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Seasonal variations in the effect of microzooplankton grazing on phytoplankton in the East China Sea

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ABSTRACT

The effect of microzooplankton grazing on phytoplankton in the East China Sea (ECS) was investigated in summer 2009 and winter 2009/2010 using the dilution technique. There were no significant differences in phytoplankton growth rates and microzooplankton grazing rates between coastal (influenced by the Changjiang River plume) and offshore (influenced by the Kuroshio) waters in either season. The mean rates of phytoplankton growth ($0.77 \pm 0.53\ d^{-1}$) and microzooplankton grazing ($0.69 \pm 0.42\ d^{-1}$) in summer ($n=26$) were significantly higher than those in winter ($0.39 \pm 0.18\ d^{-1}$ and $0.21 \pm 0.08\ d^{-1}$ for mean rates of growth and grazing, respectively) ($n=24$). In both seasons, phytoplankton growth and microzooplankton grazing rates were significantly higher at the surface than at the depth of 5% surface irradiance. Aloricate ciliates were abundant and dominated microzooplankton in the ECS. There were no significant differences in microzooplankton abundance and biomass between seasons or depths. The grazing per microzooplankton was higher in summer than in winter. Phytoplankton growth rates were positively correlated with temperature in the surface waters in summer. Microzooplankton grazing balanced the primary production in summer, while the grazing was low in winter. In winter, the low picophytoplankton and temperature may have been responsible for the low microzooplankton grazing in the ECS.

1. Introduction

The phytoplankton is an important component of biogeochemical cycling in the oceans, and plays an important role in organic carbon transportation from shelf to deep oceans (Liu et al., 1995). Environmental factors, microzooplankton feeding, benthic filter feeding zooplankton, viruses and other pathogens are related to phytoplankton growth (Martina and Justus, 2008). Microzooplankton ($<200\ \mu m$) are the major grazers of the phytoplankton, accounting for an average of 60% to 80% of the phytoplankton daily production in the oceans (Sherr and Sherr, 2002; Calbet and Landry, 2004). It is also shown that most of the production of small phytoplankton (less than 20 μm) can be consumed by microzooplankton (Strom et al., 2007).

The East China Sea (ECS) is a productive area in the west of the Pacific Ocean with one of the largest continental shelves in the world (Wong et al., 2000). There are high seasonal variabilities of temperature, salinity and nutrients due to the seasonal fluctuations of several different water masses (Gong et al., 1996). Above all, the ECS ecosystem is strongly affected by river plume such as from the Changjiang River and Qiantang River, which carry nutrient-rich fresh water into the ECS especially in summer when the river discharge peaks. On the other hand, the Kuroshio Water delivers warm, saline and oligotrophic water into the shelf water along the continental slope (Liu and Gan, 2012). In addition, waters on the shallow continental shelf are mixed vertically by strong surface cooling water during winter and re-stratified by strong surface heating during summer. Thus, the ECS is considered to be one of the most complicated continental seas and also an ideal field for ecological studies on the temporal and spatial dynamics of the biota.

Microzooplankton grazing is an important factor controlling algal blooms in spring in the ECS (Sun et al., 2003) and regulating phytoplankton biomass in the South China Sea (Huang et al., 2006;

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Huang et al., 2011; Zhou et al., 2015). As a major consumer of picophytoplankton, microzooplankton also consume 60% to 70% of the daily production produced by picophytoplankton, particularly in oligotrophic areas of the ECS (Guo et al., 2014a). The growth and grazing mortality rates for the picophytoplankton decrease from the inshore to offshore region in the ECS (Guo et al., 2014a). However, little has been examined related to the dynamics and regulation mechanisms of microzooplankton abundance and grazing on the total phytoplankton as the significant role of the microphytoplankton (Guo et al., 2014b) and nanophytoplankton (Lin et al., 2014) in the ECS ecosystem.

In this study, we quantified the microzooplankton grazing impact on the phytoplankton using the dilution technique, which has become a standard protocol for estimating the microzooplankton grazing effect (Landry and Hassett, 1982; Landry, 1993). The grazing effects were studied not only in the surface layer, but also at the depth of 5% irradiance. Factors such as light, nutrients and temperature influence phytoplankton growth and set the upper limit for biomass production and, ultimately, regulate the grazing effect (Banse, 1992). The present study set out to understand the seasonal and spatial variations in the microzooplankton grazing effect in the ECS, and the temporal variation in microzooplankton grazing between the two seasons (summer and winter), and to know what may affect the phytoplankton growth and the microzooplankton grazing effect.

2. Materials and methods

2.1. Study area and sampling

Our experiments were conducted onboard in two cruises in the ECS, one in August to September 2009 (summer cruise, 13 stations) and the other in December 2009 to January 2010 (winter cruise, 12 stations). The locations of our experimental stations are shown in Fig. 1. We used the dilution technique (Landry and Hassett, 1982) to estimate the in situ phytoplankton growth and microzooplankton grazing rates at two depths (the surface layer and the depth of 5% surface irradiance i.e. the deep layer) for each station. In summer, the depth of 5% surface irradiance represented a deep chlorophyll *a* (Chl *a*) maximum, but in winter, there was no deep Chl *a* maximum layer due to the strong mixing. These stations can be classified into three distinct water masses by hydrographic features and locations based on Gong et al. (1996) and Jiao et al. (2005): Stations with low salinity (<31) and relatively low temperature influenced by the Changjiang River plume; stations with relatively high temperature and high salinity (>34) influenced by the Kuroshio warm current; and other stations belonging to the transitional area.

2.2. Dilution experiment

Seawater was collected using Niskin bottles attached to a CTD rosette (SBE 911 PLUS). Seawater was gently siphoned into two 15-L polycarbonate carboys (Nalgene) using a polycarbonate tube. All the equipment used for incubation was acid washed and rinsed with Milli-Q water. Particle-free filtered seawater was obtained by gravity-filtering seawater through a 0.2 μm capsule (Pall Corporation). In order to comply with the dilution assumption that consumers are not food-satiated at natural prey densities (Landry and Hassett, 1982), we added nutrients in our experiments. Five 1.2 L polycarbonate bottles were used for the nutrient-added treatment (0.5 μmol L^{-1} NH_4Cl, 0.03 μmol L^{-1} KH_2PO_4, 1 nmol L^{-1} $FeCl_3$, 0.1 nmol L^{-1} $MnCl_2$) with a dilution series consisting of 14%, 27%, 50%, 73% and 100% unfiltered seawater. Two additional bottles were filled with unfiltered seawater without nutrient addition and another two identical bottles were used for initial sampling. The bottles were placed in an on deck incubator cooled using surface running seawater for 24 h. The light level of the deeper layer was simulated using neutral light screens.

Sampling for Chl *a* concentration was from the initial bottles and from bottles at the end of the incubation. Technical replicate samples of 500 to 1000 mL were filtered through 25 mm GF/F filters under low vacuum. Chl *a* samples were extracted for 24 h in 5 mL 90% acetone and analyzed onboard. Fluorometric analyses of Chl *a* were carried out with a Turner Designs Model fluorometer (Model No. Trilogy 040) (Strickland and Parsons, 1972).

The data for water temperature and salinity were recorded and generously provided by Prof. J Y. Hu from Xiamen University, China. Seawater was filtered with a 0.45 μm acetate fiber membrane before nutrient analysis, and then the samples for PO_4^{3-}, NO_2^- and NO_3^- were run on an AA3 Auto-Analyzer (Bran-Lube) on board using classical colorimetric methods (M. Dai et al., unpublished data; Dai et al., 2008).

