The influence of episodic flooding on a pelagic ecosystem in the East China Sea

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ABSTRACT

This study was designed to determine the effects of flooding on a pelagic ecosystem in the East China Sea (ECS), with a focus on plankton activity and plankton community respiration (CR). In July 2010, a flood occurred in the Changjiang River. As a comparison, a variety of abiotic and biotic parameters were monitored both during this flooding event, as well as during a non-flooding period (July 2009). During the flood, the Changjiang diluted water (CDW) zone covered almost two thirds of the ECS, which was approximately six times the area covered during the non-flooding period. The mean nitrate concentration was 3-fold higher during the 2010 flood (6.2 vs. 2.0 μM in 2009). CR was also higher in the 2010 flood: 105.6 mg C m^{-3} d^{-1} vs. only 73.2 mg C m^{-3} d^{-1} in 2009. The higher CR in 2010 could be attributed to phytoplankton respiration, especially at stations in the CDW zone that were not previously characterized by low sea surface salinity in 2009. In addition, Zooplankton (>330 μm) were another important component contributing to the high CR rate observed during the 2010 flood, a period also associated with a significant degree of fCO_2 drawdown. These results collectively suggest that the 2010 flood had a significant effect on the carbon balance in the ECS; this effect might become more pronounced in the future, as extreme rainfall and flooding events are predicted to increase in both frequency and magnitude due to climate change.

Keywords: Bacteria; Dissolved inorganic nutrients; East China Sea; Flooding; Freshwater discharge; Phytoplankton; Plankton community respiration; Yangtze River

1 INTRODUCTION

Riverine run-off has a profound effect on the production and consumption of organic carbon in coastal ecosystems (e.g., Dagg et al., 2004; Hedges et al., 1997 and references therein). Accompanying freshwater discharge, a substantial amount of dissolved inorganic nutrients (DIN) is routinely dispensed into coastal regions, thus enhancing primary productivity (PP; e.g., Dagg et al., 2004; Nixon et al., 1996). In addition, a large quantity of particulate and dissolved organic matter is discharged via riverine input (e.g., Wang et al., 2012), and high rates of microbial metabolism associated with this discharge have been observed in marine environments (e.g., Hedges et al., 1994; Malone and Ducklow, 1990). River plumes can extend for hundreds of kilometers along the continental shelf, as in the case of the Amazon River (e.g., Müller-Karger et al., 1988).

Overall, the effects of river plumes on coastal ecosystems are strongly related to the volume of the freshwater discharged (e.g., Chen et al., 2009; Dagg et al., 2004; Tian et al., 1993). Thus, understanding how freshwater discharge influences coastal ecological processes is an important factor in modeling global carbon cycling in the ocean. Under projected climate change scenarios, such heavy freshwater discharge events are predicted to become even more pronounced in the near future because of the dramatic frequency and magnitude increases in extreme rainfall events and floods predicted to occur throughout the world in the coming decades (Christensen and

Christensen, 2003; Knox, 1993; Milly et al., 2002; Palmer and Ralsanen, 2002).

The East China Sea (ECS) has an approximate area of 0.5 x 10^6 km^2 and is the largest marginal sea in the Western Pacific. A large amount of freshwater (956 km^3 yr^{-1}) is discharged annually into the ECS, notably by the Changjiang (a.k.a Yangtze) River, which is the fifth largest river in the world in terms of volume discharge (Liu et al., 2010). On average, the maximum amount of discharge occurs in July, and mean monthly discharge has ranged from 33,955 to 40,943 m^3 s^{-1} in years of normal weather during the past decade (Gong et al., 2011; Xu and Milliman, 2009). After having been discharged into the ECS, freshwater mixes with seawater to form the Changjiang diluted water (CDW) zone, the sea surface salinity (SSS) of which is ≤ 31 (e.g., Beardsley et al., 1985; Gong et al., 1996). In the CDW, especially in summer, the regional carbon balance is regulated by high rates of plankton community respiration (CR) and PP (Chen et al., 2006; Gong et al., 2003). The rates of CR are positively associated with riverine flow rates (Chen et al., 2009).

In July 2010, a large flood occurred in the Changjiang River (Gong et al., 2011). This event provided an opportunity to understand how flooding affects the ECS shelf ecosystem. Comparative analyses were conducted in which number of physical, chemical, and biological parameters (notably CR) were measured not only during this flood, but also during a period (July 2009) when the riverine flow was relatively low. The main objective of this study was to reveal the effects of riverine input, particularly the associated DIN, on the plankton activities (e.g., phytoplankton, heterotrophic bacteria, and zooplankton (>330 μm)) and how they impact on CR in the ECS between periods of non-flooding and flooding. In addition, the relationship between CR and the fugacity of CO_2 (fCO_2) was examined to determine the contribution of the plankton communities to variations in fCO_2 in periods of non-flooding and flooding.

2 MATERIALS AND METHODS

2.1 Study area and sampling protocol. This study is part of the Long-term Observation and Research of the East China Sea (LORECS) program. Samples were collected from the ECS in the summers of 2009 (June 29 to July 13) and 2010 (July 6 to 18) during two cruises on the *R/V Ocean Researcher I*. The sample stations were located throughout the ECS shelf region (Fig. 1). In July 2010, the discharge from the Changjiang River reached 60,527 $m^3 s^{-1}$, which was significantly higher than in the non-flooding year of 2009 (Gong et al., 2011; Yu et al., 2009). Water samples were collected using Teflon-coated Go-Flo bottles (20 L, General Oceanics Inc., USA) mounted on a General Oceanic Rosette® assembly (Model 1015, General Oceanics Inc.). At each station, six to nine samples were taken at depths of 3 to 50 m, depending on the depth of the water column. Sub-samples were taken for immediate analysis of DIN, chlorophyll *a* (Chl *a*), and bacterial abundance. Plankton CR was also measured on board from seawater sub-samples. The methods used to collect the hydrographic data and analyze the aforementioned response variables followed Chen et al. (2006; 2013; 2009). Descriptions of the methods used are presented briefly in the following sections. It should also be noted that portions of these results were published by Chung et al. (2014) and Gong et al. (2011).

2.2 **Physical and chemical hydrographics.** Seawater temperature, salinity, and transparency were recorded throughout the water column using a SeaBird CTD (USA). Photosynthetically active radiation (PAR) was measured throughout the water column using an irradiance sensor (4π; QSP-200L). The depth of the euphotic zone (Z_E) was taken as the penetration depth of 1% of the surface light. The mixed layer depth (M_D) was based on the potential density criterion of 0.125 units (Levitus, 1982).

A custom-made flow-injection analyzer was used for dissolved inorganic nutrient (e.g., nitrate, phosphate, and silicate) analysis (Gong et al., 2003). Integrated values for the nitrates and other variables assessed in the water column above the Z_E were estimated using the trapezoidal method, in which depth-weighted means are computed from vertical profiles and then multiplied by Z_E (e.g., Smith and Kemp, 1995). The average nitrate concentration over Z_E was calculated from the vertically integrated value divided by Z_E. This calculation was adopted to determine the values of the other measured variables.

The fugacity of CO_2 (fCO_2) in the surface waters was calculated from dissolved inorganic carbon (DIC) and total alkalinity (TA) data using a program designed by Lewis and Wallace

(1998). For details of the TA and DIC measurements, please see Chou et al. (2007).

2.3 Biological variables. The water samples taken for Chl *a* analysis were immediately filtered through GF/F filter paper (Whatman, 47 mm) and stored in liquid nitrogen. The Chl *a* retained on the GF/F filters was quantified fluorometrically (Turner Design 10-AU-005; Parsons et al., 1984). When applicable, Chl *a* was converted to carbon units using a C:Chl ratio of 52.9, which was previously estimated from shelf waters of the ECS (Chang et al., 2003). Surfer 11 (Golden Software, Inc.) was used to estimate total Chl *a* content integrated over Z_E for both the ECS and the CDW (please see below for details.). This estimation was also adopted to determine the total quantities for heterotrophic bacteria and zooplankton across Z_E. To compare, total plankton biomass was the summed biomass of phytoplankton, bacterioplankton, and zooplankton over the Z_E.

