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Picoplankton and virioplankton abundance and community structure in Pearl River Estuary and Daya Bay, South China

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**ARTICLE INFO**

Article history:
Received 27 August 2014
Revised 26 December 2014
Accepted 29 December 2014
Available online 22 April 2015

Keywords:
Picoplankton
Virioplankton
Community composition
Flow cytometry

**ABSTRACT**

By using flow cytometry techniques, we investigated the abundance and composition of the heterotrophic prokaryotes, virioplankton and picophytoplankton community in the Pearl River Estuary and Daya Bay in the summer of 2012. We identified two subgroups of prokaryotes, high nucleic acid (HNA) and low nucleic acid (LNA), characterized by different nucleic acid contents. HNA abundance was significantly correlated with larger phytoplankton and Synechococcus (Syn) abundance, which suggested the important role of organic substrates released from primary producers on bacterial growth. Although LNA did not show any association with environmental variables, it was a vital component of the microbial community. In contrast to previous studies, the total virioplankton concentration had a poor relationship with nutrient availability. The positive relationship between large-sized phytoplankton abundance and the V-I population confirmed that V-I was a phytoplankton-infecting viral subgroup. Although the V-II group (bacteriophages) was dominant in the virioplankton community, it was not related with prokaryotic abundance, which indicated factors other than hosts controlling V-II abundance or the uncertainty of virus-host coupling. With respect to the picophytoplankton community, our results implied that river input exerted a strong limitation to Syn distribution in the estuary, while picoeukaryotes (Euk) were numerically less abundant and showed a quite different distribution pattern from that of Syn, and hence presented ecological properties distinct from Syn in our two studied areas.

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**Introduction**

Picoplankton are a key component in aquatic ecosystem structure and function (Gasol et al., 1997). As the smallest known component of autotrophic organisms, picophytoplankton have been documented to be of great importance in a variety of marine or ocean provinces (Tarran et al., 2001; Pan et al., 2007; Mitbavkar et al., 2012). In offshore oceanic areas usually 50 to 90% of the chlorophyll is found in particles < 2.0 μm, while a lower contribution but often higher cell numbers is observed in more eutrophic coastal areas (Søndergaard, 1991). Studies of prokaryotic production and distribution in estuaries and coastal areas provide evidence that prokaryotes significantly influence carbon cycling processes, not only by...
assimilating photosynthetically produced dissolved organic matter (Gasol et al., 1997; Lønborg and Søndergaard, 2009; Hoikkala et al., 2012) but also by serving as an important food resource for heterotrophic flagellates and ciliates (Ducklow et al., 1999).

Although the abundance of heterotrophic prokaryotes in the coastal waters is well documented, limited studies have considered flow cytometrically defined prokaryotic sub-groups. Currently, at least two distinct groups of prokaryotes are confirmed, characterized by their relative nucleic acid content (e.g. Li et al., 1995; Troussellier et al., 1999). In general, the high nucleic acid (HNA) fraction is usually considered to be the most metabolically active and responsible for most of the activity in the microbial communities (Zubkov et al., 2001) and is preferred by viruses (Bonilla-Findji et al., 2009), while the low nucleic acid (LNA) group has been proven to be inactive or dormant and is probably less susceptible to viral infection (Magiopoulosa and Pitta, 2012). However, there have been contrasting reports showing that LNA was not substantially different from HNA; furthermore, they could form an active part of microbial communities in seawater (Zubkov et al., 2001) and in freshwater (Nishimura et al., 2005). Hence, whether LNA represented a unique group or they were merely a different physiological status of HNA was still an open question (Wang et al., 2009).

Virioplankton, being $10^4$ to $10^8$ particles/mL in seawater, often tenfold more numerous than heterotrophic prokaryotes, is the most abundant and dynamic group among the microorganisms in the marine environment (Bergh et al., 1989). They regulate nutrient cycling via a viral shunt and impact microbial community composition by “killing the winner”, i.e., controlling the abundance and diversity of competitive dominants (Suttle, 2007). Due to the selective and parasitic natures of viroplankton, one would therefore expect a close linkage between virus and host abundance and community composition (Hennes et al., 1995; Steward et al., 2000). Previous studies on viral distributions revealed positive correlations with bacterioplankton (Wommack and Colwell, 2000; Hewson et al., 2001) and with chlorophyll (Maranger and Bird, 1995). Some studies also showed higher viral counts with higher trophic states (Cochlan et al., 1993; He et al., 2009), but several works found no direct link between viroplankton abundance and trophic conditions (Corinaldesi et al., 2003).

