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PRIMARY RESEARCH PAPER

Responses of aerobic anoxygenic phototrophic bacteria to algal blooms in the East China Sea

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Abstract Aerobic anoxygenic phototrophic bacteria (AAPB) are a new functional group of heterotrophic bacteria capable of phototrophy, and are suggested to be closely related with phytoplankton. However, less known is the relationship between AAPB and dominant phytoplankton populations. In this tudy, the responses of AAPB to algal blooms (ABs) in the AB-frequent-occurrence area of the East China Sea were investigated during four cruises from March to June 2005, using an advanced 'Time-series observation-based cyanobacteria-calibrated InfraRed Epifluorescence Microscopy (TIREM)' approach. Generally, total bacterial abundances at the bloom stations were higher than or similar to those at the non-bloom stations during the same time period. Interestingly, the responses of AAPB to ABs seemed to be more diverse and complex. AAPB abundance was higher at the stations with ABs where *Thalassiosira curviseriata* Takano and *Skeletonema costatum* (Greville) Cleve, *Noctiluca scintillans* (Macartney) Kofoid et Swezy, or *Prorocentrum donghaiense* Lu and *Karenia mikimotoi* Hansen co-dominated than those at the non-bloom stations during the same time period. However at the stations with a bloom of *Akashiwo sanguinea* Hansen, AAPB abundance only accounted for ~20% of the average abundance of AAPB at the non-bloom stations. In addition, variations of AAPB's proportion to total bacterial abundance (AAPB%) in response to ABs basically followed AAPB abundance. Overall, our results suggest that the responses of AAPB to ABs are AB-species specific and somewhat independent of chlorophyll *a* concentration.

Keywords Aerobic anoxygenic phototrophic bacteria · Algal blooms · Dissolved organic carbon · Algal bloom-frequent-occurrence area · East China Sea

Introduction

Discovered 30 years ago, aerobic anoxygenic phototrophic bacteria (AAPB) represent a new functional bacterial group, with remarkably low cellular contents of bacteriochlorophyll *a* (BChl *a*), while high concentrations of carotenoids (Kolber et al., 2001). Although, AAPB are incapable of photoautotrophy and depend on heterotrophy for not less than 80% of their cellular energetics (Hunter et al., 2008), they can use sunlight for photosynthesis to supplement their normal heterotrophic diet of dissolved organic matter. Therefore, AAPB are widely distributed in marine environments and are reported to play a particularly important role in the ocean carbon cycle (Kolber

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et al., 2001). Investigations in the global oceans have shown that the distribution pattern of AAPB is more related to availability of dissolved organic carbon (DOC) from phytoplankton (Jiao et al., 2007). However, the relationship between AAPB and dominant phytoplankton populations, the major supplier of labile DOC, have not been fully studied, which is of critical importance in understanding not only AAPB dynamics but also the role of AAPB in carbon cycling in the ocean.

As an episodic event, when an algal bloom (AB) occurs, a large quantity of DOC is excreted by the dominant populations. Given that the AAPB could rely on phytoplankton produced DOC (PDOC) to a greater extent than other heterotrophic bacteria (Jiao et al., 2007), it is intriguing to explore how the AAPB respond to different ABs. In this regard, a few studies have mentioned the possible relationships between AAPB and ABs with different arguments (Mašín et al., 2006; Sieracki et al., 2006; Zhang & Jiao, 2007). For example, a short-term diatom bloom in the Sargasso Sea co-occurrenced with a high abundance of AAPB (Sieracki et al., 2006). Nevertheless in the Baltic Sea, the numbers of heterotrophic bacteria and AAPB increased slightly during a spring bloom dominated by dinophytes and/or diatoms, and then peaked in the later phase of the bloom. During an autumn bloom co-dominated by cyanobacteria, dinophytes, and chlorophytes, the relative abundance of AAPB declined to 1–2% of the total bacteria (Mašín et al., 2006). Obviously, further detailed studies are needed on AAPB dynamics following the entire duration of a phytoplankton bloom in order to contribute to a comprehensive understanding of the responses of AAPB to different types of ABs. In this study, we examined and evaluated for the first time, the dynamics of AAPB in response to several frequently occurring ABs in the coastal waters of the East China Sea.