Heterotrophic bacteria samples were fixed in paraformaldehyde at a final concentration of 0.2% (w/v) in the dark for 15 min. They were then immediately frozen in liquid nitrogen and kept at -80°C prior to analysis. The heterotrophic bacteria were stained with the nucleic acid-specific dye SYBR® Green I (emission = 530 ± 30 nm) at a 10^4-fold diluted commercial solution (Molecular Probes, Oregon, USA; (Liu et al., 2002). They were then identified and enumerated using a flow cytometer (FACSAria, Becton-Dickinson, New Jersey, USA). Known numbers of fluorescent beads (TruCOUNT Tubes, Becton-Dickinson) were simultaneously used to calculate the original cell abundance in each sample. Bacterial abundance was converted to carbon units using a conversion factor of 20×10^{-15} g C $cell^{-1}$ (Hobbie et al., 1977; Lee and Fuhrman, 1987).

Zooplankton samples were collected across the whole water column (ranging from 20 to 198 m, depending on the station), at selected stations using a 330-μm mesh net with a 160-cm diameter opening. Upon retrieval of the net, the contents of the cod-end were immediately preserved in 10% buffered formalin. Zooplankton samples were digitized to extract size information (i.e., body width and length) using the ZooScan integrated system, and the size information was used to calculate the ellipsoidal bio-volume of zooplankton (Garcia-Comas, 2010). The biomass (carbon units) of zooplankton was then calculated using the estimated bio-volume following equations of Alcaraz et al. (2003). To estimate the biomass over Z_E, the total biomass of zooplankton over the whole water column was multiplied by the fraction of "Z_E relative to depth of the water column" at all stations.

The plankton CR, which was calculated as the decrease in dissolved oxygen (O_2) during dark incubation (Gaarder and Grann, 1927), was measured in samples collected from most stations, with two initial and two dark treatment samples taken from 4-6 depths (depth intervals of 3, 5, 10, 15, 20, and/or 25 m depending on the depth of the water column) within the Z_E at each station. The treatment samples were siphoned into 350-mL biological oxygen demand (BOD) bottles and incubated for 24 hrs in a dark chamber filled with running surface water.

Maximum temperature changes were 1.33 ± 0.81 and 2.70 ± 1.43ºC (mean±SD) during each incubation in 2009 and 2010, respectively. The concentration of O_2 was measured by a direct spectrophotometry method (Pai et al., 1993). The precision of this method was calculated as the root-mean square of the difference between the duplicate samples and was found to be 0.02 and 0.03 mg L^{-1} in 2009 and 2010, respectively. The precision for initial samples in both periods was < 0.01 mg L^{-1}. The difference in O_2 concentration between the initial and the dark treatment was used to compute the CR. A respiration quotient of 1 was assumed in order to convert the respiration from oxygen units to carbon units (Hopkinson Jr., 1985; Parsons et al., 1984).

3 RESULTS and DISCUSSION

3.1 Comparison of hydrographic patterns between flooding and non-flooding periods

In 2010, the Changjiang River began to flood in late May or early June. The mean monthly water discharge was 60,527 m^3 s^{-1}, and the suggested discharge rate for flooding was 4-6 x 10^4 m^3 s^{-1}, making it the largest recorded flooding of the Changjiang River over the last decade (http://yu-zhu.vicp.net/). This rate was almost two times larger than that recorded in the non-flooding period in July 2009 (33,955 m^3 s^{-1}; (Gong et al., 2011; Yu et al., 2009). During the flood, a tremendous quantity of freshwater was delivered into the ECS, and the low salinity of the sea surface (SSS ≤ 31) covered almost two thirds of the continental shelf (Fig. 1b). The SSS in the ECS during the 2010 flood was significantly lower than during the 2009 non-flooding survey period; the mean (± SD for this and all parameters discussed henceforth) values were 30.32 (± 3.60) and 32.62 (± 2.07), respectively (Table 1). During periods of high discharge from the river, particularly during the summer, the CDW zone is generally distributed within the 60-m isobath region between the latitudes of 27 and 32° N along the coast (e.g., Beardsley et al., 1985; Gong et al., 1996). During the 2010 flood, the CDW dispersed towards the south and east and reached as far as the 100-m isobath (Fig. 1b). The substantial quantity of freshwater discharged into the ECS is also reflected in the coverage area of the CDW (e.g., Gong et al., 2011); in the 2010 flood, the CDW area (111.7 x 10^3 km^2) was approximately six times larger than in the 2009 non-flooding period (19.0 x 10^3 km^2).

Although the mean SSS differed significantly between the flooding and non-flooding periods, there was no difference in the temperature of the sea surface (SST; Table 1). The mean values of SST in 2009 (26.8 ± 1.7) and 2010 (and 26.1 ± 2.2ºC) were within the range of the mean SST of the ECS in summer (Chen et al., 2009). The mixed layer depth (M_D) did not significantly vary between survey periods: 13.7 (± 7.3) m in 2009 and 11.3 (± 6.6) m in 2010 (Table 1). However, the average M_D was shallower than documented previously in the summer in the ECS (range: from 16.8 to 28.2 m; Chen et al., 2009). The euphotic depth (Z_E) was not significantly deeper in 2009 (38.9 ± 36.4 m) than in 2010 (33.4 ± 17.3 m; Table 1). Regarding the Z_E, the average Z_E in the ECS was also shallower than in a previous study conducted during the summer (Chen et al., 2009). The shallower Z_E could have been indirectly influenced by the transmittance of the seawater. The average transparency in summer in the ECS over the 2003-2008 period was 81.9% (C.C. Chen, unpublished data). The average transparency values of the ECS in 2009 and 2010 were 76.7% and 80.5%, respectively (Table 1). The average transparency for the CDW zone was lower in 2009 (70.0%) and higher high in 2010 (78.4%) compared to the previous 6-year average (72.7%; C.C. Chen, unpublished data). This might also explain why Z_E in the CDW in 2009 was only 16.8 m (Table 1).

These findings suggest that the growth of phytoplankton might be limited by the availability of light, especially in the CDW zone in 2009. Generally, the transparency of the coastal ocean might be low during flooding periods due to riverine discharge of terrestrial matter. A low transparency value was documented in June 2003 in the ECS, during which the CDW area was 43.1 x 10^3 km^2 (~40% of the CDW area of the 2010 flood; Chen et al., 2009), and the average transparency values for the ECS and the CDW were 70.9% and 66.0%, respectively (C.C. Chen, unpublished data). The average transparency in the CDW in 2010 (78.4%) was higher than the previous 6-year average (72.7%). This could be partially explained by the fact that most large particulates from terrestrial sources might have been confined to and precipitated in the coastal region, not in the expanded CDW region (e.g., Chung et al., 2012). Furthermore, it should also be noted that the 2010 sampling period was one month after the beginning of this flood. In estuarine and coastal regions, phytoplankton blooms normally occur within 2-3 weeks after a heavy rainfall event (e.g., Hsieh et al., 2012; Meng et al., 2016; Meng et al., 2015; Mulholland et al., 2009). Therefore, it is reasonable to speculate that plankton communities were in the late phase of succession in this flood event. The transparency during the 2010 sampling period might, then, have increased due to organic matter (particulate and dissolved) having been uptaken and transferred to higher trophic levels.

In general, a large quantity of dissolved inorganic nutrients is delivered from the Chinese coast to the ECS during the wet season (May to September; Chen et al., 2013; Chen et al., 2009; Gong et al., 1996). A high concentration of nitrates in the fluvial discharge of the Changjiang River was documented in the ECS during the 2010 flood. Furthermore, there was 1) a negative linear relationship between SSS and nitrate concentration ($r^2 = 0.37$, $p < 0.001$, n = 37), 2) a negative linear relationship between SSS and silicate concentration ($r^2 = 0.60$, $p < 0.001$, n = 37), and 3) no correlation between SSS and phosphate concentration. Nitrate concentration (Table 1) was significantly higher in the surface waters of the ECS in the 2010 (6.2 ± 9.8 μM) flood than in the 2009 non-flooding period (2.0 ± 5.3 μM), and similar nitrate concentration differences were perpetuated between sampling times over Z_E (data not shown). During the 2010 flood, the mean nitrate concentration, either in the surface water or averaged over $Z_{E,}$ was higher or comparable to that documented during periods of high riverine discharge in the ECS (Chen et al., 2009; Gong et al., 1996). Nitrate levels reached 37.6 μM in the surface water during the 2010 flood, and the highest nitrate concentrations were observed within the CDW (Fig. 1d).