Investigations into the spatial distribution of prokaryotes and viroplankton have been conducted in various ecosystems (Wommack and Colwell, 2000; Clasen et al., 2008), as well as in the Pearl River Estuary (He et al., 2009). In terms of picopelagian in this estuary, the distribution is becoming increasingly well understood (Qiu et al., 2010; Lin et al., 2010; Zhang et al., 2013). However, few data are available on the abundance and community structure of picopelagian and viroplankton and their connection along the gradient in the Pearl River Estuary. On the other hand, there is still a critical lack of information about the dynamics of microbial communities, particularly viral and picopelagian interactions in Daya Bay. The aims of this study were: (1) to give a detailed picture of the community structure of picopelagian, prokaryotes and viruses; (2) to examine their statistical relationship to each other; and (3) to assess their potential links with environmental parameters in the two coastal waters.

1. Materials and methods

1.1. Description of the study area

A cruise during August 14 to September 5, 2012 was conducted with the research vessel Haijian 73 (Fig. 1). The investigated areas can be divided into 2 parts (Fig. 1): the Pearl River Estuary with 14 stations and Daya Bay with 5 stations. The Pearl River Estuary, which lies in southern Guangdong Province, is created by inflows of the Pearl River to the South China Sea. Around 53% of the river runoff empties into the estuary through the four western outlets, namely Humen (HUM), Jiaomen (JM), Hongqimen (HQM) and Hengmen (HEM). The annual average freshwater discharge from the Pearl River into the Pearl River Estuary is 10,524 m³/sec (Zhao, 1990). River discharge in dry and wet seasons is distinct, with roughly 80% of the annual input being delivered to the South China Sea during the wet season (April–September) (Zhao, 1990).

Daya Bay is a semi-closed bay. It covers an area of 600 km², with a width of about 15 km and a north–south length of about 30 km. About 60% of the area in the Bay is less than 10 m deep (Xu, 1989; Wang et al., 2006). No major river discharge into Daya Bay, but there are three small rivers that discharge into Dapeng Cove (located south-west of the bay). Most of the waters in Daya Bay originate from the South China Sea intrusion.

1.2. Station locations and sampling

Vertical profiles of salinity and temperature were recorded in situ using a YSI6600 multi-probe sensor (Yellow Springs Instrument Co., Yellow Springs, OH, USA). The probes were calibrated both before and after the cruise. Water samples were collected 0.5 m below the surface and 0.5 m above the bottom at all stations, using 5 L Niskin bottles. All nutrient parameters were the average value between the surface and bottom layers. All samples for picopelagian were also pre-filtered through 20 μm mesh netting.

DIN (dissolved inorganic nitrogen) was the sum of the concentrations of nitrate, nitrite and ammonia. Nitrate (plus nitrite) and ammonium were determined manually following the procedures of Wood et al. (1967) and Slayyk and MacIsaa (1972). The orthophosphate concentration was measured based on the methods of Armstrong et al. (1967).

