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Distinct bacterial-production–DOC–primary-production relationships and implications for biogenic C cycling in the South China Sea shelf

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Abstract. Based on two summer spatio-temporal data sets obtained from the northern South China Sea shelf and basin, this study reveals contrasting relationships among bacterial production (BP), dissolved organic (DOC) and primary production (PP) in the transition zone from the neritic to the oceanic regions. Inside the mid-shelf (bottom depth < 100 m), where inorganic nutrient supplies from river discharge and internal waves were potentially abundant, BP, DOC and PP were positively intercorrelated, whereas these three measurements became uncorrelated in the oligotrophic outer shelf and slope. We suggest that the availability of limiting minerals could affect the couplings/decouplings between the source (i.e. phytoplankton) and sink (i.e. bacteria) of organic carbon, and thus DOC dynamics. DOC turnover times were homogeneously low (37–60 days) inside the mid-shelf area and then increased significantly to values > 100 days in the outer shelf, indicating that riverine (Pearl River) DOC might be more labile. The actual mechanism for this is unknown, but might relate to higher inorganic nutrient supply from river/terrestrial sources. The positive correlation of the BP / PP ratios vs. phosphate (and nitrate) concentrations in the inner shelf implies that if anthropogenic mineral loading keeps increasing in the foreseeable future, the near-shore zone may become more heterotrophic, rendering the system a stronger source of CO_2.

1 Introduction

Dissolved organic carbon (DOC) constitutes > 90 % of total organic carbon in many aquatic ecosystems (Hedges, 1992). Thus, understanding the processes regulating DOC dynamics (accumulation and depletion) is very important for assessing biological pump and global carbon cycling (Longhurst and Harrison, 1989; Carlson et al., 1994; Giorgio et al., 1997; Hansel and Carlson, 1998; Williams and Bowers, 1999). In terms of source, DOC may come from external inputs, such as river discharge and re-suspension processes (Boss et al., 2001). Internally, DOC can be generated through biogenic (i.e. food-web) processes such as phytoplankton exudation, zooplankton grazing, viral lyses and plankton excretion. On the other hand, heterotrophic bacterioplankton (bacteria) are the organisms primarily responsible for DOC consumption (see Azam, 1998 for a review) in various aquatic ecosystems.

In the 1990s, many literatures reported DOC accumulation in productive surface waters in various ocean systems (Thingstad et al., 1997 in their Table 1). As an alternative to models based on low degradability, Thingstad et al. (1997) proposed a malfunctioning microbial-loop (MM) hypothesis, which affirmed that DOC accumulation occurs when bacterial production (a product of growth rate and biomass) was low. Their modelling work indicated that both bacterial growth and biomass could be oppressed by food-

Table 1. A list of the linear regression analysis of individual depth measurements of bacterial production vs. dissolved organic carbon derived from different study types and areas of the two summer cruises. r^2, coefficient of determination; n, sampling size.

Cruises	Area and study type	r^2	n	p value
June 2009	a. St. 2 diel	$r^2 = 0.059$	$n = 39$	0.078
	b. St. 3–9	$r^2 = 0.001$	$n = 45$	0.268
	Outer shelf (a + b)	$r^2 = 0.035$	$n = 84$	0.065
	c. St. 14 diel	$r^2 = 0.67$	$n = 39$	< 0.001
	d. St. 10–13	$r^2 = 0.45$	$n = 23$	< 0.001
	Inner shelf (c + d)	$r^2 = 0.66$	$n = 62$	< 0.001
June 2010	Inner shelf	$r^2 = 0.14$	$n = 67$	0.004
	Outer shelf	$r^2 = 0.005$	$n = 78$	0.544

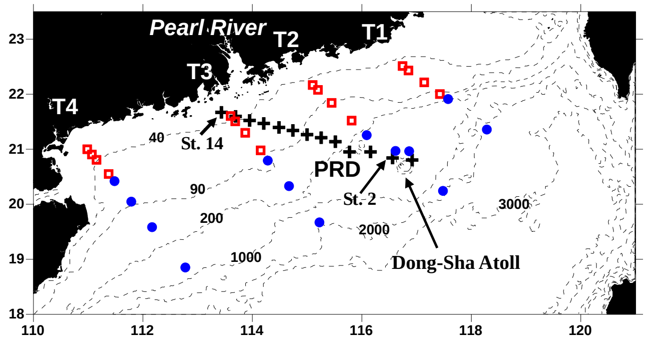

Fig. 1. Map of the South China Sea shelf showing sampling stations of the Pearl River mouth to the Dong-Sha Atoll (i.e. PRD; June 2009) and shelf-mapping (transects T1–T4, June 2010) surveys. Stations of the PRD transect survey are marked by black crosses. Stations 2 and 14 are located NW of the Dong-Sha Atoll and the Pearl River mouth, respectively. In T1–T4, inner-shelf (bottom depth < 100 m) and outer-shelf stations are indicated by symbols red squares and blue dots, respectively.

web mechanisms. The bacterial growth rate was kept low by bacteria–phytoplankton competition for inorganic nutrients (i.e. bottom-up or substrate control), and biomass was kept low by bacterivory (i.e. top-down or predators' control). Their former finding explicitly highlighted the importance of inorganic nutrient supply in controlling the relationship between bacterial production and DOC dynamics. However, the effects of inorganic nutrient supply on the ecological relationships among bacterial production (BP – DOC sink), DOC inventory and primary production (PP – DOC source) have not been examined with field data in marine systems.