Materials and methods

Study area and sampling

The coastal sea of Zhejiang province is a AB-frequent-occurrence area in the East China Sea (Fig. 1), where ABs with areas exceeding ten thousands of square kilometers have taken place for years and the frequency of ABs is much higher than in the other coastal areas of China in recent years (http://www.soa.gov.cn/hyjww/ml/news/news/webinfo/2007/10/1192695976646853.htm).

We investigated the abundance and distribution of AAPB during the four AB-tracking cruises (on board RV ZHE-HAI-HUAN-JIAN-HAO) in the coastal area of the East China Sea in 2005. The first cruise was from March 27 to April 1, the second cruise was from 9 to 12 June, the third cruise was from 15 to 17 June, and the fourth cruise was from 22 to 24 June.

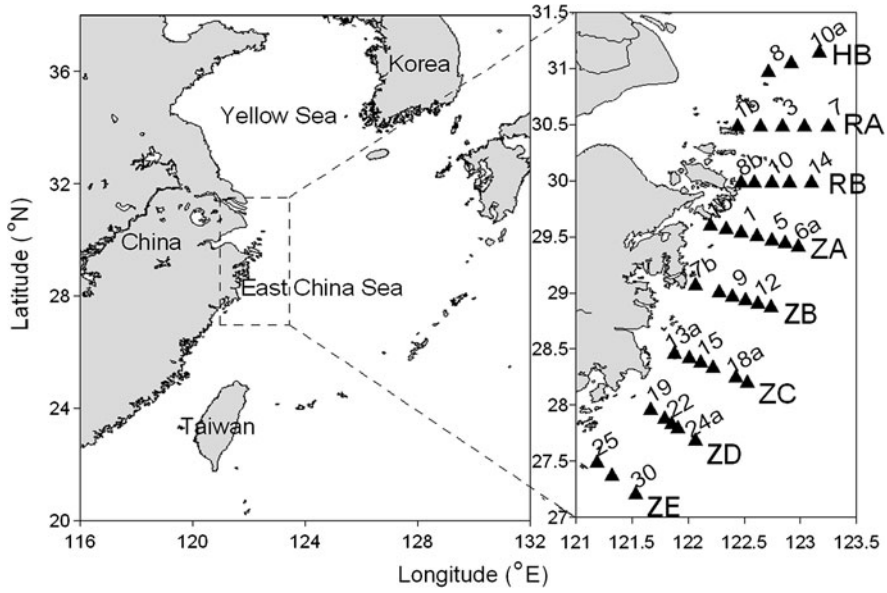

Fig. 1 Location of the stations in the East China Sea

The transects and sampling stations are shown in Fig. 1, but not all transects and stations were involved in each cruise, which depended on the area of ABs.

AAPB and total bacterial abundance

Surface seawater samples were collected using a Rosette sampler with 20 l Teflon-coated Go-Flo bottles (General Oceanic Inc., USA) mounted on a SeaBird CTD (SBE 9/11 plus, SeaBird Inc., USA). Immediately after sampling, aliquots of 20 ml seawater were filtered through a 20 μm pore-size sieve, the filtrates were fixed for 15 min with paraformaldehyde (1%, final concentration), and then filtered onto 0.2 μm pore-size black polycarbonate (PC) membranes (Millipore). A quarter of the PC filters were mounted with cover slips using 30 μl of 4:1 mixture of the antifade mountants Citifluor (Ted Pella) and Vectashield (Vector Labs) with a 10 μg ml^{-1} solution of 4′6-diamidino-2-phenylindole (DAPI). The slides were frozen for analysis after the cruise. Accurate enumeration of AAPB and total bacteria was made using the 'Time-series observation based cyanobacteria-calibrated InfraRed Epifluorescence Microscopy (TIREM)' protocol (Jiao et al., 2006).