1.3. Analysis of heterotrophic bacteria and viroplankton

For heterotrophic prokaryotes and viroplankton, triplicate sub-samples (1.8 mL) were dispensed into three sterile cryovials (2 mL) and were fixed with glutaraldehyde (final concentration 0.5%) for 30 min at 4°C, frozen in liquid nitrogen and stored at −80°C in the laboratory until analysis. Prokaryotic samples were stained with SYTO-13 (Molecular Probes Inc., Eugene, OR, USA) at a final concentration of 5 μmol/L, and left for approximately 10 min in the dark to complete the staining. For viroplankton enumeration, thawed samples were diluted in autoclaved and 0.2 μm filtered 1×TE buffer (10 mM Tris, 1 mM EDTA, pH 8) and stained with SYBR Green I (Molecular Probes®, final dilution: 5 × 10⁻⁵ of the commercial stock solution) for 10 min in the dark at 80°C water bath prior to analysis in the flow cytometer.
We used a FACScalibur bench cytometer (Becton and Dickinson) with a laser emitting at 488 nm. 10 μL of a solution of 0.92 μm Polysciences latex beads was added (final concentration 10^5 beads/mL) as an internal standard and used to normalize values of single-cell variables. Aliquots (0.4 mL) were run at low flow rate (~15 μL/min) until acquisition of 10,000 events. Prokaryotic sub-groups were defined as high HNA and LNA groups with different green fluorescence intensities (Li et al., 1995; Gasol et al., 1999; Fig. 2a). Viral sub-groups were partitioned into two fractions (V-I and V-II) based on their differences in green fluorescence and side scatter (Marie et al., 1999; Fig. 2b). Viral sub-groups were defined as high HNA and LNA groups with different green fluorescence intensities (Li et al., 1995; Gasol et al., 1999; Fig. 2a). Viral sub-groups were partitioned into two fractions (V-I and V-II) based on their differences in green fluorescence and side scatter (Marie et al., 1999; Fig. 2b).

1.4. Analysis of larger phytoplankton and picophytoplankton

Larger phytoplankton (including nano- and micro-phytoplankton) samples (1 L) were preserved in 1% acidified Lugol’s iodine solution and concentrated into a volume of 5–25 mL after sedimentation for 48 hr. Taxonomic identification and enumeration were carried out using an inverted microscope with the Utermöhl technique (Utermöhl, 1958) in the lab. For picophytoplankton counting, samples were fixed with formaldehyde (2% final concentrations) for 15 min, frozen in liquid nitrogen and analyzed within a month. We differentiated two major picophytoplankton populations (Synechococcus (Syn) and pico-eukaryotes (Euk)) based on FL2 (orange fluorescence) vs. FL3 (red fluorescence) and side scatter vs. FL3 signatures (Fig. 2c). Data were collected, saved, and analyzed with CellQUEST software (BD Biosciences, San Jose, CA, USA).

1.5. Data analysis

Significant relationships between heterotrophic prokaryotes, virioplankton, and picophytoplankton and environmental parameters were determined using Pearson’s correlation. The biological data were log-transformed to meet the normality assumptions of least squares regression analysis. Statistical analysis was performed using SPSS Statistics 17.0 for Windows. A significance level of 0.05 was used. The distribution maps of abiotic variables and biotic groups were constructed using Surfer 11.0 (Golden Software Inc., Golden, CO, USA).

![Fig. 1](image1.png)

**Fig. 1** – Stations in the Pearl River Estuary and Daya Bay during the August 2012 cruise.

![Fig. 2](image2.png)

**Fig. 2** – Representative cytograms used to determine bacterial (a), virioplankton (b) and picophytoplankton (c) abundance in the summer of 2012. HNA: high nucleic acid; LNA: low nucleic acid. V-I: phytoplankton virus; V-II: bacteriophage. SYN: Synechococcus; Euk: picoeukaryotes.
2. Results

2.1. Abiotic variables

In the summer of 2012, there was a distinct salinity gradient in the Pearl River Estuary along the north–south transect from sampling sites P1 to P12. Surface salinity at the head of the estuary, P1, was approximately 0.9‰ and reached 11.8‰ at midstream of site P9, and up to 30.5‰ at outer site P14 (Fig. 3a). In Daya Bay, the Pearl River Estuary plume water diminishes the salinity, and the high-salinity intruding waters from the South China Sea are under the influence of the weak monsoons southwesterly during summer (Wu and Wang, 2007). Hence, salinity in Daya Bay was lowest at site D1 (27‰) and reached the highest value at site D3 station (32.0‰).