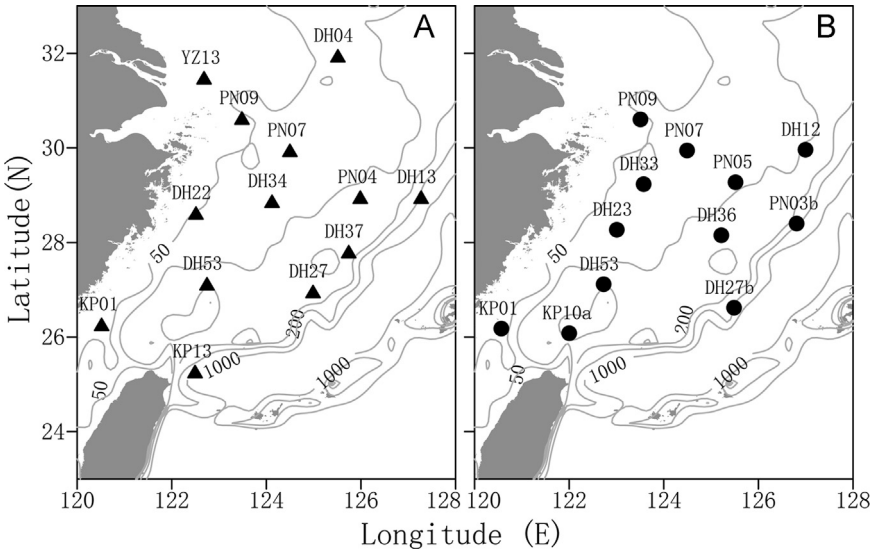

Fig. 1. Map of the sampling stations for the summer (a) and winter (b) cruises in the East China Sea.

2.3. Phytoplankton growth and microzooplankton grazing rates

Phytoplankton growth rates during the nutrient-added treatment (μ_n) and microzooplankton grazing rates (m) of phytoplankton were calculated by regressing the net growth rates in each bottle with nutrient amendment against the dilution factors (the proportions of unfiltered seawater). The m and μ_n values were calculated as the negative slope and the intercept of the linear regression equation (Landry and Hassett, 1982). The in situ phytoplankton instantaneous growth rate (μ_0) was calculated as the sum of the grazing rate and the apparent growth rate without nutrient enrichment (Landry, 1993). In the case of grazing saturation, the grazing rate was assumed to be the value of μ_n minus the net growth rate of the phytoplankton in the nutrient enriched, 100% unfiltered seawater bottle (Strom et al., 2007). The microzooplankton grazing pressure on phytoplankton standing stock (P_i, %) and primary production (P_p, %) were calculated following Verity et al. (1993):

$$P_i = 1 - e^{-\mu_0 t} \times 100\%$$

$$P_p = (e^{\mu_0 t} - e^{(\mu_0 - m)t})/(e^{\mu_0 t} - 1) \times 100\%$$

where t is the time (day); m is microzooplankton grazing rate (d^{-1}); μ_0 is phytoplankton growth rate (d^{-1}).

2.4. Microzooplankton community composition and biomass

For enumeration of the microzooplankton, water samples (500 or 1000 mL) from the dilution experiment bottles were preserved using Lugol's solution (final conc. 5%). Then the fixed samples were stored in a dark place until analysis in the laboratory. After 24 h sedimentation, the samples were concentrated to 100 mL using a silicone tube and 10 mL subsamples were chosen for enumeration. The microzooplankton was divided into two main categories: ciliates and dinoflagellates. Copepod nauplii were excluded because of their extremely low abundance. Ciliates were categorized into loricate tintinnids and aloricate ciliates, and dinoflagellates were categorized into thecate and athecate dinoflagellates. They were identified and counted according to their cilia and shapes using an inverted microscope under a magnification of 200 or 400 times (LEICA DMIRB). The ciliates were identified based on Kofoid and Campbell (1929) and Chihara and Murano (1997); and the dinoflagellates were identified following Dodge (1980) and Chihara and Murano (1997). The cells were photographed and sized using image-analysis (Software Simple PCI 6, imaging systems 705, Compix Inc.), and cell volumes were calculated assuming corresponding geometric shapes. Cellular carbon content of the ciliates was estimated on the basis of biovolumes using the equations pgC $cell^{-1} = 444.5 + 0.053 \times$ volume (non-loricate ciliates) (Verity and Langdon, 1984), and pgC $cell^{-1} = 0.19 \times$ volume (other ciliates) (Putt and Stoecker, 1989). Biovolumes of dinoflagellates were converted to cell carbon using the equation: pgC $cell^{-1} = 0.760 \times volume^{0.819}$ (Menden-Deuer and Lessard, 2000).

3. Results

3.1. Environmental properties

The physical, chemical and biological features of the study area are provided in Tables 1 and 2. Generally, the temperature, surface salinity, nitrite, nitrate and phosphate concentrations showed onshore–offshore gradients in both summer and winter. Surface water temperature was quite high and was always above 20 °C in summer while the water was relatively cool and the temperature always fell below 20 °C in winter except in offshore regions. Surface salinity ranged from 29.4 to 34.0 in summer and 31.3 to 34.6 in winter. Stations with low salinity were in the near shore regions

Table 1
Summary of environmental variables and Chl *a*-based rate estimates of phytoplankton growth (μ, d^{-1}) and microzooplankton grazing (m, d^{-1}) in the surface layer and the depth of 5% surface irradiance (deep layers) in the East China Sea during August–September 2009. *T*, temperature (°C); Sal, salinity; $NO_2^- + NO_3^-$, nitrate plus nitrite concentration (μmol L^{-1}); PO_4^{3-}, phosphate concentration (μmol L^{-1}); Chl *a*, initial chlorophyll concentration (μg L^{-1}); μ_n, phytoplankton growth rate with nutrient enrichment (d^{-1}); μ_0, phytoplankton growth rate without nutrient enrichment (d^{-1}); m, mortality rate (d^{-1}). BLQ: below the limit of determination (0.10 μmol L^{-1} for NO_x: $NO_2^- + NO_3^-$, 0.08 μmol L^{-1} for PO_4^{3-}).

Stn.	Date	Time	Depth	*T*	Sal	NO_x	PO_4^{3-}	Chl *a*	μ_n	μ_0	m	R^2
YZ13	22-Aug	7:00	0	26.08	33.71	15.35	0.61	3.23	1.73	1.63	1.40	0.96
YZ13	24-Aug	7:00	10	21.55	33.38	13.65	0.79	2.40	−0.35	−0.72	0.00	0.21
PN09	24-Aug	22:20	0	29.51	29.40	/	/	0.45	1.28	1.22	1.18	0.86
PN09	24-Aug	22:20	25	25.63	33.72	4.69	0.45	1.23	0.33	0.25	0.00	0.72
DH04	27-Aug	9:00	0	28.26	29.78	BLQ	BLQ	0.39	1.15	1.03	0.71	0.85
DH04	27-Aug	9:00	15	27.43	29.74	2.45	BLQ	0.51	0.40	0.62	0.70	0.84
DH22	20-Aug	12:45	0	29.96	30.62	2.22	0.25	1.22	2.10	1.86	1.31	0.84
DH22	20-Aug	12:45	10	26.68	33.53	5.55	0.53	7.94	0.17	0.20	0.34	0.95
KP01	18-Aug	9:15	0	28.68	33.31	0.22	0.10	1.25	1.08	0.82	0.93	0.97
KP01	18-Aug	9:15	15	26.56	33.73	2.32	0.28	3.15	0.84	0.85	0.39	0.85
KP13	19-Aug	8:15	0	27.45	33.58	0.10	0.08	0.93	1.48	0.96	1.54	0.96
KP13	19-Aug	8:15	50	22.10	34.42	6.63	0.56	1.17	0.51	0.42	0.33	0.98
DH53	19-Aug	18:15	0	30.28	33.51	0.09	BLQ	0.42	0.43	0.16	0.25	0.68
DH53	19-Aug	18:15	50	23.25	33.98	7.28	0.34	1.24	0.87	0.80	1.02	0.33
DH37	21-Aug	20:10	0	29.66	33.52	BLQ	BLQ	0.15	2.00	1.52	0.72	0.94
DH37	21-Aug	20:10	50	24.84	34.08	2.64	0.29	1.37	0.41	0.22	0.23	0.83
DH34	22-Aug	9:15	0	29.52	32.62	BLQ	0.12	0.23	2.32	1.44	0.97	0.97
DH34	22-Aug	9:15	25	27.58	33.46	0.64	0.15	2.88	0.26	0.31	0.83	0.66
PN07	25-Aug	8:45	0	29.61	33.63	BLQ	BLQ	0.26	0.85	0.64	0.50	0.86
PN07	25-Aug	8:45	40	27.42	33.74	1.03	0.18	1.19	0.52	0.31	0.32	0.75
PN04	25-Aug	23:00	0	29.89	33.69	BLQ	BLQ	0.22	0.91	0.99	0.57	0.72
PN04	25-Aug	23:00	50	28.45	33.79	BLQ	BLQ	0.69	0.26	0.24	0.04	0.02
DH27	21-Aug	8:00	0	29.08	34.01	BLQ	BLQ	0.20	2.07	1.26	0.58	0.85
DH27	21-Aug	8:00	50	22.87	34.14	5.35	0.42	0.96	0.13	0.07	0.41	0.81
DH13	26-Aug	9:35	0	29.35	33.74	/	0.10	0.20	0.85	0.78	1.20	0.82
DH13	26-Aug	9:35	75	25.34	34.23	0.84	0.20	0.57	0.13	0.09	0.17	0.83

Table 2
Summary of environmental variables and Chl *a*- based rate estimates of phytoplankton growth (μ, d^{-1}) and microzooplankton grazing (m, d^{-1}) in the surface layer and the depth of 5% surface irradiance (deep layers) in the East China Sea during December 2009 to January 2010. See Table 1 for the abbreviations.

