

Plankton respiration in the northern South China Sea during summer and winter

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Abstract

Plankton respiration is an important part of the carbon cycle and significantly affects the balance of autotrophic assimilation and heterotrophic production in oceanic ecosystems. In the present study, respiration rates of the euphotic zone plankton community (CR_{eu}), size fractionated chlorophyll *a* concentration (Chl *a*), bacterial abundance (BAC), and dissolved oxygen concentration (DO) were investigated during winter and summer in the northern South China Sea (nSCS). The results show that there were obvious spatial and temporal variations in CR_{eu} in the nSCS (ranging from 0.03 to 1.10 $\mu\text{mol}/(\text{L}\cdot\text{h})$), CR_{eu} in winter ($(0.53\pm 0.27) \mu\text{mol}/(\text{L}\cdot\text{h})$) was two times higher than that in summer ($(0.26\pm 0.20) \mu\text{mol}/(\text{L}\cdot\text{h})$), and decreased gradually from the coastal zone to the open sea. The distribution of CR_{eu} was affected by coupled physical-chemical-biological processes, driven by monsoon events. The results also show that CR_{eu} was positively correlated with Chl *a*, BAC, and DO, and that BAC contributed the highest CR_{eu} variability. Furthermore, the results of the stepwise multiple linear regression suggest that bacteria and phytoplankton were the dominant factors in determining CR_{eu} ($R^2 = 0.82, p < 0.05$) in the nSCS. Based on this relationship, we estimated the integrated water column respiration rate (CR_{int}) within 100 m of the investigated area, and found that the relationship between the biomass of the plankton community and respiration may be nonlinear in the water column.

Key words: northern South China Sea, plankton community, respiration, phytoplankton, bacteria

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1 Introduction

Plankton respiration, the ability of planktonic organisms to consume oxygen and release CO_2 , is the key link to organic-inorganic transformation in oceanic ecosystems, as well as one of the most important aspect of studies of the carbon cycle. The total respiration of the marine ecosystem consumes up to 186 Gt/a organic carbon ($17.2 \text{ Pmol}/\text{a O}_2$), which is approximately equal to the oceanic gross primary production, and most of the organic carbon consumption is associated with plankton respiration (Williams and del Giorgio, 2005). Although plankton respiration exists throughout the water column, the respiration rate is usually higher in the upper layer where photosynthesis occurs and biological events are concentrated. It was estimated that the planktonic community respiration in the euphotic zone alone may be responsible for approximately 50% of the total organic carbon consumption in the open ocean (del Giorgio and Duarte, 2002).

The respiration of plankton communities is usually expressed as the consumption rate of dissolved oxygen. Plankton

respiration rates are mainly dependent on the biomass of plankton communities and their metabolic activities, which are controlled by environmental factors such as temperature, nutrients, and dissolved organic carbon (Williams and del Giorgio, 2005). Temperature is a critical factor for controlling the metabolic rate of plankton communities, and therefore, on a global scale, the respiration of plankton communities increases gradually from the polar regions to the tropical areas with increasing temperatures (Rivkin and Legendre, 2001; Garcia-Corral et al., 2017). The respiration of the plankton community in the Antarctic Ocean has been shown to be 14.1–52.8 $\text{mmol}/(\text{m}^2\cdot\text{d})$, while the mean value in a tropical area was 32.3–131.3 $\text{mmol}/(\text{m}^2\cdot\text{d})$ (Zhang, 1999). The variation in the respiration rate is significantly affected by the biomass dominant species in the plankton community, and therefore, heterotrophic bacteria, phytoplankton, or zooplankton probably control plankton respiration in the different ecosystems. In some productive coastal zones, community respiration rate has been shown to be positively correlated with phytoplankton biomass, where more than 60% of the change in

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respiration in the upper layer could be explained by changes in gross primary productivity (Pringault et al., 2009). However, in the oligotrophic open sea area, the oxygen consumption of heterotrophic bacteria usually contributed more than 50% of community respiration (Schwaerter et al., 1988; Rivkin and Legendre, 2001). Moreover, it was reported that zooplankton grazing was enhanced in a late spring bloom, and that plankton community respiration was also related to protozoan biomass to a certain degree (Ahrens and Peters, 1991; Chen et al., 2003). Ocean circulation and river input can carry a large quantity of nutrients and dissolved organic carbon that affect horizontal transportation or vertical movement, where violent fluctuations in nutrient concentration can significantly affect the biomass of plankton communities, thereby influencing community respiration rates. Therefore, a certain degree of coupling exists between plankton respiration and physical processes.

In comparison with photosynthesis, there are relatively few investigations of plankton community respiration in China's seas. Previous researchers have found that plankton community respiration at the Changjiang (Yangtze River) Estuary exhibited extremely wide distributions in characteristics that gradually decreased from the estuary to the open sea, and that plankton community respiration was positively correlated with bacterial abundance (Ning and Coudé, 1991). Li et al. (2002) combined apparent oxygen utilization and the range and thickness of an anoxic area to calculate the oxygen consumption of an anoxic area near the Changjiang Estuary, which was estimated to be approximately 1.59×10^6 t. Subsequent investigations in the East China Sea determined that the factors governing plankton community respiration in different trophic systems were distinct, where bacteria were found to be the main contributors of plankton community respiration in the mesotrophic system, protozoans were the dominant contributors of plankton community respiration in the oligotrophic system, and the influence of temperature on plankton community respiration was small (Chen et al., 2003). Research in the Taiwan Strait also verified that the correlation between plankton community respiration and chlorophyll *a* concentration in winter and summer was not significant, thereby indicating that phytoplankton was not the main contributor to community respiration rate (Huang et al., 2005). Wang et al. (2014) compared plankton community respiration and primary production in the Taiwan Strait and in the nSCS during summer, and reported the distribution patterns of autotrophic and heterotrophic regions. In the South China Sea, several studies have indicated that primary production exhibits significant seasonal variation and is coupled with monsoon-driven patterns of ocean circulation (Liu et al., 2002; Ning et al., 2004). However, research on seasonal variations in plankton community respiration in the South China Sea is lacking, and even less research has focused on the relationship between plankton community respiration and ecological factors here.

In the present study, we described distributions in the rates of plankton community respiration in the euphotic zone (CR_{eu}) during different monsoon seasons in the nSCS. We conducted a comprehensive observation of ecological factors, and *in situ* incubation measurements of CR_{eu} during two seasonal cruises (winter and summer). The relationships between CR_{eu} and ecological factors were also analyzed. This work aimed to provide basic data for studying the micro-ecology and carbon cycle of the nSCS, and help to understand the coupling between plankton communities and the environmental forces at the regional scale.

