendre and Le Fèvre, 1995). In recent studies, the contribution of picoplankton to global oceanic carbon flux is highlighted to be more important than previous recognized, which can be proportional to their net production through incorporation in larger feeders producing high sinking rate (e.g. mesozooplankton) or aggregation of direct sinking (Richardson and Jackson, 2007). As the major consumer of picoplankton, microzooplankton undertake the most important role in trophic carbon transfer between picoplankton and higher trophic levels. It is estimated that microzooplankton consumption accounted for an average of 60 % to 80 % of phytoplankton daily production throughout global oceans (Calbet and Landry 2004), and the rest mortality may include grazing of larger zooplankton, viral attacks, and programmed cell death. In tropical open ocean systems, microzooplankton grazing is thought to be the major source regulating picoplankton abundance (Landry et al., 1998; Calbet and Landry 1999). Furthermore, as revealed by previous nutrient manipulation experiments, protist grazers could respond quickly to picoplankton physiological change induced by nutrient fluctuations and thus control picoplankton abundance through enhanced grazing (Landry et al., 2000; Worden and Binder, 2003). However, the top-down mortality pressures has been much less studied than the bottom-up environmental forcing, when exploring picoplankton dynamics in a specific ecosystem.

The East China Sea (ECS) situates on the western edge of northwest Pacific, and covers one of the most extensive continental shelves in the world. Serving as a transitional area, ECS plays an important role in linking terrestrial and oceanic regions, and regulating the regional carbon budget through the “continental shelf pump” (Liu et al., 2000). Physical environment of ECS is highly variable, dictated by the distinct seasonality in mid-latitude and influenced by anthropogenic stresses from landmass (Gong et al., 2003; Uematsu et al., 2010), as well as mixing among several principal water types. Tremendous amount of nutrient-rich freshwater from Yangtze River, one of the biggest rivers by discharge volumes, flows into the ECS, with an annual mean of about $3 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ (Beardsley et al., 1985; Gong et al., 1996). Besides, the warm, saline and oligotrophic Kuroshio current intrudes and mixes with the shelf water along

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the continental slope (Liu and Gan, 2012), creating a gradient of nutrients, as well as chlorophyll and primary production from nearshore to Kuroshio waters (Gong et al., 2000).

The diverse environmental conditions lead to a sharp cross-shelf gradient of physicochemical properties in the upper water column of the ECS and make it an interesting place to explore the temporal and spatial variabilities of biota. Picoplankton have been the subject of research in ECS in the past (Chiang et al., 2002; Chang et al., 2003; Jiao et al., 2005; Pan et al., 2005). However, most of these studies either focused on just one specific population, or were with limited spatial and temporal coverage. The integrated impact and relative strength of both bottom-up and top-down forcing that drives the picoplankton population dynamics remains poorly understood. In this study, we used the dilution technique (Landry and Hassett, 1982) and flow cytometer based measurement of growth and grazing mortality associated with specific picoplankton populations in the dynamic shelf ecosystems of the ECS. Our goals are to better understand the complex trophic interaction in microbial food webs of different marine environments, and to evaluate both the bottom-up and top-down controls in regulating the trophic transfer in microbial food webs.

2 Methods

2.1 Cruise information

The study was conducted in the East China Sea during two “CHOICE-C” cruises of the R/V *Dongfanghong* in summer (18–27 August 2009) and winter (14 December 2009–4 January 2010). Fifty and 67 stations setting on 7 transects were investigated during summer and winter cruise respectively (Fig. 1). Characterized by distinct hydrographic features and the locations, stations can be roughly divided into 3 water systems: stations in coastal water affected by Yangtze River input was defined as salinity of near or below 31 psu (Gong et al., 1996); stations of Kuroshio warm current located in outer

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and deep water region with relatively high temperature and high salinity was defined as salinity near or higher than 34 psu (Gong et al., 1996; Jiao et al., 2005); and stations situated between the two was defined as transitional station. Temperature and salinity were determined by CTD probes (model and manufacturer).

Nutrient samples were collected after filtering seawater through 0.45 μm acetate fiber membrane. The inorganic nutrients including NO_3^- , NO_2^- , PO_4^{3-} and SiO_3^{2-} were analyzed using the Technicon AA3 Auto-Analyzer (BRAN-LUEBBE) onboard (M. Dai, unpublished data).

Chlorophyll *a* concentration was obtained using High Performance Liquid Chromatography (HPLC) following the modified method of Furuya et al. (1998) (B. Huang, unpublished data).

2.2 Flow cytometric analysis of picoplankton abundance

Picoplankton samples were collected at every station from 3–8 depths of upper 150 m using Niskin bottles attached to a CTD rosette system for enumeration of population abundance. Collected seawater (1.8 mL) was fixed with 0.5 % (final conc.) seawater buffered paraformaldehyde immediately after collection and stored at -80°C before analysis. Abundances of autotrophic picoplankton (Pro, Syn and peuk) were enumerated using a Becton-Dickson FACSCalibur flow cytometer under the High flow rate ($\sim 60 \mu\text{L min}^{-1}$), according to the side scattering (SSC) and red/orange auto-fluorescences emitted by chlorophyll/phycoerythrin (Olson et al., 1993). Yellowish green fluorescence beads (1 μm , Polysciences) were added as an internal standard to calibrate and normalize the fluorescence and light scattering signals. Biovolumes of Pro, Syn and peuk were converted from normalized signals of side-scattering (SSC) using empirically determined equations (Chen et al., 2011) and were then converted to carbon using the conversion factor of 0.28, 0.28, 0.22 $\text{pg C } \mu\text{m}^{-3}$, respectively (Zubkov et al., 1998; Liu et al., 2007).

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2.3 Dilution experimental set up and rate estimation

Dilution experiments were conducted at 12 stations in summer and 14 stations in winter at both surface and depth of chlorophyll maximum (DCM) layer (at station DH02, DH04, and YZE in winter, experiment was only conducted at surface). Seawater samples were collected using an acid-washed plastic bucket or a Niskin bottle attached to a CTD rosette system.

Growth rate and grazing mortality of picoplankton populations were measured by the dilution technique (Landry and Hassett, 1982) following protocols of Landry et al. (2003). Five 1.2 L bottles were used to establish a set of nutrient-enriched dilution series consisting of 15 %, 27 %, 50 %, 73 % and 100 % natural seawater pre-filtered by 200 μm mesh. Duplicate sets were used for each dilution experiment. Measured amount of filtered seawater prepared by gravity flow through a 0.2 μm filter capsule (Pall Corporation) was added to experimental bottles, following with gently filling the bottles with natural seawater. All five bottles were added with inorganic nutrients (final concentrations of 0.5 $\mu\text{mol L}^{-1}$ NH_4Cl , 0.03 $\mu\text{mol L}^{-1}$ KH_2PO_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 natural seawater without nutrient amendment were run in parallel with nutrient amended bottles to account for potential nutrient limitation. The bottles were incubated in an on-deck incubator with temperature controlled by running seawater and in situ light simulated by covering with neutral density screen. Prior to each experiment, all incubation bottles, capsules, tubing and carboys were washed with 10 % HCl and rinsed thoroughly with distilled water and ambient seawater. The capsules were soaked in 10 % HCl for more than 2 h before the first use and were washed with 10 % HCl, distilled water and ambient seawater between each experiment (Landry et al., 1995). Picoplankton samples for flow cytometric analysis were taken from initial seawater and all experimental bottles after incubation.

Picoplankton growth rate with nutrient amendment (μ_n) and grazing mortality (m) were calculated from the linear regression relationship between net growth rate (with

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nutrient) and dilution factor (the proportion of natural seawater in dilution treatment) (Landry et al., 2003). The instantaneous growth rate (μ_0 , growth rate in water without nutrient addition) was determined by adding the grazing rate to the population net growth rate in bottles without nutrient addition (k_0). To assess the biomass production (P) and grazing loss (G) on picoplankton populations, following formulas were used according to Landry et al. (2003):

$$P = \mu_0 \cdot C_m$$

$$G = m \cdot C_m$$

$$C_m = C_0 \left[e^{(\mu_0 - m)t} - 1 \right] / (\mu_0 - m)t$$

where C_m is mean concentration of picoplankton carbon biomass during the incubations, C_0 is the initial concentration of picoplankton carbon biomass, and t is incubation time (1 d). The percentage of production of each picoplankton population that was consumed by microzooplankton was calculated as m/μ_0 .