We argue that strong couplings among BP, DOC and PP takes place in area/time with abundant nutrients supply. Under nutrient-limited conditions, BP, PP and DOC would be out of phase, with no positive correlations among them. Note that the MM hypothesis concentrated on the mechanisms in explaining DOC accumulation, while the effects of nutrient supply on the algae–bacteria–DOC relationships was the major focus of this research. With several summer data sets collected from the South China Sea shelf, this study provides, for the first time, evidence indicating that the availability of limiting nutrients could be the major factor in shaping the relationships among BP, PP and ambient DOC concentrations in marine systems.

2 Materials and methods

2.1 Study site and sampling

Two types of cruise surveys covering spatio-temporal variation were conducted in the South China Sea (SCS; Fig. 1) shelf. For spatial study, one transect from the Pearl River mouth to the Dong-Sha Atoll (i.e. transect PRD, 13 stations, cruise # OR3 1379) and one shelf-mapping (four transects, T1–T4; 29 stations; cruise # OR1 929) surveys across the SCS shelf were conducted in June 2009 and June 2010, respectively. In these transect and self-mapping studies, water samples were taken from six depths. The deepest sampling depth (DSD) of each station was bottom-depth (BD) dependent. For stations with BD > 100 m, the DSD was set at 100 m; for stations with BD < 100 m, the DSD was set at the depth 10–15 m above the BD. The mixed layer depth (MLD) was defined as the depth where its temperature was 0.25 °C lower than that of the surface (Levitus, 1982).

In the June 2009 (i.e. the PRD) cruise, two anchored studies were performed at stations (Fig. 1) located at the Pearl River mouth (St. 14; BD ∼30 m) and at the north-west off the Dong-Sha atoll (St. 2; BD ∼250 m) respectively. In these two anchored studies, water-column sampling was performed every three hours. CTD (Conductivity-Temperature-Density) was cast hourly. At each station, water samples were taken within the upper water column (25 and 100 m for stations 14 and 2, respectively) from six depths. Profiles of temperature, salinity, fluorescence and underwater PAR (photosynthetically available radiation) were recorded by sensors attached to the CTD rosette (General Oceanic Inc. Model 1015).

2.2 Inorganic nutrients and dissolved organic carbon

Inorganic nutrient concentrations were measured following the methods of Parsons et al. (1984). In presentation, only phosphate (PO_4) data were shown since the nitrate (NO_3) samples of the PRD survey were ruined during storage processes. A good correlation was observed between NO_3 and PO_4 (Fig. 2) in the shelf-mapping study (cruise # OR1 929). Samples for dissolved organic carbon were filtered through a Whatman GF/F filter precombusted at 550 °C. Filtrates

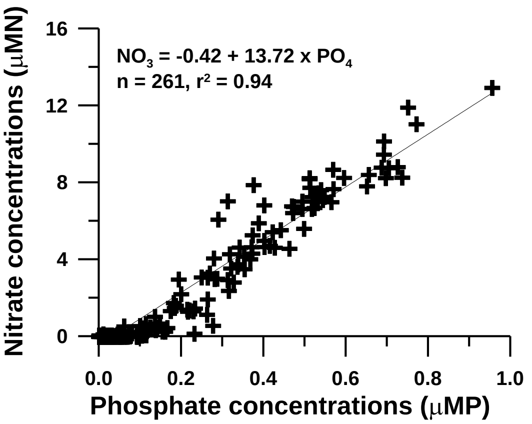

Fig. 2. Scatter plot of nitrate vs. phosphate concentrations derived from the data set of the shelf-mapping cruise conducted in June 2010. The regression line is significant at the $p = 0.01$ level.

were filled into precombusted 40 mL glass vials (Kimble). After the addition of several drops of 80 % H_3PO_4 (Emsure, Merck), vials were sealed with precombusted aluminium foil and screw caps with Teflon-coated septa. Before analysis, samples were acidified with 2 mL of 80 % H_3PO_4 and purged with CO_2-free O_2 at a flow rate of 350 mL min^{-1} for > 10 minutes. Samples were analysed by means of high temperature catalytic oxidation method with a Shimadzu TOC 5000. All samples were blank- (20-25 µM) corrected with the deep-sea water (−3000 m) from the South China Sea (DOC, 45–50 µM).