2 Materials and methods

2.1 Study area and sampling

Samples were collected during winter and summer of 2009 in the nSCS ($18^{\circ}30' - 23^{\circ}00'N$, $111^{\circ}00' - 117^{\circ}00'E$). The winter cruise was from 11 to 23 February 2009 and comprised 22 stations (two transects perpendicular to the coast line and two transects parallel to the coast line, Fig. 1). The summer cruise was from 12 to 23 August 2009, and also comprised 22 stations (same configuration as the winter cruise, Fig. 1). To understand the spatial variation of the different variables, the nSCS was categorized into the coastal zone (<50 m), continental shelf region (50–200 m), and open sea (>200 m) according to depth.

Samples of seawater were collected for the determination of temperature (*T*), dissolved oxygen concentration (DO), chlorophyll *a* concentration (Chl *a*), and bacterial abundance (BAC) using 5 dm³ Niskin bottles at the following depths: surface layer (0 m), 10 m, 25 m, 50 m, 100 m, 150 m, and 200 m. There were seven and five sample stations for measuring CR_{eu} in winter and summer, respectively. Sampling depths corresponded to light levels of 100%, 10%, and 1% of the surface irradiance. Water samples in each layer were pre-screened through 200 μ m mesh to remove larger zooplankton, and were then incubated in parallel.

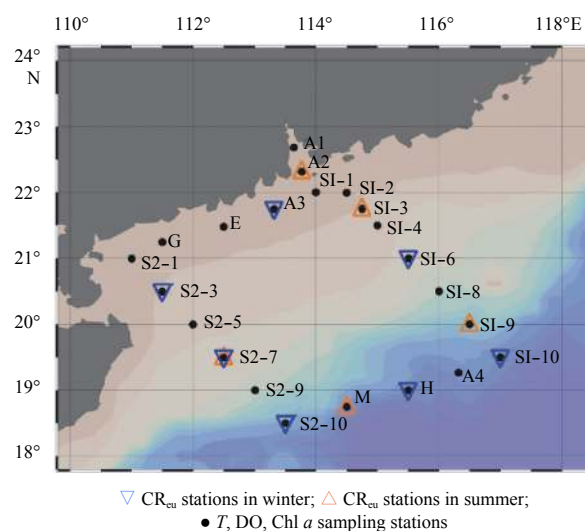


Fig. 1. Sampling stations (●) in the northern South China Sea (nSCS) during winter and summer of 2009.

2.2 Methods of measurement

2.2.1 Plankton community respiration

Plankton community respiration rates are usually represented by the difference in dissolved oxygen between initial and dark treatments (Robinson et al., 2002; Chen et al., 2003). In this study, plankton community respiration was determined by measuring the change in the rate of DO during a dark incubation period. Owing to limits imposed by the plan of the cruise, and by logistical support, only a very few stations were reached between midnight and dawn, and thus water samples for CR_{eu} were collected in the morning of each sampling day (6:00–12:00). First, each pre-screened water sample was aliquoted into two 250 cm³ acid-washed black glass bottles (black bottles were pre-sterilized after being immersed in diluted hydrochloric acid for 8 h and repeatedly washed (Pringault et al., 2009) until they overflowed). The bottles were then carefully sealed using a silica gel plug with

electrodes, paying careful attention to eliminating air bubbles in the bottles during this process. Next, the bottles were placed in a large incubation tank on deck to maintain the *in situ* temperature by pumping surface seawater into the tank (Ganf, 1974; Markager et al., 1992; Xu et al., 2006). As the study area included estuary and upwelling regions with higher activities of heterotrophic organisms, a 6 h incubation time was chosen to avoid the influence of the growth of microzooplankton and bacterioplankton. DO was determined in culture bottles using a six-channel oxygen meter with high-sensitivity SI1302 microcathode oxygen electrodes (Strathkelvin Instruments, Ltd, North Lanarkshire, Scotland), and probes were calibrated by iodometry before each incubation experiment according to the National Standards of the PRC (2008b). The dissolved oxygen meter recorded DO values once per second, and plankton community respiration rates were calculated by the differences in DO during the incubation period.

2.2.2 Measurements of environmental parameters

Sampling and procedures to determine *T*, salinity, and DO were conducted according to the method of China National Specifications Oceanographic Survey Standards (National Standards of the PRC, 2008a, b).

Bacterial abundance was analyzed by FCM (flowcytometry; FACSCalibur, Becton Dickinson Co., USA) according to Marie et al. (1999). A 5 cm³ subsample of water was fixed with paraformaldehyde (1%), quick-frozen in liquid nitrogen, and stored at -80°C in the laboratory. After thawing at room temperature, an aliquot (0.5 cm³) of the water sample was stained with SYBR Green-I in the dark for approximately 10 min before measurement by FCM (Marie et al., 1999). Fluorescence at >650 nm (FL3 instrument channel) was ascribed to Chl *a*. Fluorescence centered on (585±21) nm (FL2) was ascribed to phycoerythrin. Forward angle light scatter (FSC) and side angle light scatter (SSC) indicated the relative size and refractive properties of cells (Booth, 1988). The raw data were processed using CellQuest software (Becton Dickinson Co.) and were saved in a list mode file. Identification of three major groups of phPico—Syn, Pro and PEuk—was based on interactive analysis of bivariate cyto grams (Marie et al., 1999), using CellQuest software (Becton Dickinson Co.) as well.

Chl *a* was measured using the acetone extraction fluo-

rescence method (Holm-Hansen et al., 1965) using a Turner Designs fluorometer. For the determinations of size-fractionated Chl *a*, water samples were filtered through 20-μm mesh (for the retention of net-phytoplankton), a Nuclepore filter (pore size: 2.0 μm) for the retention of nano- and net-phytoplankton, and a Whatman GF/F filter for the retention of pico-, nano-, and net-plankton after incubation. After analyzing the content of each filter, the three fractions could be easily calculated.

2.2.3 Data analysis

The integrated value of CR_{eu}, DO, *T*, and Chl *a* were calculated according to Eq. (1):

$$Y = \sum_1^{n-1} \frac{(X_i + X_{i+1})}{2} \times (D_{i+1} - D_i), \quad (1)$$

where *Y* was the integrated value of each station, *n* was the number of sample layer, *X_i* was the parameter value at layer *i*, and *D_i* was the sample depth of layer *i*, 1 ≤ *i* ≤ *n*-1.

The integrated average value of each parameter was calculated by Eq. (2):

$$Y_{\text{avg}} = Y/Z_{\text{max}}, \quad (2)$$

where *Y_{avg}* was the integrated average value of each station, and *Z_{max}* was the maximum depth of the sample layer.