2.4 Data analysis

Flow cytometric data were analyzed using WinMDI software 2.9 (Joseph Trotter, Scripps Research Institute, La Jolla, CA, USA). Contour plots were generated using Ocean Data View (Schlitzer, 2006). Spearman rank-order correlation analysis was used to detect significant relationships between variables. Stepwise multiple-regression analysis was performed to assess the relative influence of potential factors controlling picoplankton abundances (temperature, salinity, $\text{NO}_3 + \text{NO}_2$, PO_4 , and Chl a concentration). The data used for stepwise multiple-regression analysis were log-transformed to satisfy a roughly normal distribution.

3 Results

3.1 Hydrographical condition in ECS

Contrasting patterns of hydrographical condition were observed between summer and winter. The sea surface temperature ranged from 23.19 to 30.73 °C in summer and from 9.2 to 23.6 °C in winter (Fig. 2a and b). Surface salinity was generally lower in summer (ranging from 17.22 to 34.0) than in winter (ranging from 27.1 to 34.6). Both temperature and salinity showed increasing gradients from inshore to offshore region (Fig. 2, Table 1). In summer, inshore regions of ECS was strongly affected by freshwater discharged from Yangtze River, resulting in a strong plume of low salinity water spreading to near 125° (Fig. 2c). However, the influence of river input was much weaker in winter (Fig. 2d). A dramatic increase of surface temperature can be observed in Kuroshio region in winter, which was about 10.5 °C and 4.5 °C higher respectively than that of coastal and mixing regions.

The surface NO₃+NO₂ (N) and PO₄ (P) concentrations were much higher in winter (median value of 5.27 μmol L⁻¹ for N and 0.37 μmol L⁻¹ for P) than in summer (median value of below detection limit for both N and P) due to strong vertical mixing in winter (Fig. 2e–h). Affected by river discharge, the nutrient concentrations in the plume region were very high (with averaged N concentration of 9.69 and 23.34 μg L⁻¹ respectively in summer and winter), and showed a clear decreasing trend from inshore plume region to offshore Kuroshio region (Fig. 2e and f; Table 1). The N/P ratio was generally lower in summer than in winter, and demonstrated different regional patterns in both seasons (Fig. 2i and j). The area of P limitation was mostly confined in the coastal regions in the ECS, especially in the Yangtze River plume region, while the offshore region is mainly N-limited. Generally, the area of P limitation was larger in summer than that in winter.

The surface Chl *a* concentration was highly variable in summer (ranging from 0.07 to 35.3 μg L⁻¹ with median value of 0.20 μg L⁻¹), decreasing dramatically across the shelf

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(Fig. 2k). However, the Chl *a* concentration in winter was generally evenly distributed (ranging from 0.29 to 0.68 $\mu\text{g L}^{-1}$ with median value of 0.44 $\mu\text{g L}^{-1}$) (Fig. 2l).

We selected the PN transect, a well-studied transect from Yangtze River estuary, across the continental shelf, to offshore region, to illustrate the vertical pattern of hydrographical parameters (Fig. 3). In summer, strong stratification was observed, with higher temperature, lower salinity and lower nutrient concentrations in the surface layer, whereas in winter, the hydrographic parameters were homogenous through the whole water column due to strong wind-induced mixing. This pattern lead to a different pattern and location of chl *a* maximum zone in the two seasons: a chlorophyll maximum occurred in the subsurface layer (at ~ 20 m in plume region and ~ 50 m in transitional and Kuroshio regions) in summer, but no clear subsurface chlorophyll maximum was observed and high chlorophyll concentration was usually located in up-surface layer in winter.

3.2 Distribution patterns of picoplankton abundance

Pro – The average abundance (over top 150 m after integration using a trapezoid rule) of *Pro* was 4.0×10^4 cells mL^{-1} in summer, which was about one magnitude higher than the value of 6.0×10^3 in winter. Their distribution was largely confined in oligotrophic waters in transitional and Kuroshio regions, but absent in plume zones (Fig. 4a and b). The average abundance of *Pro* in transitional and Kuroshio zones was comparable in summer, but much higher in Kuroshio region than in transitional region in winter (Table 1). Both spearman rank order correlation test (all surface data points) and stepwise multiple regression (data of 0 for *Pro* removed) revealed that *Pro* abundance were negatively correlated with nutrient concentrations and salinity in both seasons (Table 2). Negative correlation between *Pro* abundance and Chl *a* concentration was observed in summer for the whole area, while a positive correlation was obtained in winter (Table 2). At stations with *Pro* existence, temperature was the most important bottom-up variable that controlled the abundance distribution, explaining respectively 45 % and 86 % of variance in summer and winter. Salinity and P concentration attributed to an additional

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14 % and 5 % of Pro variance in summer and winter, respectively (Table 3). Vertically, taking PN transect as an example, the abundance of Pro exhibited a subsurface maxima around 20 m in transitional region, and 40 m in Kuroshio region in summer; they distributed homogenously from 0–60 m in the offshore region during winter (Fig. 5a and b).

Syn – The average abundance of *Syn* was also much higher in summer (average 9.8×10^4 cells mL⁻¹) than in winter (average 6.2×10^3 cells mL⁻¹), which was similar to that of Pro. Relatively high abundance was observed in plume and transitional regions in summer (Fig. 4c), which was about 2.1 and 6.5 times higher than that in Kuroshio regions (Table 1). Inversely, in winter, the highest abundance was observed in Kuroshio region (Table 1), exceeding that in plume and transitional regions for 6.4 and 29 folds (Fig. 4d). No significant correlations were observed between *Syn* abundance and bottom-up factors in summer (Table 2). In winter, *Syn* abundance was positively correlated with temperature, which accounted for 71 % of abundance variation (Tables 2 and 3).

Peuk – The abundance of *peuk* was comparable in the two seasons with average value of about 4×10^3 cells mL⁻¹. Though they were less abundant compared with Pro and *Syn*, they contributed significantly to picoplankton biomass (Table 1). *Peuk* exhibited very different distribution patterns in the two seasons: in summer, the average abundance decreased by ~2–3 times from plume region to the transitional and Kuroshio regions; whereas it increased dramatically by 5.2 and 9.8 times from plume region to transitional and Kuroshio region respectively in winter (Table 1; Fig. 4e and f). In contrast to Pro, *peuk* tended to distribute in regions with lower salinity and higher nutrient and Chl *a* concentration in summer, indicated by correlation analysis (Table 2), with N concentration explaining 44 % of the abundance (Table 3). In winter, the distribution of *peuk* was similar to Pro and *Syn*, which was positively correlated with temperature, salinity and Chl *a* concentration, but negatively correlated with nutrient concentrations. Among those bottom-up factors, temperature accounted for 65 % of the abundance variance, the percentage of which was lower than Pro and *Syn*. The

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highest abundances of Syn and peuk occurred at around 10 m to 20 m depths in in-shore region and 40 m in offshore region in summer, while in surface in winter (Fig. 5c–f).

3.3 Growth and grazing of picoplankton populations and their associations with environmental variables

Flow cytometry-based estimation for growth rate and grazing mortality of picoplankton populations were depicted spatially in Fig. 6. Out of 49 experiments (24 in summer and 25 in winter), positive mortality rates ($m \geq 0.1$) were obtained in 16 experiments for Pro, 32 for Syn, and 41 for peuk; and most of the negative or near-zero mortality rates were observed in winter.

Pro – Averaged growth rate for Pro was 0.36 d^{-1} in summer and 0.46 d^{-1} in winter (Table 5), and showed little nutrient limitation indicated by $\mu_0 / \mu_n > 1$ except in Kuroshio region in summer ($\mu_0 / \mu_n = 0.87$) (Table 4). Vertically, higher growth rates were observed at DCM in summer, but at surface in winter (Fig. 6g and h; Table 5). Averaged grazing mortality for Pro was 0.46 d^{-1} in summer, which accounted for 84 % of Pro production. In winter, averaged grazing mortality deceased to about half (0.22 d^{-1}) of the summer rates, accounting for just 45 % (ranged from 12–133 %) daily production in average (Table 5). Grazing mortality showed a general decreasing trend from transitional region to Kuroshio region, except high values at surface layer in summer and DCM layer in winter at Kuroshio station DH 13. Negative correlation was observed between grazing mortality and salinity ($r = -0.576$, $p < 0.001$; Table 6). Microzooplankton consumed a higher proportion of Pro production in transitional region during summer and in Kuroshio region during winter (Table 4).

