Distinct distribution pattern of abundance and diversity of aerobic anoxygenic phototrophic bacteria in the global ocean

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Summary
Aerobic anoxygenic phototrophic bacteria (AAPB) are an important bacterial group with capability of harvesting light energy, and appear to have a particular role in the ocean’s carbon cycling. Yet the significance of AAPB relative to total bacteria (AAPB%) in different marine regimes are still controversial, and variation trend of genetic diversity of AAPB along environmental gradients remains unclear. Here we present the first comprehensive observation of the global distribution of AAPB in the Pacific, Atlantic and Indian oceans, revealing a general pattern of high abundance of AAPB and AAPB% in coastal waters than oceanic waters. The Indian Ocean contained relatively high AAPB% compared with the other two oceans, corresponding to the high primary production in this region. Both abundance of AAPB and AAPB% were positively correlated with the concentration of chlorophyll a, while the diversity of AAPB decreased with increasing chlorophyll a values. Our results suggest that AAPB abundance and diversity follow opposite trends from oligotrophic to eutrophic regimes in the ocean.

Introduction
Aerobic anoxygenic phototrophic bacteria (AAPB) represent a group of newly recognized bacteria that can utilize light energy and play a particular role in carbon cycling in the ocean (Kolber et al., 2000; 2001). The percentage of AAPB in total bacteria (AAPB%) is a key to evaluate the significance of such a role of AAPB in marine ecosystems. As the bacterial chlorophyll a (BChl. a)-based phototrophic function in AAPB is a supplement to their normal heterotrophic diet of dissolved organic carbon (DOC) (Beatty, 2002; Suyama et al., 2002; Koblizek et al., 2003), it is thus expected to make AAPB more competent when starved of organic carbon electron donors in respiration, and provides AAPB with a selective advantage in oligotrophic environments (Kolber et al., 2000; 2001; Beatty, 2002). However, current literature data on the relative abundance of AAPB in marine environments are still controversial. High AAPB% in oceanic water was reported by certain research groups (Kolber et al., 2001; Cottrell et al., 2006; Masin et al., 2006), while other researchers found relatively high AAPB% in coastal waters (Sieracki et al., 2006). Most recently, an approximate estimation based on pufM-pufL-bchX gene to recA gene copy numbers from global ocean sampling (GOS) data also showed the highest AAPB% occurring at coastal sites (Yutin et al., 2007); and the metagenomic analysis of the GOS data indicated great variability in AAPB genetic diversity with specific AAPB assemblages adapted to open ocean or coastal areas respectively (Yutin et al., 2007). However, as the GOS samples were in the 0.1–0.8 μm size range, and AAPB are usually larger than other bacteria (Yurkov and Beatty, 1998; Sieracki et al., 2006), the diversity of AAPB and relative significance of AAPB drawn from the GOS data may have been underestimated (Yutin et al., 2007). In addition, variation trend of overall diversity of AAPB from oligotrophic to eutrophic regimes remains unknown. Therefore, in order to better understand the distribution pattern of abundance and diversity of AAPB across different environmental provinces, a larger-scale systematic survey covering the world oceans would be desired.

During 2005 and 2006, a global cruise (R/V Ocean No.1) in memorial of the 600-year anniversary of the Admiral Zheng He’s expedition voyages (1405–1433) to the occident provided an opportunity to collect samples from the Pacific, Atlantic and Indian oceans. Together with other cruises to the West Pacific marginal seas including the East and South China Seas, the sampling sites in the present study covered tropical, subtropical and temperate...
zones, and included coastal, shelf and oceanic waters (Fig. 1). Time-series observation-based infrared epifluorescence microscopy (TIREM) protocol was employed for accurate enumeration of AAPB (Jiao et al., 2006). Genetic diversity of AAPB was examined in representative environments by analysing the puffM gene (photosynthetic reaction centre small-subunit gene), which encodes the M subunit in the photosynthetic reaction centre (Beja et al., 2002; Yutin et al., 2007).