Environmental parameters

Temperature and salinity were measured using the SeaBird CTD, and these data were provided by D. D. Zhu (Second Institute of Oceanography, State Oceanic Administration). Samples for chlorophyll *a* analysis were collected on 0.7 μm pore-size GF/F filter papers (Whatman) and determined using a Turner-Design-Model 10 fluorometer (Sigma, USA) (Parsons et al., 1984). Chlorophyll *a* data were provided by W. Y. Huo (South China Sea Institute of Oceanology, Chinese Academy of Sciences) and D. D. Lu (Second Institute of Oceanography, State Oceanic Administration). Aliquots of 1–2 l seawater were fixed with formaldehyde (5%, final concentration), and then transported to the laboratory for phytoplankton analysis. After sedimentation for 24 h, the fixed seawater was concentrated to an appropriate extent via being filtered through a 10 μm-mesh net according to the density of phytoplankton. Then, 0.1 ml of the concentrated seawater was taken for phytoplankton species identification and its quantitative count was carried out using phytoplankton-counting chamber under Olympus BH-2 light microscope.

Statistical analysis

All AAPB and bacterial measurements were replicated for at least five times, and the data were expressed as mean values ± SE (standard error). The SE for AAPB's proportion to total bacterial abundance (AAPB%) was not provided because AAPB% was obtained from a ratio of the average abundance of AAPB to that of bacteria. To assess bacterial variation among different ABs, an independent sample *t* test was used to determine whether the measured data had significantly different mean values. The homogeneity assumption was checked using Levene's test, and the normality assumption was checked using box-plot analysis.

Results

Hydrological parameters

In the study area, higher values of temperature and salinity were found in the offshore area than in the inshore area during the four cruises (Fig. 2), which was influenced by the Taiwan warm current (Jiao et al., 2002). Whereas opposite patterns were observed for the distribution of phosphate and nitrate concentrations, with higher values being present at the inshore stations due to the Yangtze River dilution (Zhang et al., 2008a, b).

ABs succession in the study area

In late March, ABs were first dominated by diatoms (mainly *Thalassiosira curviseriata* Takano and *Skeletonema costatum* (Greville) Cleve) with a maximum of 1×10^6 cells l^{-1} at ZD-24a on March 31 in the AB-frequent-occurrence area of the East China Sea (Xie, 2006). This turned into a progression of dinoflagellate blooms beginning with *Karenia mikimotoi* Hansen and *Prorocentrum donghaiense* Lu, and finally *Noctiluca scintillans* (Macartney) Kofoid et Swezy and *Akashiwo sanguinea* Hansen in early June (Xie, 2006). The total area of the *K. mikimotoi* and *P. donghaiense* (10^7 cells l^{-1}) co-dominated