Syn – Averaged growth rate for Syn was 0.81 d^{-1} in summer, and 0.58 d^{-1} in winter. The growth rate was positively correlated with ambient N concentrations ($r = 0.343$, $p < 0.05$; Table 6) and negatively correlated with salinity ($r = -0.312$, $p < 0.05$; Table 6). Nutrient limitation occurred in summer, especially in Kuroshio region with μ_0 / μ_n ratio of 0.64 and at all surface layer with μ_0 / μ_n ratio of 0.82. Grazing mortality of Syn averaged

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0.63 d⁻¹ in summer, which was almost 2 times higher than the value of 0.32 d⁻¹ in winter, equaling to 79 % (ranged from 21 % to 235 %) and 47 % (ranged from 24 % to 82 %) of daily Syn production in summer and winter respectively. It was positively correlated with temperature ($r = 0.447$, $p < 0.01$; Table 6) and microzooplankton abundance ($r = 0.451$, $p < 0.01$; Table 6), and negatively correlated with salinity ($r = -0.481$, $p < 0.01$; Table 6). Both growth and grazing rates declined from plume to Kuroshio region in two seasons (Fig. 6c–g, Table 4), with a high growth rate of 2.58 d⁻¹ observed at plume station YZ13 in summer. The proportion of microzooplankton consumption on Syn was highest in plume region in summer, reaching growth and grazing balance with averaged m/μ of 1.08; but the highest percentage shifted to transitional region in winter.

Peuk – Averaged growth rate for peuk was almost identical to that of Syn, which was 0.85 d⁻¹ in summer and 0.56 d⁻¹ in winter. The growth rate was negatively correlated with salinity ($r = -0.520$, $p < 0.01$; Table 6) and positively correlated with ambient N concentration ($r = 0.433$, $p < 0.01$; Table 6). Microzooplankton grazing rate was 0.68 d⁻¹ in summer, which was 3 times higher than 0.22 d⁻¹ in winter, consuming 74 % (ranged from 24 % to 119 %) and 57 % (ranged from 11 % to 144 %) of peuk production in summer and winter respectively. Higher growth rate and grazing mortality were observed at surface layer and plume region (Fig. 6e–k, Table 4). The grazing mortality of peuk was positively correlated with temperature ($r = 0.415$, $p < 0.01$; Table 6) and microzooplankton abundance ($r = -0.408$, $p < 0.01$; Table 6) and negatively correlated with salinity ($r = -0.507$, $p < 0.02$; Table 6). The percentage of peuk production consumption was similar in three regions in both seasons (Table 4), which was different from that of Pro and Syn.

Microzooplankton abundance, which can indicate the grazing pressure, was higher in summer than in winter, and higher in surface water than in DCM (Table 5). Spatially, it showed decreasing trends from inshore or transitional region to offshore region in both seasons (Table 4). An extremely high abundance of 14 000 cells mL⁻¹ was obtained at station YZ13 in Yangtze River plume in summer. Ciliate dominated the

microzooplankton composition in ECS, accounting for 78.5 % and 92.6 % in summer and winter respectively.

Growth and grazing estimates of Syn and peuk were significantly and positively correlated (Fig. 7b and c). The slope of linear regression curve for Syn was close to one (0.87), and larger than that of peuk (0.56).

Negative correlations were obtained between grazing mortality and abundance for Syn and peuk, and the correlation is significant in summer for peuk (Fig. 8b and c). There was no overall relationship found between the grazing mortality and cell abundance for Pro, although a significant negative correlation exist for winter data. Interestingly, growth rates for all three populations were negatively correlated with their abundances, though the relationship was not significant sometimes (Fig. 8d–f)..

3.4 Seasonal and spatial variations of picoplankton biomass and their contribution to microzooplankton carbon consumption

The standing stock of carbon biomass (C_0) in summer and winter showed opposite distribution patterns. In three regions from inshore to offshore, C_0 decreased with average value of 10.96, 8.77 and 3.64 ng mL⁻¹ respectively in summer, and increased with average value of 1.58, 5.83 and 6.00 ng mL⁻¹ respectively in winter (Fig. 9a). In summer, the proportion of Syn biomass decreased from plume region to Kuroshio region, while that of Pro demonstrated an increasing trend. In winter, peuk dominated in all three regions with its carbon biomass occupying 66–90 % of total biomass.

Similar to C_0 , the composition of carbon biomass that consumed by microzooplankton (G) varied in both seasonal and spatial scales. Microzooplankton consumed 10.05, 2.92, and 1.30 ng mL⁻¹ in coastal, transitional, and Kuroshio regions in summer, and 1.54, 2.03, and 1.21 ng mL⁻¹ respectively in winter (Fig. 9b). Among the total picoplankton carbon consumed by microzooplankton, ~ 50 % was contributed by peuk and the rest ~ 50 % came from Pro and Syn in summer; while in winter the contribution of peuk became more important, reaching ~ 80 %. Spatially, in summer, Pro was a more important food for microzooplankton in Kuroshio region than transitional region, accounting

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for 25 % and 15 % in the two regions respectively; whereas the grazing loss of Syn exhibited the opposite trend, accounting for 47 %, 38 %, and 19 % in total picoplankton carbon loss in plume, transitional and Kuroshio region respectively. In winter, the composition of biomass grazing loss was similar in three regions, with peuk dominating the composition.

4 Discussion

4.1 Effect of environmental factors on picoplankton abundance distribution

According to regional and seasonal change of hydrographic variables, the study area covers a broad range of biogeochemical provinces and bears strong seasonality. Three water systems could be clearly observed: Yangtze River plume region with relatively low temperature and low salinity; offshore Kuroshio region with relatively warm and saline water; and the transitional region cover the shelf between the two regions. Driven by the diverse hydrographical conditions, picoplankton distribution changed dramatically spatially and seasonally.

Responses of picoplankton populations to bottom-up factors in this study are consistent with previous documented physiology and reports from other seas. Being abundant in summer and nutrient-depleted Kuroshio region and absent in eutrophic plume region, Pro showed their preference of stratified, oligotrophic and warm habitat, which is in accordance with findings in other tropical and subtropical regions (Liu et al., 1998; Campbell et al., 1997). In summer, among all bottom-up factors, nutrient concentration was most important in shaping Pro distribution when temperature was relatively high, indicated by the significant negative correlation between Pro abundance and nutrient concentration (Table 3). It has been suggested that Pro minimized their genome during evolution (Dufresne et al., 2003) and lack genes responsible for nutrient-uptake regulation and lost their capability to utilize NO_3 (Rocap et al., 2003; Martiny, 2006; Martiny et al., 2009). Besides, the strong-mixing induced limited ability for chromatic adaptation,

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and the disadvantage of Pro to absorb green light in high Chl *a* regions also contributed to low Pro abundance in winter and coastal regions (Bouman, 2006).

The abundance of Syn was also much higher in summer than in winter in ECS, which is in agreement with previous studies conducted in ECS and other coastal regions (Agawin et al., 1998; Jiao et al., 2005; Chen et al., 2009). On the other hand, high Syn abundance has been observed in winter in some tropical and subtropical oceans (Olson et al., 1990; Campbell et al., 1997; Liu et al., 2007). Such different patterns may attribute to the combined effects of temperature and nutrient. Compared with Pro, Syn were reported to be more nutrient dependent and adapted to environment with intermediate nutrient level (Liu et al. 1998; Chen et al., 2011). It has been reported that the optimal N concentration for Syn growth in was 0.25 μM in Mediterranean Sea and 0.1–3 μM in Arabian Sea, and high N concentration of about > 8 μM could inhibit Syn growth (Liu et al., 1998; Agawin et al., 2000a). In addition to nutrient, Syn growth has also been showed to increase with enhancement of temperature (Agawin et al., 1998; Li, 1998; Jiao et al., 2005). Therefore, in some highly stratified tropical and subtropical oligotrophic oceans, the enhanced nutrient availability by winter mixing can trigger a “bloom” of Syn (Olson et al., 1990; Liu et al., 2007). In ECS, however, due to dramatic seasonal variation of temperature and relatively mesotrophic environment, Syn appear to best distribute in regions with intermediate temperature, nutrient and Chl *a* concentration.

