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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 contrast 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 where inorganic nutrient supplies from river discharge and internal waves were potentially abundant, BP, DOC and PP were positively inter-correlated, whereas these three measurements became uncorrelated in the oligotrophic outer-shelf and slope. A previously proposed malfunctioning microbial-loop hypothesis was extended to address the availability of limiting mineral could affect the couplings/de-couplings between the source (i.e. phytoplankton) and sink (i.e. bacteria) of biogenic organic carbon, and thus DOC dynamics. The positive correlation of the BP/PP ratios vs. phosphate 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, to understand the processes regulating DOC dynamics (accumulation and depletion) is very important in 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. Internally, DOC can be generated from 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

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the organisms primarily responsible for DOC consumption (see Azam, 1998 for 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" theory, which affirmed that DOC accumulation occurred when bacteria production (a product of growth rate and biomass) was low. Their modeling work indicated that both bacteria growth and biomass could be oppressed by food-web mechanisms. Bacterial growth rate was kept low by bacteria–phytoplankton competitions for inorganic nutrients (i.e. bottom-up or substrate control), and biomass was kept low by bacteriovory (i.e. top-down or predators control). Their former finding explicitly highlighted the importance of inorganic nutrients supply in controlling the relationship between bacterial production (BP; DOC sink) and primary production (PP; DOC source). However, the applicability of this theory has not been examined with field data in marine systems.

We proposed an "Extended Malfunctioning Microbial-loop (i.e. EMM)" hypothesis which argues that strong couplings among BP, DOC and PP takes place in area/time with abundant nutrients supply. Under nutrient-limited condition, BP, PP and DOC would be out of phase with no positive correlations among them. 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 nutrient could be the major factor in shaping the relationships among BP, PP and ambient DOC concentrations in marine system. With two summer data sets collected from the South China Sea shelf, this study provides for the first time evidence indicating that the availability of limiting mineral could be the major factor in shaping the relationships among BP, PP and ambient DOC concentrations in marine systems.

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2 Materials and methods

2.1 Study site and sampling

Two types of cruise surveys covering tempo-spatial variation were conducted at the South China Sea (SCS; Fig. 1) shelf. For spatial study, one transect form 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. For the former, two anchored stations located outside the Pearl River mouth (St. 14; bottom depth ~ 30 m) and north-west off the Dong-Sha atoll (St. 2; bottom depth ~ 250 m) of the PRD cruise were visited. In these two anchored studies, water-column sampling was performed every 3 h. CTD was casted hourly. At each station, water samples were taken within the euphotic zone (25 m and 100 m for Sts. 14 and 2 respectively) from 6 depths. Profiles of temperature, salinity, fluorescence and underwater PAR (photosynthetic available radiance) 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 Whatman GF/F filter pre-combusted at 550 °C. Filtrates were filled into pre-combusted 40 mL glass vials (Kimble). After the addition of several drops of 80 % H_3PO_4 (Emsure; Merck), vials were sealed with pre-combusted aluminum 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 min. Samples were analyzed

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by high temperature catalytic oxidation method with a SHIMADZU, TOC 5000. All samples were blank (20–25 µM) corrected with the deep seawater (~ 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. Details see Shiah et al. (2003). 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 tempo–spatial (horizontal) variation of the bulk properties of measured variables, depth-averaged value at given station was obtained by dividing depth-integrated (trapezoidal method) value by the deepest sampling depth of that station. Statistical analysis was performed using the software of SPSS® V12.0.

3 Results

3.1 Diel patterns of the anchored study

3.1.1 The Pearl River mouth (St. 14)

As affected by the freshwater input from the Pearl River and tidal effects, a strong vertical gradient of Sigma-t ($3 \sim 23\,\mathrm{kg\,m^{-3}}$; Fig. 3a) occurred with lower values in the surface, and then increased with depth. Phosphate (PO_4) ranged $< 0.001 \sim 0.172\,\mu\mathrm{MP}$, with a layer of high values occurring at shallow-waters ($5 \sim 10$ 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 shallow-depth high values disappeared (Fig. 3b). Vertical profiles of dissolved organic carbon (DOC; $62 \sim 160\,\mu\mathrm{MC}$; Fig. 3c) and bacterial production (BP; $2.2 \sim 17.2\,\mathrm{mgC\,m^{-3}\,d^{-1}}$; Fig. 3d) over 24 h were in phase (see analysis below), with two higher anomalies, one of which observed at the bottom-waters (depth > 20 m) during night-time, and the other one appeared at the surface-waters during day-time.