2.3 Bacterial production and primary production

Bacterial activity was measured by ^{3}H-thymidine incorporation (Fuhrman and Azam, 1982). Bacterial biomass (BB) and production (BP) in C units were derived with a thymidine and a carbon conversion factor of 1.8×10^{18} cell mole^{-1} and 2×10^{-14} gC cell^{-1}, respectively (for details see Shiah et al. (2003)). Bacteria carbon demand was calculated by dividing bacterial production by a globally averaged bacterial growth efficiency of 20 % (Ducklow and Carlson, 1992). Primary production was measured by the ^{14}C assimilation method (Parsons et al., 1984) with 10 neutral density filters (LEE filters) and incubated for 1–3 h in a self-designed tank with an artificial light source (−2000 µE m^{-2} s^{-1}). After incubation and acidification (0.5N HCl), the radioactivity collected in the 0.2 µm polycarbonate (PC) filter was then counted in a scintillation counter (Packard 2200) (See Shiah et al. (2003) for details).

2.4 Data management and statistical analysis

To compare the spatio-temporal (horizontal) variation of the bulk properties of measured variables, the depth-averaged value at a given station was obtained by dividing the depth-integrated (trapezoidal method) value by the DSD of that station. Statistical analysis was performed using SPSS® V12.0 software.

3 Results

3.1 Diel patterns of the anchored study

3.1.1 The Pearl River mouth (station 14)

As affected by the freshwater input from the Pearl River and tidal effects, a strong vertical gradient of σ_T (3–23 kg m^{-3}; Fig. 3a) occurred with lower values in the surface, and then increased with depth. PO_4 ranged from < 0.001 to 0.172 µMP, with a layer of high values occurring at shallow waters (5–10 m depth) during the first four sampling points (i.e. night-time) and the other one in the deep waters (> 20 m depth) after the high values at shallow depth disappeared (Fig. 3b). Vertical profiles of dissolved organic carbon (DOC, 62–160 µMC; Fig. 3c) and BP (2.2–17.2 mgC m^{-3} d^{-1}, Fig. 3d) over 24 h were in phase (see analysis below), with two higher anomalies, one of which observed in bottom waters (depth > 20 m) during night-time, and the other one appearing in surface waters during daytime.

3.1.2 The Dong-Sha Atoll (station 2)

The σ_θ profile (Fig. 4a, 21.2–24.8 kg m^{-3}) signalled diurnal tide. PO_4 concentrations (Fig. 4b, 0.015–0.536 µMP) changed positively with salinity (33.89–34.52 psu; $r = +0.96$, $n = 54$, $p < 0.001$). DOC concentrations (Fig. 4c, 53–99 µMC) generally were high in the surface waters and decreased with depth. Occasionally, high DOC values (concentrations > 80 µMC) could be observed at the mid- or deep waters. DOC showed a negative correlation with salinity ($r = -0.40$, $n = 54$, $p < 0.01$). BP varied fourfold, ranging from 1.14 to 4.55 mgC m^{-3} d^{-1} (Fig. 4d), and showed no correlation with DOC (see analysis below).

3.2 Vertical structures of the PRD transect and the shelf-mapping studies

The vertical structures of the four transects (i.e. T1–T4) of the shelf-mapping study were quite similar to that of the PRD study. Data of the PRD transect were used for illustration. Along the PRD transect, σ_T (Fig. 5a) ranged from 14.0 to 24.5 kg m^{-3}. PO_4 concentrations (Fig. 5b, 0.006–0.592 µMP) were high in the near-shore area and decreased seaward. Outside the near-shore area, P depletion occurred in the surface water extending to depths of 20–50 m. DOC (Fig. 5c) ranged from 60 to 107 µMC with two distinctively high anomalies, one of which occurred at the Pearl River mouth and the other at the upper water column outside the mid-shelf area. BP (Fig. 5d, 1.1–9.8 mgC m^{-3} d^{-1}) varied ∼9-fold, with higher values in the near-shore area, and then

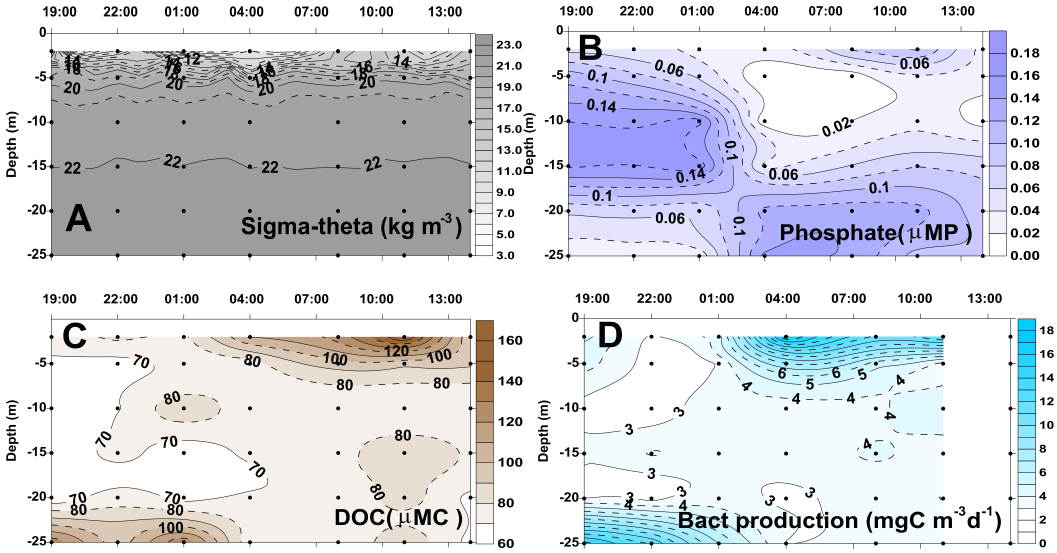

Fig. 3. Depth contours of measurements collected from the anchored study of station 14 located at the Pearl River mouth. The top axis shows sampling time of day.