The regression model was calculated and analyzed using R-studio. Correlations between CR_{eu} and ecological factors were fitted using a type-II linear regression. In addition, a step-by-step regression method was used to conduct multiple linear regression analyses of the relationships between CR_{eu} and ecological factors.

3 Results

3.1 Hydrographical and biological variables in the nSCS

The integrated average values of environmental parameters measured within the water column (<200 m) in the nSCS are presented in Table 1. The results show that the distribution of environmental parameters in the nSCS exhibit significant seasonal

Table 1. Integrated averages of the rates of plankton community respiration (CR_{eu}) and related environmental parameters in the northern South China Sea (nSCS) during the winter and summer of 2009

Parameter	Winter			Summer			
	Coastal zone	Continental shelf	Open sea	Coastal zone	Continental shelf	Open sea	
<i>T</i> /°C	20.2±1.2 <i>n</i> =8	21.7±0.8 <i>n</i> =6	21.3±0.9 <i>n</i> =8	26.6±2.1 <i>n</i> =8	25.1±1.0 <i>n</i> =6	20.6±0.5 <i>n</i> =8	
DO/μmol·dm ⁻³	551.12±56.54 <i>n</i> =8	499.78±21.62 <i>n</i> =6	422.87±31.97 <i>n</i> =8	394.95±74.65 <i>n</i> =8	434.59±16.32 <i>n</i> =6	378.25±13.30 <i>n</i> =8	
Chl <i>a</i> /mg·m ⁻³	Sum	3.05±3.05 <i>n</i> =8	0.39±0.09 <i>n</i> =6	0.18±0.04 <i>n</i> =8	1.86±1.69 <i>n</i> =8	0.26±0.05 <i>n</i> =6	0.09±0.03 <i>n</i> =8
	Net	1.66±2.20 <i>n</i> =8	0.05±0.04 <i>n</i> =6	0.01±0.00 <i>n</i> =8	1.04±1.04 <i>n</i> =8	0.03±0.02 <i>n</i> =6	0.01±0.00 <i>n</i> =8
	Nano	0.86±0.72 <i>n</i> =8	0.10±0.05 <i>n</i> =6	0.03±0.01 <i>n</i> =8	0.58±0.74 <i>n</i> =8	0.06±0.03 <i>n</i> =6	0.02±0.00 <i>n</i> =8
Pico	0.53±0.36 <i>n</i> =8	0.24±0.07 <i>n</i> =6	0.14±0.04 <i>n</i> =8	0.25±0.17 <i>n</i> =8	0.18±0.04 <i>n</i> =6	0.07±0.02 <i>n</i> =8	
BAC/10 ⁶ cell·cm ⁻³	1.3±0.4 <i>n</i> =8	0.9±0.1 <i>n</i> =6	0.6±0.1 <i>n</i> =8	1.3±0.3 <i>n</i> =8	0.8±0.2 <i>n</i> =6	0.4±0.0 <i>n</i> =8	
CR _{eu} /μmol·L ⁻¹ ·h ⁻¹	0.82 <i>n</i> =1	0.63±0.15 <i>n</i> =3	0.36±0.15 <i>n</i> =3	0.67 <i>n</i> =1	0.35±0.01 <i>n</i> =2	0.09±0.04 <i>n</i> =2	

Note: *T* represents temperature, DO dissolved oxygen, BAC bacterial abundance, and Chl *a* chlorophyll *a* concentration; and these parameters were calculated in water column. CR_{eu} represents the rates of plankton community respiration, and was calculated in euphotic zone. Values are mean±standard deviation and *n* number of sample stations.

differences and spatial variation. In the winter, T , DO, Chl a and BAC were $(21.8 \pm 2.1)^\circ\text{C}$, $(484.55 \pm 64.52) \mu\text{mol}/\text{dm}^3$, $(0.73 \pm 1.58) \text{mg}/\text{m}^3$, and $(0.9 \pm 0.4) \times 10^6 \text{cell}/\text{cm}^3$, respectively. In terms of horizontal distribution, T increased with increasing distance from the coastline, while DO, Chl a and BAC gradually decreased from the coastal zone to the open sea. The contributions of net-, nano- and pico-fractions to Chl a were 49%, 27% and 24%, respectively. In terms of vertical distribution, T decreased with increasing water depth. Coastal water was uniform owing to vertical mixing, and thermocline intensity was weak in the nSCS (Fig. 2).

In comparison with winter, the entire study area was characterized by high T ($(24.8 \pm 4.8)^\circ\text{C}$), low DO ($(419.46 \pm 77.71) \mu\text{mol}/\text{dm}^3$), and low biomass (including Chl a ($(0.50 \pm 1.23) \text{mg}/\text{m}^3$) and BAC ($((0.8 \pm 0.4) \times 10^6 \text{cell}/\text{cm}^3)$) in summer. In terms of horizontal distribution, T , Chl a and BAC gradually decreased from the coastal zone to the open sea; however, the highest value of DO was encountered in the continental shelf area. Net-, nano and pico-fractions contributed 50%, 29% and 21% to Chl a , respectively, which was similar in comparison with that in winter. In terms of vertical distribution, the intensity of the thermocline in the summer was relatively strong. The thermocline in the coastal zone appeared at a depth of 20–30 m, while the thermocline of the open sea appeared at 50–75 m layer (Fig. 2). Both Chl a and BAC presented the phenomenon of subsurface maximum, significantly (Le et al., 2015; Zeng et al., 2017).

3.2 CR_{eu} in the northern South China Sea

3.2.1 Distribution of CR_{eu}

The distribution of CR_{eu} at depths with 100%, 10% and 1% of surface incident irradiance in winter and summer is shown in Fig. 3. The CR_{eu} in winter was significantly higher than that in summer. The CR_{eu} ranged between 0.10–1.10 $\mu\text{mol}/(\text{L}\cdot\text{h})$ and 0.03–0.67 $\mu\text{mol}/(\text{L}\cdot\text{h})$ in winter and summer, respectively. The mean value of CR_{eu} in winter was $(0.53 \pm 0.27) \mu\text{mol}/(\text{L}\cdot\text{h})$, which

was approximately two times the summer value ($(0.26 \pm 0.20) \mu\text{mol}/(\text{L}\cdot\text{h})$). The horizontal distribution of CR_{eu} at each layer was similar in winter and summer, both decreasing from the coastal zone to the open sea (Fig. 3 and Table 1). CR_{eu} in both the coastal zone and the continental shelf in winter remained high (0.82 and $(0.63 \pm 0.15) \mu\text{mol}/(\text{L}\cdot\text{h})$, respectively), while in the summer, the highest CR_{eu} ($0.67 \mu\text{mol}/(\text{L}\cdot\text{h})$) was encountered in the coastal zone.