Different from the significant changing abundance of Pro and Syn with seasons, the average abundance of peuk was almost the same in the two seasons, although temperature accounted for 65 % of the abundance variance in winter, among the hydrographical factors. Therefore, it was most likely that succession of species composition in response to hydrographic conditions in different seasons occurred, which demonstrated high diversity of peuk (Diez et al., 2001; Worden, 2006). Peuk were more abundant in coastal areas than oceanic areas in summer, with an opposite trend in winter. This pattern can be captured most obviously in areas near Yangtze River estuary, where peuk abundance was highest in summer, but lowest in winter. This seasonal distribution may

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be due to either low temperature in coastal area or different light availability in Yangtze River plume, which was also important in regulating picoplankton distribution patterns.

4.2 Variations of picoplankton growth and mortality rates

The average growth rates over the study area for Pro, Syn and peuk were 0.36, 0.89, 0.9 d⁻¹ in summer and 0.46, 0.58, 0.56 d⁻¹ in winter. The values are within the range of recent studies conducted in marginal or coastal seas (Hirose et al., 2007; Chen et al., 2009), while they are generally higher than the values in open ocean (Landry et al., 2003; Landry et al., 1995; Liu et al., 2002b; Paterson et al., 2007) and study in ECS in last decade (Chang et al., 2003).

Seasonally, consistent with the abundance of picoplankton, growth rates were higher in summer than in winter due to the factor of temperature, which has been often identified as the major factor causing the seasonal variations in growth rates (Agawin et al., 1998, 2000b). Spatially, however, high picoplankton population abundance did not coincide with high growth rate, indicated by negative associations between growth rate and abundance of picoplankton populations (Fig. 8). The nutrient input from Yangtze River discharge influenced the growth rate picoplankton remarkably across the shelf. As the freshwater plume diminishing from inshore to offshore, the growth rate estimates of Syn and peuk decreased with increasing salinity and decreasing N concentration (Table 7) High average growth rate of > 1 d⁻¹ for Syn and peuk was observed in plume region in summer, with maximum value of > 2.5 d⁻¹ at station YZ13 located in Yangtze River estuary. This observation is consistent with previous findings of high growth rates in the river plume regions (Chang et al., 2003; Chen et al., 2009). The spatial mismatching between picoplankton abundance and their corresponding growth rates leads to our speculation that the top down grazing control may exert a great role on picoplankton distribution in ECS.

Similar with growth rate, we observed significant and negative correlations between grazing mortality and seawater salinity for all three populations, suggesting the important role of Yangtze River in affecting the intensity of top-down control. Nutrient status

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has been reported to exert a strong influence on functional response of grazers (Worden and Binder, 2003). The increased nutrient concentrations in plume area could improve the food quality of picoplankton as prey, indicated by larger cell size and high cellular Chl *a* fluorescence in plume area than in Kuroshio region (data not shown), and thus enhanced the grazing activity of microzooplankton (Worden and Binder, 2003).

It is generally believed that microzooplankton biomass is the major factor affecting grazing rate. The significant positive correlations between microzooplankton abundance and grazing mortality of Syn and peuk in this study support this point. The highest grazing mortality (1.97 d^{-1} for Syn and 2.58 d^{-1} for peuk) was captured at station YZ13, where microzooplankton abundance ($14\,000 \text{ cells mL}^{-1}$) was 1–2 orders of magnitude higher than that at other stations. However, Pro did not exhibit above relations with microzooplankton abundance, suggesting that their major grazer is nanoflagellates rather than ciliates (Christaki et al., 1999; Guillou et al., 2001; Callieri et al., 2002).

Moreover, temperature also imposed great control on protist grazing of Syn and peuk, suggested by significant and positive association between the two parameters. Increased microzooplankton grazing during warm season and reduced grazing during cold season have been reported in many studies (e.g., Calbet et al., 2008; Lawrence and Menden-Deuer, 2012). The effect of temperature on grazing mortality could be due to either numerical response of protist grazers, evidenced by the significant positive correlation between microzooplankton abundance and temperature, or functional response of increased protist metabolic activities resulted from higher temperature (Peters, 1994). About 84 %, 78 %, 73 % and 45 %, 47 %, 57 % of biomass production of Pro, Syn and peuk respectively in summer and winter are consumed by microzooplankton in average. The lower proportion in winter could be the result of a larger degree of decrease in grazing than in growth, which suggested a weaker top-down control of grazing in winter. A number of studies have pointed out that the temperature dependency of metabolic rates is different for autotrophs and heterotrophs (Allen et al. 2005; Lopez-Urrutia et al. 2006; Rose and Caron 2007; Chen et al., 2012). According to previous studies, the activation energy of heterotrophic metabolism (0.65 eV) is

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about twice of that of autotrophic phytoplankton (0.32 eV). Here, picoplankton growth rate decreased for 0.78, 1.53, and 1.61 fold in winter than in summer, while their grazing mortality decreased for 2.09, 1.97, and 3.09 fold, respectively.

4.3 Top down controls on picoplankton biomass by microzooplankton grazing in ECS

Highly correlated picoplankton growth rate and grazing mortality estimates suggest a close coupling between picoplankton production and consumption, underlying the capacity for protist to rapidly respond to variations in their prey resources and highlighting the importance of microzooplankton grazing as top down control on picoplankton (Landry et al., 2000; Chen et al., 2009). The strong top down control of grazing on picoplankton may also be because of the numerical dominance of small heterotrophic flagellates ($< 20 \mu\text{m}$) in protist communities, whose abundance are one to several orders of magnitude higher than ciliates (Sherr et al., 1997; Chiang et al., 2003; Tsai et al., 2010; Choi et al., 2012). It is believed that nanoflagellates rather than ciliates are the major grazers of Pro and Syn (Christaki et al., 1999; Guillou et al., 2001; Callieri et al., 2002)..

The different correlation coefficients between grazing mortality and abundance of three populations suggested different potential mechanism of top down control. For peuk, the seasonal change of abundance is very small, which is very different from Pro and Syn. High grazing pressure in summer which can keep the abundance of peuk in check may be one of the possible reasons, evidenced by higher m/μ in summer and the negative correlation between grazing mortality and peuk abundance. However, although the seasonal pattern of m/μ and m/μ of Syn was similar to that of peuk, its grazing mortality did not demonstrated significant negative relationship with its abundance. On the other hand, there was no apparent correlation between Pro abundance and its mortality rate. Such different significance level of relationships was possibly due to the feeding preference on the three picoplankton populations by different grazers (Christaki et al., 1999; Guillou et al., 2001; Callieri et al., 2002). The physiological

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characters of three populations, such as cell size, cell surface properties, nutritional content could also attribute to the feeding behavior of microzooplankton (Christaki et al., 1998; Monger et al., 1999). Considering the clear seasonal change in the abundance of Pro and Syn and their narrower spatial distribution compared with peuk, we believe that the bottom-up factors might be more important in determining the population distribution.

There were very few studies focused on the vertical pattern of grazing mortality of picoplankton populations. We find higher growth rate of three picoplankton populations in surface than DCM layer in both seasons, indicating light extinction greatly diminishes picoplankton growth rate at DCM layers. Our observation was consistent with previous studies which showed decreased growth rates with decreasing light levels (Landry et al., 1995, 2011b; Verity et al., 1996). However, the degree of decrease for grazing mortality at DCM compared with surface was not as significant as that of growth rate, particularly in winter. Therefore, microzooplankton grazed a higher proportion of picoplankton production at DCM layer in winter, which may be one of reasons for the higher abundance of picoplankton in surface layer. As the strong wind induced mixing during winter results in a homogenous physical and chemical condition in the surface mixing layer, the protist community maybe similar in surface and DCM layers. Although light has been reported to stimulate the grazing activity of some protists (Strom, 2001), this stimulatory effect should not be as strong as the light effect on phytoplankton growth rate. In summer, the percentage of protist-consumed picoplankton production was similar in surface and DCM layer because growth rate and grazing mortality decreased by a similar degree in DCM layer compared with surface. Different protist composition and lower temperature resulted from stratification may be the reasons for reduced grazing mortality in DCM layer.