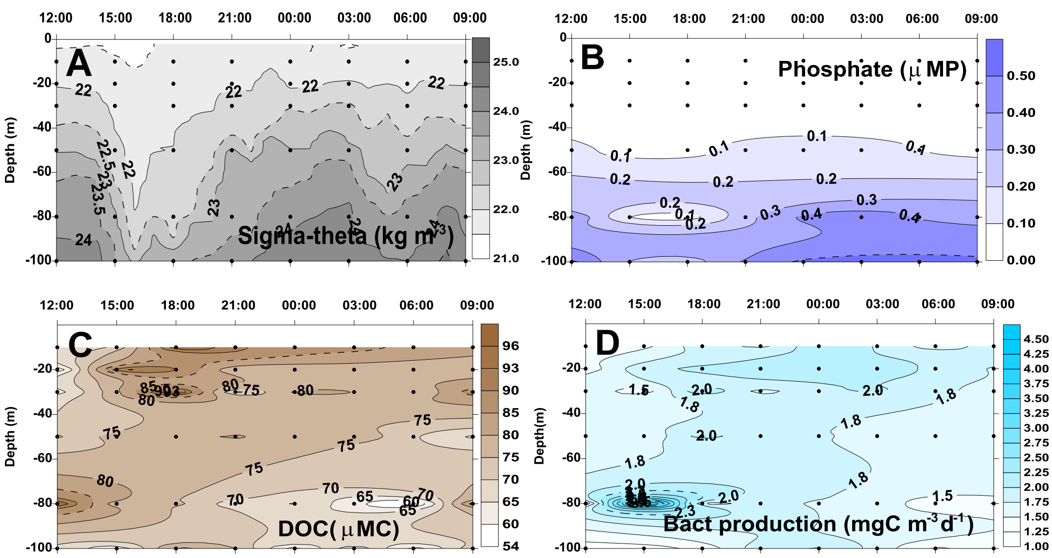

Fig. 4. Depth contours of measurements collected from the anchored study of station 2 located northwest of the Dong-Sha Atoll. The top axis shows sampling time of day.

decreased dramatically seaward. Outside the near-shore area, BP values were high at the surface and then decreased with depth. High BP in the bottom waters could also be observed at the inner-shelf stations.

Table 1 reveals the relationship between individual depth measurements of BP and DOC. We found that the BP vs. DOC relationship differed between inner-shelf and outer-shelf regions in both cruises. For the anchored and PRD transect studies, BP was positively correlated with DOC in the inner-shelf (bottom depth < 100 m) stations, while those of the outer shelf showed no correlation. This phenomenon was observed again in the shelf-mapping study, in which BP increases linearly with rising DOC only in the inner shelf. The BP–DOC correlation was not seen in regions of deeper water (Fig. 1, marked by blue dots).

3.3 Horizontal patterns of the shelf-mapping study

Depth-averaged salinity (31.27–34.48 psu, figure not shown) showed strong gradient with fresher water in the inner shelf, with salinity increasing seaward. Concentrations of depth-averaged PO_4 (IPO_4, 0.01–0.49 µMP; Fig. 6a) were