In terms of vertical distribution, the CR_{eu} maximum mainly appeared at the subsurface layer in both seasons, with the exception of the coastal zones. From the surface to the bottom of the euphotic zone, the CR_{eu} values at each sample depth were (0.56 ± 0.26) , (0.56 ± 0.24) and $(0.47 \pm 0.33) \mu\text{mol}/(\text{L}\cdot\text{h})$, respectively, in winter. The CR_{eu} maximum in the coastal zone generally appeared at the surface, while in the continental shelf and open sea, it generally appeared at depths with light attenuated to 10% of the surface irradiance. In summer, CR_{eu} values at depths with 100%, 10% and 1% of surface incident irradiance were (0.19 ± 0.10) , (0.22 ± 0.15) and $(0.26 \pm 0.25) \mu\text{mol}/(\text{L}\cdot\text{h})$, respectively. The CR_{eu} maximum appeared at depths with light attenuated to 1% in the summer. It is worth noting that, Sta. A2 was not taken into consideration for this calculation, as only data for surface CR_{eu} was obtained during the experiment.

3.2.2 Relationships between CR_{eu} and ecological factors

By comparing CR_{eu} and ecological factors in the different regions of the nSCS (Table 1), it could be seen that CR_{eu} and ecological factors exhibited distinct differences between the different regions of the nSCS. In the winter, T was lower than in the summer, where the temperature difference between winter and summer was 1–6°C. However, for CR_{eu} , the values for DO, Chl a and BAC were higher in winter than in summer, and their distributions were relatively consistent with each other. In terms of horizontal distribution, the values for CR_{eu} , Chl a and BAC in the coastal zone were significantly higher than those in the contin-

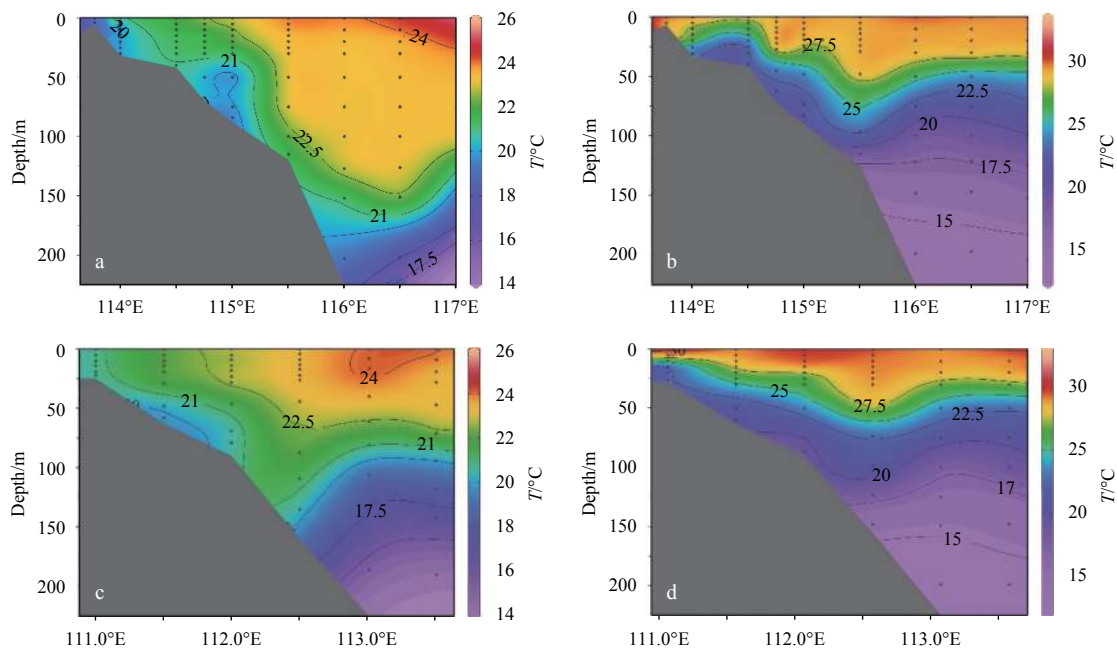


Fig. 2. Vertical distribution of temperature (T) in the northern South China Sea (nSCS) during the winter and summer of 2009. a and c. Stations sampled in winter, b and d. stations sampled in summer, a and b. Transect S1, and c and d. Transect S2.