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5 Summary

Seasonally, bottom-up factors imposed more important control in winter than in summer; they could explain as much as 80–90 % of the variance of the abundance of 3 picophytoplankton populations in winter, but only 40–60 % in summer. Among all environmental factors, temperature was the most important one affecting the distribution patterns of picophytoplankton in ECS, particularly in winter. Microzooplankton consumed an average of ~ 60 %, 69 % and 65 % biomass production of Pro, Syn and peuk, respectively, in ECS, and the proportion of m/μ was higher in summer than that in winter due to a steeper decrease in grazing than in growth, suggesting a stronger top-down control effect in summer.

Spatially, on one hand, gradient of bottom-up factors caused by Yangtze River input and Kuroshio intrusion exerted important influence on picoplankton abundance (Table 2). On the other hand, grazing mortality of all three populations were observed being significantly and negatively associated with salinity, suggesting the important role of Yangtze River in affecting the intensity of top-down control.

Vertically, picoplankton exhibited highest abundance at DCM layer in summer, while at surface in winter. Both growth rate and grazing mortality were higher at surface than at the DCM in two seasons. Microzooplankton grazed a higher proportion of picoplankton production at DCM layer in winter but a higher proportion at surface layer in summer, which may be one of reasons for the higher abundance of picoplankton in surface layer in winter and in DCM layer in summer. Light, degree of stratification/mixing and protist community structure are possible reasons for causing the vertical patterns.

Among the three populations, Pro was mainly controlled by temperature as it only appears in warm, low-nutrient and stratified environment, while grazing imposes important control on peuk biomass and distribution. For Syn, their maximum abundance was found in environment with intermediate nutrient concentrations and they were consumed by microzooplankton with the highest proportion of production in average,

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suggesting both bottom-up and top-down factors imposed important controls on their distribution.

Relative strength and balance between bottom-up and top-down control has been indicated to shift in different regions and in different size class of phytoplankton. As the ECS possess a great deal of variability in both spatial and temporal scales on physical, chemical and biological parameters, understand the relative importance and interactive mechanism of bottom-up and top-down control in regulating picoplankton biomass and composition, and consequently the dynamics of biogeochemical cycling of carbon in the subtropical marginal seas remain a challenge.

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Table 1. Summary of environmental factors and biomass of picoplankton populations in the three water systems in ECS.

	Summer			Winter		
	plume	transitional	Kuroshio	plume	transitional	Kuroshio
temperature (°C)	28.32 (23.19–30.73)	29.54 (28.49–30.28)	28.92 (27.45–29.87)	10.93 (9.24–12.69)	17.01 (13.23–19.32)	21.45 (18.65–23.55)
salinity (psu)	28.17 (17.22–32.04)	33.38 (32.40–33.68)	33.80 (33.53–34.03)	29.87 (27.05–31.37)	33.41 (30.5–34.41)	34.50 (34.19–34.62)
[Chl <i>a</i>] ($\mu\text{g L}^{-1}$)	2.73 (0.30–35.3)	0.22 (0.07–0.93)	0.13 (0.08–0.20)	0.44 (0.34–0.56)	0.45 (0.32–0.68)	0.48 (0.29–0.65)
$\text{NO}_2^- + \text{NO}_3^-$ ($\mu\text{g L}^{-1}$)	9.69 (0.10–40.94)	0.11 (0.10–0.22)	0.10 (0.10–0.11)	23.34 (13.43–40.06)	7.92 (2.61–22.68)	2.05 (0.29–4.49)
PO_4^{3-} ($\mu\text{g L}^{-1}$)	0.26 (0.08–0.71)	0.09 (0.08–0.17)	0.17 (0.08–0.66)	0.79 (0.54–1.24)	0.46 (0.23–0.93)	0.16 (0.16–0.32)
SiO_3^{2-} ($\mu\text{g L}^{-1}$)	9.69 (0.20–36.08)	2.99 (1.18–6.95)	1.09 (0.67–1.98)	24.17 (15.49–37.83)	10.50 (4.54–26.30)	3.43 (0.83–5.67)
Pro abund (cells mL^{-1})	4182 (0–42 126)	75 958 (0–214 488)	48 559 (9452–138 626)	0	341 (0–4259)	23 804 (696–71 042)
Syn abund (cells mL^{-1})	97625 (7013–380 179)	46124 (14 044–156 847)	7042 (3343–9351)	737 (0–1327)	4773 (611–13256)	13 435 (5826–31 273)
peuk abund (cells mL^{-1})	6542 (799–64 300)	5413 (1972–12 344)	1834 (1259–3206)	939 (0–1704)	4189 (943–8560)	5771 (2914–9972)
Pro C / total C	0.56 % 0–4.69 %	11.30 % 0–37.48 %	14.86 % 3.97–24.85 %	0 0	0.06 % 0–8.3 %	3.78 % 0.09–10.09 %
Syn C / total C	11.72 % 0.37–63.51 %	22.53 % 5.47–72.20 %	5.64 % 3.60–8.75 %	0.81 % 0.59–1.17 %	3.19 % 0.76–6.74 %	6.93 % 2.90–12.78 %
peuk C / total C	10.09 % 0.62–26.91 %	19.97 % 0.04–35.23 %	14.24 % 9.49–16.08 %	8.70 % 7.12–10.42 %	18.06 % 7.06–40.93 %	19.20 % 12.05–30.30 %
picoplankton C / total C	22.49 % 0.99–79.38 %	48.39 % 1.60–88.16 %	34.74 % 22.64–45.26 %	9.50 % 7.96–11.04 %	21.31 % 7.98–44.12 %	29.92 % 21.17–47.36 %

Detection limit of $0.1 \mu\text{mol L}^{-1}$ and $0.08 \mu\text{mol L}^{-1}$ were respectively used for $[\text{NO}_2^- + \text{NO}_3^-]$ and $[\text{PO}_4^{3-}]$ calculation when the concentration was undetectable.

C / Chl ratio of 50 was used to calculate the total phytoplankton carbon biomass.

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Table 2. Spearman's rank correlation coefficient between environmental factors and abundances of picoplankton populations.

	temp	sal	N	P	Chl	Pro_abund	Syn_abund	Peuk_abund
summer								
Pro_abund	0.277	0.782**	−0.696**	−0.354*	−0.801**	1	−0.145	−0.247
Syn_abund	0.036	−0.236	−0.008	0.004	0.147	−0.145	1	0.552**
peuk_abund	−0.195	−0.419**	0.415**	0.315*	0.396**	−0.247	0.552**	1
winter								
Pro_abund	0.846**	0.869**	−0.770**	−0.791**	0.337*	1	0.837**	0.666**
Syn_abund	0.905**	0.857**	−0.818**	−0.843**	0.456**	0.837**	1	0.874**
peuk_abund	0.778**	0.668**	−0.626**	−0.660**	0.515**	0.666**	0.874**	1

Surface data were used for the correlation test; summer: $N = 44$, winter: $N = 47$; *:correlation is significant at 0.05 level, **: correlation is significant at 0.01 level.

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Table 3. Summary of multiple stepwise regression analysis between picoplankton abundances and environmental variables.

variables entered		R^2	R^2 exchange	Beta	F	p
summer						
log_Pro	Log_T	0.452	0.452	0.469	16.498	0.001
	Log_S	0.591	0.139	0.425	13.735	< 0.001
log_peuk	Log_N	0.437	0.437	0.661	31.852	< 0.001
winter						
log_Pro	Log_T	0.863	0.863	0.536	112.981	< 0.001
	Log_P	0.915	0.053	−0.455	91.748	< 0.001
log_syn	Log_T	0.711	0.711	0.537	108.237	< 0.001
	Log_Ch1	0.820	0.109	0.306	98.121	< 0.001
log_peuk	Log_P	0.844	0.024	−0.277	76.026	< 0.001
	Log_T	0.653	0.653	1.133	82.675	< 0.001
	Log_Ch1	0.763	0.11	0.27	69.257	< 0.001
	Log_S	0.812	0.048	−0.459	60.281	< 0.001

All the picoplankton abundances were log transformed with removal of zero values.