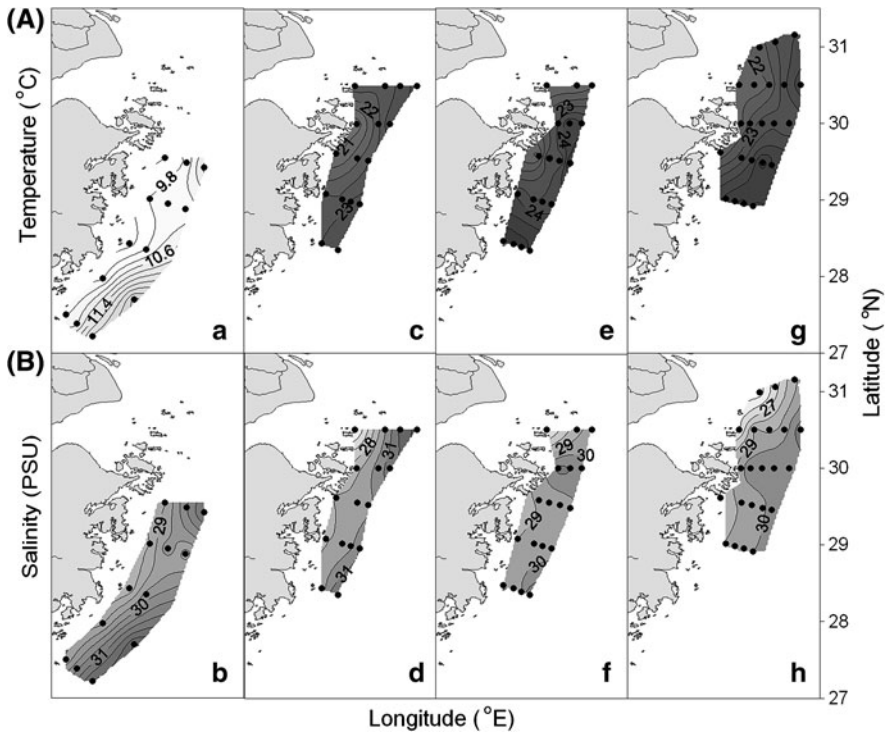

Fig. 2 Surface distributions of temperature (**A**) and salinity (**B**) in the first (*a*, *b*), second (*c*, *d*), third (*e*, *f*), and fourth (*g*, *h*) cruises in the algal bloom-frequent-occurrence area of the East China Sea

bloom was estimated to be more than 17,000 km^2 (Zhu et al., 2009).

Distribution patterns of chlorophyll *a*, AAPB, and total bacteria

For the first cruise, chlorophyll *a* concentration varied from 0.52 to 14.95 μg l^{-1}, with AAPB abundance for 0.12 ± 0.04–1.55 ± 0.10 × 10^4 cells ml^{-1}, total bacterial abundance for 1.67 ± 0.09–8.54 ± 0.46 × 10^5 cells ml^{-1}, and AAPB% for 0.38–2.72%. Higher values of chlorophyll *a* concentration were found in the offshore area than in the inshore direction during this cruise. There was a pronounced plume center with a maximum value of 14.95 μg l^{-1} in the south-eastern part of this area, which was mainly contributed by *T. curviseriata* and *S. costatum* (Fig. 3a). Accordingly, the maximum values of AAPB and total bacteria were present in the south-eastern part of the study area. In addition, AAPB% was also found to be high in this part, though it was not the maximum in this study area.

For the second cruise, chlorophyll *a* concentration ranged from 0.24 to 43.43 μg l^{-1}, with AAPB abundance being 2.35 ± 0.15–23.85 ± 0.80 × 10^4 cells ml^{-1}, total bacterial abundance being 8.56 ± 0.28–55.17 ± 2.15 × 10^5 cells ml^{-1}, and AAPB% being 2.59–9.85%. *P. donghaiense* and *K. mikimotoi* bloomed simultaneously along the ZA transect during this cruise, where high chlorophyll *a* concentration was concomitant with high abundances of AAPB and total bacteria (Fig. 3e–g). However, no distinct high value patch was found for AAPB% (Fig. 3h) along the ZA transect.

ABs frequently occurred during the third cruise, where chlorophyll *a* concentration with 0.34–18.05 μg l^{-1}, AAPB abundance with 1.30 ± 0.04–23.58 ± 2.56 × 10^4 cells ml^{-1}, total bacterial abundance with 8.41 ± 0.25–20.27 ± 0.42 × 10^5 cells ml^{-1}, and AAPB% with 1.01–16.58% were observed (Fig. 3i–l). A *N. scintillans* bloom was found along the ZB transect, but chlorophyll *a* concentration was not high, since *N. scintillans* is heterotrophic and without chlorophyll *a*. Nevertheless, a high-value center of AAPB abundance was present in this bloom region (Fig. 3j). *A. sanguinea* bloomed at station ZA-5, where AAPB abundance remained at the lowest level of 1.30 × 10^4 cells ml^{-1}. Overall, the