Stn.	Date	Time	Depth	T	Sal	NO_x	PO_4^{3-}	Chl *a*	μ_n	μ_0	m	R^2
DH53	3-Jan	8:00	0	20.14	34.53	2.28	0.16	0.73	0.61	0.62	0.35	0.56
DH53	3-Jan	8:00	50	19.86	34.54	2.79	0.19	0.73	0.32	0.37	0.16	0.87
DH36	30-Dec	0:10	0	19.18	34.40	2.91	0.23	0.58	0.52	0.50	0.19	0.76
DH36	30-Dec	0:10	50	19.31	34.46	2.55	0.20	0.57	0.20	0.17	0.14	0.99
DH23	31-Dec	20:30	0	17.90	34.31	4.30	0.28	0.64	0.35	0.32	0.10	0.90
DH23	31-Dec	20:30	25	17.92	34.30	4.29	0.28	0.64	0.34	0.31	0.12	0.99
PN05	27-Dec	6:30	0	18.81	34.03	4.22	0.33	0.44	0.34	0.34	0.16	0.89
PN05	27-Dec	6:30	50	18.84	34.03	4.23	0.32	0.49	0.19	0.18	0.13	0.98
PN07	27-Dec	14:10	0	17.35	34.04	5.27	0.36	0.53	0.50	0.49	0.25	0.47
PN07	27-Dec	14:10	25	17.37	34.04	5.26	0.37	0.53	0.26	0.21	0.11	1.00
PN09	28-Dec	13:00	0	16.19	33.98	5.04	0.39	0.57	0.41	0.33	0.37	0.64
PN09	28-Dec	13:00	25	16.20	33.98	5.03	0.38	0.51	0.26	0.24	0.26	0.87
DH33	29-Dec	12:50	0	18.20	34.18	2.97	0.24	1.07	0.61	0.60	0.29	0.79
DH33	29-Dec	12:50	25	18.16	34.18	3.01	0.23	0.54	0.33	0.25	0.06	0.98
KP01	4-Jan	18:30	0	14.99	31.30	17.50	0.78	1.25	0.51	0.50	0.23	0.82
KP01	4-Jan	18:30	15	15.35	31.80	16.19	0.75	0.57	0.19	0.18	0.11	0.06
DH12	25-Dec	14:30	0	19.54	34.19	4.49	0.32	0.45	0.79	0.75	0.08	0.66
DH12	25-Dec	14:30	25	19.49	34.19	4.62	0.32	0.38	0.37	0.41	0.03	0.32
PN03b	25-Dec	17:15	0	22.90	34.02	0.34	BLQ	0.67	0.21	0.17	0.07	0.64
PN03b	25-Dec	17:15	50	22.85	34.61	0.49	BLQ	0.71	−0.19	−0.14	0.09	0.95
DH27b	30-Dec	10:15	0	23.19	34.57	0.59	BLQ	0.37	0.38	0.36	0.29	0.73
DH27b	30-Dec	10:15	50	23.28	34.61	0.52	BLQ	0.38	0.19	0.23	0.24	0.93
KP10a	4-Jan	8:30	0	19.60	34.57	4.44	0.28	0.47	0.87	0.84	0.26	0.50
KP10a	4-Jan	8:30	25	19.57	34.57	4.56	0.28	0.43	0.56	0.56	0.20	0.92

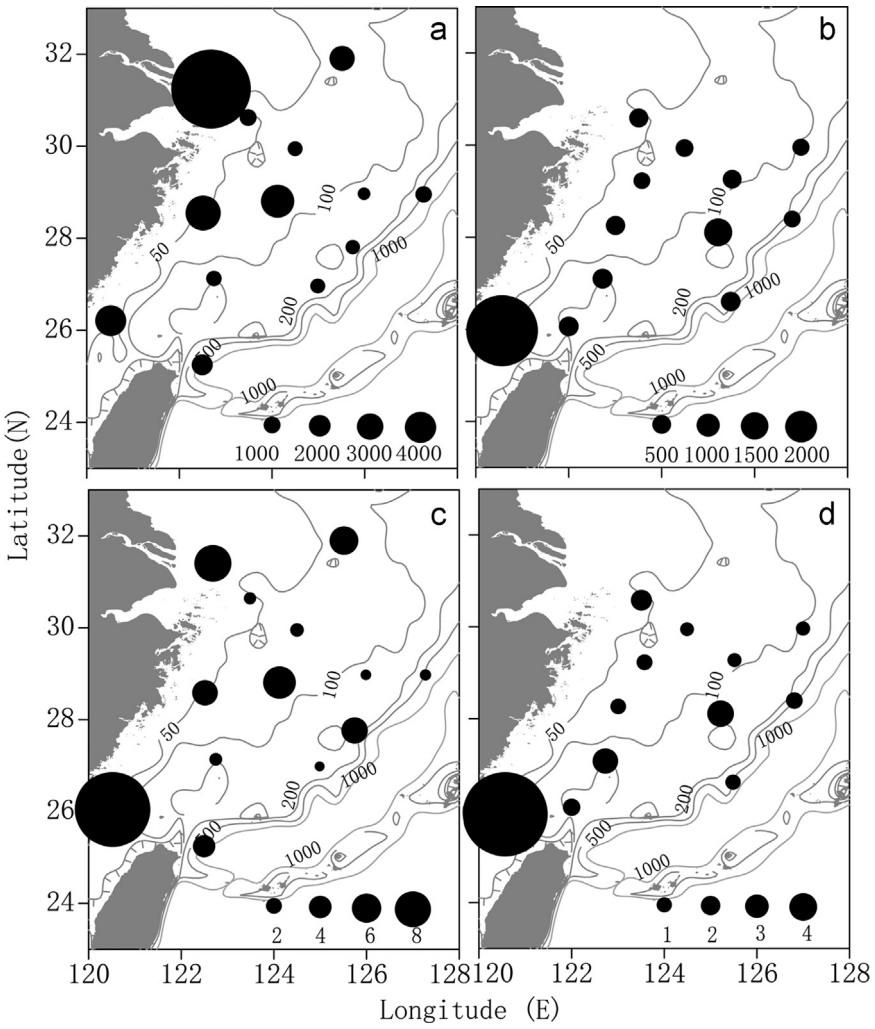

Fig. 2. Surface distribution of total microzooplankton abundance (a, b, cells L^{-1}) and biomass (c, d, μg C L^{-1}) during summer (left) and winter (right) in the East China Sea.

and affected by the freshwater discharge of the Changjiang River. The concentrations of nitrate and phosphate were often near or below the detection limit in summer but were above the detection limit in winter because of the strong vertical mixing. The surface nitrite, nitrate and phosphate concentrations also showed similar patterns that were higher in inshore than in offshore regions. Surface Chl *a* concentration in summer ranged from 0.15 to 3.23 μg L^{-1} with a mean value of 0.70 μg L^{-1} and the high values were shown at inshore stations (Stns. YZ13 and KP01). Chl *a* concentrations in winter ranged from 0.37 to 1.25 μg L^{-1} with a mean value of 0.67 μg L^{-1}. Compared to the surface layer, Chl *a* concentrations and salinity were significantly higher in the 5% I_0 layers ($p < 0.05$), but the temperature was slightly lower than at the surface in summer ($p = 0.053$). Because of the strong mixing, the values for Chl *a* and temperature showed no significant difference in the different layers in winter ($p > 0.05$). Nitrite, nitrate and phosphate concentrations could be detected in the 5% I_0 layers in summer and also in the surface water and 5% I_0 layers in winter.