R^2 : correlation coefficient of multiple determination;

R^2 exchange: change in multiple R^2 caused by entering a new variable in a single step (hierarchical analysis);

Beta: standardized regression coefficient;

F & p : F test results. Results of $F > 1$ and $p < 0.001$ represent the improvement due to fitting the regression model is much greater than the inaccuracy within the model, which means the final model significantly improves our ability to predict the outcome variable.

Abbreviations: T : temperature; S : salinity; N : $\text{NO}_2 + \text{NO}_3$; P : PO_4 ; Ch1: chlorophyll a .

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Table 4. Comparison of m/μ , m/μ_0 , and μ_0/μ_n of three populations in plume, transitional and kuroshio regions in summer and winter.

	Summer			Winter		
	plume	transitional	Kuroshio	plume	transitional	Kuroshio
Pro- m		0.34 (0.15)	0.92 (0.85)		0.19 (0.13)	0.28 (0.13)
Pro- μ_0		0.35 (0.18)	0.38 (0.01)		0.50 (0.37)	0.44 (0.17)
Pro- m/μ_0		1.09 (0.63)	0.46 (0.51)		0.39 (0.04)	0.47 (0.41)
Pro- μ_0/μ_n		1.24 (0.10)	0.87 (0.01)		0.97 (0.12)	1.11 (0.37)
Syn- m	1.11 (0.76)	0.41 (0.23)	0.37 (0.17)	0.44	0.29 (0.11)	0.31 (0.21)
Syn- μ_0	1.08 (1.31)	0.74 (0.40)	0.55 (0.40)	1.04	0.67 (0.40)	0.39 (0.43)
Syn- m/μ_0	1.08 (0.62)	0.57 (0.20)	0.88 (0.82)	0.043	0.55 (0.25)	0.32 (0.14)
Syn- μ_0/μ_n	1.08 (0.66)	0.85 (0.32)	0.64 (0.15)	1.21	1.03 (0.12)	1.10 (0.44)
peuk- m	1.17 (0.72)	0.35 (0.17)	0.76 (0.56)	0.72	0.16 (0.08)	0.25 (0.16)
peuk- μ_0	1.53 (1.05)	0.41 (0.33)	0.92 (0.37)	1.21	0.61 (0.51)	0.37 (0.53)
peuk- m/μ_0	0.76 (0.07)	0.74 (0.33)	0.66 (0.59)	0.60	0.54 (0.43)	0.62 (0.29)
peuk- μ_0/μ_n	1.20 (0.32)	0.81 (0.27)	0.98 (0.14)	0.96	1.03 (0.15)	0.79 (0.26)
total						
microzoo	3995	1514	1285		1069	649
plankton	(4295)	(1525)	(667)		(1767)	(662)
abundance						

Values of $\mu < 0.1$ and $m < 0.1$ were removed when calculating m/μ .
The numbers in parenthesis are standard errors of the mean.

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Table 5. Comparison of m , μ , m/μ_0 , and μ_0/μ_n of three populations at surface and DCM layers in summer and winter.

	Summer			Winter		
	surface	DCM	avg.	surface	DCM	avg.
Pro- m	0.52 (0.50)	0.34 (0.17)	0.46 (0.40)	0.23 (0.12)	0.19 (0.19)	0.22 (0.14)
Pro- μ_0	0.31 (0.11)	0.39 (0.17)	0.36 (0.16)	0.61 (0.20)	0.32 (0.15)	0.46 (0.22)
Pro- m/μ_0	1.52 (0.99)	0.85 (0.71)	1.12 (0.87)	0.36 (0.18)	0.51 (0.54)	0.45 (0.38)
Pro- μ_0/μ_n		1.15 (0.21)	1.15 (0.21)	1.04 (0.02)	1.07 (0.28)	1.08 (0.20)
Syn- m	0.72 (0.70)	0.49 (0.28)	0.63 (0.56)	0.35 (0.07)	0.27 (0.24)	0.32 (0.18)
Syn- μ_0	0.84 (1.07)	0.75 (0.35)	0.81 (0.82)	0.71 (0.42)	0.40 (0.15)	0.58 (0.37)
Syn- m/μ_0	0.91 (0.63)	0.82 (0.31)	0.79 (0.51)	0.47 (0.24)	0.45 (0.23)	0.47 (0.22)
Syn- μ_0/μ_n	0.83 (0.31)	1.45 (1.39)	1.09 (0.86)	1.09 (0.36)	1.05 (0.13)	1.07 (0.28)
peuk- m	0.84 (0.67)	0.41 (0.31)	0.68 (0.59)	0.25 (0.18)	0.19 (0.17)	0.22 (0.17)
peuk- μ_0	1.07 (1.03)	0.51 (0.43)	0.85 (0.87)	0.74 (0.52)	0.30 (0.18)	0.56 (0.46)
peuk- m/μ_0	0.80 (0.26)	0.71 (0.30)	0.74 (0.27)	0.48 (0.28)	0.66 (0.46)	0.57 (0.37)
peuk- μ_0/μ_n	0.90 (0.20)	1.11 (0.41)	0.99 (0.32)	0.95 (0.14)	1.00 (0.25)	0.96 (0.18)
total	2785	1639	2303	1118	659	878
microzooplankton abundance	(3840)	(1242)	(2878)	(1841)	(613)	(1361)

Values of $\mu_0 < 0.1$ and $m < 0.1$ were removed when calculating m/μ_0 .
The numbers in parenthesis are standard errors of the mean.

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Table 6. Spearman's rank correlation coefficient between environmental factors and m and μ of picoplankton populations.

	temperature	salinity	chl	N	P	microzooplankton
pro_ m	0.321	−0.576**	−0.260	0.653*	0.086	0.179
syn_ m	0.447**	−0.481**	0.100	0.136	0.055	0.451**
peuk_ m	0.415**	−0.507**	0.032	0.037	0.081	0.408**
pro_ μ_0	−0.411	0.077	0.601*	0.235	−0.014	0.324
syn_ μ_0	0.043	−0.312*	0.049	0.343*	0.200	0.218
peuk_ μ_0	0.051	−0.520**	0.125	0.433**	0.246	0.288

*: correlation is significant at 0.05 level, **: correlation is significant at 0.01 level.

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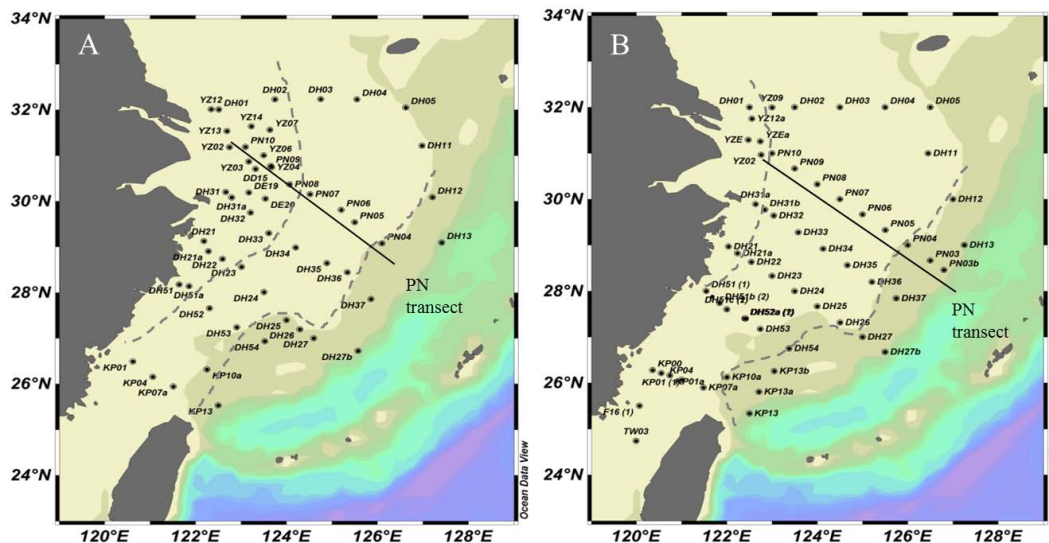


Fig. 1. Location of investigated stations in **(A)** summer and **(B)** winter. Plume, transitional, and Kuroshio regions were divided by the grey dotted line. PN transect were labelled by the black line.