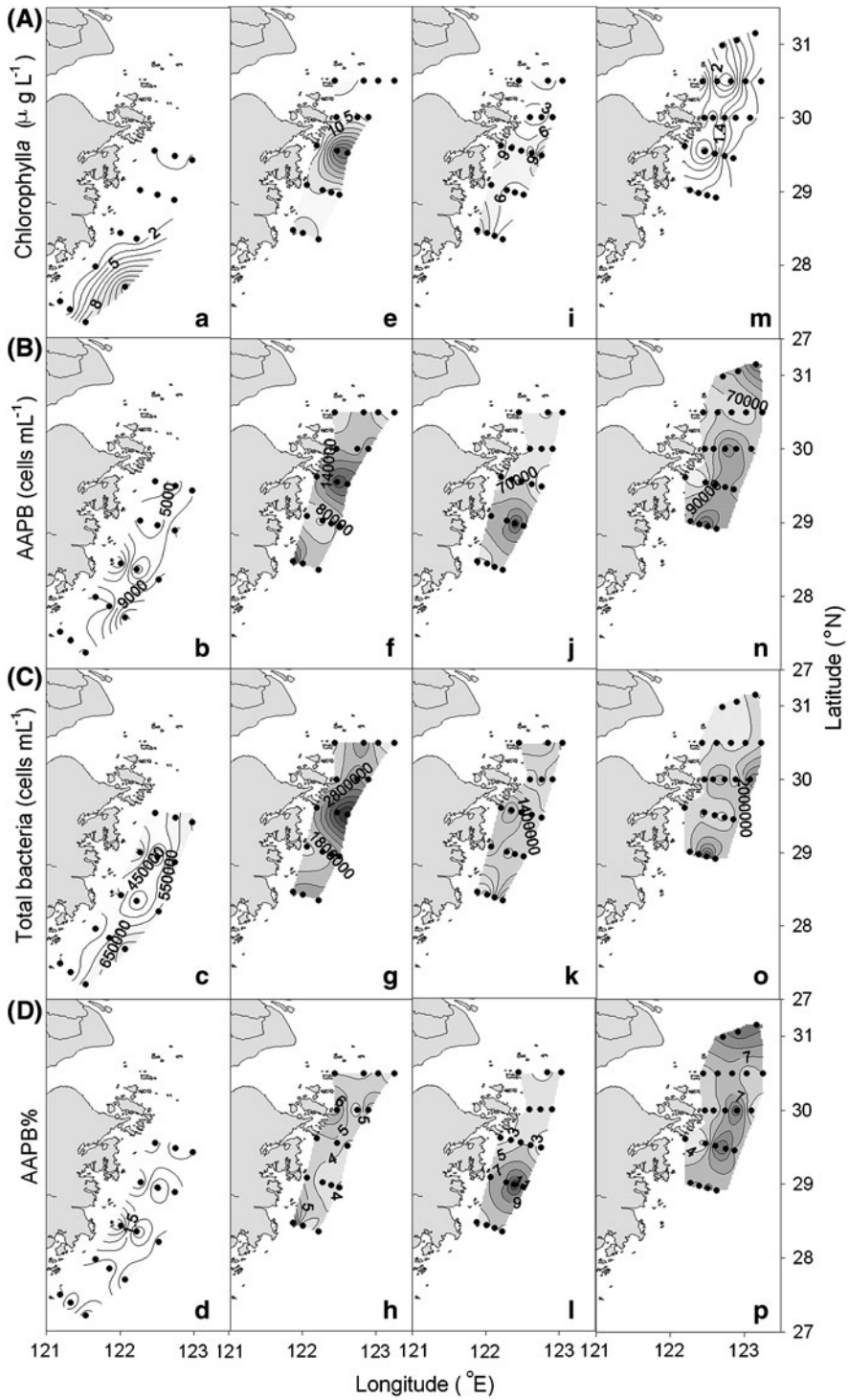

Fig. 3 Surface distributions of chlorophyll *a* concentration (**A**), AAPB abundance (**B**), total bacterial abundance (**C**), and AAPB% (**D**) in the first (*a*–d), second (*e*–*h*), third (*i*–*l*), and fourth (*m*–*p*) cruises in the algal bloom-frequent-occurrence area of the East China Sea

distribution of total bacteria was even throughout the study area during this cruise, which resulted in a similar response of AAPB% to ABs as did AAPB (Fig. 3l).