The phosphate concentration in the surface water (Table 1) did not differ between the 2009 non-flooding period (0.13 ± 0.17 μM) and the 2010 flood (0.17 ± 0.30 μM), nor did it differ in the CDW zone between study years (0.23 and 0.13 μM, respectively). However, it should be noted that there was one station with extremely high phosphate concentration (1.71 μM) in the surface water in the CDW zone during the 2010 flood (Fig. 1f), during which the mean molar ratio of nitrate to phosphate (N/P) over the entire ECS was 22.3 ± 20.9. The high N/P molar ratio was even more pronounced in the CDW; it was higher than the Redfield ratio for N:P (i.e., 16) at 14 of the 20 stations and averaged 40.4 (± 22.6). This value was comparable to that of the CDW during high riverine flow periods in the ECS in summer (Chen et al., 2006). During the non-flooding period, the N/P molar ratio was lower than 16, with a mean value of 11.5 (± 20.8).

It has been suggested that phytoplankton growth might be regulated by the availability of nutrients, or the N/P ratio of the available nutrient pool, in the ECS (Gong et al., 1996; Harrison et al., 1990). The results of this study indicate that in the 2009 non-flooding period, phytoplankton biomass might have been regulated by the availability of dissolved inorganic nitrogen to a greater extent than it was during the 2010 flood. Phytoplankton biomass might have also been limited by nitrate and silicate levels in 2010. Based on nutrient levels and the N/P molar ratio, however, phytoplankton growth was more likely limited by phosphate, especially in the CDW zone during the 2010 flood (please refer to Sect. 3.2 for details.). Phytoplankton growth limited by different inorganic nutrients has been observed in estuaries and coastal regions, such as Chesapeake Bay in the United States (Fisher et al., 1992; Harding, 1994). In the ECS, phosphates have been frequently found as a factor limiting phytoplankton growth, especially in the CDW (Chen et al., 2004; Gong et al., 1996; Harrison et al., 1990).

3.2 Plankton activity associated with the Changjiang River flood

Following the discharge of fluvial nutrients into the ECS, phytoplankton are generally abundant in the CDW region. The Chl *a* concentration in the CDW even reached bloom criteria (> 20 mg Chl m^{-3}) in past years in the ECS (Chen et al., 2009; Chen et al., 2003). Surprisingly, the phytoplankton biomass was not as high as expected in this study, even though a high nitrate concentration was observed during the 2010 flood. The mean values of Chl *a* in the surface water of the ECS in 2009 and 2010 were 0.98 (± 1.52) and 1.26 (± 1.27) mg Chl m^{-3}, respectively (Table 1). However, these mean values were still at the high end of the Chl *a* concentration range normally documented in the ECS in the mid-summer through July/August period (Chen et al., 2009). In both periods, the phytoplankton biomass in the surface water was generally higher in the CDW than in other regions of the ECS (Fig. 1g and h). For example, in the 2010 flood, the maximum Chl *a* value reached 5.32 mg Chl m^{-3} in the CDW (Table 1; Fig. 1h). In the 2010 flood, the Chl *a* values were positively correlated with nitrate and silicate concentrations (all $p < 0.001$), but not phosphate concentrations ($p = 0.09$), in the surface water. The linear relationship between Chl *a* and phosphate values in the surface water, however, became significant ($p < 0.001$) if one outlier with a markedly high phosphate concentration (1.71 μM) was excluded from the analysis (Fig. 1f). In the 2009 non-flooding period, the Chl *a* concentration was significantly, positively, and linearly correlated with concentrations of all measured nutrients: nitrate, silicate, and phosphate ($p < 0.01$ in all cases).

The spatial distribution pattern of Chl *a* documented in this study was similar to that found in previous studies of the ECS (Gao and Song, 2005; Gong et al., 2011), and phytoplankton biomass in the surface water (Table 1), or averaged over Z_E (data not shown), did not differ significantly between 2009 and 2010. In the 2010 flood, primary production (PP) in the surface water was 62.1 (±33.8) mg C m^{-3} d^{-1}, comparable to values documented in the ECS in summer by (Chen et al., 2009). In contrast, the PP:Chl *a* value was higher in the 2010 flood (27.1 ± 17.2 mg C mg Chl^{-1} d^{-1}) compared to that documented value (19.7 ± 5.5 mg C mg Chl^{-1} d^{-1}) by Chen et al. (2009). Gong et al. (2011) estimated that over the past decade, the average rate of carbon fixation during flooding periods was about three times higher than during non-flooding periods, and the carbon fixation rate reached 176.0 x 10^3 tons C d^{-1} in the CDW during the 2010 flood (Gong et al., 2011).

In summer, heterotrophic bacterioplankton are generally more abundant in the CDW of the ECS than in other regions (Chen et al., 2006; Chen et al., 2009). Chen et al. (2006) suggested that the growth of bacteria along the coast might be stimulated by the substantial amount of organic matter derived from both autochthonous marine production and fluvial runoff. This spatial distribution pattern was also observed in 2009 and 2010. In the 2009 non-flooding period, the mean bacterial biomass in the surface water of the CDW was 77.5 (± 55.7) mg C m^{-3}, over 2-fold higher than in all other areas (31.0 ± 18.6 mg C m^{-3}). Their mean values in the 2010 flood were 24.4 (± 18.6) and 15.0 (± 11.5) mg C m^{-3} in the CDW and other regions, respectively. Further analyses revealed that the bacterial biomass in the surface water was positively and linearly associated with Chl *a* concentrations in both 2009 ($p < 0.01$) and 2010 ($p < 0.05$). This finding applies to the values averaged over Z_E in both periods (both $p < 0.01$). However, the mean Chl *a* concentrations in the surface water were slightly higher in 2010 than in 2009 (Table 1).

In general, an increased amount of organic matter is delivered through fluvial discharge into the ECS during periods of high riverine flow (e.g., Wang et al., 2012). Although these results suggest that the bacterial biomass might be higher in the flooding period than in the non-flooding period, this difference was not verified when using averaged bacterial biomass values in this study. The bacterial biomass in the surface water was significantly higher in the 2009 non-flooding period than during the 2010 flood, with mean values of 39.8 (± 33.7) and 20.4 (± 16.5) mg C m^{-3}, respectively (Table 1). The average bacterial biomass over Z_E was even more pronounced in 2009 than in 2010 (data not shown). However, the total bacterial biomass in the CDW zone was two times higher in 2010 than in 2009, with values of 47.7 and 21.0 x 10^6 kg C, respectively (Table 2). A potential cause of the low average bacterial biomass observed during the 2010 flood might be protozoan grazing. Protozoa have been recognized as important microbial grazers in the ECS and in many coastal ecosystems (e.g., Chen et al., 2009; Chen et al., 2003; Sherr and Sherr, 1984). Although protozoan abundance was not measured in this study, a high production rate of nanoflagellates was observed in the southern ECS, with mean values of 0.46 μg C l^{-1} h^{-1} during periods of high riverine flow (Tsai et al., 2005).

Zooplankton, especially microzooplankton, are amongst the most important contributors to plankton CR (Calbet and Landry, 2004; Hernández-León and Ikeda, 2005; Hopkinson Jr. et al., 1989). Unfortunately, microzooplankton was not measured in this study. Instead, zooplankton (> 330 μm) were sampled across the whole water column. However, the average biomass of zooplankton over Z_E can be still estimated, and mean values for the 2010 flood and 2009 non-flooding period were calculated as ,105.7 (± 144.4) and 22.6 (± 25.7) mg C m^{-3}, respectively; this differences was statistically significant ($p < 0.01$). The average zooplankton biomass over Z_E for the CDW zone was 90-fold higher in 2010 than in 2009 (Table 2), suggesting that the flood may have had a significant effect on zooplankton biomass.

3.3 Effects of the Changjiang River flooding on plankton community respiration

Plankton CR is typically defined as the integrated rate of organic carbon consumption by plankton communities (e.g.., Hopkinson Jr. et al., 1989; Rowe et al., 1986). In summer, the mean CR rate in the surface waters of the ECS ranges from 52.2 to 128.4 mg C m^{-3} d^{-1} (Chen et al., 2006; Chen et al., 2009), and it is significantly correlated with fluvial discharge from the Changjiang River (Chen et al., 2009). In this study, the CR in the surface water ranged from 2.7 to 311.9 mg C m^{-3} d^{-1}, with a mean value of 73.2 (± 76.9) mg C m^{-3} d^{-1} in the 2009 non-flooding period (Table 1). During the 2010 flood, the mean rate in the surface water of 105.6 (± 66.7) mg C m^{-3} d^{-1} was significantly higher than in 2009 ($p < 0.01$; Table 1), and CR ranged from 10.9-325.3 mg C m^{-3} d^{-1} (Table 1). The CR rate averaged over the Z_E was statistically similar in both years ($p = 0.08$), with mean values of 76.8 (±53.0) and 66.8 (±68.4) mg C m^{-3} d^{-1}, respectively. In terms of spatial distribution, higher CR rates were mostly observed in the CDW region in both sampling periods, especially along the coast (Fig. 2). Nevertheless, it should be noted that the CDW zone was much larger in 2010 than in 2009.