In the Pearl River Estuary, DIN concentration approached the maximal value (116.6 μM) at the head of the estuary and decreased sharply to 32.3 μM at the southernmost P14 station (Fig. 3b). However in Daya Bay, DIN concentration was extremely low, ranging from 1.5 to 2.5 μM. The horizontal distribution revealed that the DIN concentration increased from east to the west in Daya Bay, probably because of high-nutrient-loaded discharges of effluents from culture zones in west coastal waters. The distribution pattern of orthophosphate was similar to that of DIN, with peak values at the head of the Pearl River Estuary and western region of Daya Bay (Fig. 3c). With regard to its averaged concentration, it was much higher in the Pearl River Estuary (0.48 μM) than in Daya Bay (0.14 μM).

2.2. Heterotrophic prokaryotes and virioplankton abundance and their community composition

In our study, total averaged abundance of prokaryotes in the Pearl River Estuary was 10.31 × 10^5 cells/mL, ranging from 3.51 to 17.23 × 10^5 cells/mL, while total prokaryote abundance in Daya Bay waters was 14.55 × 10^5 cells/mL, varying from 3.61 to 19.56 × 10^5 cells/mL. Specifically, two bacterial sub-groups (LNA and HNA) were observed at all stations during this summer cruise. LNA abundance contributed up to 52.9% of total prokaryotic abundance in Daya Bay and 76.3% in the Pearl River Estuary waters, respectively. Its absolute abundance ranged from 2.82 (P13) to 17.13 × 10^5 cells/mL (site P2) in the two studied areas. Mean HNA abundance was 3.96 × 10^5 cells/mL, varying from 0.02 (site P4) to 10.92 × 10^5 cells/mL (D2) in these two coastal waters (Fig. 4a).

Total virioplankton density was slightly higher than total prokaryotic abundance (Fig. 4b). The averaged virioplankton abundance in the Pearl River Estuary was 19.10 × 10^5 cells/mL, ranging in (7.42–34.32) × 10^5 cells/mL, and the highest density occurred at P4 station in the eastern section. Mean viral abundance in Daya Bay (36.32 × 10^5 cells/mL) was almost two-fold greater than that in the Pearl River Estuary, and the highest abundance occurred at site D2 station. Two viral subgroups (V-I and V-II) were consistently observed at all stations in both regions. The viral community was dominated by V-II, which represented up to 73.9% of total virioplankton abundance in both studied areas. Spatial distribution patterns for these two viral groups were similar in the two studied regions. On the whole, V-I abundance varied from 1.89 (site P11) to 33.32 × 10^5 cells/mL (site D2), with a mean value of 6.68 × 10^5 cells/mL, while mean V-II abundance was 16.96 × 10^5 cells/mL, varying from 5.53 (P11) to 38.94 × 10^5 cells/mL (site D2).

2.3. Phytoplankton abundance and community composition

The average density of larger phytoplankton was 6.02 × 10^3 cells/mL, ranging in (1.11–42.39) × 10^3 cells/mL in these two waters. In Daya Bay, the highest phytoplankton abundance
occurred in site D2 station, which was closed to aquacultural area. In the Pearl River Estuary, peak values were observed either near the northern river outlets (site P1) or in the downstream of site P14 station (Fig. 5). In general, diatoms, including \textit{Skeletonema costatum}, \textit{Thalassiosira subtilis}, \textit{Pseudonitzschia delicatissima}, and \textit{Pseudonitzschia pungens}, along with \textit{Chaetoceros} species, dominated the phytoplankton assemblages in this period.

Picophytoplankton was ubiquitous in the study areas, with average abundance being almost two orders of magnitude lower than those of prokaryotes. The total picophytoplankton concentration was \(6.51 \times 10^4\) cells/mL (\((0.63-14.71) \times 10^4\) cells/mL) in Daya Bay and \(1.89 \times 10^4\) cells/mL (\((0.86-4.52) \times 10^4\) cells/mL) in the Pearl River Estuary water, respectively. Euk and Syn were present throughout all of monitoring sites, whereas Prochlorococcus populations were not detected in this study. Syn cell numbers increased along the estuary axis, and the maximum value (\(4.09 \times 10^4\) cells/mL) occurred at the outer reach of the estuarine zone, (site P14 station) where the salinity was high and nutrient concentrations were low. In Daya Bay, Syn showed the highest abundance (\(12.20 \times 10^4\) cells/mL) in the northeast section of the Bay (D5 station), where nutrient levels were quite low as well (Fig. 6a).