In summer, the 13 stations could be distinguished into three distinct water masses: Stns. YZ13, PN09, DH04 and DH22 were affected by the Changjiang river plume; Stns. DH13 and DH27 by the Kuroshio Water; while the others belonged to the mixed waters between the river plume and the Kuroshio Water. In winter, there were only two types of water systems because of the relatively low river plume and land runoff. Stns. DH12, PN03b, DH27b and KP01a were influenced by the Kuroshio Water and the others belonged to the mixed waters.

3.2. Microzooplankton community dynamics

The abundance and biomass of microzooplankton in summer and in winter are shown in Figs. 2–4. Microzooplankton abundance in the surface layer in summer ranged from 120 to 4800 cells L^{-1} with a mean value of 1833 ± 1673 (mean ± SD) cells L^{-1}, except for the extremely high value at Stn. YZ13 (14,000 cells L^{-1}). The averaged abundance in the surface layer in summer ($n = 13$) was higher than that in winter ($n = 12$), but it was not significantly ($p > 0.05$) (Figs. 2 and 3). In winter, microzooplankton abundance ranged from 268 to 1556 cells L^{-1} with a mean value of 550 ± 356 cells L^{-1}, except for the extremely high value at Stn. KP01 (6563 cells L^{-1}) (Figs. 2 and 4). The highest cell abundance in summer was recorded at Stn. YZ13, where aloricate ciliates were dominant and nutrient concentrations were high.

Oligotrichs and non-loricate choreotrichs dominated at most of the stations in both seasons. *Strombidium conicum, Strombidium tintinnodes, Strombidium epidemum, Strombidium capitatum, Strobilidium spiralis* were the main species of aloricate ciliates found in the ECS. *Mesodinium rubra* was also found at some stations in summer. Although the abundance of loricate ciliates was low, the diversity was high including *Tintinnopsis* spp., *Eutintinnus* spp., *Condonellopsia morchella, Acanthostomella minutissima* and *Ascampbelliella retusa.* The abundance of heterotrophic dinoflagellates was also high at some stations in summer.

Microzooplankton biomass varied from 0.23 to 19.67 μg C L^{-1} with a maximum at KP01, and with a low concentration at DH27 in

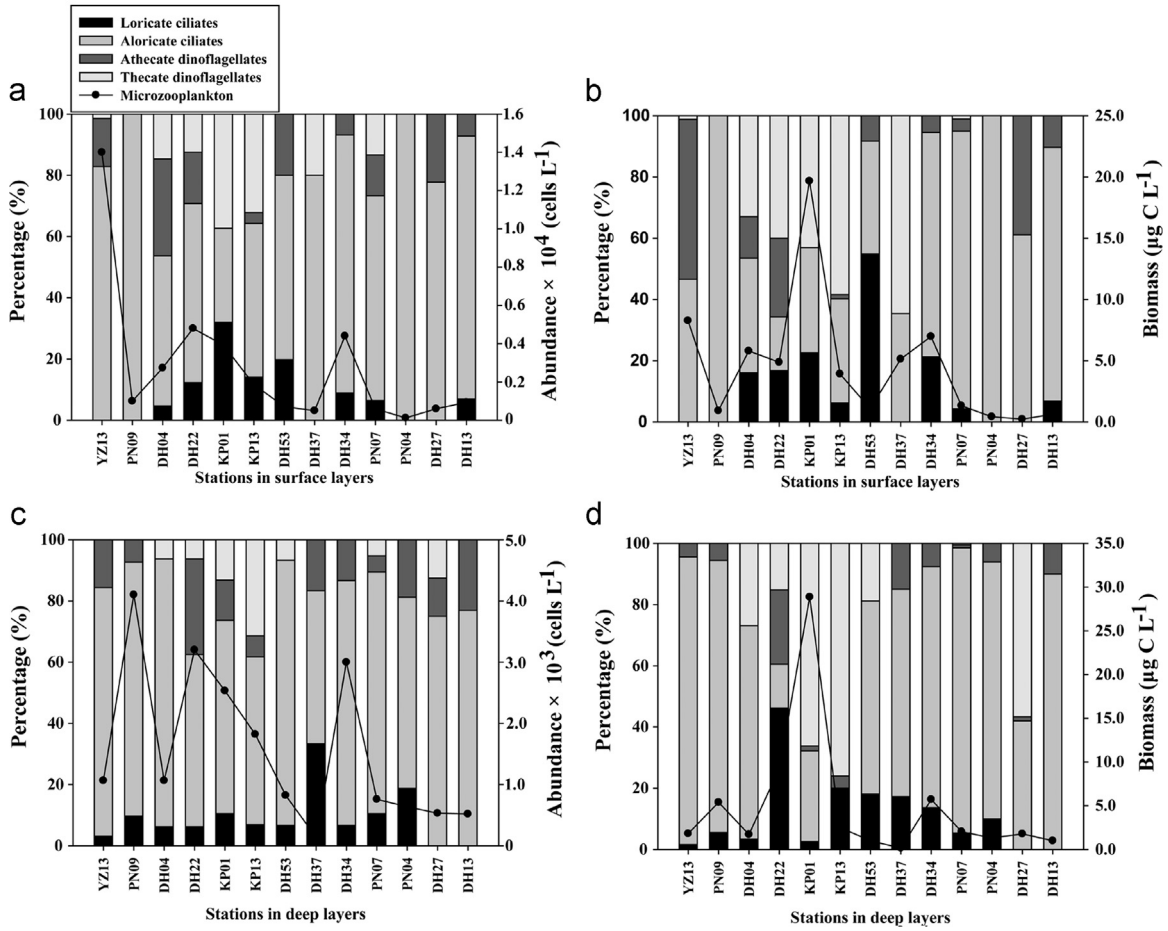

Fig. 3. Microzooplankton abundance and the percentage contribution of different groups in the surface layer and deep waters (a, c cells L^{-1}), and biomass and the percentage contribution of different groups (b, d μg C L^{-1}) in the surface layer and deep waters in summer in the East China Sea.