CR rates were regressed against biomass of phytoplankton, heterotrophic bacteria, and zooplankton (> 330 μm). However, it should be noted that microzooplankton was not measured in this study and excluded from our analysis. In this study, CR was significantly correlated with both Chl *a* concentration and bacterial biomass for both periods in surface water and when averaged over Z_E (all $p < 0.01$; Fig. 3). The contribution of phytoplankton and/or bacterioplankton to CR is substantial in the ECS, even though the relative contribution varies spatially and temporally (Chen et al., 2006; Chen et al., 2009; Chen et al., 2003) Given the importance of phytoplankton and bacterioplankton to CR rates in both years, as well as their high densities measured herein, it seems likely that these microbial groupings contributed substantially to the CR rate in both 2009 and 2010.

Surprisingly, the mean Chl *a* concentration was slightly higher in 2010 than in 2009, though bacterial biomass was significantly lower in 2010 than in 2009 (Table 1). However, the CR rate was still higher in 2010 than in 2009. In a further analysis, the differences (i.e., 2010 minus 2009) in the average CR, Chl *a* concentration, and bacterial biomass over Z_E at the same station were calculated. The extent of such differences in CR was significantly related to differences in Chl *a* concentration ($p < 0.001$) and bacterial biomass ($p < 0.01$; Fig. 4). The linear relationships were also statistically significant if the values of the differences in the surface water were used (all $p < 0.01$; data not shown). Among the positive CR difference values (i.e., 20 of 33), 15 stations were also characterized by positive differences in Chl *a* concentrations; only 2 stations had positive differences in bacterial biomass. Interestingly, the stations with positive Chl *a* concentration difference values were mostly located within the CDW region in 2010, with the exception of the CDW in 2009. These results suggest that the higher CR in the 2010 flood might be attributed to phytoplankton, especially in the CDW. The mean Chl *a* concentration was only slightly higher in 2010 than in 2009. Therefore, it is reasonable to speculate that the differences in CR rate in both periods might have been partially caused by variation in the composition of the phytoplankton communities. Although the CR attributed to different components of the phytoplankton community was not measured in this study, it was been documented elsewhere; for instance, dinoflagellates have higher carbon-specific respiration rates that many other phytoplankton types (e.g., Lopez-Sandoval et al., 2014).

In addition, zooplankton might also be amongst the potential contributors to the higher CR rate observed in 2010 than in 2009. As stated above, the biomass of zooplankton was significantly higher in 2010 than in 2009. However, the linear relationships between CR and zooplankton biomass over Z_E were not statistically significant in 2009 or 2010. To further explore how plankton communities contributed to CR, the CR rate was regressed against total plankton biomass (i.e., summed biomass of phytoplankton, bacterioplankton, and zooplankton) for both periods, and the linear relationships between CR and total plankton biomass (mg C m^{-3}) over Z_E were significant in both 2009 ($p < 0.001$) and 2010 ($p < 0.01$; Fig. 5).

Similarly significant relationships between CR and total planktonic biomass have also been observed in the summer in the ECS, and phytoplankton and bacterioplankton might be the most important components contributing to CR at such times (Chen et al., 2006). In this study, autotrophic plankton biomass (i.e., phytoplankton) accounted for 41.3% and 45.6% of total planktonic biomass in 2009 and 2010, respectively. As for heterotrophic plankton biomass, bacterioplankton attributed to 38.7% and 11.3% and zooplankton contributed for 20.0% and 43.1% of total plankton biomass in 2009 and 2010, respectively. This suggests that phytoplankton and bacterioplankton might be the most important components attributing to CR in the 2009 non-flooding period. In contrast, during the 2010 flood, the CR rate might have been mostly driven by phytoplankton and zooplankton metabolic activity.

All such conjectures are based on stocks, and biomass might not be directly related to the concurrent CR rate. By using physiological and allometric relationships of variant plankton communities, the plankton CR rate could be estimated from stock values, and significant correlations have indeed been found between measured and estimated rates (Chen et al., 2009). Furthermore, it also should be noted that microzooplankton might be another important contributor to CR, though they were unfortunately not assessed herein.

3.4 Implications of plankton community respiration on coastal ecosystems of the ECS

A further comparative analysis was conducted to determine whether the CR rate affected the fugacity of CO_2 (fCO_2) in the seawater. In 2009, the fCO_2 in the surface water was in the range of 118.7-599.8 μatm, with mean values of 362.9 ± 101.2 μatm (Table 1). This mean value is close to the mean (369.6 μatm) observed in the ECS in August in prior years (Chen et al., 2006). In the

2010 flood, the mean value (297.6 μatm) of fCO_2 in the surface water was significantly lower than in 2009, and ranged from 178.7 to 454.2 μatm (Table 1). It is well known that fCO_2 is temperature dependent, and it increases as the temperature increases (e.g., Goyet et al., 1993). The effect of temperature on the large variation in fCO_2 observed between the 2009 non-flooding period and the 2010 flood was trivial; the SST difference of 0.7ºC between 2009 and 2010 would only equal a fCO_2 decrease of approximately 10 μatm (Table 1).

The effect of freshwater input on fCO_2 in the surface water in the ECS has also been suggested to be relatively minor compared to the inter-annual variation of fCO_2 (Chen et al., 2013). To evaluate this, conservative mixing was applied by using TA and DIC data between freshwater and seawater end-members. Provided that the proportional contributions from freshwater and seawater endmembers are f_1 and f_2 ($f_1+f_2=1$), respectively, the conservative mixing TA and DIC values for a given water sample can be expressed by the following equations:

$$TA_{mix}=TA_{fw}xf_1+TA_{sw}xf_2$$

$$DIC_{mix}=DIC_{fw}xf_1+DIC_{sw}xf_2$$

where the subscripts "mix", "fw", and "sw" represent values of conservative mixing, freshwater, and seawater endmembers, respectively. The TA and DIC data reported by Zhai et al. (2007) for the Changjiang River in summer were used as the freshwater endmembers (both TA_{fw} and

DIC_{fw}=1743 μmol kg^{-1}), and the surface data at station K in July 2009 and 2010 were chosen to represent the seawater endmembers (TA_{sw}=2241 μmol kg^{-1} and DIC_{sw}=1909 μmol kg^{-1} in 2009; TA_{sw}=2240 μmol kg^{-1} and DIC_{sw}=1904 μmol kg^{-1} in 2010). Subsequently, the hypothetical fCO_2 from conservative mixing was calculated from the TA_{mix} and DIC_{mix} data using CO2SYS version 2.1 (Pierrot et al., 2006), in which the carbonic acid dissociation constants were adopted from Mehrbach et al. (1973) and refitted by Dickson and Millero (1987). The uncertainty in this simulation mainly derives from errors in the estimations of TA_{mix} and DIC_{mix}. Assuming the errors of the calculated TA_{mix} and DIC_{mix} are ±5 μmol kg^{-1}, this may result in an uncertainty of ±13 μatm in the simulated fCO_2. The simulated results show that the effect of mixing freshwater and seawater on fCO_2 was nearly the same in both periods. However, a large variation in fCO_2 in the surface water was estimated; it varied from 375.4 to 439.8 μatm as salinity varied from 20.38 to 33.96. This finding implies that surface water fCO_2 in the ECS might increase dramatically, especially during the devastating flood of 2010 where low SSS (≤ 31) characterized almost 70% of the ECS shelf (Fig. 1b). However, in the 2010 flood, surface water with low fCO_2 was observed in the ECS. Therefore, vigorous photosynthetic processes might be a potential cause for the reduction of fCO_2 in the surface water during periods of flooding. Compared to PP values observed in summer in the ECS in previous years (Chen et al., 2009), PP was indeed high during the 2010 flood (Table 1; Chen et al., 2009). Gong et al. (2011) also estimated that over the past decade, the carbon fixation rate during flooding was about three times higher than during non-flooding periods. However, no significant correlation was found between fCO_2 and PP in the 2010 flood, though this may simply be due to having a small sample size for PP. Nevertheless, fCO_2 was significantly correlated with Chl *a* concentration in the pooled 2010 flood dataset ($p < 0.001$). This significant relationship indirectly supports the hypothesis that the reduction in fCO_2 in the 2010 flood might be associated with vigorous phytoplankton metabolic activity.