3.1.2 The Dong-Sha atoll (St. 2)

Sigma-t profile (Fig. 4a; $21.2 \sim 24.8\,\mathrm{kg\,m^{-3}}$) signaled diurnal tide. PO_4 concentrations (Fig. 4b; $0.015 \sim 0.536\,\mu\mathrm{MP}$) changed positively with salinity ($33.89 \sim 34.52$ psu; $r = +0.96$, $n = 54$, $p < 0.001$). DOC concentrations (Fig. 4c; $53 \sim 99\,\mu\mathrm{MC}$) generally were high in the surface-waters, and decreased with depth. Occasionally, high DOC values (concs. $> 80\,\mu\mathrm{MC}$) 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 4-fold ranging $1.14 \sim 4.55\,\mathrm{mgC\,m^{-3}\,d^{-1}}$ (Fig. 4d), and showed no correlation with DOC (see analysis below).

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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 was used for illustration. Along the PRD transect, Sigma-t (Fig. 5a, 14.0 ~ 24.5 $kg\,m^{-3}$) were lower near the coast and in the surface-waters, and then increased seaward and with depth. PO_4 (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 ~ 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 decreased seaward dramatically. Outside the near shore area, BP values were high at the surface then decreased with depth. High BP in the bottom-waters could also be observed at the inner-shelf stations.

Table 1 revealed the relationship between individual depth measurements of BP and DOC. We found 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 (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 was observed to increase linearly with rising DOC only in the inner-shelf. The BP-DOC correlation was not seen in deeper water region (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 then increased seaward. Concentrations of depth-averaged PO_4 (IPO_4; 0.01 ~ 0.49 µMP; Fig. 6a) were low in the inner-shelf, and then increased seaward. Higher IPO_4 values were recorded at the N-E and S-W corners of

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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, then increased again from mid- to outer-shelf. Depth-averaged BP (IBP; Fig. 6c) ranged 0.5 ~ 9.6 $\mathrm{mgC\,m^{-3}\,d^{-1}}$ with a seaward decreasing trend. Depth-averages of primary production (IPP; Fig. 6d) varied > 50-fold with a range of 0.4 ~ 20.6 $\mathrm{mgC\,m^{-3}\,d^{-1}}$.

Figure 7 portrayed 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. 7a and b). Moreover, in these shallow water regions, IDOC vs. IPP (Fig. 7b and e) and IPP vs. IBP (Fig. 7c and f) also indicated positive relationships. In the outer-shelf, IBP neither correlated with IDOC nor with IPP. Noted the relationship between IPP and IDOC in the outer-shelf of the shelf-mapping cruise (Fig. 7e) was a negative one. Additionally, we found the ratios of IBP to IPP (23 ~ 426 %) within the mixed layer depth (i.e. MLD) in the inner-shelf region could be expressed as a positive function of phosphate concentrations (Fig. 8). The ratio (21 ~ 136 %) vs. IPO_4 relationship in the outer-shelf was insignificant.

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 activities. This eu-trophic to oligotrophic gradient may serve as an ideal experimental site to examine our EMM hypothesis, that is, 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 of the major rivers along the south China coast, such as the Pearl River, peak in summer. Another advantage is that the warmer water temperature and ample sunlight in

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summer may potentially create a non-physical limiting environment for bacteria and phytoplankton activities respectively.

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, and citations therein). As internal waves propagate westward from the Luzon Strait to the SCS-shelf, they are in forms of depression waves moving downward in deep-water region, and elevation waves moving upward in shallow-water area. The elevation waves occur in 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), and this means 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 suspected that bacterial and algal growth in the whole water column of this shallow area was probably not nutrient-limited. 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. 7a–f) responses 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 EMM hypothesis.

The anchored observations suggest that the EMM hypothesis can be applied to explain the coupling/decoupling at an hourly scale. St. 14, located at the river mouth of the Pearl River, could hardly be a mineral-limited system (Fig. 3b), which resulting in synchronous changes of the vertical and horizontal structures of BP and DOC over one diel cycle in this nutrient-rich environment (Fig. 3c and d). Alternatively, the growth of bacteria and phytoplankton at St. 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 indicated that bacteria and algal activities in mineral-limiting environment/condition oscillated but were never in phase (Thingstad et al., 1997).