Results and discussion

Global distribution pattern of AAPB abundance and its association with autotrophs

In surface water among the three oceans, the Indian Ocean had the highest AAPB% (3.79 ± 1.72%) followed by the Atlantic (1.57 ± 0.68%) and the Pacific (1.08 ± 0.74%) (Fig. 1). This pattern is similar to that of the biomass of cyanobacteria especially Synechococcus whose biomass was 4.43, 2.57 and 1.81 mg C m⁻³ in the Indian, Atlantic and Pacific Oceans respectively. The distinguished high AAPB% in the Indian Ocean is also consistent with significantly higher primary production in the Indian Ocean than in the other two oceans (Koblentz-Mishke et al., 1970; Mackey et al., 1995; Beaufort et al., 1997; Gregg et al., 2003; Perez et al., 2005). Within the Indian Ocean, high values of AAPB% occurred at the sites with high concentration of chlorophyll a (Chl. a) . In general, the coastal/shelf waters of the marginal seas had higher AAPB% (4.46 ± 2.41% with the maximum of 13.51%) than oceanic waters (1.52 ± 1.30%) (Fig. 1).

In addition to the surface distribution, vertical distribution of AAPB was also investigated at selected sampling sites (representative cases shown in Fig. 2). Unlike heterotrophic bacteria (non-AAPB), AAPB were confined to the euphotic zone. In general, AAPB followed Chl. a concentration and carbon biomass of cyanobacteria (Prochlorococcus and Synechococcus) along the depth profile regardless of stratification (Fig. 2A–C). One exception was the extremely oligotrophic Western North Pacific Gyre (WNPG) (Schlitzer, 2004) where AAPB were present at shallower depths than cyanobacteria (Fig. 2D). In the WNPG, as the phytoplankton (mainly cyanobacteria) did not thrive in the upper 100 m layer, AAPB only maintained a minimum abundance throughout the euphotic water column, with a weak maximum occurring at near surface probably benefiting from light (Fig. 2D). These observations suggest that AAPB are associated with phytoplankton.

Indeed, both AAPB abundance and AAPB% were correlated significantly to Chl. a concentration in all the oceans as well as in the Western Pacific marginal seas in all seasons (Fig. 3; Table 1). In contrast, correlations between non-AAPB and Chl. a were less significant in most cases, even no correlation in some cases of the coastal waters. More interestingly, AAPB were correlated significantly with the biomass of cyanobacteria, while less or no significant correlation existing between non-AAPB and cyanobacterial biomass (Table 2). It is still unclear why AAPB have a closer relationship with phytoplankton than non-AAPB. As Chl. a concentration can be an indicator of phytoplankton biomass (Leavitt et al., 1999; Malej...
et al., 2003) and phytoplankton can release highly labile DOC (Chen and Wangersky, 1996; Malej et al., 2003) supporting bacterial growth (Nishii et al., 2001), the closer tie between AAPB and phytoplankton suggests that AAPB could rely on the labile DOC to a greater extent than non-AAPB. Thus, the high abundance of AAPB and even higher AAPB% in coastal waters is likely due to high availability and high percentage of labile DOC there (Søndergaard and Middelboe, 1995). On the other hand, the close correlation between AAPB and phytoplankton could also be partially a result of similar dependence of both organisms on light. Further studies are needed in order to fully understand the trophic mechanism of AAPB.

The global distribution trend of AAPB with respect to trophic regimes revealed in this study is in agreement with results from other relatively large-scale investigations, such as that by Schwalbach and Fuhrman (2005) based on scattered sampling over the oceans, and that by Sieracki and colleagues (2006) from the coast of the Gulf of Maine to the Sargasso Sea ranging from 31.85°N/64W to 160.21°E, 19.66°N.

![Abundance of AAPB or non-AAPB (cells m⁻¹)](image)

![Cyanobacterial Carbon Biomass (mg C m⁻³)](image)

![Depth profiles of AAPB abundance (black line with closed circle), non-AAPB abundance (line with closed square), Chl. a concentration (line with closed triangle), biomass of cyanobacteria (doted line with open square) and temperature (doted line) at representative locations: (A) Central Indian Ocean (75.85°E, 10.01°S); (B) Southern Indian Ocean (70.04°E, 25.32°S) (oligotrophic); (C) Tropical Eastern North Pacific (131.06°W, 10.71°N); and (D) Western North Pacific Gyre (160.21°E, 19.66°N) (extremely oligotrophic). Error bars indicate standard deviation of triplicate measurements.]