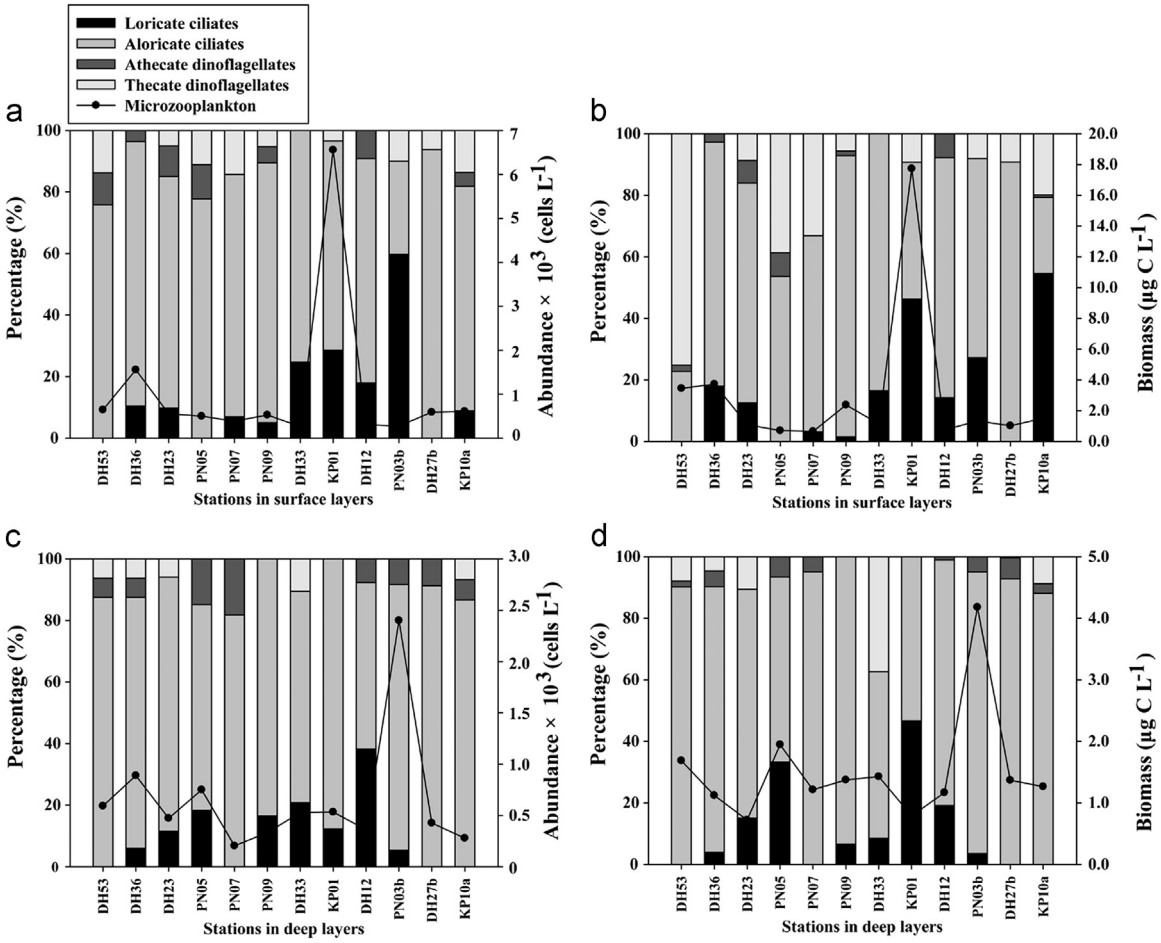

Fig. 4. Microzooplankton abundance and the percentage contribution of different groups in the surface layer and deep waters (a, c cells L^{-1}) , biomass and the percentage contribution of different groups (b, d μg C L^{-1}) in the surface layer and deep waters in winter in the East China Sea.

summer. The microzooplankton biomass varied from 0.71 μg C L^{-1} at Stn. PN05 to 3.73 μg C L^{-1} at Stn. DH36 in the winter surface waters. The average total biomass was 4.25 ± 5.42 μg C L^{-1} in the surface layer in summer and 1.54 ± 1.01 μg C L^{-1} in winter. Surface microzooplankton biomass in winter was lower than that in summer, but it was not significantly ($p > 0.05$). The thecate dinoflagellates, especially *Protoperidinium* sp., although with low abundance, contributed substantially to the relatively high biomass in winter (e.g. Stns. DH53, PN05) and in summer (e.g. KP01). Microzooplankton biomass at Stn. KP01 was high in both seasons. The microzooplankton abundance was positively correlated with Chl *a* concentration in the surface layer in summer ($p < 0.05$). Positive correlations were obtained between Chl *a* concentration and microzooplankton biomass in the surface layer in both summer and winter ($p < 0.05$).

Microzooplankton abundance in the 5% I_0 layers varied from 140 to 4100 cells L^{-1} with an average value of 1554 ± 1255 cells L^{-1} in summer. The abundance in winter ranged from 203 to 2400 cells L^{-1} with an average value of 644 ± 586 cells L^{-1}. The average microzooplankton biomass in the 5% I_0 layers was 4.81 ± 7.66 in summer and 1.52 ± 0.90 μg C L^{-1} in winter. Microzooplankton abundance and biomass showed no significant difference between the surface waters and the 5% I_0 layers in either season ($p > 0.05$). In the 5% I_0 layers, the abundance and biomass in summer were higher than those in winter but also not significantly ($p > 0.05$).

3.3. Phytoplankton growth and microzooplankton grazing rates

Phytoplankton growth and microzooplankton grazing rates are shown in Tables 1 and 2. Positive mortality rates ($m \geq 0.1$) were used for data analysis. Phytoplankton growth rates (μ_0) ranged from 0.16 to 1.86 d^{-1} (mean ± SD = 1.11 ± 0.48 d^{-1}) and microzooplankton grazing rates (m) ranged from 0.25 to 1.54 d^{-1} (mean ± SD = 0.93 ± 0.41 d^{-1}) in the surface layer in summer. In winter, both μ_0 (0.17 to 0.84 d^{-1}, mean ± SD = 0.49 ± 0.17 d^{-1}) and m (0.10 to 0.37 d^{-1}, mean ± SD = 0.25 ± 0.08 d^{-1}) in the surface layer were significantly lower than those in summer ($p < 0.05$) (Tables 1 and 2; Fig. 5). The phytoplankton growth and microzooplankton grazing rates were distributed evenly with no regional differences in summer or in winter ($p > 0.05$). However, in the mixed waters and Kuroshio regions, μ_0 and m in summer were significantly higher than those in winter ($p < 0.05$).

In the 5% I_0 layers in summer, phytoplankton growth rates varied from 0.07 to 0.85 d^{-1} with a maximum in Stn. KP01, and with a low concentration at Stn. DH27. The microzooplankton grazing rates varied from 0.17 to 1.02 d^{-1} with a mean value of 0.39 ± 0.28 d^{-1}. In winter, the mean phytoplankton growth rate was 0.27 ± 0.13 d^{-1}, ranging from 0.17 to 0.56 d^{-1} and the mean microzooplankton grazing rate was 0.16 ± 0.06 d^{-1}, ranging from 0.11 to 0.26 d^{-1} in deep waters. Phytoplankton growth rates (μ_0) and microzooplankton grazing rates (m) in the surface layer were significantly higher than in the deep layers in both seasons ($p < 0.05$).

In terms of the ratio of μ_0/μ_n, which indicates the degree of nutrient-limitation, in winter the phytoplankton growth rate

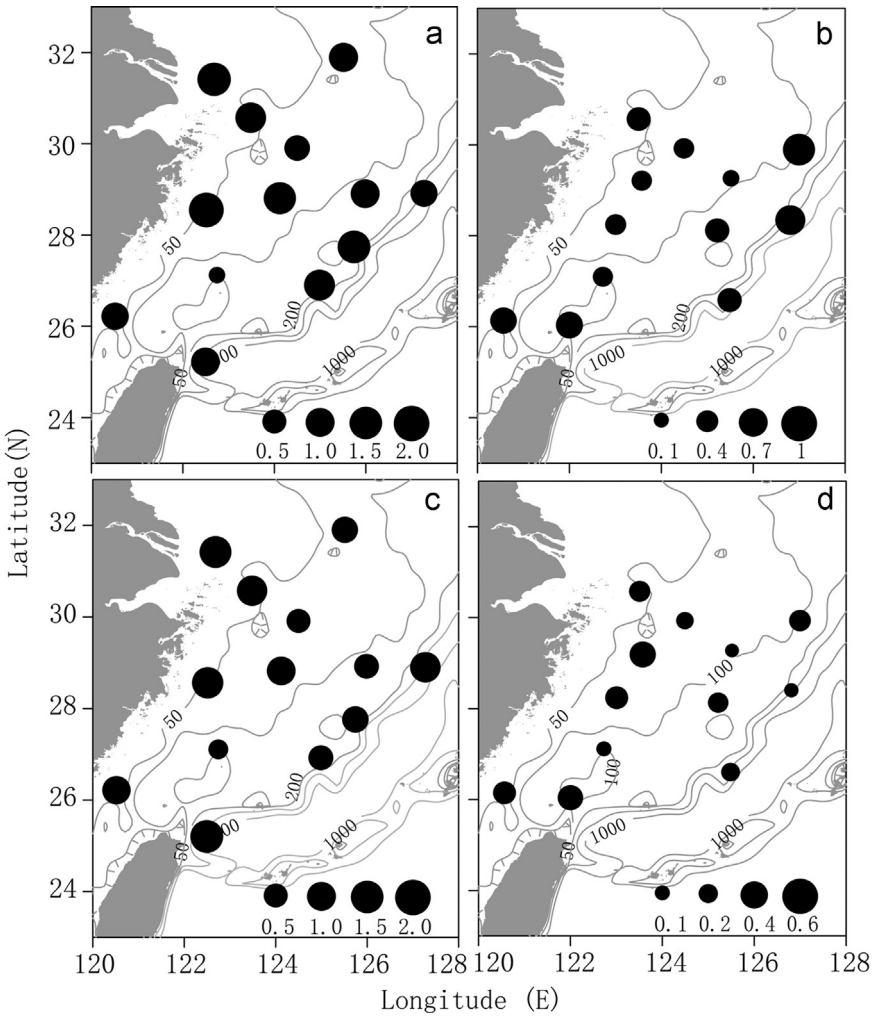

Fig. 5. Surface distribution of phytoplankton growth rates (a, b, d^{-1}) and microzooplankton grazing rates (c, d, d^{-1}) during summer (left) and winter (right) in the East China Sea.