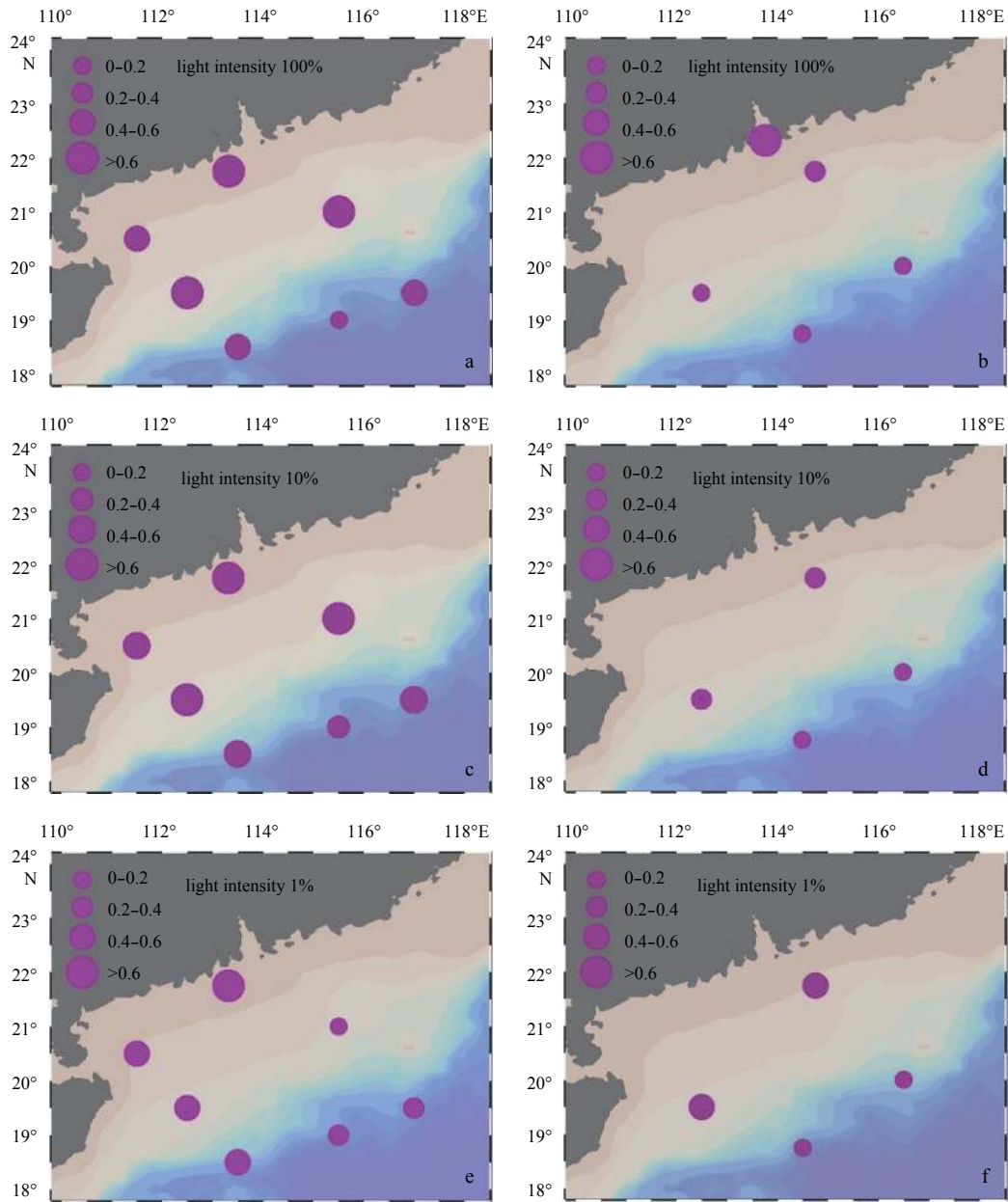


Fig. 3. Distribution of the rates of plankton community respiration (CR_{eu}) in the northern South China Sea (nSCS) during the winter and summer. a, c, e. CR_{eu} in winter and b, d, f. CR_{eu} in summer.

ental shelf and open sea. DO presented a progressively decreasing trend from the coastal zone and continental shelf to the open sea. Because thermal conductivity was higher in the continental shelf than in the ocean, T increased with increasing distance to the coastline in the winter, but gradually decreased with increasing distance to the coastline in the summer. From the aforementioned results, it can be seen that there is a high consistency between CR_{eu} and ecological factors in the different areas of the nSCS.

To understand the influence of the aforementioned ecological factors on CR_{eu} , linear regression was used to analyze relationships between CR_{eu} and T , DO, BAC, and Chl a in the euphotic zone (Fig. 4). The results show that biological factors (Chl a and BAC) were significantly positively correlated with CR_{eu} . The most significant correlation was observed between BAC and CR_{eu} , where BAC could explain 55% of the variability in CR_{eu} , and Chl a

could explain 36%. Of the abiotic factors, DO was significantly positively correlated with CR_{eu} ($R^2=0.45$, $p<0.05$), while T displayed a relatively weaker negative correlation with CR_{eu} ($R^2=0.20$, $p<0.05$).

4 Discussion

4.1 Variation in CR_{eu} and environmental control

In the South China Sea, in general, there is a significant concomitant relationship between physical, chemical and biological process at the large- and mesoscales (Ning et al., 2004), such as biological processes in the upper layers were greatly affected by monsoon-driven oceanic movements. In summer, estuary and coastal upwellings are induced by the prevailing southwest monsoon, but the upper water of the whole sea area generally presents as oligotrophic, with a lower plankton community biomass

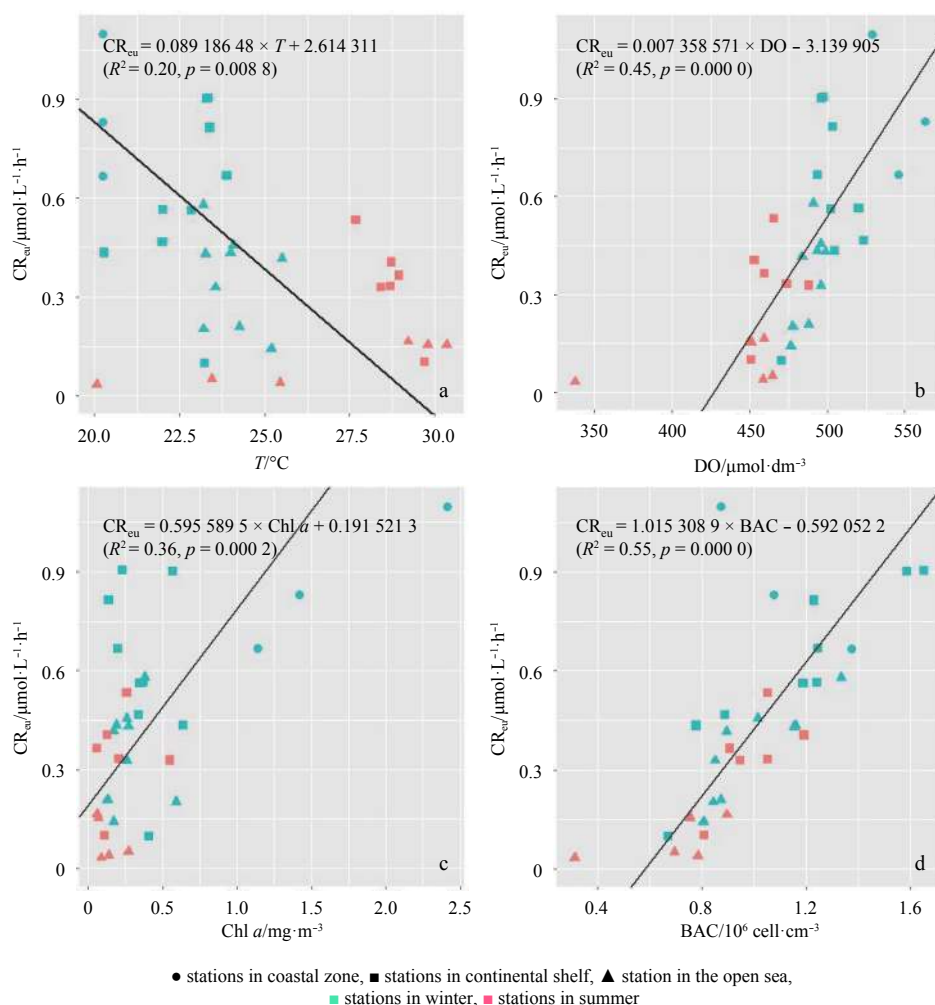


Fig. 4. Relationships between the rates of plankton community respiration (CR_{eu}) and temperature (T), dissolved oxygen (DO), chlorophyll a concentration ($\text{Chl } a$), and bacterial abundance (BAC) in the euphotic zone of the northern South China Sea.