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That heterotrophic bacteria can take up, and compete with phytoplankton for limiting nutrients in oligo-trophic environments has been well documented (Azam, 1998; Thingstad et al., 2005, and citations therein). 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 modeling results (Thingstad et al., 2005) 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 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. The EMM hypothesis was formed based on the major conclusions of the studies of Thingstad et al. (2005) and Tseng et al. (2010).

The results and our proposed EMM 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. 6b and e). But the newly produced DOC would be quickly depleted by bacteria (Fig. 6a and d), creating a more heterotrophic system (i.e. higher IBP/IPP ratios, Fig. 8) in the shelf and a stronger CO_2 source.

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

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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 & 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

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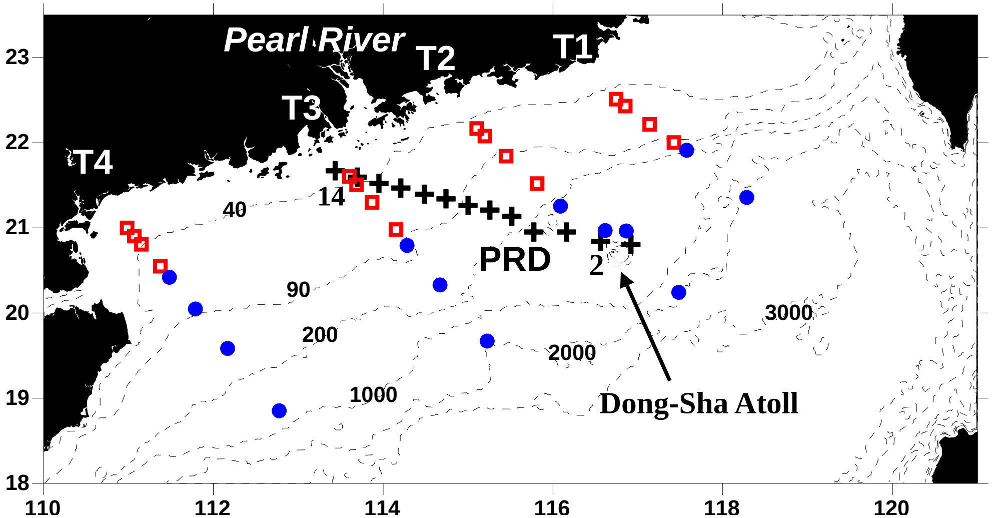

Fig. 1. Map of the South China Sea shelf showing sampling stations of the PRD (June 2009) and shelf-mapping (transects T1 ~ T4; June 2010) surveys. Stations of the PRD transect survey are marked by black crosses. Stations 2 and 14 located at the NW of the Dong-Sha atoll and the Pearl River mouth, respectively.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

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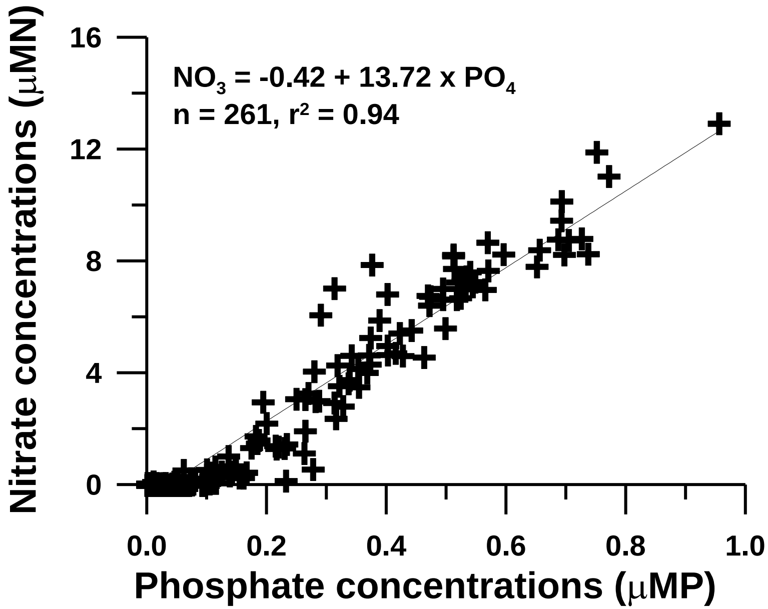

Fig. 2. Scatter plot of nitrate vs. phosphate concentrations derived from the data set of the shelf-mapping cruise conducted in June 2011. Regression line is significant at $p = 0.01$ level.