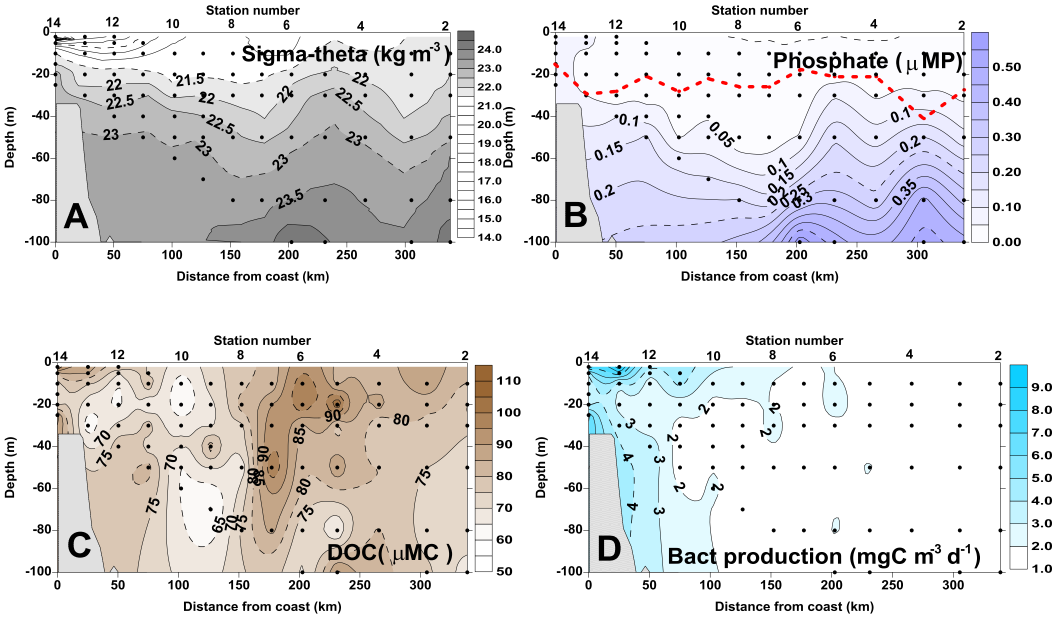

Fig. 5. Depth contours of measurements collected from the PRD transect study in June 2009. Data of stations 2 and 14 used here were the averages of the anchored investigations. The red dashed line in panel B indicates the mixed layer depth.

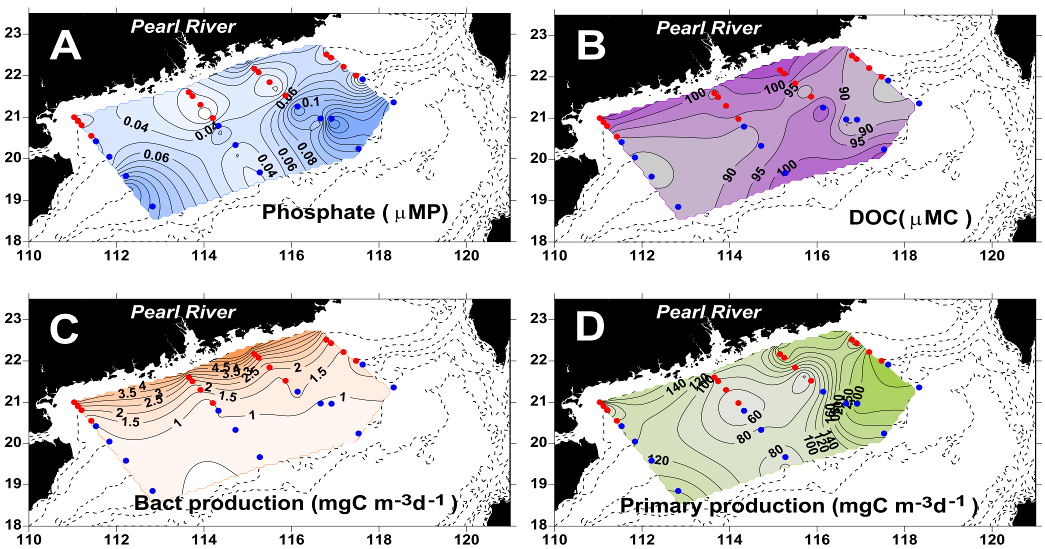

Fig. 6. Contour plots of the depth-averaged measurements collected from the June 2010 cruise in the South China Sea shelf. Inner-shelf (bottom depth < 100 m) and outer-shelf stations are indicated by red and blue dots, respectively.

low in the inner shelf and increased seaward. Higher IPO_4 values were recorded at the SE and SW corners of the sampling area. These two high anomalies resulted from high PO_4 concentrations in the deep waters (Fig. 5b) after integration and averaging processes. Depth-averaged DOC (IDOC; Fig. 6b, 65–116 µMC) declined seaward, and then increased again from the mid- to outer shelf. Depth-averaged BP (IBP, Fig. 6c) ranged from 0.5 to 9.6 $mgC\,m^{-3}\,d^{-1}$ with a seaward decreasing trend. Depth averages of primary production (IPP, Fig. 6d) varied > 50-fold with a range of 0.4–20.6 $mgC\,m^{-3}\,d^{-1}$.

Surface-water DOC concentrations of the shelf-mapping (71–169 µMC) investigation changed negatively with salinity (Sal; 28.69–34.22 psu; $r = -0.54$, $n = 28$, $p < 0.05$), and the PRD transect (DOC, 63–160 µMC; Sal, 15.54–33.92 psu) study showed the same trend ($r = -0.42$, $n = 28$, $p < 0.05$; Fig. 7a). Note that most of the DOC readings of these two studies deviated from the conservative mixing line derived