owing to the influence of strong anti-cyclonic circulation on the basin scale (Liu et al., 2002). However, in the winter when the northeast monsoon prevails, the temperature decreases and the vertical mixing effect becomes strong. Coastal waters, driven by the northeast monsoon, move towards the southwest, and bring abundant nutrients into the South China Sea. Meanwhile, a large and strong cyclonic western boundary current forms in the western South China Sea, thereby causing an upwelling of lower layers, and thus supplements nutrients in the euphotic zone (Behrenfeld and Falkowski, 1997). Hence, the primary productivity in winter increases, which supports the higher standing stock of phytoplankton during this time. In addition, the dissolved organic matter, either released from the phytoplankton or from the process of zooplankton consuming phytoplankton, can be used by bacteria for growth and propagation to enhance bacterial abundance (Liu et al., 2007). High levels of nutrients would also lead to higher BAC, for bacteria can only effectively use dissolved organic matter when sufficient quantities of inorganic nutrients are present (Tupas and Koike, 1990; Cotner et al., 1997; Donachie et al., 2001). This study also demonstrates that the intensity of the thermocline was relatively weak in the winter (Fig. 2), and the biomass of the plankton community (both $\text{Chl } a$ ($(0.73 \pm 1.58) \text{ mg}/\text{m}^3$) and BAC ($(0.9 \pm 0.4) \times 10^6 \text{ cell}/\text{cm}^3$)) in the water column in winter was significantly higher than that in the summer

($(0.50 \pm 1.23) \text{ mg}/\text{m}^3$ and $(0.8 \pm 0.4) \times 10^6 \text{ cell}/\text{cm}^3$, respectively). In addition, owing to the dual influences of the infusion of eutrophic rivers and offshore upwelling, high levels of nutrients and a high plankton community biomass are commonly reported in the coastal zone as opposed to in the open sea (Smith, 2006; Liu et al., 2007; Legrand et al., 2015). Similarly, high values of both $\text{Chl } a$ and BAC encountered in the coastal zone were observed in the present study, along with a relatively high nutrient concentration, while the lowest values appeared in the open sea (Table 1).

The distribution of CR_{eu} , which also exhibited high temporal and spatial variability in the nSCS, was consistent with data for $\text{Chl } a$ and BAC . Seasonally, CR_{eu} was substantially higher in the winter ($(0.53 \pm 0.27) \mu\text{mol}/(\text{L}\cdot\text{h})$) than in summer ($(0.26 \pm 0.20) \mu\text{mol}/(\text{L}\cdot\text{h})$). In terms of horizontal distribution, the CR_{eu} observed in the coastal zone and continental shelf ((0.82 ± 0.20) and $(0.50 \pm 0.25) \mu\text{mol}/(\text{L}\cdot\text{h})$, respectively) were quite higher than that observed in the open sea ($(0.25 \pm 0.17) \mu\text{mol}/(\text{L}\cdot\text{h})$). The highest CR_{eu} was observed in the continental shelf during winter, while it was observed in the coastal zone during summer. In terms of vertical distribution, the highest CR_{eu} occurred in the layers where the $\text{Chl } a$ and BAC maxima appeared. Previous studies indicate that plankton respiration is positively correlated with the biomass of the plankton community (Robinson et al., 2002; Chen et al., 2003). However, as the composition and biomass of the

plankton community change concomitantly with the nutritional conditions and physicochemical environment, there is also a change in the respiration rate. In the East China Sea, bacteria were shown to be the main contributor of plankton respiration when nitrate concentrations were greater than 0.3 mmol/m³; however, when nitrate concentration was not greater than 0.3 mmol/m³, protozoans governed the respiration of the plankton community (Chen et al., 2003). In addition, a study on plankton respiration in the eastern Atlantic found that BAC and Chl *a* could explain the variability in the respiration of the plankton community by 70% and 61%, respectively (Robinson et al., 2002). In comparison with the aforementioned ocean regions, nutrients in the nSCS were relatively abundant, and the nitrate concentration at most stations was greater than 0.3 mmol/m³. Thus, it is unlikely that phytoplankton and bacterial biomass decreased, and that protozoans became the major component of plankton respiration as a result of nutrient limitation. The results of the present study indicate that CR_{eu} in the nSCS was significantly and positively correlated with BAC and Chl *a*, where Chl *a* could explain 36% of the variability in CR_{eu}, and BAC could explain 55% of the variability in CR_{eu}, suggesting that heterotrophic bacteria are the main contributors to plankton respiration in the nSCS, and that phytoplankton and heterotrophic bacteria affect the majority of CR_{eu} in a cooperative manner.

Our results also indicate that the abiotic factors *T* and DO were weakly correlated with CR_{eu}, with relatively lower *R*², when compared with the correlations between CR_{eu} and biotic factors. In the nSCS, CR_{eu} was negatively correlated with *T* (*R*²=0.20, *p*<0.05), which was inconsistent with the reports of a previous study conducted in the Chesapeake Bay, where the seasonal variation in CR_{eu} was positively correlated with temperature (Sampou and Kemp, 1994). Generally, plankton respiration demonstrates a significant sensitivity to fluctuations in temperature, where increasing temperature would accelerate the respiration rate (Ganf, 1974). In general, *Q*₁₀—the temperature sensitivity coefficient—of plankton respiration has been shown to be approximately 2.4 (Jankowski et al., 2014). In other words, with every 10°C increase in temperature, plankton respiration would also increase 2.4 times the original value. The temperature-dependent nature of plankton respiration has also been demonstrated in the North Atlantic Ocean Gyre (García-Corral et al., 2014). However, the respiration rate of the plankton community in this case was also controlled by the biomass of the plankton community (García-Corral et al., 2014), where this was mainly dependent on nutrient level and the concentration of dissolved organic carbon. In the nSCS, the increasing temperature would enhance the thermocline, thereby preventing the high-nutrient water under the thermocline to be transported into the euphotic zone, which restrains the growth of phytoplankton. Therefore, increased temperature indirectly reduces primary production in the water, and consequently lowers the biomass of phytoplankton and bacteria (Liu et al., 2007; Le et al., 2015; Hao et al., 2016), thereby decreasing the respiration of the plankton community. According to the results of the present study, we believe that in the nSCS, the effect of biomass on CR_{eu} is more pronounced than temperature. This could be the main reason for the negative correlation between CR_{eu} and *T* observed in the nSCS. In addition, the CR_{eu} in the nSCS was positively correlated with DO (*R*² = 0.45, *p*<0.05). The results of a previously published study indicated that in waters with relatively abundant levels of nutrients, low levels of DO (31.25–62.50 μmol/dm³) would limit the respiration of the plankton community, and thus the influence of DO above the limited value on respiration was not very significant (Sam-