![Fig. 2.](image)

Table 1. Correlation coefficients among AAPB%, AAPB abundance or non-AAPB abundance and chlorophyll a (Chl. a) in the western Pacific marginal seas.

<table>
<thead>
<tr>
<th>Items</th>
<th>East China Sea</th>
<th>South China Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer</td>
<td>Spring</td>
</tr>
<tr>
<td>AAPB% versus Chl. a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>r</td>
<td>0.68</td>
<td>0.65</td>
</tr>
<tr>
<td>p</td>
<td>&lt; 0.05</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>n</td>
<td>9</td>
<td>42</td>
</tr>
<tr>
<td>AAPB versus Chl. a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>r</td>
<td>0.82</td>
<td>0.66</td>
</tr>
<tr>
<td>p</td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>n</td>
<td>9</td>
<td>42</td>
</tr>
<tr>
<td>Non-AAPB versus Chl. a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>r</td>
<td>0.33</td>
<td>0.32</td>
</tr>
<tr>
<td>p</td>
<td>–</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>n</td>
<td>9</td>
<td>42</td>
</tr>
</tbody>
</table>

a. The fitting function used is: y = ae^bx.

–, data not shown when P > 0.05.
44.085°N/68°W, as well as that by Yutin and colleagues (2007) estimated on *pufM-pufL-bchX* gene to *recA* gene copy numbers from the GOS data set. It is likely that field observations may yield opposite distribution trend of AAPB between eutrophic and oligotrophic sites if investigation coverage is not large enough, such as the cases of the Atlantic Bights (ranging from 36°N/73°W to 38°N/74.43°W; Cottrell *et al.*, 2006) and Baltic Sea (ranging from 54.44°N/19.042°W to 55.3°N/18°W; Masin *et al.*, 2006). Abundance of AAPB and AAPB% are also influenced by factors beyond light and substrate, such as difference in community structures and interactions.

![Fig. 3. Correlations between AAPB%, AAPB abundance or non-AAPB abundance and chlorophyll a (Chl. a) in surface water of the Pacific, Atlantic and Indian oceans (the fitting function used is: \( y = ae^{bx} \)).](image)

44.085°N/68°W, as well as that by Yutin and colleagues (2007) estimated on *pufM-pufL-bchX* gene to *recA* gene copy numbers from the GOS data set. It is likely that field observations may yield opposite distribution trend of AAPB between eutrophic and oligotrophic sites if investigation coverage is not large enough, such as the cases of the Atlantic Bights (ranging from 36°N/73°W to 38°N/74.43°W; Cottrell *et al.*, 2006) and Baltic Sea (ranging from 54.44°N/19.042°W to 55.3°N/18°W; Masin *et al.*, 2006). Abundance of AAPB and AAPB% are also influenced by factors beyond light and substrate, such as difference in community structures and interactions.

![Table 2. Correlation coefficients among AAPB%, AAPB abundance or non-AAPB abundance and carbon biomass of cyanobacteria (Synechococcus and Prochlorococcus) in the Pacific, Atlantic, Indian oceans.](table)

<table>
<thead>
<tr>
<th>Items</th>
<th>Pacific, Atlantic and Indian oceans</th>
<th>Indian ocean</th>
</tr>
</thead>
<tbody>
<tr>
<td>AAPB% versus carbon biomass of cyanobacteria</td>
<td>0.66</td>
<td>0.78</td>
</tr>
<tr>
<td>( r )</td>
<td>(&lt; 0.01)</td>
<td>(&lt; 0.01)</td>
</tr>
<tr>
<td>( p )</td>
<td>135</td>
<td>21</td>
</tr>
<tr>
<td>AAPB versus carbon biomass of cyanobacteria</td>
<td>0.74</td>
<td>0.79</td>
</tr>
<tr>
<td>( r )</td>
<td>(&lt; 0.01)</td>
<td>(&lt; 0.01)</td>
</tr>
<tr>
<td>( p )</td>
<td>135</td>
<td>21</td>
</tr>
<tr>
<td>Non-AAPB versus carbon biomass of cyanobacteria</td>
<td>0.40</td>
<td>0.50</td>
</tr>
<tr>
<td>( r )</td>
<td>(&lt; 0.01)</td>
<td>(&lt; 0.05)</td>
</tr>
<tr>
<td>( p )</td>
<td>135</td>
<td>21</td>
</tr>
</tbody>
</table>