For the fourth cruise, chlorophyll *a* concentration varied from 0.31 to 2.58 μg l^{-1}, with AAPB abundance of 3.14 ± 0.12–19.08 ± 1.14 × 10^4 cells ml^{-1}, total bacterial abundance of 8.54 ± 0.31–42.34 ± 1.26

$\times 10^5$ cells ml^{-1}, and AAPB% of 1.88–12.17% (Fig. 3m–p). Blooms were almost absent during this cruise except in the middle of the ZA transect where *N. scintillans* bloomed, and both AAPB abundance and AAPB% remained at a relatively high level (Fig. 3n, p). No significant correlations were found between chlorophyll *a* and AAPB or total bacteria.

Variations of AAPB and total bacteria with various blooms

To sum up, diatom blooms occurred in late March–early April, while dinoflagellate blooms formed in June in this AB-frequent-occurrence area. Following the bloom co-dominated by *P. donghaiense* and *K. mikimotoi*, total bacterial abundance was significantly higher at the bloom stations than at the non-bloom stations during the second cruise (*t* test, $P < 0.01$). However, no significant increase was found when a *T. curviseriata* and *S. costatum*, *N. scintillans* or *A. sanguinea* bloom occurred (Fig. 4C).

AAPB abundance was significantly higher at the stations where *P. donghaiense* and *K. mikimotoi* co-bloomed (about twice as high) than at the non-bloom stations during the second cruise (*t* test, $P < 0.01$). In addition, AAPB abundance at the stations with *T. curviseriata* and *S. costatum* co-dominated bloom was 2.7 times higher than the average at the non-bloom stations during the first cruise (Fig. 4B). When *N. scintillans* bloomed, AAPB abundance was 2.67 and 1.31 times higher than the average of the non-bloom stations during the third and fourth cruise, respectively. The smaller change during the fourth cruise was probably due to lysis induced by virus infection, since distinctly large numbers of virus particles were observed in the microscopic view