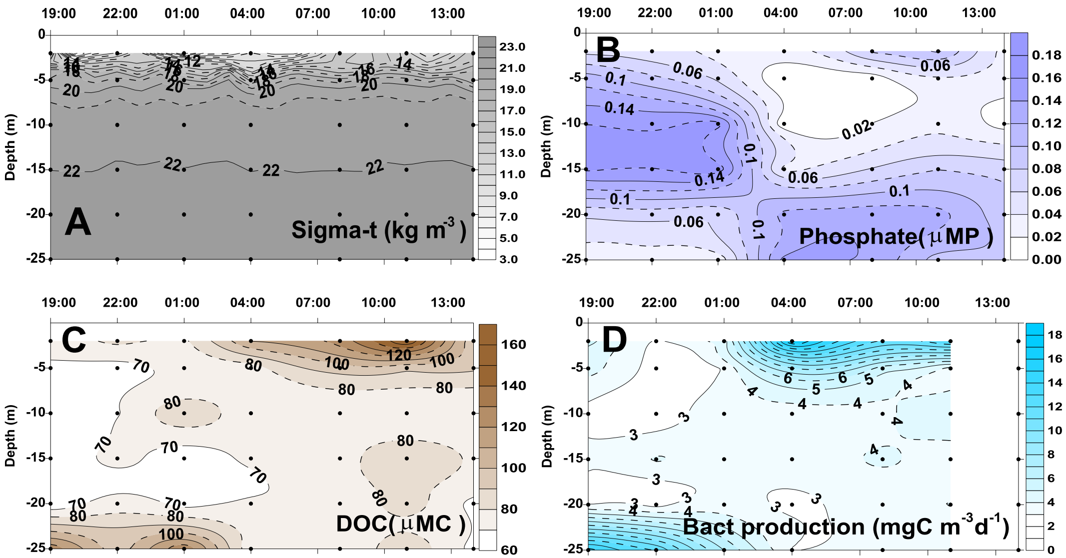

Fig. 3. Depth contours of measurements collected from the anchored study of St. 14 located at the Pearl River mouth. The top axis shows sampling time of the day.

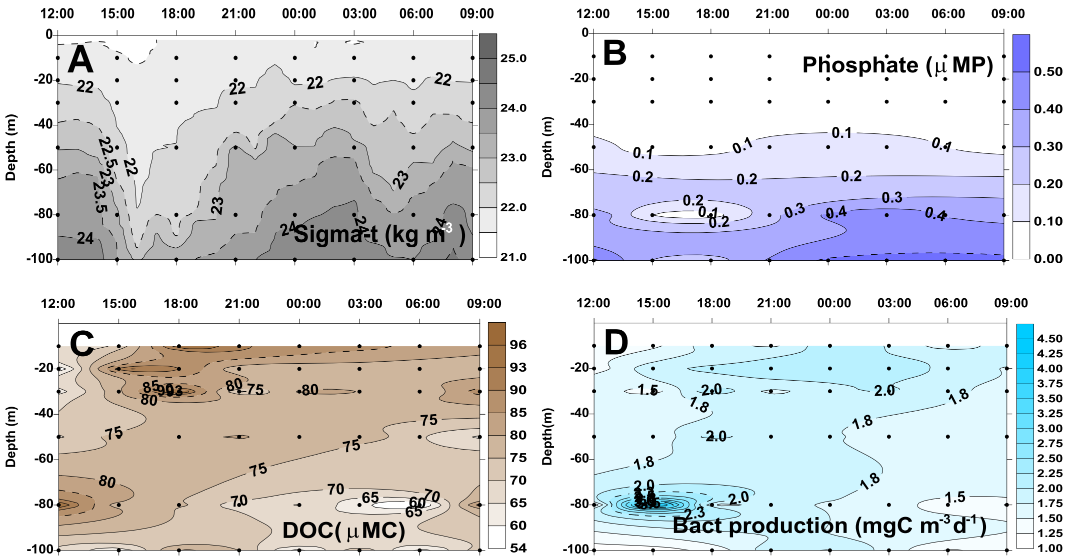

Fig. 4. Depth contours of measurements collected from the anchored study of St. 2 located at the north-west off the Dong-Sha atoll. The top axis shows sampling time of the day.