Furthermore, negative linear relationships were observed between fCO_2 and CR in the surface water during both the 2009 non-flooding period ($p < 0.01$) and the 2010 flood ($p < 0.001$; Fig. 6). Significant linear relationships were also found using pooled data from each period (all $p < 0.001$). CR has been assumed to be an integrated response of overall plankton activity. These results imply that fCO_2 in the surface water (or the entire water column) is related to plankton activities. To explore the variation in fCO_2 between the non-flooding and flooding period, the difference in fCO_2 and CR at the same station was estimated. Surprisingly, a negative linear relationship was found between the difference in fCO_2 and CR of the flooding and non-flooding periods ($p = 0.001$; Fig. 7). As previously stated, compared to the 2009 non-flooding period, the increase in CR rate in the 2010 flood might be associated with the increase in phytoplankton biomass (Fig. 4a). These results indicate that the significant amount of fCO_2 absorption in the 2010 flood was related to the strength of plankton activity, particularly phytoplankton at stations that were not characterized by low SSS in the 2009 non-flooding period.

4 CONCLUSIONS

Riverine run-off has a profound effect on organic carbon production and consumption in coastal ecosystems across the globe, and these effects will become even more pronounced as storm frequency and magnitude increase in the coming decades. During the 2010 flooding of the Changjiang River, a large quantity of freshwater was discharged into the ECS, and the CDW zone covered almost two thirds of the continental shelf; this represents a 6-fold greater area than during a more typical, non-flooding period (2009). Higher nitrate concentrations, mostly in the river's fluvial discharge, were also measured in the ECS during the flood. Although the phytoplankton biomass showed no significant difference between 2009 and 2010, bacterial biomass in the surface water was significantly higher in the 2009 non-flooding period. Despite this, CR was still higher during the 2010 flood than in the 2009 non-flooding period. The temporal difference (2010 minus 2009) in CR was significantly related to the respective differences in Chl *a* concentration, suggesting that higher CR in the 2010 flood might have been attributed to a higher biomass of phytoplankton, especially at stations located within the CDW region (most of which were not characterized by low SSS in the 2009 non-flooding period). In addition to phytoplankton, zooplankton (> 330 μm) may also have contributed significantly to the high CR rate observed in the 2010 flood. This could be evidenced from the fact that zooplankton biomass in 2010 accounted for 43.1% of the total plankton biomass. Finally, a negative linear relationship was found between the temporal differences (i.e., 2010 minus 2009) in CR vs. fCO_2. This finding implies that a tremendous quantity of fCO_2 was uptaken during phytoplankton photosynthesis during the flood period. Overall, these results suggest that plankton activity increased due to the substantial input of dissolved inorganic nutrients discharged by the river during the flood. This effect was especially pronounced at stations not previously characterized by low SSS, indicating that the effects of flooding on the ECS shelf ecosystem might be scaled to the magnitude of the flood.

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Table 1. The mean ± SD values for different variables measured in the surface water of the ECS during non-flooding (2009) and flooding (2010) periods, with range of values in parentheses. The mean ± SD values for stations in the area of the Changjiang Diluted Water (CDW) region are in brackets. Variables include transparency (CTD_{TM}; %), salinity (SSS), temperature (SST; ºC), fugacity of CO_2 (fCO_2; μatm), nitrate concentration (NO_3^-; μM), phosphate concentration (PO_4^{3-}; μM), silicate concentration (SiO_4^-; μM), chlorophyll *a* concentration (Chl *a*; mg Chl m^{-3}), bacterial biomass (BB; mg C m^{-3}), and plankton community respiration (CR; mg C m^{-3} d^{-1}). The euphotic depth (Z_E; m) and mixed layer depth (M_D; m) are also shown for each year. Mann-Whitney rank-sum test were used to test temporal differences. For reference, it should be noted that the difference between the CDW zone and the other region in the ECS in each year was significant for most of variables ($p < 0.05$), except nitrate and phosphate in 2009.

Variable	2009 (non-flooding period)	2010 (flood)
Z_E	38.9±36.4 (1.3–190.6) [16.8±7.4]	33.4±17.3 (10.1–82.2) [24.8±10.7]
M_D	13.7±7.3 (5–37) [7.3±3.6]	11.3±6.6 (4–35) [7.9±2.6]
CTD_{TM}	76.7±12.2 (37.2–86.3) [70.0±4.9]	80.5±5.4 (67.7–88.5) [78.4±4.3]**
SSS	32.62±2.07 (23.80–34.11) [29.24±2.52]	30.32±3.60 (19.33–34.27)* [27.95±3.03]
SST	26.8±1.7 (23.3–29.6) [25.0±0.9]	26.1±2.2 (21.0–30.0) [25.1±1.7]
fCO_2	362.9±101.2 (118.7–599.8) [230.4±105.3]	297.6±79.0 (178.7–454.2)* [248.6±54.5]
NO_3^-	2.0±5.3 (0.0–24.3) [4.0±9.1]	6.2±9.8 (0.0–37.6)* [10.3±11.3]*
PO_4^{3-}	0.13±0.17 (0.00–0.83)	0.17±0.30 (0.00–1.71)

	[0.13±0.07]	[0.23±0.37]
SiO_4^-	5.8±5.9 (1.5–24.5) [9.8±7.2]	6.4±7.8 (0.6–36.4) [9.1±9.2]
Chl *a*	0.98±1.52 (0.12–4.41) [2.23±1.46]	1.26±1.27 (0.03–5.32) [1.83±1.35]
BB	39.8±33.7 (10.6–184.8) [54.9±39.6]	20.4±16.5 (3.6–90.2)** [24.4±18.6]**
CR	73.2±76.9 (2.7–311.9) [172.0±109.2]	105.6±66.7 (10.9–325.3)* [142.0±61.2]

*: $p < 0.01$; **: $p < 0.001$

Table 2. Total area (x 10^3 km^2) of the East China Sea (ECS) and Changjiang Diluted Water (CDW) region (in brackets), as well as bacterial (BB; x 10^6 kg C) and zooplankton (Zoo; x 10^6 kg C) biomass over the euphotic depth integrated for the entire ECS and the CDW region (in brackets) during non-flooding (2009) and flooding (2010) periods.

Variables	2009 (non-flooding period)	2010 (flood)
Area	186.0 [19.0]	182.7 [111.7]
BB	222.5 [21.0]	87.3 [47.7]
Zoo	410.3 [6.2]	920.6 [560.8]

FIGURE LEGENDS

Fig. 1. Contour plots of salinity (SSS) and concentrations of nitrate (NO_3^-), phosphate (PO_4^{3-}), and chlorophyll *a* (Chl *a*) in the surface water (2-3 m) in the ECS during non-flooding (2009; left most panels) and flooding (2010; right-most panels) periods. Bottom depth contours are shown as dashed lines both here and in Fig. 2. The sampling stations in both periods are marked by an ex (x) both here and in Fig. 2. The contour intervals of SSS and concentrations of nitrate, phosphate, and Chl *a* are 0.5, 1.0 μM, 0.1 μM, and 0.5 mg Chl m^{-3}, respectively, and the values of the respective contour lines (bold) are = 31, 3.0 μM, 1.0 μM, and 1.0 mg Chl m^{-3}, respectively The range for each parameter is shown at the top of each panel.

Fig. 2. Contour plots of plankton community respiration (CR; mg C m^{-3} d^{-1}) over the euphotic zone of the ECS during a) non-flooding (2009) and b) flooding (2010) periods. The contour interval is 10 mg C m^{-3} d^{-1}. The CR range is shown at the top of each panel.

Fig. 3. Relationships between plankton community respiration (CR; mg C m^{-3} d^{-1}) and a) chlorophyll *a* concentration (Chl *a*; mg Chl m^{-3}) and b) bacterial biomass (mg C m^{-3}) for all data from non-flooding (2009; ●) and flooding (2010; ○) periods. Linear regressions of data from 2009 (solid lines) and 2010 (dashed lines), as well as the respective r^2 and p values, have also been included.