estimates for the nutrient addition treatments (μ_n) were almost the same as the estimates without nutrient addition (μ_0), and the ratio was 0.95 and 0.97 in the surface and 5% I_0 layers, indicating no nutrient limitation. The μ_0/μ_n ratio had average values of 0.72 in the surface waters and 0.90 in the 5% I_0 layers in summer (Fig. 6). The μ_0/μ_n value was scattered over a wide area, from 0.37 to 0.94 in the surface waters and 0.54 to 1.55 in the 5% I_0 layers, suggesting that nutrients became a limiting factor in summer.

High phytoplankton growth rates were measured at Stns. YZ13 and DH22 in summer with high nitrate concentrations in the plume region. The percentages of phytoplankton standing stock (P_i) and primary production (P_p) that were consumed by microzooplankton were 22 to 78 and 65 to 150 in summer in the surface layer. In the 5% I_0 layers, the rates of P_i and P_p were $25 \pm 20\%$ and $127 \pm 135\%$. In winter, the rates of P_i and P_p were $22 \pm 6\%$ and $59 \pm 22\%$ in the surface layer and $14 \pm 5\%$ and $64 \pm 27\%$ in the 5% I_0 layers (Fig. 7). Our results indicated that the phytoplankton standing stock and primary production were controlled more by the microzooplankton in summer than in winter, and more phytoplankton standing stock was controlled by microzooplankton in

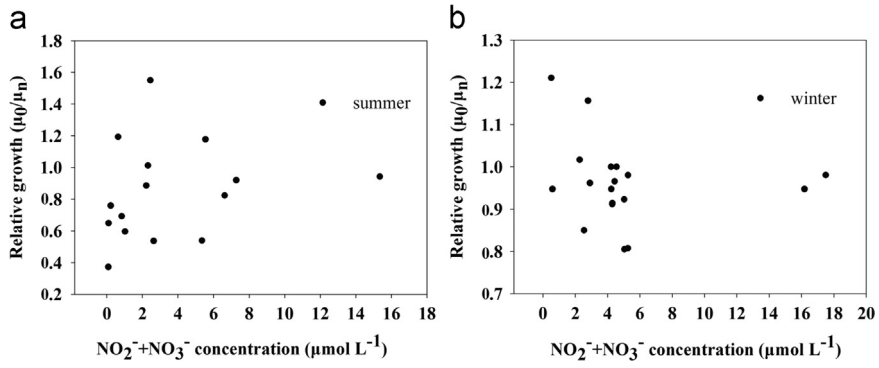

Fig. 6. Relationships between phytoplankton relative growth rate (μ_0/μ_n) and nitrate concentrations for dilution experiments conducted in the East China Sea in summer 2009 and winter 2009/2010.

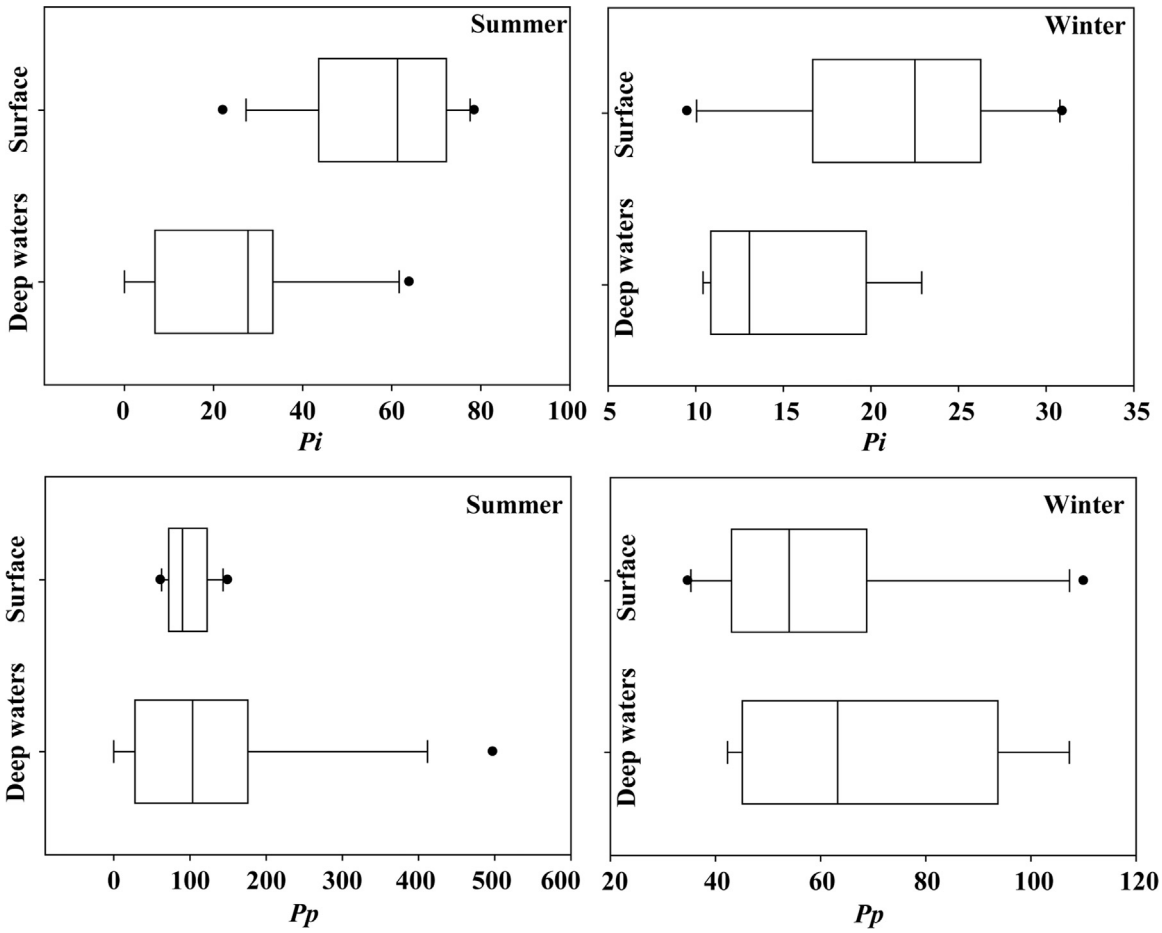

Fig. 7. Box plots of the microzooplankton grazing pressure on phytoplankton standing stock (P_i, %) and primary production (P_p, %) in the East China Sea in summer 2009 and winter 2009/2010.

Table 3
Pearson correlation coefficients between environmental variables and phytoplankton growth rates and microzooplankton grazing rates in different seasons in the East China Sea. *T*, temperature (°C); Chl *a*, initial chlorophyll concentration (μg L^{-1}); $NO_2^- + NO_3^-$, nitrate plus nitrite concentration (μmol L^{-1}); PO_4^{3-}, phosphate concentration (μmol L^{-1}); MZP abundance, microzooplankton abundance (cells L^{-1}); MZP biomass, microzooplankton biomass (μg C L^{-1}); μ_n, phytoplankton growth rate with nutrient enrichment (d^{-1}); μ_0, phytoplankton growth rate without nutrient enrichment (d^{-1}); *m*, mortality rate (d^{-1}).