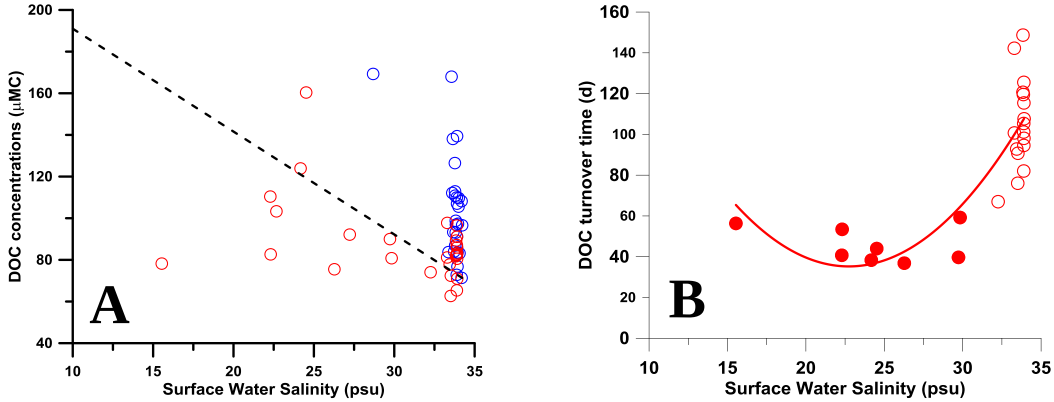

Fig. 7. Scatter plots of **(A)** surface salinity vs. surface DOC concentrations of the PRD transect (red open circles) and shelf-mapping (blue open circles) studies, and **(B)** surface salinity vs. DOC turnover time of the PRD transect study. The black dashed line in **(A)** indicates the conservative mixing line derived from He et al. (2010). The red solid line in **(B)** is significant ($r^2 = 0.72$, $n = 25$) at a p level of 0.01. The red solid circles in **(B)** indicate data inside the mid-shelf area.

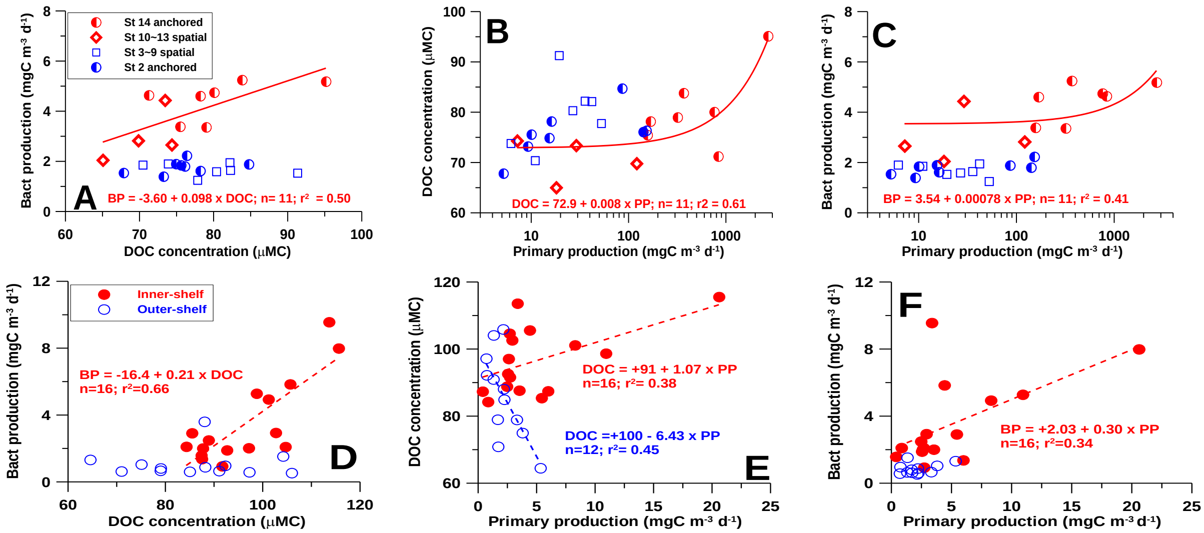

Fig. 8. Scatter plots of the depth averages of bacterial production vs. DOC concentrations vs. primary production of the PRD transect study **(A–C)** and the shelf-mapping study **(D–F)**. Solid and dashed lines indicate significance at the $p < 0.01$ level. x–y axes in log scale are for better representation.

from a previous Pearl River estuary study (He et al. (2010), their Fig. 3f). The distinct salinity ranges of these two cruises indicated that the PRD transect study was much more affected by the Pearl River than the shelf-mapping study (Fig. 7a). In the PRD transect study, DOC turnover times (i.e. DOC concentration divided by bacterial carbon demand) were homogeneously low (37–60 days) inside the mid-shelf (Sal < 30.00 psu) area, and then increased significantly to values > 100 days in the outer shelf (Fig. 7b).

Figure 8 portrays the relationships among the depth-integrated averages of IBP, IDOC and IPP. Similar to the results shown in Table 1, we saw positive correlations between IBP and IDOC in the inner shelf on both cruises (Fig. 8a and d). Moreover, in these shallow-water regions, IDOC vs. IPP (Fig. 8b and e) and IPP vs. IBP (Fig. 8c and f) also indicated positive relationships. In the outer shelf, IBP neither correlated with IDOC nor with IPP. Note that the relationship between IPP and IDOC in the outer shelf of the shelf-mapping cruise (Fig. 8e) was a negative one. Furthermore, the ratios of IBP to IPP (23–426 %) within the MLD in the inner-shelf region could be expressed as a positive function of phosphate (Fig. 9) and nitrate (data not shown; $r^2 = 0.55$, $n = 16$, $p < 0.01$) concentrations. The relationships of the ratios (21–136 %) vs. IPO_4 and the ratios vs. INO_3 (depth-averaged nitrate) in the outer shelf were insignificant.