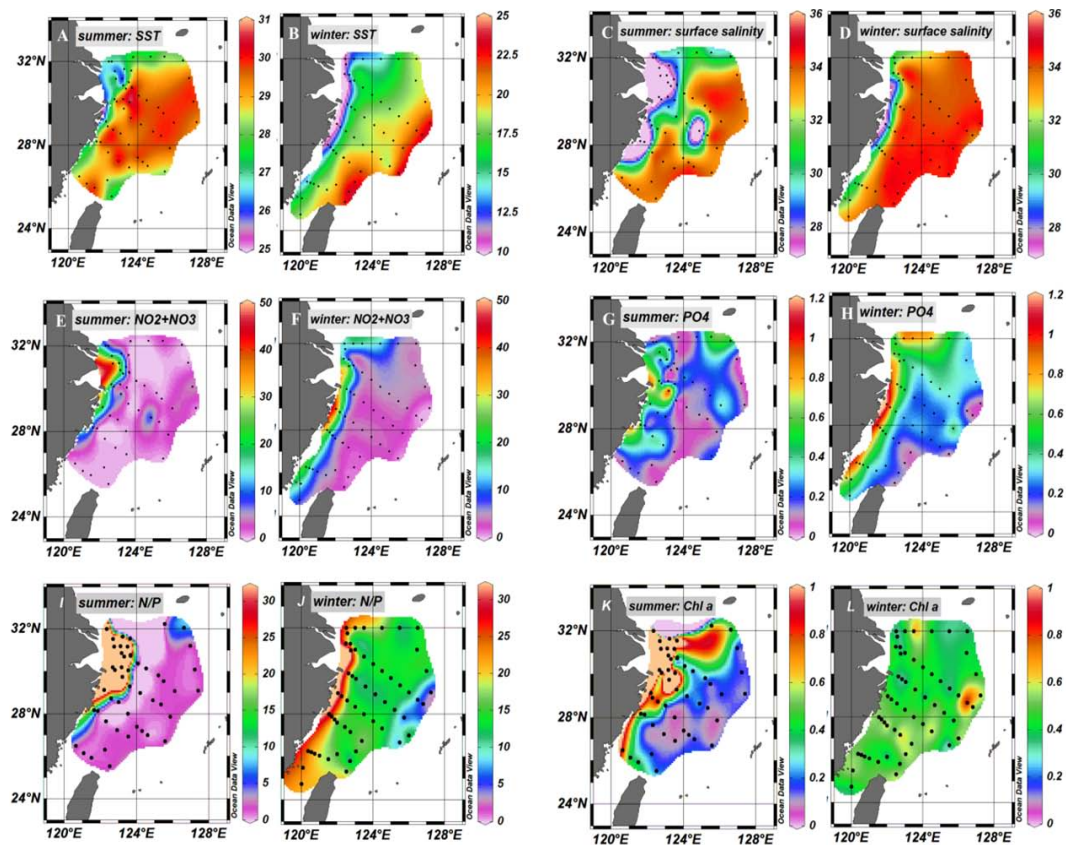


Fig. 2. Spatial distributions of sea surface (A, B) temperature, (C, D) salinity (psu), (E, F) $\text{NO}_2^- + \text{NO}_3^-$ ($\mu\text{g L}^{-1}$) concentration ($\mu\text{g L}^{-1}$), (G, H) PO_4^{3-} concentration ($\mu\text{g L}^{-1}$), (I, J) N/P molar ratio, and (K, L) Chl *a* concentration ($\mu\text{g L}^{-1}$) in summer (18–27 August 2009) and winter (14 December 2009–4 January 2010).

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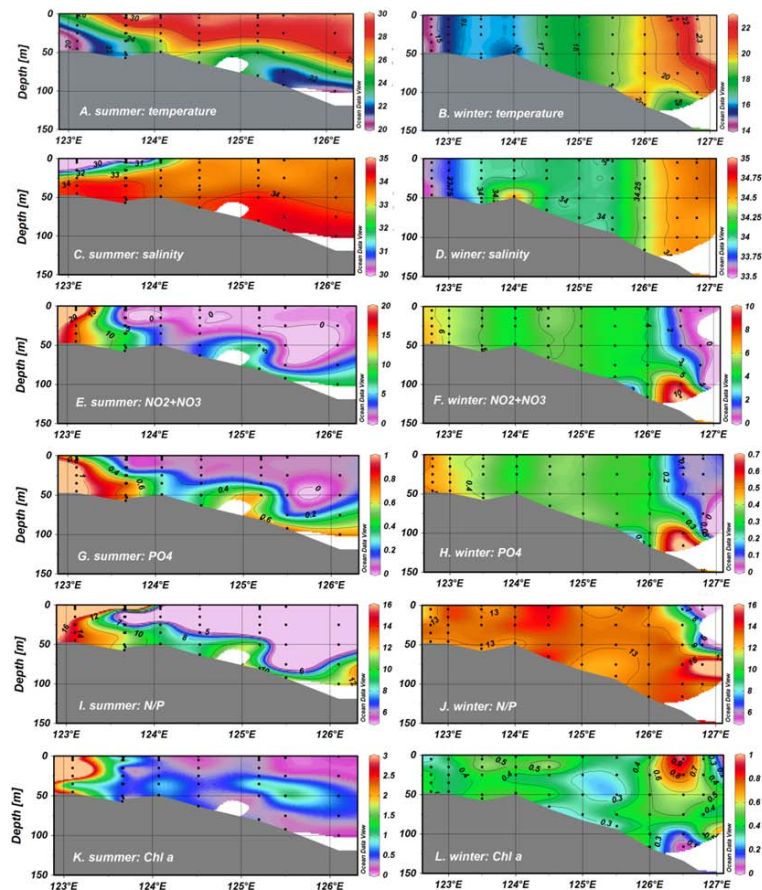


Fig. 3. Vertical distributions of **(A, B)** temperature, **(C, D)** salinity (psu), **(E, F)** $\text{NO}_3^- + \text{NO}_2^-$ concentration ($\mu\text{g L}^{-1}$), **(G, H)** PO_4^{3-} concentration ($\mu\text{g L}^{-1}$), **(I, J)** N/P molar ratio, and **(K, L)** Chl *a* concentration ($\mu\text{g L}^{-1}$) in summer and winter along PN transect.

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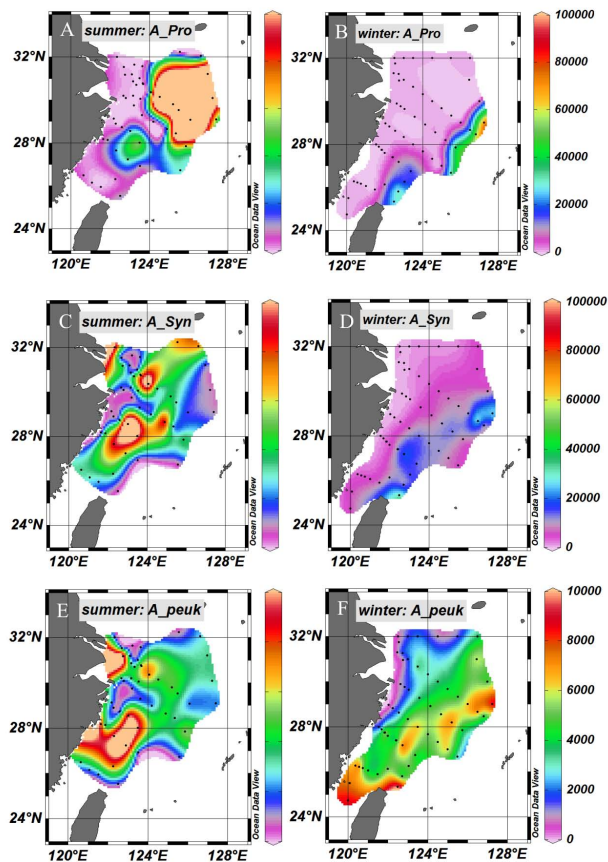


Fig. 4. Spatial distributions of abundances (cells mL⁻¹) of **(A, B)** *Prochlorococcus* (Pro), **(C, D)** *Synechococcus* (Syn), and **(E, F)** piceoekaryotes (Peuk) averaged over 0–150 m during summer and winter.