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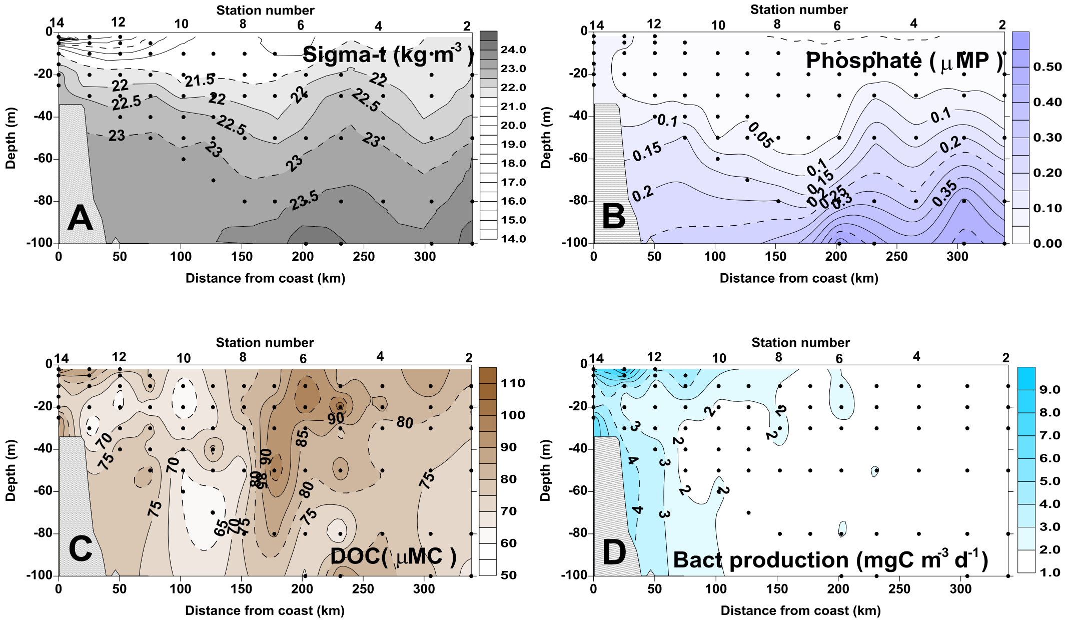

Fig. 5. Depth contours of measurements collected from the PRD transect study in June 2009. Data of Sts. 2 and 14 used here were the averages of the anchored investigations.

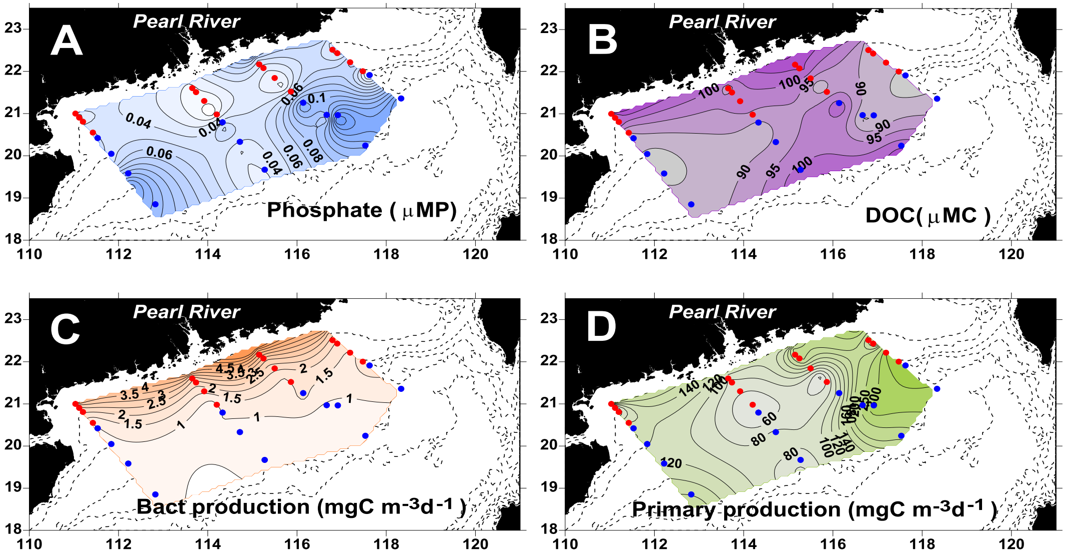

Fig. 6. Contour plots of the depth-averaged measurements collected from the June 2010 cruise in the South China Sea shelf. Inner-shelf (bottom depth < 100 m) and outer-shelf stations are indicated by symbols of red squares and blue dots respectively.