Euk had a lower abundance than Syn in Daya Bay, with an average value of \((0.60-3.94) \times 10^4\) cells/mL. Euk showed the highest abundance in D2 station (\(3.94 \times 10^4\) cells/mL) (Fig. 6b); whereas in the Pearl River Estuary, the mean density of Euk was \(0.91 \times 10^4\) cells/mL, with the highest counts at P11 station (\(1.62 \times 10^4\) cells/mL).

3. Discussion

3.1. Microbial characteristics of prokaryotic sub-groups

Coffin and Sharp (1987) stated that the location of peak microbial abundance within the estuary was a function of substrate availability, i.e., labile dissolved organic matter (DOM). Many investigators have observed significant correlations between prokaryotes and chlorophyll (or phytoplankton abundance) in various ecosystems including the Chesapeake Bay (Ducklow et al., 1999), the Mississippi River Plume (Liu et al., 2004) and northern South China Sea (Ning et al., 2005). Nevertheless, we discovered that the association between total prokaryotes and phytoplankton density was weak, with one of the subgroup of prokaryotes — HNA— showing a closer relationship with phytoplankton (Table 1).

This is the first study, to our knowledge, to evaluate the microbial community structure based on flow cytometry characteristics in Daya Bay waters. Heterotrophic prokaryote abundances (14.55, range \((3.61-19.56) \times 10^5\) cells/mL) in Daya Bay are comparable to those reported by Hamasaki et al. (1999) for Sagami Bay and lower than those reported by Koepfler et al. (1993) for the Chesapeake Bay and Bai et al. (2004) for Jiaozhou Bay, while prokaryote abundance measured in the Pearl River Estuary were within the range recorded in several previous studies (Zhou et al., 2011; Yuan et al., 2011; Zhang et al., 2013).

Jellett et al. (1996) suggested that the percent contribution of HNA cells to the microbial community (%HNA) could be used as an active cell index. Typical %HNA values in the field ranged from 15% to 95% (Gasol et al., 1999). However, present %HNA values (ranging from 0.23% to 62.71%) were more variable.
than previous reported data. We considered that the most likely explanation for the varying HNA proportion and abundance was a positive relationship with phytoplankton biomass (Li et al., 1995; Sherr et al., 2006). The existence of a tight trophic linkage or “coupling” between the HNA fraction and phytoplankton abundance (including larger phytoplankton and Syn abundance) was in accordance with the results of Sarmento et al. (2008) and Li et al. (2010). Furthermore, recent work demonstrated that there was a tighter correlation between HNA and larger phytoplankton density \( (r = 0.58, p < 0.01; \text{Table 1}) \) when compared with the HNA-Syn correlation \( (r = 0.51, p < 0.05; \text{Table 1}) \). This is a direct indication that the HNA population was more dependent on diatom-mediated DOM, because larger-sized diatoms were always dominant in eutrophic coastal waters (e.g., the Pearl River Estuary and Daya Bay) and pico-sized phytoplankton served as a major contributor to primary production only in open oceans (Zhang et al., 2013).

In terms of the LNA group, some studies have suggested that LNA apparently depends less than HNA on phytoplankton substrates for growth and metabolism (Morán et al., 2007, 2011), which was in agreement with our observation. Furthermore, LNA abundance showed weak associations with all environmental parameters except total prokaryotic counts. Based on cell numbers, the LNA fraction had more or at least an equal share compared to the HNA group in the current study, which confirmed that the LNA subgroup was an important component in our coastal waters. However, the significance of LNA cells to the total microbial community remains questionable from a physiological point of view (Sherr et al., 2006; Scharek and Latasa, 2007).