*a.* The fitting function used is: \( y = ae^{bx} \).
among the members (Sieracki et al., 2006). On top of that, data by different means may also result in differences in conclusions; for example, the \textit{pufM} gene to \textit{recA} gene ratio-based approach can only give approximate estimation of the relative significance of AAPB; the infrared fluorescence microscopy could suffer positive errors in oceanic waters where cyanobacteria are abundant and could be mistaken as AAPB (Zhang and Jiao, 2003). In the present study, the TIREM protocol (Jiao et al., 2006) was employed on board the cruises to ensure accurate enumeration of AAPB throughout the investigations.

**Decreasing AAPB diversity with increasing Chl. a gradient and its implications**

To better understand the population structure of AAPB in different environments, we analysed 10 clone libraries (total 500 clones) of the AAPB’s diagnostic gene \textit{pufM} (Beja et al., 2002; Schwalbach and Fuhrman, 2005) from 10 different sites of global ocean surface water (Fig. 1). Total 208 distinct \textit{pufM} sequences were obtained based on the cut-off of 1% sequence difference. The \textit{pufM} gene phylogeny showed that AAPB are highly diverse and represented by the bacteria from alpha-, beta- and gammaproteobacterial classes (Fig. 4). About a quarter of \textit{pufM} sequences from our samples clustered with well-known genera \textit{Roseobacter} and \textit{Erythrobacter} of alphaproteobacteria. The \textit{Roseobacter}-like and \textit{Erythrobacter}-like clones were distributed across the eutrophic and oligotrophic marine regions. However, about 10% of distinct sequences recovered from South China Sea and North Central Pacific formed a unique cluster within the \textit{Erythrobacter} group but had no their culture counterpart. Moreover, a large portion (93/208) of the environmental \textit{pufM} sequences was closely related to gammaproteobacteria. It is noteworthy that these gammaproteobacteria-like clones were from both oligotrophic and eutrophic waters. Gammaproteobacterial AAPB were dominant in the high-Chl. \textit{a} regions (Fig. 5), consistent with that common gammaproteobacteria are well known for their adaptability and opportunism (Bouvier and del Giorgio, 2002; Bernhard et al., 2005). Cho and colleagues (2007) also found that a bacterial group – OM60 clade containing gammaproteobacterial AAPB – were abundant in coastal oceans.

The recent GOS efforts revealed that AAPB compositions vary between different oceanic regions with specific assemblages adapted to oligotrophic and eutrophic environments respectively (Yutin et al., 2007). However, the limited sampling number (total 41 samples in GOS phase I from the surface waters of North Atlantic and Eastern North Pacific; Rusch et al., 2007) and the relatively narrow size fractionation (0.1–0.8 \textmu m pore size) (Yutin et al., 2007) leave rooms for further recognition of diversity of AAPB and its variation trends with environmental gradients. Covering Atlantic, Indian and Pacific oceans, and with sampling range of 0.22–200 \textmu m, our global ocean survey on AAPB diversity showed that \textit{Roseobacter}-, \textit{Erythrobacter}- and Gammaproteobacteria-related AAPB were all widely distributed over the major ocean regimes. The revealed great diversity in AAPB is reflected not only by newly found abundant gammaproteobacteria-like \textit{pufM} sequences (Hu et al., 2006) but also isolates of \textit{Erythrobacter} AAPB spread over the oceans (Koblizek et al., 2003), and even a group of gamma-AAPB strains from the North Sea (Fuchs et al., 2007) and the coast of Oregon, USA (Cho et al., 2007). More importantly, we found that the genetic diversity of AAPB tended to decrease with increasing Chl. \textit{a} gradient. This was evident when a significant inverse correlation between diversity of AAPB (measured by the Shannon index) and the concentration of Chl. \textit{a} was found (Fig. 5). The inverse relationship between AAPB diversity and Chl. \textit{a} is in contrast to the positive correlation between abundance of AAPB and Chl. \textit{a} discussed above.