pou and Kemp, 1994). In the present study, the minimum values of DO in winter and summer in the nSCS were 286.07 μmol/dm³ and 177.55 μmol/dm³, respectively, which were both substantially higher than the DO concentration that is considered to be limiting in plankton community respiration. Thus, the DO in the study area would not impose a restriction on CR_{eu}. The positive correlation observed between DO and CR_{eu} could be a result of the following scenarios: (1) DO increased with increasing primary productivity, where approximately 10% of the primary productivity was released in the form of soluble inorganic carbon, thereby accelerating the growth of bacteria; (2) DO was generally positively correlated with phytoplankton biomass, which was also the main contributor of respiration under conditions of darkness (Markager et al., 1992; Zheng et al., 1992). Therefore, taken together, the aforementioned information indicates that abiotic factors do not directly influence the variability of CR_{eu} in a significant manner, but they mainly exert indirect effects on the variability of CR_{eu} via their effects on biotic factors.

4.2 Comparisons with previous studies

In comparison with the published findings regarding respiration in subtropical ocean waters, the distribution of CR_{eu} in the nSCS presented consistency in a general trend, and also preserved the peculiarity of the investigated area (Table 2). On one hand, the CR_{eu} in the study area decreased sharply from the coastal zone to the open sea, which was consistent with trends of plankton respiration gradually decreasing from the inner to the outer southeastern continental shelf in the USA (Pomeroy et al., 2000) and the continental shelf regions of the Mediterranean and the East China Sea (Le Ferla et al., 2006; Chen et al., 2003). Affected by factors such as the input of terrestrial organic matter and near shore upwelling, nutrients in the coastal zone and the continental shelf are relatively rich, and effectively support the high plankton community biomass observed in these regions, which causes the relatively higher respiration of plankton communities in the coastal zone and inner continental shelf (Iriarte et al., 1991; Chen et al., 2003). On the other hand, plankton community respiration in the winter in the nSCS was significantly higher than that in the summer, in contrast to the findings of a higher-latitude continental shelf near Georgia, USA (Jiang et al., 2010). Bearing in mind the *Q*₁₀ value of plankton (2.4) (Jankowski et al., 2014), the temperature difference between winter and summer in the continental shelf of Georgia was between 10–20°C (which exerted a significant influence on CR_{eu}), while the temperature difference between winter and summer in the present study was approximately 1–6°C, and appears to have had little influence on the respiration of the plankton community.

A comparison between the CR_{eu} in the nSCS and that of open sea regions of similar latitudes can be seen in Table 2. This comparison shows that the CR_{eu} in the nSCS in summer was higher than the values observed in oligotrophic regions (e.g., Central North Pacific Ocean Gyre, North Atlantic Subtropical Gyre, Eastern Tropical Atlantic Gyre) (Williams and Purdie, 1991; González et al., 2001; Robinson et al., 2002), and was slightly lower than that in the open sea areas of upwelling with relatively abundant nutrients (North West African Upwelling) (Robinson et al., 2002).

It is also important to note that variations in sampling and incubation time could lead to slight differences in the resulting measurements of plankton respiration. As aforementioned, it is ideal to collect water samples before dawn to ensure consistency between metabolic level and the circadian rhythm of plankton communities (Gasol et al., 1998). However, some studies have indicated that the activities of bacteria and the abundance of het-

Table 2. Comparison of rate of plankton community respiration (CR_{eu}) in the euphotic zones of subtropical oceans

Region	Season	$T/^\circ C$	CR_{eu} (calculated by O_2)/		Reference
			$mmol \cdot m^{-3} \cdot d^{-1}$	$mmol \cdot m^{-2} \cdot d^{-1}$	
South-eastern USA continental shelf (28.0°–34.0°N, 78.0°–83.0°W)					
Inner shelf	winter	ND	26.4	ND	Pomeroy et al. (2000)
Middle shelf	winter	ND	16.8	ND	Pomeroy et al. (2000)
At the edge of the Gulf Stream	winter	ND	7.2	ND	Pomeroy et al. (2000)
Continental shelf off Georgia, USA (30.8°–32.2°N, 79.5°–81.5°W)	winter	10.0–30.0	0.3–3.3	ND	Jiang et al. (2010)
nSCS (18.5°–22.0°N, 111.0°–117.0°E)	winter	20.2–25.5	4.6–19.6	548	this study
South-eastern USA continental shelf (28.0°–34.0°N, 78.0°–83.0°W)					
Inner shelf	summer	ND	22.8	ND	Pomeroy et al. (2000)
Middle shelf	summer	ND	31.2	ND	Pomeroy et al. (2000)
At the edge of the Gulf Stream	summer	ND	24	ND	Pomeroy et al. (2000)
CNPO (Central North Pacific Ocean Gyre; 28.0°–29.0°N, 154.0°–155.0°W)	summer	24.9–25.3	0.1–1.6	53	Williams and Purdie (1991)
NAS (North Atlantic Subtropical Gyre; 28.0°–38.0°N, 38.0°–18.0°W)	summer	20	ND	142	González et al. (2001)
ETRA (Eastern Tropical Atlantic Gyre; 15.5°S–14.2°N)	summer	22.2–28.9	ND	159	Robinson et al. (2002)
NWAF (North West African Upwelling; 14.9°–21.2°N)	summer	22.6	ND	211	Robinson et al. (2002)
nSCS (18.5°–22.0°N, 111.0°–117.0°E)	summer	25.5–30.3	1.7–16.0	208	this study

Note: Data are represented as means and ranges. ND means no data.

erotrophic flagellates were the highest at midnight or during early morning (Kuipers et al., 2000). Therefore, collecting water samples before dawn could result in the estimated respiration rate of plankton communities to seem high, while collecting water samples during the daytime could result in an underestimation. Thus, in the present study, the later collection times may have resulted in an underestimation of the respiration rate. Likewise, differences in incubation may also result in differences in respiration rate estimation. In general, the incubation time is 24 h. Under the assumption that the respiration rate increases linearly with time, a 24 h incubation is ideal to record the complete diurnal variation of plankton community respiration. However, Bender et al. (1999) points out that the accelerated growth, grazing, and death of microzooplankton in the absence of large grazers during the incubation period in bottles may result in underestimations of plankton community respiration rates, and that using short incubation times can, at least partially, alleviate this problem. In the present study, the incubation time was 6 h, which could have caused a slight overestimation of CR_{eu} , even though it weakened the bottle effect. Despite the sampling and incubation times in the present study, the differences in CR_{eu} between this study and other similar studies are not substantial, and trends in the large-scale distribution of CR_{eu} tendency are comparable. Therefore, we suggest that the error from methodological variation did not exert a significant influence on large-

scale seasonal variations in respiration and spatial tendencies.