3.2. Abundance and community structure of virioplankton

Virioplankton abundance ranged in \((7.42 – 72.26) \times 10^5/mL\), with a mean of \(13.30 \times 10^5/mL\) in the present studied areas. Because methods for counting viruses vary, viral abundance comparisons can be persuasive only between studies using the same technique; hence, only cell counts determined by flow cytometry are listed in \(\text{Table 2}\). The abundance range overlaps with the data reported for other coastal or estuarine waters, i.e., Changjiang Estuary and the Northern Yellow Sea, but is lower than that in Zuari Estuary and the coastal English Channel (\(\text{Table 2}\)). There is evidence showing the enhancement of viral abundance with increased nutrient availability (Maranger and Bird, 1995; Hewson et al., 2001; Danovaro et al., 2003). With a higher standing stock of prokaryotes and phytoplankton, it can directly stimulate viral development (Cochlan et al., 1993; Maranger and Bird, 1995) by providing more hosts for viruses.

![Fig. 6](image-url)

**Fig. 6** – Spatial distribution of two picophytoplankton groups in the summer of 2012.

### Table 1 – Pearson correlation coefficients between prokaryotes, virioplankton, picophytoplankton and phytoplankton abundance and abiotic environmental variables in Pearl River Estuary and Daya Bay during summer of 2012.

<table>
<thead>
<tr>
<th></th>
<th>HNA</th>
<th>LNA</th>
<th>TP</th>
<th>VI</th>
<th>VII</th>
<th>TV</th>
<th>PP</th>
<th>Syn</th>
<th>Euk</th>
<th>SAL</th>
<th>NO_3-N</th>
<th>NH_4-N</th>
<th>PO_4-P</th>
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<td>%HNA</td>
<td>0.98</td>
<td>-0.29</td>
<td>0.46</td>
<td>0.34</td>
<td>0.30</td>
<td>0.33</td>
<td>0.59**</td>
<td>0.45</td>
<td>0.01</td>
<td>0.29</td>
<td>-0.25</td>
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</tr>
<tr>
<td>HNA</td>
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<td>0.57</td>
<td>0.39</td>
<td>0.32</td>
<td>0.36</td>
<td>0.58**</td>
<td>0.51*</td>
<td>0.14</td>
<td>0.34</td>
<td>-0.29</td>
<td>-0.40</td>
<td>-0.20</td>
<td></td>
</tr>
<tr>
<td>LNA</td>
<td>0.16</td>
<td>0.71**</td>
<td>0.12</td>
<td>0.11</td>
<td>0.12</td>
<td>-0.12</td>
<td>-0.05</td>
<td>0.32</td>
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<td>0.22</td>
<td>0.19</td>
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</tr>
<tr>
<td>TP</td>
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<td>0.71**</td>
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<td>0.34</td>
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<td>0.25</td>
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</tr>
<tr>
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<td>0.34</td>
<td>0.38</td>
<td>0.33</td>
<td>0.28</td>
<td>0.30</td>
<td>-0.02</td>
<td>0.05</td>
<td>-0.16</td>
<td></td>
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<tr>
<td>V-II</td>
<td>0.32</td>
<td>0.11</td>
<td>0.34</td>
<td>0.82**</td>
<td>0.92**</td>
<td>0.58*</td>
<td>0.37</td>
<td>0.40</td>
<td>0.43</td>
<td>-0.26</td>
<td>-0.38</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>TV</td>
<td>0.36</td>
<td>0.12</td>
<td>0.38</td>
<td>0.92**</td>
<td>0.98**</td>
<td>0.36</td>
<td>0.02</td>
<td>0.05</td>
<td>0.32</td>
<td>0.04</td>
<td>-0.59*</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>PP</td>
<td>0.58**</td>
<td>-0.12</td>
<td>0.33</td>
<td>0.58</td>
<td>0.36</td>
<td>0.46</td>
<td>0.48</td>
<td>0.22</td>
<td>0.50*</td>
<td>-0.30</td>
<td>-0.33</td>
<td>-0.18</td>
<td></td>
</tr>
<tr>
<td>Syn</td>
<td>0.51*</td>
<td>-0.05</td>
<td>0.28</td>
<td>0.37</td>
<td>0.02</td>
<td>0.16</td>
<td>0.48</td>
<td>0.44</td>
<td>0.72**</td>
<td>-0.76**</td>
<td>-0.26</td>
<td>-0.63*</td>
<td></td>
</tr>
<tr>
<td>Euk</td>
<td>0.14</td>
<td>0.32</td>
<td>0.30</td>
<td>0.40</td>
<td>0.05</td>
<td>0.18</td>
<td>0.22</td>
<td>0.44</td>
<td>0.22</td>
<td>-0.04</td>
<td>0.29</td>
<td>0.06</td>
<td></td>
</tr>
</tbody>
</table>