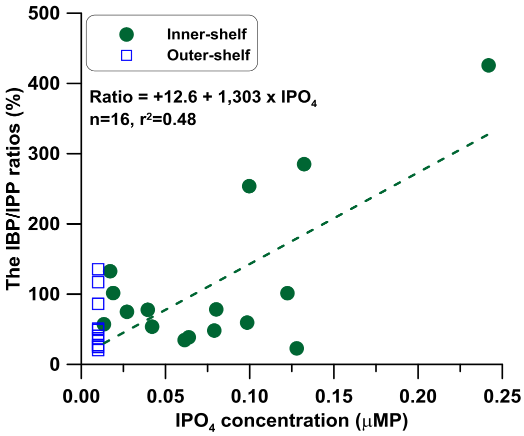

Fig. 9. Scatter plot of the ratio of depth-averaged bacterial production (IBP) to depth-averaged primary production (IPP) vs. depth-averaged phosphate concentration (IPO_4) within the mixed layer depth of the inner and outer shelf. The phosphate data of the outer shelf were < 0.01 µMP after integration and averaging processes (cf. Fig. 5b). The dashed regression line is significant at the $p = 0.01$ level. Data source: the shelf-mapping study in June 2010.

4 Discussions and conclusions

Continental shelves are ecosystems connecting lands and oceans. As affected by the import of terrestrial materials through river discharge, the shelves usually exhibit strong gradients of inorganic nutrients and thus biological activity. This eutrophic to oligotrophic gradient may serve as an ideal experimental site to examine our hypothesis, i.e. the effects of inorganic nutrient supply on the coupling/decoupling of BP with PP and thus DOC dynamics.

An advantage of using summer data sets in this analysis is that it better contrasts the nutrient conditions between inner and outer shelf. This is due to the discharge peak of the major rivers along the coast of southern China peak in summer, such as the Pearl River. Another advantage is that the warmer water temperature and ample sunlight in summer may potentially create a non-physical limiting environment for bacterial and phytoplankton activity, respectively. On the other hand, the N : P molar ratio (Fig. 2) was also less than 16 to 1, suggesting a potential N limitation for primary production (Redfield et al., 1963).

The South China Sea is one of the few marine systems possessing significant internal waves and tides (Chang et al., 2006; Jan et al., 2008; Alford et al., 2010). As internal waves propagate westward from the Luzon Strait to the SCS shelf, they disperse in the form of depression waves moving downward in deep-water region and elevation waves moving upward in shallow-water areas. The elevation waves occur in the area where its bottom depth is less than twice of the MLD (Liu et al., 1998).

The averaged MLD in SCS is about 50 m (e.g. Qu et al., 2007; Wong et al., 2007), meaning that the area with a bottom depth $<$ ca. -100 m (infer Fig. 1) might receive continuous extra nutrient supply from the bottom waters via elevated internal wave processes in spite of strong stratification in summer. In other words, we suspect that bacterial and algal growth in the whole water column of this shallow area was probably not nutrient-limited (see below). Therefore, it is of no surprise to see a cutoff at the 100 m depth for the different BP–DOC (Table 1) and IBP–IDOC–IPP (Fig. 8a–f) relationships in shallow- and deep-water regions. More specifically, the positive coupling of IBP–IDOC–IPP relationship in the nutrient-rich inner-shelf area and the non-coupling of IBP–IDOC–IPP relationships in the oligotrophic outer-shelf area justifies the adequacy of our hypothesis.

The anchored observations suggest that our hypothesis can be applied to explain the coupling/decoupling at an hourly scale. Station 14, located at the river mouth of the Pearl River, is a nutrient-rich system (Fig. 3b), resulting in synchronous changes of the vertical and horizontal structures of BP (Fig. 3c) and DOC (Fig. 3d) over one diel cycle. Alternatively, the growth of bacteria and phytoplankton at station 2 were very possibly limited by nutrient supply due to its remoteness from land, strong stratification in summer and the lack of elevation internal waves (bottom depth -250 m) property. This indicates that bacterial and algal activity in a mineral-limiting environment/condition oscillated but were never in phase (Thingstad et al., 1997).

As mentioned previously, under the MM scenario, bacterial biomass could be kept low by bacterivory. We do not have the virus and flagellate data, thus making the top-down control analysis impossible. However, multiple linear regression analysis (Edwards, 1985) of BB and Bµ (independent variables) on BP (dependent variable) can be used to evaluate the relative importance of the former two in shaping the variance of BP. Our analysis indicates that for all the outer-shelf data (see Fig. 8, blue symbols), the equation can be expressed as $BP = -0.16 + 0.14(\pm 0.01) \times BB + 7.55(\pm 0.46) \times B\mu$ ($n = 105$, $r^2 = 0.73$, $p < 0.001$). The partial regression coefficients (i.e. slope/mean) of BB and Bµ were both significant, with values of 0.012 and 47.97, respectively. This means that Bµ was 3849-fold (47.97/0.012) more powerful than BB in affecting BP.