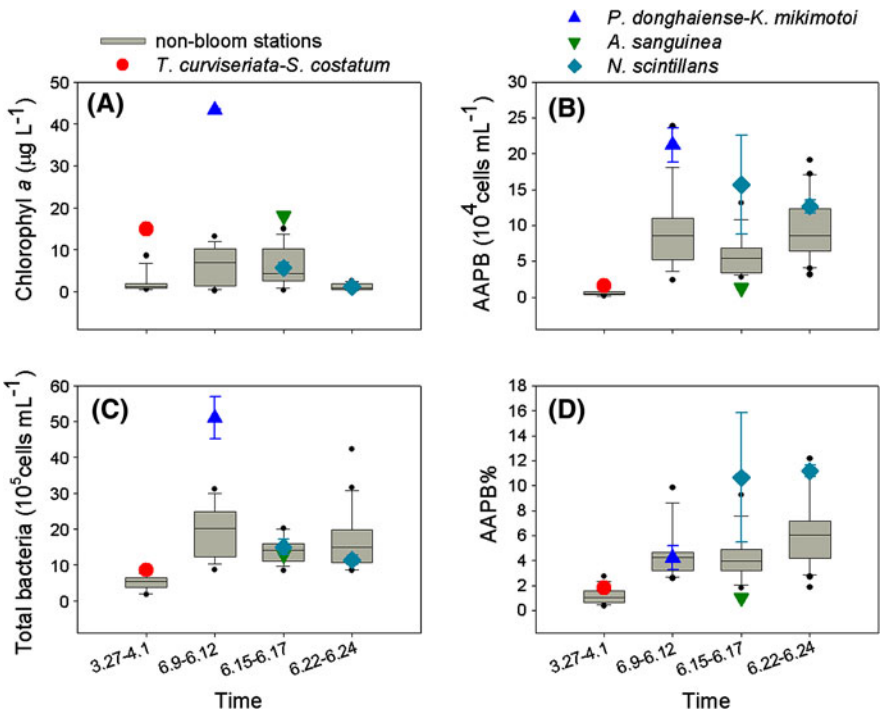

Fig. 4 Comparison of chlorophyll *a* concentration (**A**), AAPB abundance (**B**), total bacterial abundance (**C**), and AAPB% (**D**) between the bloom and non-bloom stations in the algal bloom-frequent-occurrence area of the East China Sea. All data from the four cruises were plotted and the data from the non-bloom stations were expressed by plotting the median, 10th, 25th, 75th, and 90th percentiles as *vertical boxes* with *error bars*. The data from the bloom stations were expressed by plotting the average with standard deviations as *error bars*. Red solid circle, *Thalassiosira curviseriata–Skeletonema costatum* bloom; blue solid triangle, *Prorocentrum donghaiense–Karenia mikimotoi* bloom; dark green solid inverse triangle, *Akashiwo sanguinea* bloom; dark cyan solid diamond, *Noctiluca scintillans* bloom

fields at this time (data not shown). On the contrary, at the stations with a bloom of *A. sanguinea*, AAPB abundance was only one-fifth of the average of the non-bloom stations during the same time period.

Generally, variations in AAPB% between bloom and non-bloom stations followed AAPB abundance, expect at *P. donghaiense* and *K. mikimotoi* co-blooming stations, where quite high abundance of total bacteria resulted in an indistinctive increase in AAPB% (Fig. 4D).

Discussion

Uncoupling of AAPB and chlorophyll *a* concentration in the AB-frequent-occurrence area

Although AAPB and bacterial abundances are strikingly correlated with chlorophyll *a* concentration on a regional or global scale (Bird & Kalff, 1984; Cole et al., 1988; Kolber, et al., 2000; Goericke, 2002; Jiao et al., 2007), our study showed that the temporal and spatial variability of chlorophyll *a* concentration was different from those of AAPB and total bacterial abundance, as well as AAPB% in this study area. Our previous study in the East China Sea has shown that the distribution of AAPB followed that of chlorophyll *a* in spring, autumn and winter when chlorophyll *a* concentrations were reasonably low, while this relationship was lost in the summer when phytoplankton bloomed, suggesting that some factors other than chlorophyll *a* affected AAPB's distribution (Zhang & Jiao, 2007). We speculated that organic material released by the blooming phytoplankton (e.g., PDOC) might be a key factor in controlling cell abundance and regulating the relationship between bacterial biomass and chlorophyll *a* concentration in this AB-frequent-occurrence area (Jiao et al., 2007). Some could be readily assimilated by bacteria (Cole et al., 1988; Myklestad, 2000; Kormas, 2005), while some, e.g., toxins exudates, could be harmful to bacterial growth (Doucette, 1995). Meanwhile, with changes in the dominating phytoplankton, the species composition of AAPB would probably be changing (Waidner & Kirchman, 2005; Jiao et al., 2007). Thus, different species of AAPB might display different responses to ABs, due to species-dependent physiology (Rathgeber et al., 2004).

Response diversity of AAPB to different types of blooms

Our study showed that AAPB were more sensitive to phytoplankton blooms than other heterotrophic bacteria (non-AAPB), since that AAPB showed more varied responses to ABs. Interestingly, our study demonstrated that the changes of AAPB and AAPB% were AB-species specific. It is probably due to quantitative and qualitative differences in the DOC released by different phytoplankton species (Grossart et al., 2005; Kormas, 2005).