		Surface layer			5% Surface irradiance layer		
	Parameter	μ_n	μ_0	m	μ_n	μ_0	m
Summer	Temperature	0.02*	0.03*	0.27	0.78	0.85	0.89
	Salinity	0.23	0.05*	0.08	0.94	0.37	0.32
	$NO_2^- + NO_3^-$	0.86	0.70	0.41	0.51	0.58	0.52
	PO_4^{3-}	0.38	0.55	0.98	0.88	0.96	0.71
	Chl *a*	0.21	0.36	0.72	0.65	0.84	0.83
	MZP abundance	0.06*	0.02*	0.01*	0.99	0.58	0.61
	MZP biomass	0.59	0.43	0.75	0.24	0.14	0.82
Winter	Temperature	0.88	0.65	0.51	0.87	0.55	0.31
	Salinity	0.58	0.54	0.46	0.34	0.29	0.30
	$NO_2^- + NO_3^-$	0.87	0.81	0.39	0.72	0.60	0.26
	PO_4^{3-}	0.44	0.40	0.67	0.41	0.39	0.60
	Chl *a*	0.25	0.23	0.61	0.95	0.96	0.16
	MZP abundance	0.55	0.54	0.90	0.20	0.26	0.41
	MZP biomass	0.42	0.41	0.55	0.84	0.95	0.51

* $p < 0.05$.

the surface layer than in the 5% I_0 layers ($p < 0.05$).

The phytoplankton growth rate in surface waters was positively correlated with temperature, and the grazing rate was positively correlated with microzooplankton abundance in summer ($p < 0.05$). However, in winter, no significant correlation was found between environmental variables and either m or μ_0 ($p > 0.05$) (Table 3, Fig. 8).

4. Discussion

This study provided a dataset of microzooplankton abundance, phytoplankton growth and microzooplankton grazing rates with spatial coverage of the ECS in both surface and subsurface layers. These data are important for assessing the biogeochemical cycling in this marginal sea. Our results demonstrated distinct seasonal contrasts.

4.1. Effect of environmental factors on microzooplankton distribution

Microzooplankton abundance and biomass in the ECS in our study were at the same level compared with other regions (Quevedo and Anadón, 2001). Microzooplankton abundance and metabolism are affected by many factors, such as temperature, oxygen and nutrients (Carson and Hutchins, 2013). Water temperature may affect the metabolic rates, and oxygen concentration directly affects ciliate distribution (Dolan, 1991). However, we found difference but not significant in abundance and biomass in the different layers and different seasons, which may have indicated that

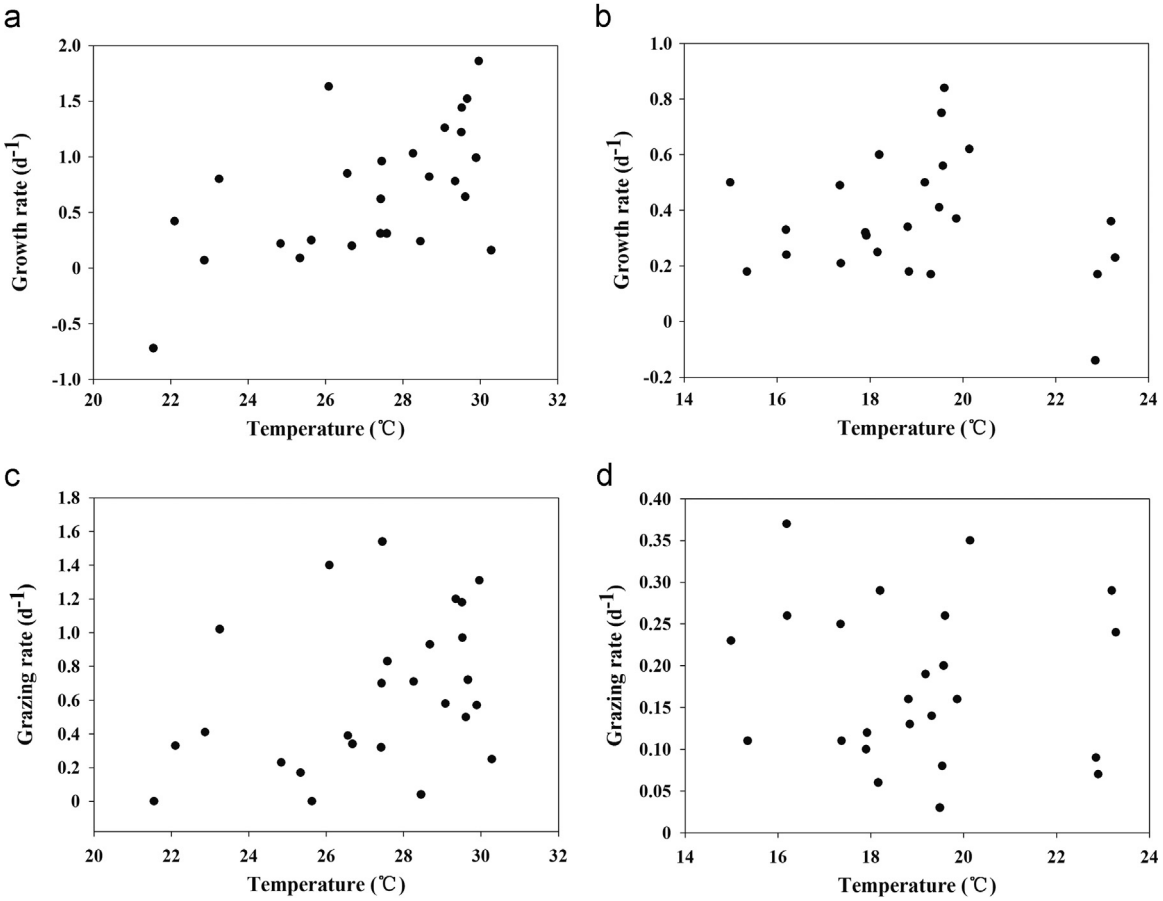

Fig. 8. Relationships between phytoplankton growth rate (a, b, μ_0, d^{-1})/microzooplankton grazing rate (c, d, m, d^{-1}) and temperature during summer (left) and winter (right) in the East China Sea.

the effects of temperature on microzooplankton abundance and biomass were unclear and complicated in our study area.

However, in the transitional regions, we found microzooplankton abundance in summer was higher than in winter ($p < 0.01$). Low nutrients may limit the growth of phytoplankton (Paasche and Erga, 1988), and so the higher nutrient concentrations in summer may have stimulated the phytoplankton growth, thus increasing the microzooplankton abundance indirectly. In our study area, nitrate and nitrite concentrations were detectable only in five stations in the surface waters in summer which may also confirm that nutrients indirectly affect microzooplankton abundance and biomass by influencing phytoplankton biomass and productivity (Dolan, 1991).

Aloricate ciliates especially the oligotrich ciliates were dominant in both seasons which is also found by Ota and Taniguchi (2003). The relatively abundance (%) of loricate ciliates was lowest in summer, but the relatively abundance of heterotrophic dinoflagellates was lowest in winter (Figs. 3 and 4). High microzooplankton biomass is found in high productivity waters, as are a large number of heterotrophic dinoflagellates (Matthew et al., 2007), and so perhaps, in the ECS in winter, the low abundance of heterotrophic dinoflagellates accompanied the low productivity waters.

4.2. Variations of phytoplankton growth and microzooplankton grazing rates

Although the differences in microzooplankton biomass and abundance were not significant, the phytoplankton growth and microzooplankton grazing rates were significantly higher in the surface waters than in the deep layers in both seasons. In the Changjiang River Water, the nutrient concentrations and light availability in the surface waters were higher than in the deep layers and therefore the growth rate in these waters also tended to be higher than in the deep layers. In the Kuroshio Water and mixed waters, although nutrient concentrations were higher in the deep layers compared to those in the surface waters in summer, the significantly lower phytoplankton growth rates in the deeper layers indicated that light intensity could have limited the growth of phytoplankton, which is observed in many other studies (for example, Landry et al., 1995; Chen et al., 2013).