In the coastal zone, supplies of organic substrate (i.e. DOC) from autochthonous and allochthonous sources may affect bacterial growth simultaneously. DOC export from the Pearl River mouth to the shelf area was estimated 0.53×10^9 gC d^{-1} (He et al., 2010). Similar to the finding of He et al., (2010, their Fig. 3f), we also observed a sharp removal of DOC in the inner-shelf area of the PRD transect study (Fig. 7a), which reflected the contribution from bacterial degradation. Our result indicates that DOCs in this area were turned over (by bacteria) differentially: the closer to the Pearl River/coast, the faster the DOC turnover rate (Fig. 7b).

Three possible mechanisms were proposed. DOC originated from Pearl River might be chemically more labile than those at the outer brim of the inner shelf, or the higher inorganic nutrient supply of the river mouth facilitate bacterial activity resulting in shorter DOC turnover time (Fig. 7b, more discussion below), or bacteria community structures were different. Note that this study does not have any related data to back up the three speculations listed above. We merely point out the phenomenon and suggest the potential mechanisms. For example, we were not able to identify the relative contribution from allochthonous and autochthonous sources quantitatively. We did not examine DOC consumptions at the river and ocean members to determine their bioavailability. It is interesting that the turnover timescale inside the mid-shelf area reported here (37–60 days, Fig. 7b) was quite similar to that ($\sim$22 days) found in incubation experiments conducted outside the Pearl River mouth area by Hung et al. (2007).

That heterotrophic bacteria can take up and compete with phytoplankton for limiting nutrients in oligotrophic environments has been proposed (Azam 1998; Thingstad et al., 2005, and citations therein). It has been documented that in nutrient-deficient systems, bacteria were responsible for the major uptake of the limiting nutrient due to its superior competition (smaller size, and thus larger surface-to-volume ratio) capacity (Currie and Kalff 1984; Thingstad et al., 1997; Vadstein, 2000). Phytoplankton–bacteria interactions may span from symbiotic to pure parasitic relationship (for a review, see Grossart et al. (2005)). Whether these relationships tend to be the former or the latter greatly depends on environmental conditions (e.g. nutrient supply) and presumably on the function of bacteria present. Competition on the same limiting resource is critical in shaping the interactions (i.e. production ratio, Fig. 9) between bacteria and phytoplankton. Grossart (1999) demonstrated that growth of both bacteria and algae was significantly enhanced when inorganic nutrients were rich. On the other hand, bacteria could inhibit algal growth when inorganic nutrients were limiting. The positive correlation of the IBP / IPP ratios to IPO_4 in the inner-shelf area (Fig. 9) further suggested that bacteria had a much higher P requirement than phytoplankton (Vadstein et al., 1988, 1993) and that bacteria could be much more sensitive than algae to P pulse.

Many mesocosm or bottle experiments have revealed that the addition of limiting nutrients could facilitate bacterial DOC degradation. Shiah et al. (1998) showed that DOC turn-over rate in the western equatorial Pacific could be enhanced two- to ninefold when inorganic nutrients were added. Similar findings were also reported in the Baltic and the Mediterranean seas (Zweifel et al., 1993), the North Atlantic (Kirchman et al., 1991), the Gulf of Mexico (Pomeroy et al., 1995) and even in estuarine ecosystems (Shiah and Ducklow, 1995).

The interactions between bacteria and algae will eventually affect DOC dynamics (accumulation vs. depletion) in aquatic systems. Several studies of DOC accumulation in marine systems have been reported (Billen and Fontigny, 1987; Ittekkot et al., 1981; Copin-Montegut and Avril, 1993; Carlson et al., 1994). However, only modelling results (Thingstad et al., 1997) were used to further identify the mechanisms, and so far there have been no marine field data. In a subtropical reservoir study, Tseng et al. (2010) suggested that the extra supply of a limiting mineral (phosphate) delivered by typhoon could substantially elevate bacterial activity, resulting in significant DOC depletion during summer. It is noted that the results of Tseng et al. (2010) were derived from a freshwater ecosystem; we assume that their major conclusion is still applicable to marine systems. Our hypothesis was formed based on the major conclusions of the studies of Thingstad et al. (1997) and Tseng et al. (2010).

The results and our proposed hypothesis might have a noteworthy implication for the organic-C cycling in river-dominated continental margins, such as the Pearl River plume in the northern SCS. The nutrient loadings into the East and South China Sea shelves have increased exponentially during the last two decades (Dai et al., 2010; Xu et al., 2010), a trend that is likely to continue in the foreseeable future. As the mesotrophic area expands within the shelf, more and more DOC will be produced through elevating primary production (Fig. 8b and e). But the newly produced DOC would be quickly depleted by bacteria (Fig. 8a and d), creating a more heterotrophic system (i.e. higher IBP / IPP ratios, Fig. 9) in the shelf and a stronger CO_2 source. This coincided with the finding of Jiao et al. (2011), which argued that the elevation of anthropogenic nutrient discharge into the coastal and shelf sea might potentially amplify microbial activity (i.e. bacterial respiration) so that the system might be acting more as a CO_2 source.

In conclusion, this study proposes and demonstrates that the supply of inorganic nutrients might affect the coupling or decoupling between the production of bacteria and phytoplankton in the South China Sea water during summer. The applicability of our hypothesis to other shelf systems and seasons (e.g. winter) awaits further testing.

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