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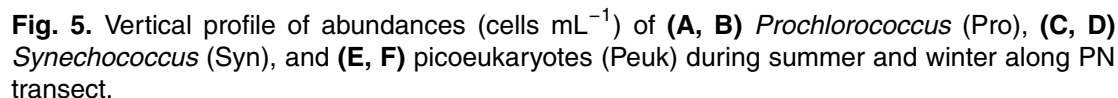
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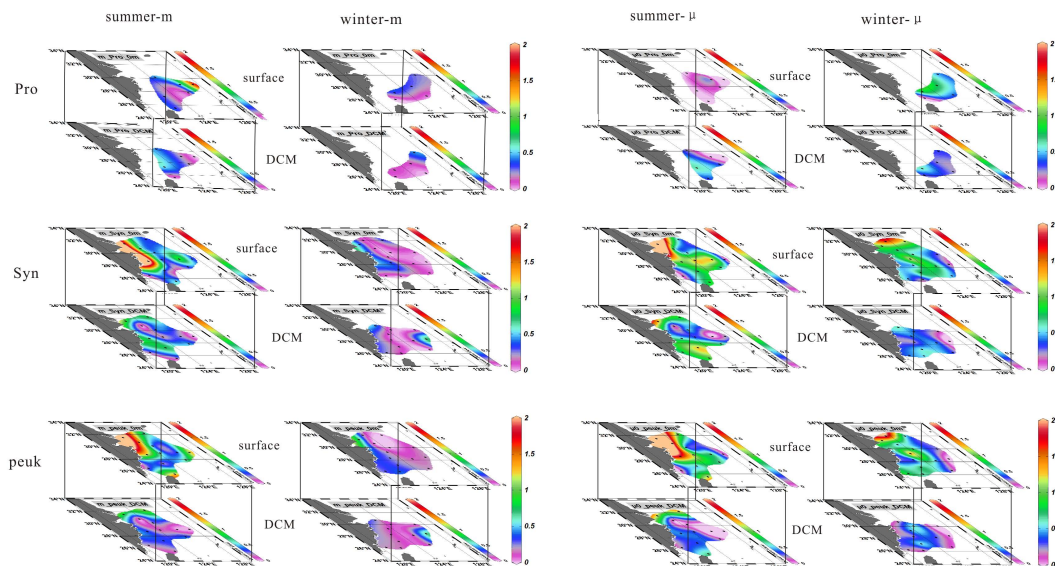


Fig. 6. Spatial pattern of (A–F) grazing mortality (m) and (G–L) growth rate (μ) of picoplankton populations in (A, C, E, G, I, K) summer and (B, D, F, H, J, L) winter. The two layers are surface and deep chlorophyll maximum (DCM) layer.

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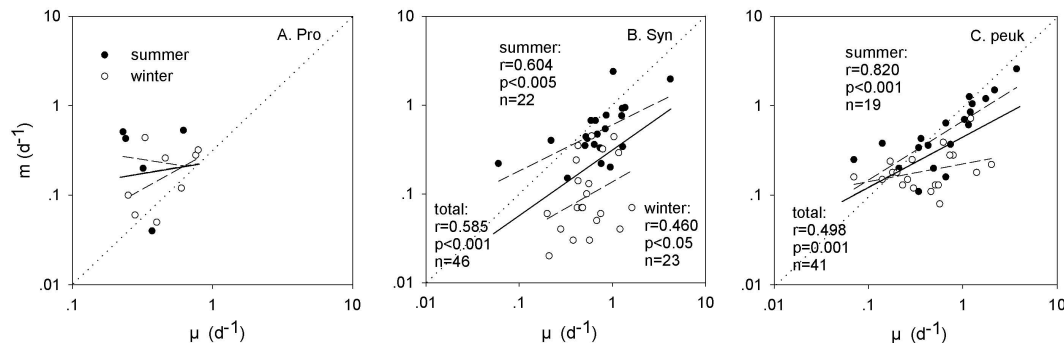


Fig. 7. Relationship between grazing mortality (m) and growth rate (μ) of **(A)** *Prochlorococcus* (Pro), **(B)** *Synechococcus* (Syn) and picoeukaryotes (peuk). The dotted line is a 1:1 line for the two parameters. The short dash line and solid line are the regression curves for each season separately and two seasons together, respectively. r , p and n are correlation coefficients, statistical significance levels and number of data point.

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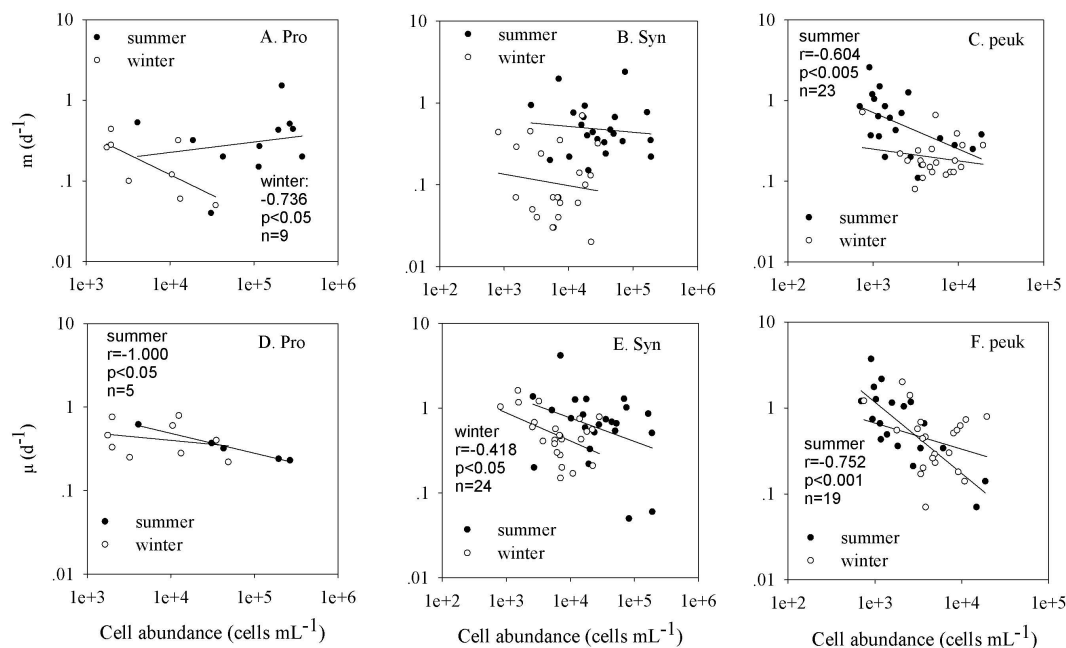


Fig. 8. Relationship between cell abundance and **(A–C)** grazing mortality (m) and **(D–F)** growth rate (μ). Solid lines are the regression curves of each season. r , p and n are correlation coefficients, statistical significance levels and number of data point.

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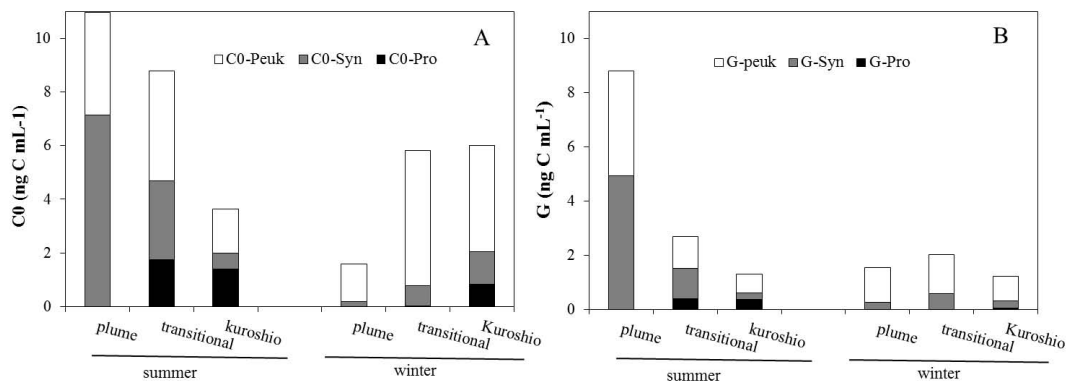


Fig. 9. Seasonal and regional composition of **(A)** picoplankton carbon biomass (C0) and **(B)** their contribution to microzooplankton carbon consumption (G).

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