Compared with the non-bloom stations from the same cruise, the average abundance of AAPB at the bloom stations co-dominated by *T. curviseriata* and *S. costatum* increased 2.7 times, while 1.66 and 1.54 times increase was observed for total bacterial abundance and AAPB%, respectively. But at the stations with a bloom of *A. sanguinea*, both AAPB abundance and AAPB% decreased to about one fifth of those at the non-bloom stations, while little difference was observed for bacterial abundance (Fig. 4). The response of AAPB and total bacteria to the diatom bloom co-dominated by *T. curviseriata* and *S. costatum* was in accordance with the previous study which showed a high AAPB abundance along with a diatom bloom in the Sargasso Sea in March (Sieracki et al., 2006). In addition, previous studies have shown a distinct difference between the DOC released by *S. costatum* and by *A. sanguinea* (formerly *Gymnodium nelsoni*) (Hellebust, 1965; Daugbjerg et al., 2000; Marcus & Murray, 2001), i.e., among the three electrodialysis fractions of the media from algal cultures, *S. costatum* excretes more low-molecular-weight substances (which can be easily assimilated by bacteria) than *A. sanguinea* (Hellebust, 1965). Therefore, distinctly increased AAPB and total bacterial abundance as well as AAPB% in a diatom bloom versus a decrease or little change in an *A. sanguinea* bloom might partly be caused by the distinct compositions of organic matter excreted by between *S. costatum* and *A. sanguinea*. Another possible explanation for the response of AAPB to the *A. sanguinea* bloom is grazing pressure. *A. sanguinea* is mixotrophic and can ingest phytoplankton species that are smaller than themselves (Jeong et al., 2005). Thus, *A. sanguinea* could probably have preyed upon some AAPB cells, and induced a decrease in AAPB abundance, since they are under greater grazing pressure due to being

larger than average heterotrophic bacteria (Mašín et al., 2006; Sieracki et al., 2006; Zhang et al., 2008a, b). However, further work is needed to confirm whether intensifying grazing pressure happens to AAPB when *A. sanguinea* blooms.

When *P. donghaiense* and *K. mikimotoi* bloomed simultaneously, the abundance of both AAPB and total bacteria increased about two times compared with those at the non-bloom stations during the same time period (*t* test, $P < 0.01$). It was concurrent with the fairly high concentrations of chlorophyll *a*, which was about seven times higher compared with those at the non-bloom stations (Fig. 4A).

N. scintillans, with a diameter of about 200–1000 μm, is an opportunistic omnivorous dinoflagellate whose survival and propagation are dependent on devouring phytoplankton, microzooplankton, the nauplii and eggs of macrozooplankton, organic detritus, and so on (Yılmaz et al., 2005). Thus, when *N. scintillans* bloomed, this would greatly reduce the grazing pressure of microzooplankton upon AAPB, with concomitant increase of AAPB abundance and AAPB%. Non-AAPB are under less intensive grazing pressure by microzooplankton than AAPB due to their smaller cell size (Sieracki et al., 2006; Lami et al., 2007), so they showed less response to the *N. scintillans* bloom. Meanwhile, *N. scintillans* likes to prey on phytoplankton, and concomitantly large quantity of DOC would be excreted to seawater during the prey process, which could favor the growth of AAPB population as AAPB could rely on PDOC to a greater extent than non-AAPB (Jiao et al., 2007). However, the distinct increase in virus particles was also observed under the microscope during the *N. scintillans* bloom period of the fourth cruise (data not shown), which could induce less increase of AAPB than that in the third cruise.

Conclusions

Our study showed that in the AB-frequent-occurrence area of the East China Sea, total bacterial abundances at the bloom stations were higher than or similar to those at the non-bloom stations. However, the responses of AAPB to the ABs were more variable and complicated. AAPB abundance significantly increased when *P. donghaiense–K. mikimotoi*, *T. curviseriata–S. costatum*, or *N. scintillans* bloomed. At the stations with a bloom of *A. sanguinea*, AAPB abundance remained at a quite low level. In addition, variations of AAPB% in response to ABs commonly followed AAPB abundance. Taken together, our results suggest that the responses of AAPB to ABs are AB-species specific and somewhat independent of chlorophyll *a* concentration.

It should be noted that any seasonal study of the abundance and activity of coastal bacteria based on weekly, or even daily, samples might not be comprehensive if strong daily changes in bacterial abundance and activity are expected to be associated with the development of phytoplankton populations, such as daily migrations of dinoflagellates (Gasol et al., 2005). Therefore, more investigations are needed to exactly explore how AAPB respond to ABs at more complex spatio-temporal scales, before their effects on the marine carbon cycle and microbial loop processes can be fully understood.

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