Significant correlations are indicated in bold with the level of significance \(p < 0.05, \text{**}p < 0.01\). TP, total prokaryotes; TV, total virioplankton; PP, phytoplankton; SAL, salinity.
Contrary to the expectation, virioplankton abundance in the Pearl River Estuary did not display a decreasing pattern seaward or higher cell counts than that in Daya Bay.

Based on flow cytometric properties, Marie et al. (1999) distinguished two populations of viruses and proposed that the V-I population could be infectious to phytoplankton, whereas the V-II population was tightly coupled to heterotrophic bacteria. We found a significant relationship between phytoplankton abundance and V-I ($r = 0.58$, p < 0.05; Table 1), but no significant correlation between prokaryotes and V-II, although the majority of virus in this study were bacteriophages. The poorer correlation does not discount the possibility that bacterioplankton are significant host organisms of V-II. We considered factors other than the host influencing the dynamics of V-II abundance or the weak linkage of virus–host interactions in the study areas.

### 3.3. Distribution patterns of picophytoplankton populations

It has been indicated that river input may exert a negative effect on Syn distribution (Liu et al., 2004; Pan et al., 2007; Zhang et al., 2013). In this context, Syn abundance showed an increasing pattern along the salinity gradient in the estuary (Table 1, Fig. 6a). Taking the two coastal waters as a whole, Syn abundance was lower in the Pearl River Estuary with higher nutrient concentrations because Syn concentration was inversely related with nitrate and orthophosphate levels.

In the East China Sea, pico-eukaryotes exhibited quite different distribution patterns to Syn and other picoplankton (Jiao et al., 2002), which also can be seen in recent work (Fig. 6b). In the present observation, we did not find any relationship between Euk abundance and environmental variables. Jiao et al. (2002) explained that the species composition of pico-eukaryotes changed over regions and water masses, therefore, the distribution pattern should not be simply attributed to the effects of physico-chemical factors. On the other hand, this subgroup seemed not as sensitive as Syn to riverine nutrients, hence, Euk made a significant contribution to total picophytoplankton abundance in the inner estuary in our study and some other near-shore waters (Jiao et al., 2005; Lin et al., 2010).

### 4. Conclusions

In terms of two subgroups of prokaryotes (HNA and LNA groups), we found a tight trophic linkage between HNA, phytoplankton density and Syn abundance, suggesting the growth and distribution of this group were dependent on substrates produced by primary producers. On the other hand, LNA showed no significant correlation with environmental variables, but made a great contribution to the total microbial community in some regions. Contrary to some other studies, our limited scale study demonstrated that virioplankton abundance did not increase with elevated nutrient availability. The positive association between phytoplankton abundance and V-I population confirmed a close connection between the V-I subgroup and its host of phytoplankton. Most of the virioplankton in this survey were in the V-II (bacteriophages) population, but poorer correlation was found between V-II abundance and the prokaryotic concentration. Hence, we speculated that probably that there were factors other than the host influencing the dynamics of V-II abundance in the study areas. Syn abundance increased along the salinity gradient and was inversely related with nitrate and orthophosphate, indicating that river input exerted a negative effect on Syn distribution. To our knowledge, this is the first study simultaneously covering picoplankton (prokaryotes and picophytoplankton), virioplankton and larger phytoplankton in the Pearl River Estuary and Daya Bay, and in addition, our study also reveals their community compositions and related key environmental variables.

### Acknowledgments

We thank Jianlin Zhang for flow cytometry analyses. This study was supported by the National Basic Research Program (973 Program) of China (Nos. 2015CB452905, 2015CB452903), the Strategic Priority Research Program of the Chinese Academy of Sciences (No. XDA11020205), Fund of Key Laboratory of Global Change and Marine-Atmospheric Chemistry, SOA, (GCMA-C1209) and Public science and technology research funds projects of ocean (201105015-06).


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