4.3 Possibility of estimating respiration rate by environmental factors

The correlations between plankton community respiration and environmental parameters have been previously used to estimate plankton community respiration, either partially or entirely (Jensen et al., 1990; Chen et al., 2003). In addition, it has been shown that the correlation between plankton community respiration and a single parameter was significantly lower than the correlation between plankton community respiration and multiple parameters (Chen et al., 2003). In the present study, the biomass, physical environment, and community structure were considered in the multiple linear regression (since DO in the investigated area was much higher than the DO concentration limiting plankton respiration, it was not considered here). As indicated in Table 3, in the regression group with two variables, the combination of BAC and Chl *a* was the closest predictor of CR_{eu} , and could explain 82% of the variation in CR_{eu} , indicating that bacteria and chlorophyll were the main factors influencing plankton respiration in the nSCS. After adding the variable of temperature, and using the size-fractionated chlorophyll concentration instead of Chl *a*, R^2 did not significantly increased, indicating that temperature and community structure have little predictive effect on CR_{eu} . Thus, the combination of BAC and Chl *a*

Table 3. Results of multiple linear regression between CR_{eu} and related factors in the northern South China Sea (nSCS)

Factor		Function	R^2
T	Chl <i>a</i>	$CR_{eu} = -0.0159 \times T + 0.30018 \times Chl\ a + 0.69598$	0.38
T	BAC	$CR_{eu} = -0.032013 \times T + 0.70614 \times BAC + 0.503764$	0.67
BAC	Chl <i>a</i>	$CR_{eu} = 0.69414 \times BAC + 0.31192 \times Chl\ a - 0.39158$	0.82
T	BAC Chl <i>a</i>	$CR_{eu} = -0.010008 \times T + 0.686117 \times BAC + 0.276569 \times Chl\ a - 0.123779$	0.83
T	BAC Net	$CR_{eu} = -0.018753 \times T + 0.707924 \times BAC + 1.144718 \times Net + 0.106085$	0.86
T	BAC Net Nano	$CR_{eu} = -0.01309 \times T + 0.803224 \times BAC - 0.331087 \times Net + 1.043628 \times Nano - 0.140226$	0.87
T	BAC Net Nano Pico	$CR_{eu} = -0.021476 \times T + 0.82322 \times BAC - 0.411904 \times Net + 1.342398 \times Nano - 0.291136 \times Pico + 0.095266$	0.89

Note: Net, Nano and Pico represent the concentration of net-Chl, nano-Chl and pico-Chl, respectively. The units of CR_{eu} , T , BAC, Chl *a*, Net, Nano, and Pico are $\mu mol/(L \cdot h)$, $^\circ C$, $10^6\ cell/mL^3$, mg/m^3 , mg/m^3 , mg/m^3 , and mg/m^3 , respectively.

could be the most effective predictor of the distribution of CR_{eu} in the nSCS.

Based on the multiple linear regression equation of CR_{eu} , BAC and Chl *a*, and the measurements of Chl *a* and BAC in the water column at each station, plankton respiration in the water column (CR_{int}) within 100 m of the study area was estimated. The average CR_{int} in winter and summer in the nSCS was (17.32 ± 20.27) $mmol/(m^3 \cdot d)$ and (11.81 ± 12.18) $mmol/(m^3 \cdot d)$, respectively, which is consistent with the distribution of CR_{eu} . However, CR_{int} below the euphotic zone of the open ocean—estimated from the multiple linear regression equation of CR_{eu} , BAC and Chl *a*—contained negative values. The reason might be the inconsistencies in plankton biomass and respiration inside and outside the euphotic zone. The changes in bacterial metabolism, which was caused by the sharply decreasing temperature from the upper euphotic zone to deeper layers, might have resulted in the above-mentioned inconsistency. It has been found in controlled experiments on respiration that when the controlled-environmental temperature is 5°C lower than the *in situ* temperature, plankton respiration dropped by about 20%–50%, and bacterial respiration also presented significant temperature dependency (Wang, 2014). Our observations indicated that the average temperature in the 100–200 m deep waters was 7.6°C lower than the average temperature in the waters above 100 m. The rapid drop in temperature possibly caused the decrease in bacterial metabolism below the euphotic zone, thereby causing a greater decrease in plankton respiration. Moreover, there were differences in the quality and quantity of organic substances available for consumption by the microbial communities in the upper and deeper layers of the ocean (Jiao et al., 2014). The dissolved organic matter brought from the outside and the dissolved organic carbon generated by primary productivity mainly exist in the euphotic zone, and nutrient concentration in the euphotic zone is relatively high and easily utilized by bacteria; below the euphotic zone, the growth of bacteria is slow because of the inefficient degradation of dissolved organic matter and the low availability of nutrient substances. Hence, owing to the changes in conditions such as temperature and nutrient availability in the water column, there may have been a nonlinear relationship between plankton biomass and respiration outside the euphotic zone. Using the empirical relationship obtained from the parameters in the euphotic zone may lead to an overestimation of plankton respiration in the water column.

5 Conclusions

In this study, we conclude that plankton respiration in the euphotic zone of the nSCS is higher in winter than in summer, and respiration in the coastal zone is higher than that in the open sea, thereby exhibiting significant seasonal and spatial variations. Plankton respiration was positively correlated with plankton community biomass, indicating a close coupling effect between plankton respiration and primary productivity, which is also driven by monsoon-circulation processes. Similar to in other oligotrophic ocean systems, heterotrophic bacteria are the main contributor to respiration. Because respiration is controlled by the biomass of plankton communities, temperature is not a dominant factor in the upper layer of the nSCS, and the influence of temperature on seasonal variations in plankton respiration is lower than that of nutrient availability. In addition, we have demonstrated that there is a significant error in estimating plankton respiration throughout the water column when using the empirical relationship between plankton respiration and ecological factors in the euphotic zone. This indicates that the relationship

between plankton respiration and ecological factors may change as the depth changes. In future, the respiration of plankton communities throughout the water column and possible substitute factors should be considered when making estimations. More importantly, it is necessary to integrate observations of primary production and plankton respiration to describe variations in net community production to further elucidate the details of the organic carbon budget in the South China Sea.

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