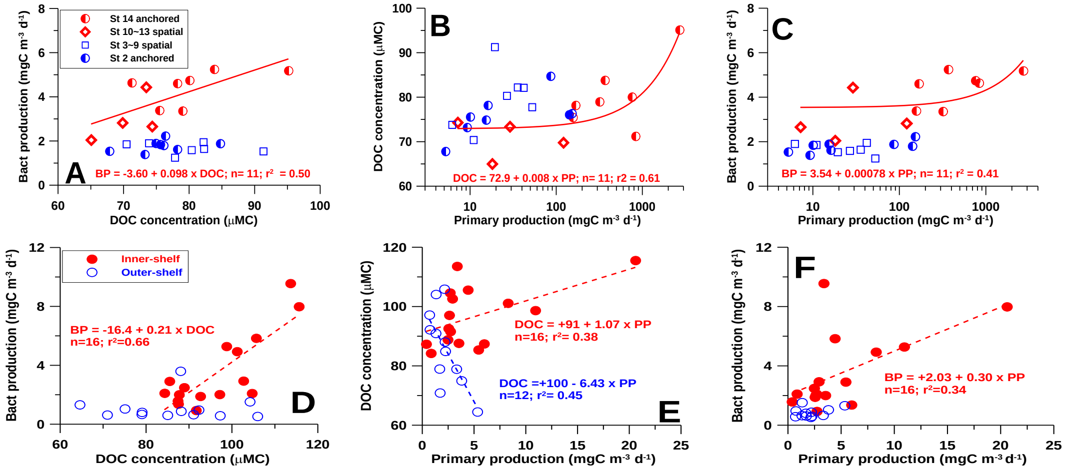

Fig. 7. The scatter plots of the depth-averages of bacterial production vs. DOC concentrations vs. primary production of the PRD transect study (A ~ C) and the shelf-mapping study (D ~ F). Solid and dash lines indicate significant at $p < 0.01$ level. x–y–axes in log scale are for better presentation.

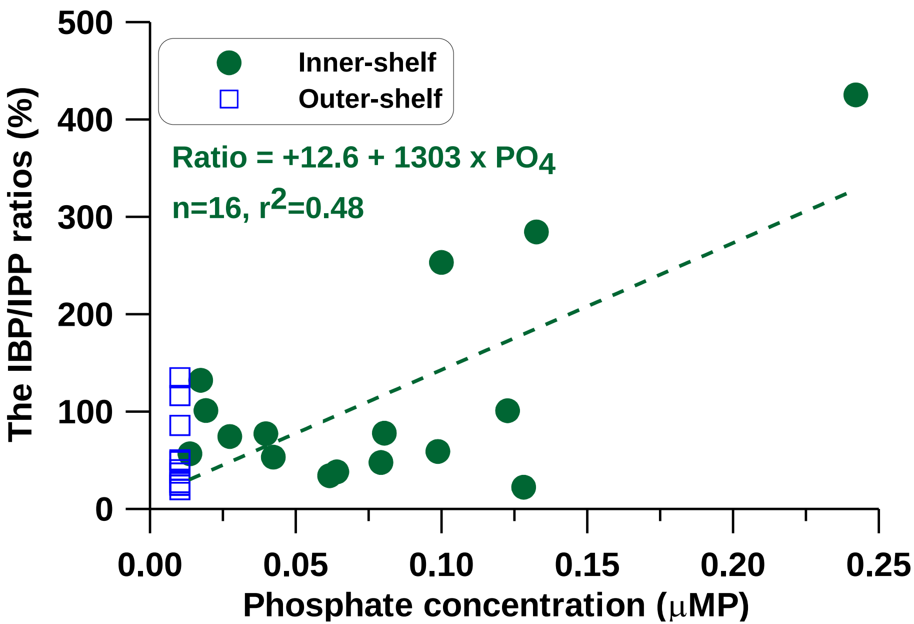

Fig. 8. Scatter plot of the ratio of bacterial production (IBP) to primary production (IPP) vs. depth-averaged phosphate concentration within the mixed layer depth of the inner- and outer-shelf. The phosphate data of the outer-shelf were < 0.01 μMP after integration and averaging processes (c.f. Fig. 6a). Dash regression line is significant at $p = 0.01$ level.

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