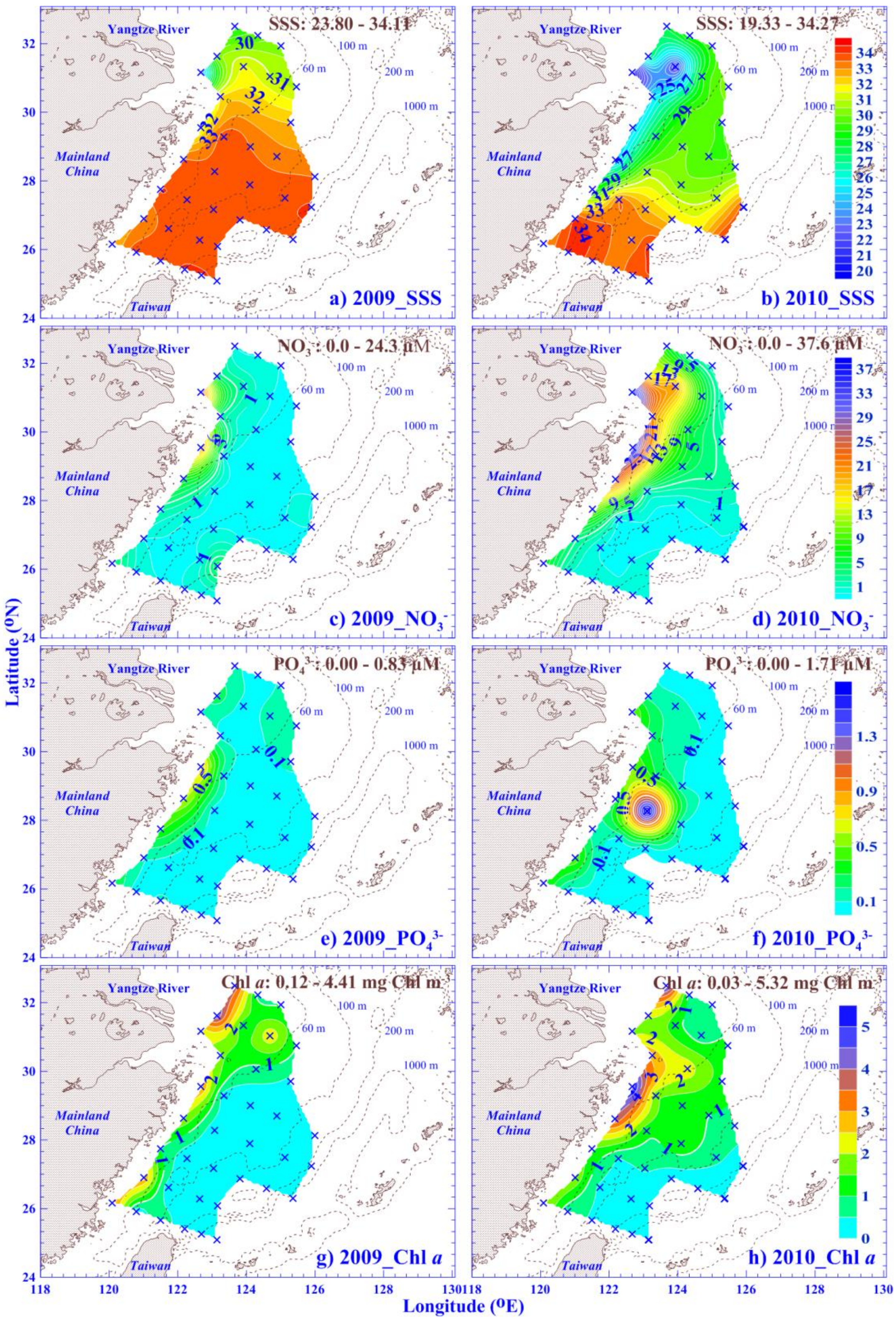
Fig. 4. Differences (Δ) between 2010 and 2009 in plankton community respiration (CR; mg C m^{-3} d^{-1}) versus a) chlorophyll *a* (Chl *a*; mg Chl m^{-3}) and b) bacterial biomass (mg C m^{-3}) over the euphotic zone at the same station. The r^2 and p values have been shown for the best-fit linear regression line (solid line). For reference, the vertical and horizontal dashed lines represent inter-year differences of zero (i.e., $\Delta = 0$).

Fig. 5. Relationship between plankton community respiration (CR) and total plankton biomass

(expressed per carbon unit) over Z_E in 2009 (●; solid line) and 2010 (○; dashed line). The respective r^2 and p values are shown for each linear regression line. Total plankton biomass was the summed biomass of phytoplankton, bacterioplankton, and zooplankton. Please refer to the “Materials and Methods” for details of the carbon conversion for plankton communities.

Fig. 6. Relationships between the fugacity of CO_2 (fCO_2) and plankton community respiration (CR) in the surface water in 2009 (●; solid line) and 2010 (○; dashed line). The respective r^2 and p values are shown for each linear regression line.

Fig. 7. Differences (Δ) between 2010 and 2009 in fCO_2 (μatm) and plankton community respiration (CR; mg C m^{-3} d^{-1}) in the surface water at the same station. For reference, the vertical and horizontal dashed lines represent the inter-annual differences of zero (i.e., $\Delta = 0$).



SSS: 23.80 - 34.11
SSS: 19.33 - 34.27
a) 2009_SSS
b) 2010_SSS
c) 2009_NO3-
d) 2010_NO3-
e) 2009_PO43-
f) 2010_PO43-
g) 2009_Chl a
h) 2010_Chl a
Chl a: 0.12 - 4.41 mg Chl m-3
Chl a: 0.03 - 5.32 mg Chl m-3
Yangtze River
Mainland China
Taiwan
Latitude (oN)
Longitude (oE)

707 Fig. 1

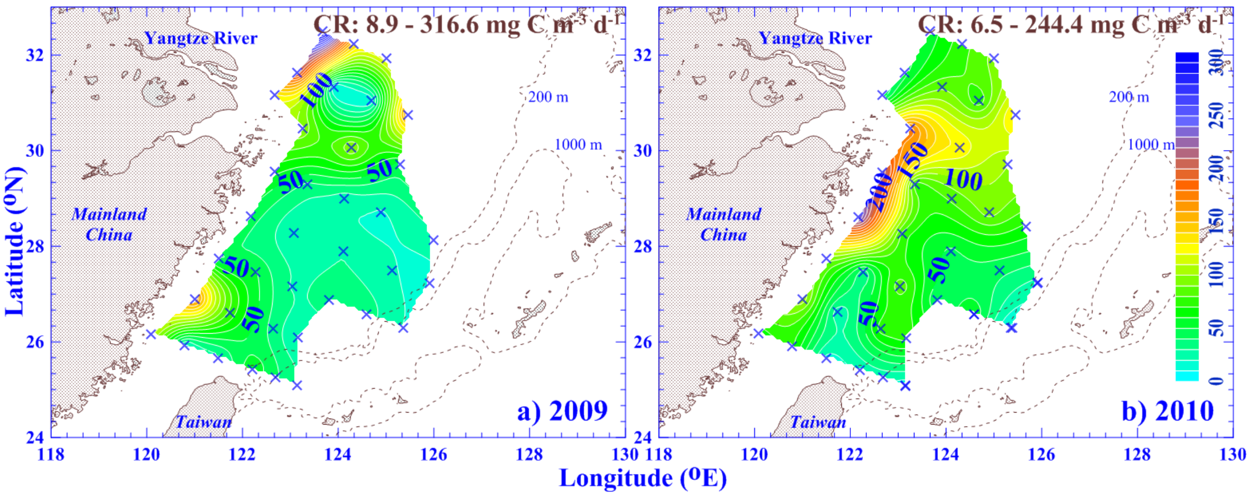

CR: 8.9 - 316.6 mg C m^{-3} d^{-1}
CR: 6.5 - 244.4 mg C m^{-3} d^{-1}
Yangtze River
Mainland China
Taiwan
200 m
1000 m
a) 2009
b) 2010
Latitude (^{o}N)
Longitude (^{o}E)
118
120
122
124
126
128
130
24
26
28
30
32
50
100
150
200
0
250
300