Generally, phytoplankton growth rates and microzooplankton grazing are closely coupled (Cáceres et al., 2013). Light may promote the digestion of food vacuoles in some protists (Strom, 2001), but some conflicting results also suggest that some protists may grow better in the dark (Jakobsen and Strom, 2004). Thus, it was not clear whether light could affect the microzooplankton grazing directly. Our results showed that m/μ_0 was lower in the surface layer than in the deep layers in both seasons, which is also suggested in previous studies (Quevedo and Anadón, 2001; Landry et al., 2011). One explanation for this phenomenon is that the phytoplankton growth rates were falling rapidly under the exponential decline of the light from the surface to the deep, but that microzooplankton grazing rates decrease more slowly than phytoplankton growth rates with depth (Landry et al., 2011).

Seasonally, phytoplankton growth rates and microzooplankton grazing rates in the surface layer in summer were significantly higher than in winter, consistent with other studies (Sunju et al., 2007). In our study, the temperature in winter was significantly lower than in summer, and temperature could be one important

factor affecting both rates, but more sensitive for grazing rates (Chen et al., 2012). Rose and Caron (2007) find that the herbivory grazing effect may be enhanced with increasing temperature. Therefore, the lower feeding impact in winter (low m/μ_0) may have been caused by a larger decrease of microzooplankton grazing in winter than of phytoplankton growth rates. At the same time, temperature is not the only factor affecting these rates, and light intensity is a very important factor affecting the growth rates of the phytoplankton. In winter, the light level is usually 2.9 times lower than in summer in the ECS, which induced a higher primary production in summer (Gong et al., 2003). As well as temperature and light intensity, nutrients were impact factors for phytoplankton growth. Although the nutrient concentrations were low in most places during summer, microzooplankton excretion may contribute a substantial part of the nutrients utilized by the phytoplankton (Zhou et al., 2015), but this is difficult to quantify directly.

Phytoplankton community structure is a key factor influencing trophic pathways in the pelagic system (Legendre and Rassoulzadegan, 1996). Phytoplankton is also an important factor which can have a threshold effect for the microzooplankton. Thus, Frost (1975) points out that the microzooplankton may cease grazing if the ambient phytoplankton biomass is low. Christaki et al. (2001) note that the nano-flagellates and small ciliates, as the grazers of *Synechococcus*, cease to feed when the prey density falls below a critical level in indoor incubation. Although the evidence for thresholds of food concentration for natural microzooplankton grazing is limited (Lessard and Murrell, 1998), Landry et al. (1984) suggest that the threshold of *Synechococcus* abundance, which corresponds significantly to grazing by nano-flagellates at 6×10^4 cells mL^{-1}, is 15 μg C L^{-1} with a conversion factor of 250 fgC $cell^{-1}$ (Kana and Glibert, 1987). In our study, the diet biomass during the winter cruise was 1.58 μg C L^{-1} which was far below the threshold of *Synechococcus* biomass, and may have resulted in the low grazing rates. Data from Guo et al. (2014a) concerning phytoplankton composition show that *Synechococcus* and *Prochlorococcus*are more abundant in summer than in winter in the surface waters. The nutrients in winter were higher than in summer but, as Raven (1986) points out, small phytoplankton are better adapted to an oligotrophic environment because of their larger surface-to-volume ratio, which gives them an advantage in competing with larger cells for dissolved nutrients at low concentrations. Tsai et al. (2005) and Liu et al. (2009) also note that both the abundance and growth rate of *Synechococcus* increase as the water temperature increases. This phenomenon is similar to the early results of Chang et al. (1996) and Waterbury and Valois (1993), who indicate that *Synechococcus* abundance is closely related to the water temperature. Thus, in the cold season of the year, when *Synechococcus* biomass was far below the grazing threshold, the grazing rate on it would be low, and the weak grazing effects signaled that low temperature was an important factor limiting trophic links during the winter.

Microzooplankton graze over a wide size range of phytoplankton cells, from picophytoplankton to large cells (Zhou et al., 2011). In the same cruises, Guo et al. (2014a) also investigated picophytoplankton growth and grazing in the ECS (Table 4). The average growth rates and grazing rates for *Prochlorococcus*, *Synechococcus* and picoeukaryotes were also higher in summer than in winter. The rates were also higher in the surface water in both seasons than in the 5% I_0 layers. Compared with our results, the grazing rates of the microzooplankton on phytoplankton in winter and in the 5% I_0 layers in summer are lower than on picophytoplankton, whereas in the surface layer in summer, the grazing rates are at the same level. Picophytoplankton abundance was lower in winter than in summer (Chen et al., 2009; Guo et al., 2014a), but the relatively higher growth and grazing rates on picophytoplankton from Guo et al. (2014a) may indicate a close coupling between picophytoplankton and microzooplankton in the ECS in both seasons. It is also suggested that microzooplankton benefit more from picophytoplankton than from large phytoplankton. In the South China Sea, higher growth rates of pico-cells than microphytoplankton are observed, but the microzooplankton grazing impacts on nano- and microphytoplankton are higher than those on picophytoplankton (Zhou et al., 2015). In the ECS, nano- and microphytoplankton, especially diatoms, are abundant in the shelf area, whereas the Kuroshio Water is dominated by picophytoplankton (Chen, 2000; Furuya et al., 2003). Field studies on the size-based grazing of microzooplankton are few in the ECS, and need further study.

Table 4
Comparison between the work of Guo et al. (2014a) study on phytoplankton growth rate (μ_0, d^{-1}) and microzooplankton grazing rate (m, d^{-1}) data (mean) in the ECS using the dilution technique.

Study	μ_0	m
Guo et al. (2014a)	*Prochlorococcus*	
	Summer surface: 0.31 ± 0.11	Summer surface: 0.52 ± 0.50
	Winter surface: 0.61 ± 0.20	Winter surface: 0.29 ± 0.03
	Summer 5% I_0: 0.39 ± 0.17	Summer 5% I_0: 0.34 ± 0.17
	Winter 5% I_0: 0.32 ± 0.15	Winter 5% I_0: 0.19 ± 0.19
	Synechococcus	
	Summer surface: 0.84 ± 0.66	Summer surface: 0.72 ± 0.70
	Winter surface: 0.71 ± 0.42	Winter surface: 0.21 ± 0.16
	Summer 5% I_0: 0.64 ± 0.29	Summer 5% I_0: 0.49 ± 0.28
	Winter 5% I_0: 0.40 ± 0.15	Winter 5% I_0: 0.23 ± 0.23
	picoeukaryotes	
	Summer surface: 1.07 ± 0.83	Summer surface: 0.85 ± 0.68
	Winter surface: 0.74 ± 0.52	Winter surface: 0.27 ± 0.17
	Summer 5% I_0: 0.57 ± 0.42	Summer 5% I_0: 0.41 ± 0.31
	Winter 5% I_0: 0.30 ± 0.18	Winter 5% I_0: 0.19 ± 0.17
Our study	Summer surface: 1.11 ± 0.48	Summer surface: 0.93 ± 0.41
	Winter surface: 0.49 ± 0.17	Winter surface: 0.25 ± 0.08
	Summer 5% I_0: 0.28 ± 0.39	Summer 5% I_0: 0.39 ± 0.28
	Winter 5% I_0: 0.27 ± 0.13	Winter 5% I_0: 0.16 ± 0.06

5. Conclusions

On average, the abundance and diversity of microzooplankton in both seasons were high with abundant aloricate ciliates. The lowest abundance of microzooplankton in summer was that of the loricate ciliates whereas it was the heterotrophic dinoflagellates in winter. In this dynamic ecosystem, temperature plays an unclear role in microzooplankton distribution, and nutrients indirectly affected microzooplankton abundance and biomass as well. However, the impacts of temperature on microzooplankton grazing and phytoplankton growth rates were clear. They closely correlated in both seasons and in both layers, with significantly higher rates in summer and the surface waters. The feeding impact in summer was high (high m/μ_0), but decreased in winter (low m/μ_0) which may have been caused by a larger decrease of microzooplankton grazing in winter than of phytoplankton growth rates. Microzooplankton grazing could be assigned as responsible for the dynamics of the phytoplankton community, as well as the temperature in both seasons. The microzooplankton benefitted

more on the picophytoplankton than the large phytoplankton. However, the size-based grazing of microzooplankton needs further study.

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