Fig. 2

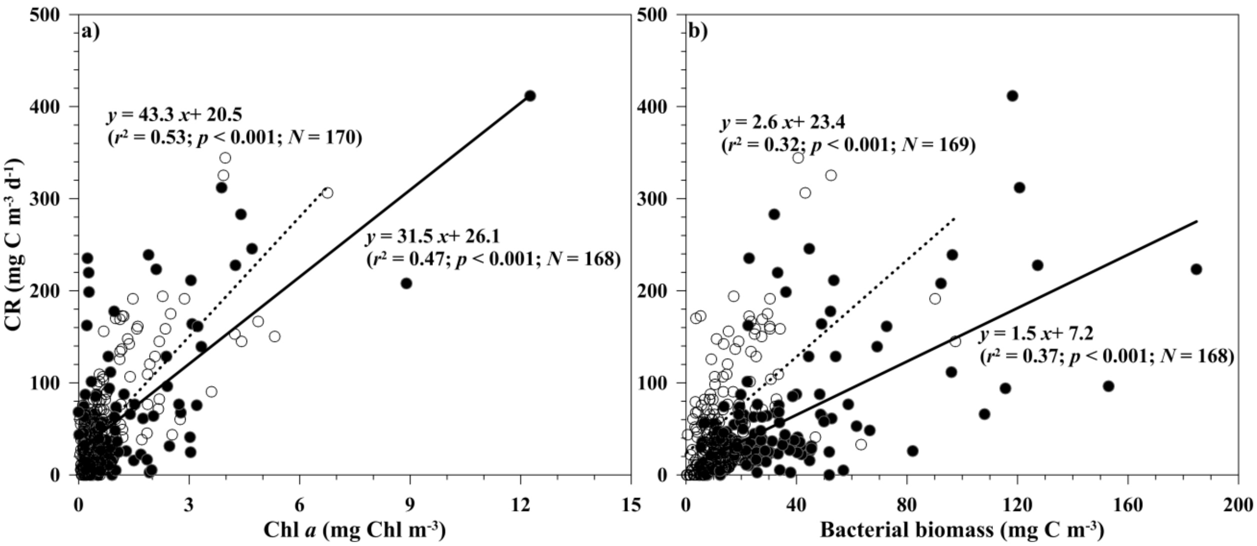

a)
y = 43.3 x+ 20.5
(r² = 0.53; p < 0.001; N = 170)
y = 31.5 x+ 26.1
(r² = 0.47; p < 0.001; N = 168)
CR (mg C m⁻³ d⁻¹)
Chl a (mg Chl m⁻³)
0
100
200
300
400
500
0
3
6
9
12
15
b)
y = 2.6 x+ 23.4
(r² = 0.32; p < 0.001; N = 169)
y = 1.5 x+ 7.2
(r² = 0.37; p < 0.001; N = 168)
Bacterial biomass (mg C m⁻³)
0
40
80
120
160
200

Fig. 3

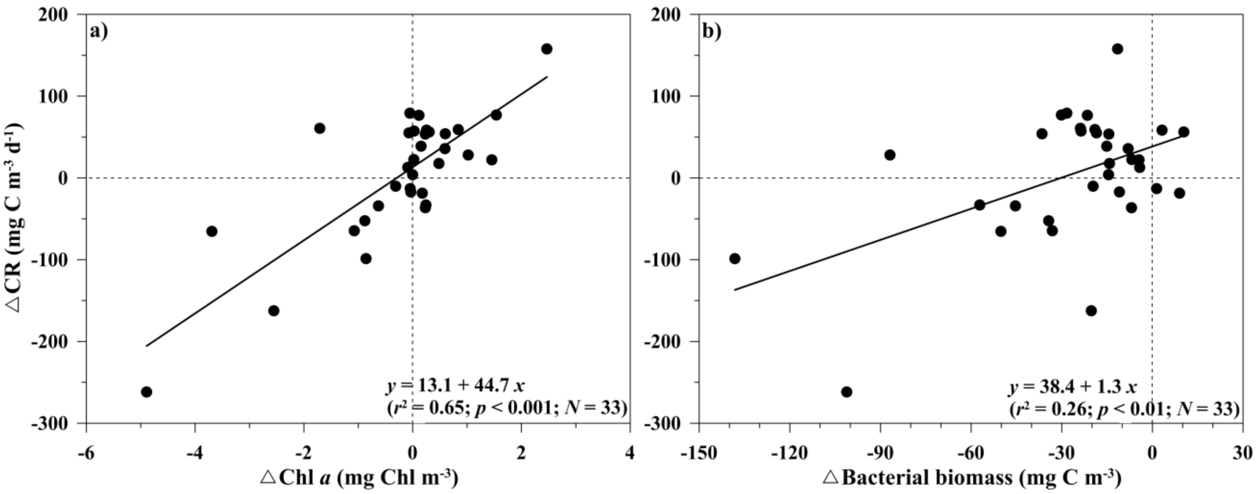
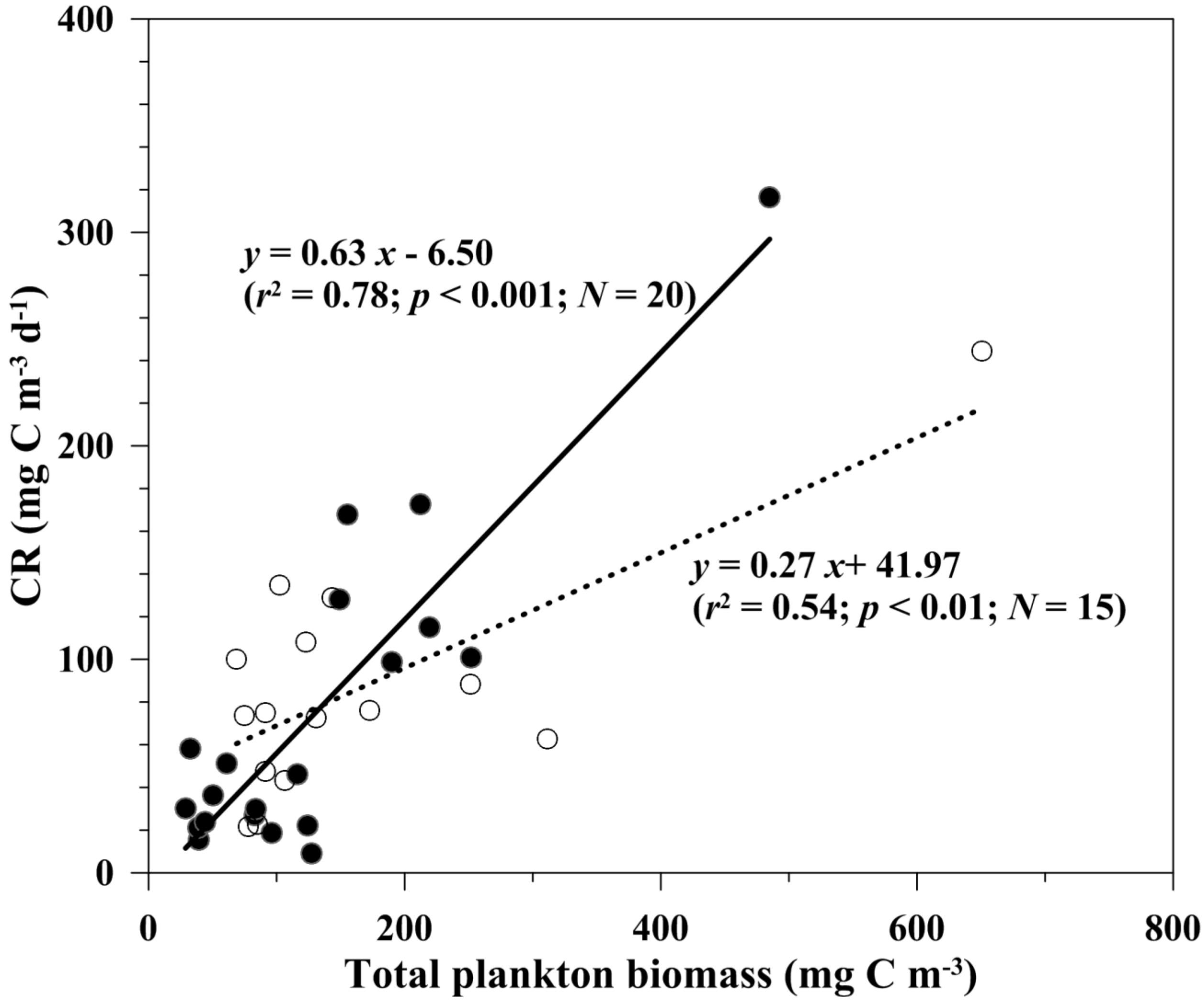
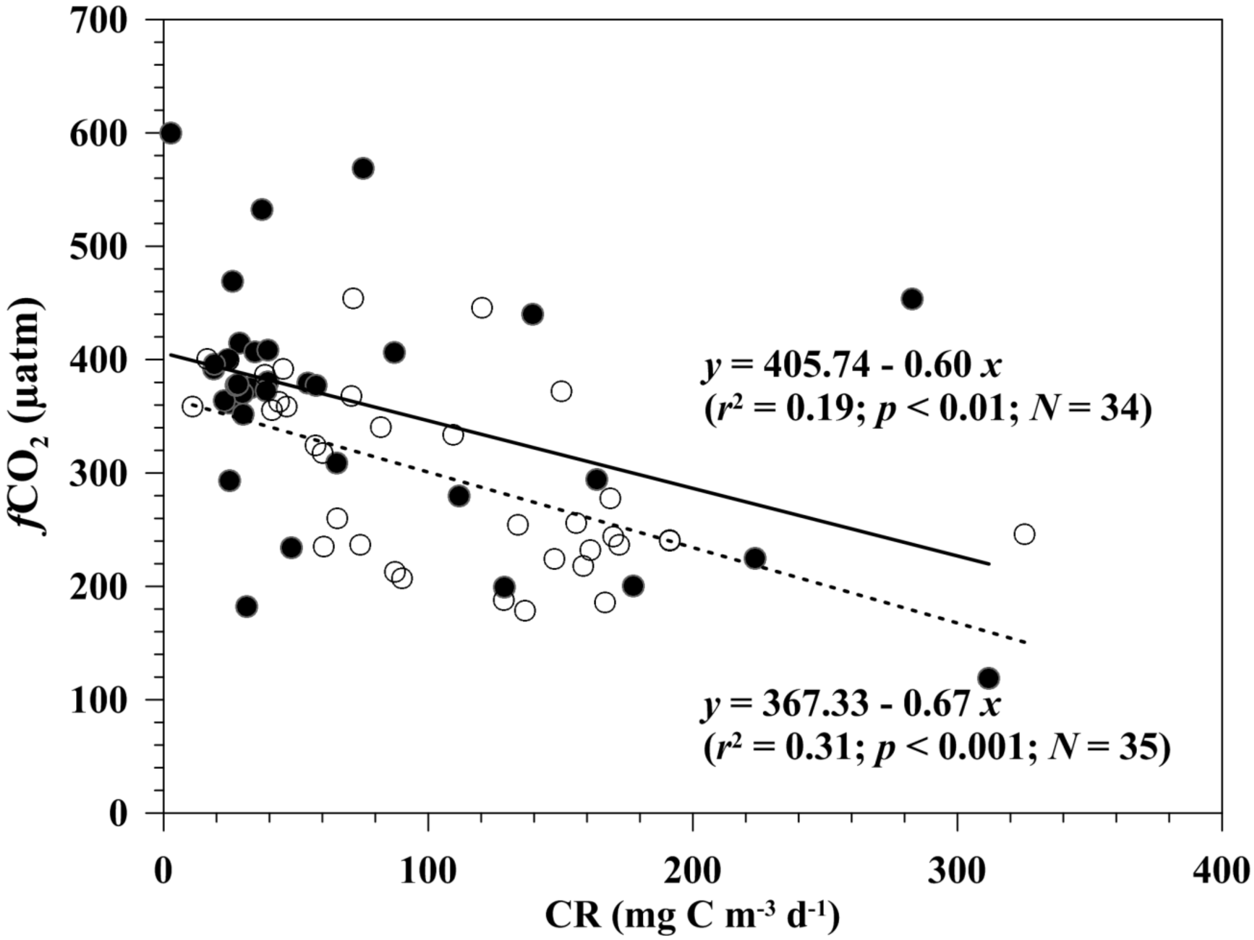

a)
b)
△CR (mg C m-3 d-1)
△Chl a (mg Chl m-3)
△Bacterial biomass (mg C m-3)
y = 13.1 + 44.7 x
(r2 = 0.65; p < 0.001; N = 33)
y = 38.4 + 1.3 x
(r2 = 0.26; p < 0.01; N = 33)
200
100
0
-100
-200
-300
-6
-4
-2
0
2
4
-150
-120
-90
-60
-30
0
30

Fig. 4



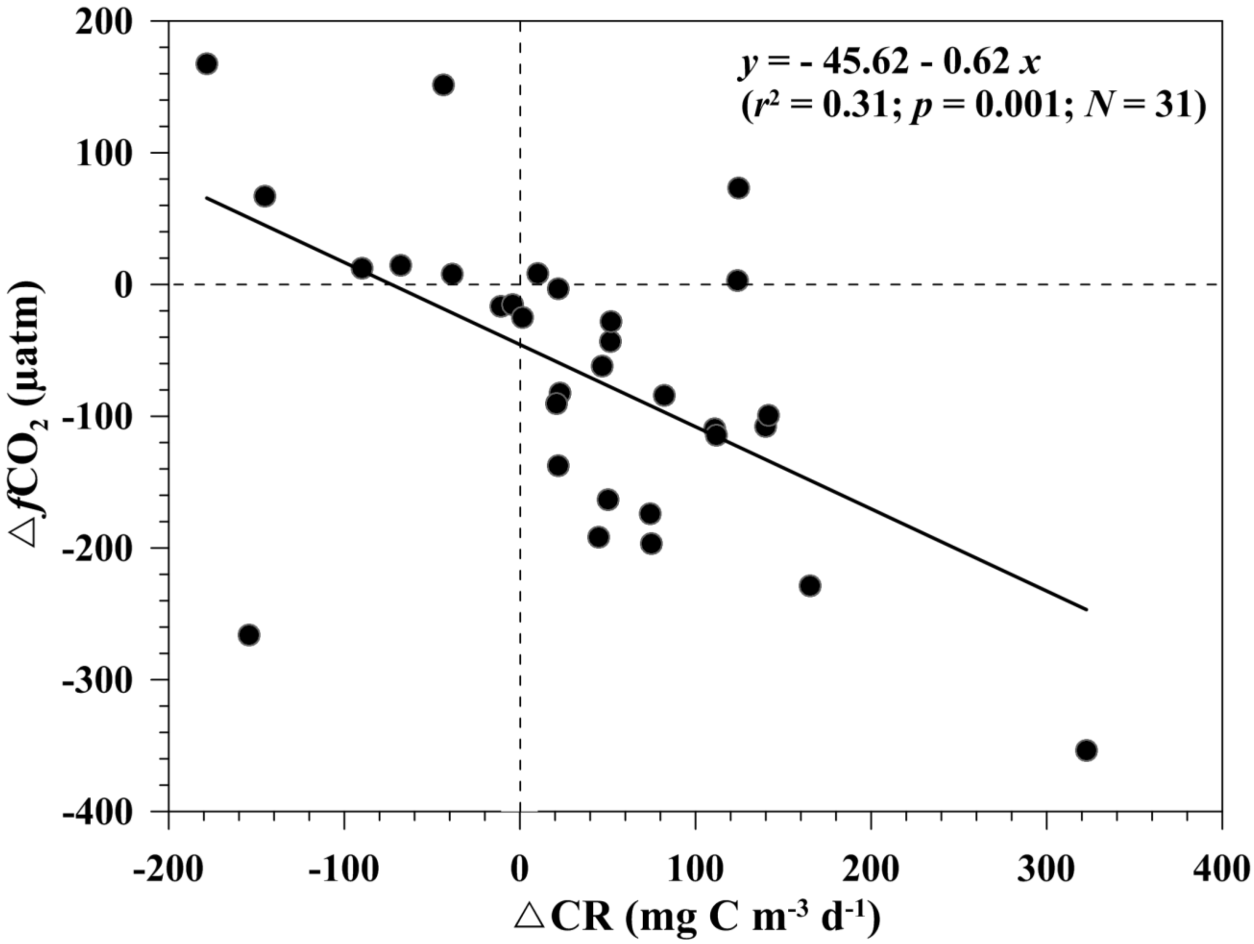
400
300
200
100
0
CR (mg C m-3 d-1)
y = 0.63 x - 6.50
(r2 = 0.78; p < 0.001; N = 20)
y = 0.27 x+ 41.97
(r2 = 0.54; p < 0.01; N = 15)
0
200
400
600
800
Total plankton biomass (mg C m-3)

714 Fig. 5



700
600
500
400
300
200
100
0
fCO2 (µatm)
y = 405.74 - 0.60 x
(r² = 0.19; p < 0.01; N = 34)
y = 367.33 - 0.67 x
(r² = 0.31; p < 0.001; N = 35)
0
100
200
300
400
CR (mg C m-3 d-1)

715 Fig. 6



y = - 45.62 - 0.62 x
(r² = 0.31; p = 0.001; N = 31)
200
100
0
-100
-200
-300
-400
△fCO2 (µatm)
-200
-100
0
100
200
300
400
△CR (mg C m-3 d-1)

716 Fig. 7