It has been proposed that all proteobacteria have descended from a common purple photosynthetic bacterial ancestor (Xiong et al., 2000). In evolution, some of them may have lost their photosynthetic genes, while others have retained these genes (Beatty, 2002). The polyphyletic feature of \textit{pufM} genes in gamma-AAPB cultures revealed by Cho and colleagues (2007) seemingly supports such possibility. Assuming the above theory is applicable to AAPB, along such an evolution direction, AAPB species could have further lost their photosynthetic genes and gradually become heterotrophic bacteria as the ocean became richer and richer in DOC. The decreasing trend in diversity of AAPB along increasing Chl. \textit{a} gradient observed in this study provides somewhat a reflecting evidence for the above proposed evolution (Xiong et al., 2000; Beatty, 2002). In the present ocean, river run-offs transport terrestrial organic matters into coastal waters, resulting in high availability of carbon source there. In such environments, AAPB species would be more readily to loose their photosynthetic genes and autotrophic lifestyle, resulting lower diversity than in oligotrophic environments. Phototrophic mechanisms in AAPB and their relationship with eutrophication in the ocean are still poorly understood, but remain as an interesting research area for future work.

**Closing remarks**

In the present study, our global ocean survey revealed that AAPB are able to maintain high diversity but low abundance in oligotrophic waters, and become more abundant but less diverse in eutrophic waters. The oligotrophic ocean (such as the Western North Pacific Gyre)
Fig. 4. Phylogenetic analysis of partial purF gene sequences from global oceans. The phylogenetic tree was constructed using the neighbour-joining algorithm. Bootstrap values (100 replicates) greater than 50% are indicated above branches. All purF nucleotide sequences obtained in this work that show >1% difference and reference sequences from cultures were included. Sequences with < 3% difference were combined into a single group. Scale bar represents the 2% nucleotide substitution percentage. Chloroflexus aurantiacus was used as outgroup.
may maintain diverse AAPB species but not necessarily high abundance as previously expected (Kolber et al., 2001; Beatty, 2002). The close tie between AAPB and phytoplankton we observed in variety of marine environments provided evidence for the dependence of abundance of AAPB on availability of organic substrates, which seemed to be more decisive than light in distribution pattern of abundance of AAPB in the ocean. The opposite conclusions about geographic distribution pattern of AAPB along environmental gradients in the literature (Kolber et al., 2001; Schwalbach and Fuhrman, 2005; Cottrell et al., 2006; Masin et al., 2006; Sieracki et al., 2006; Yutin et al., 2007) are likely due to investigation scale, methodology and particular reasons case by case. Further studies on multiple controlling mechanisms of AAPB are necessary. The decreasing diversity of AAPB with eutrophic gradient observed in the present study is somewhat consistent with the proposed evolution direction of phototrophic bacteria (Xiong et al., 2000; Beatty, 2002). The revealed great diversity of AAPB suggests that many new AAPB species can be isolated from variety of marine environments for in-depth study towards a better understanding of AAPB’s role in marine ecosystems. The contrasting variation trends of abundance and diversity of AAPB along environmental gradients are of great interests for future studies.

**Experimental procedures**

**Determination of AAPB abundance by TIREM**

The TIREM protocol is as described by Jiao and colleagues (2006). Briefly, subsamples for bacterial analysis were collected using 100 ml brown polypropylene bottles. Immediately after sampling, aliquots of 20 ml of seawater were fixed with paraformaldehyde (2%, final concentration) and stained with 4′6-diamidino-2-phenylindole (DAPI) (5 μg ml⁻¹, final concentration) and then filtered onto 0.2 μm pore-size black polycarbonate (PC) membranes (Whatman) for microscopic observation. The filters were mounted on slides, and a small drop of immersion oil and a coverslip added. The slides were frozen before analysis. Infrared fluorescence from BChl. a was the diagnostic signal of AAPB. Cells were viewed with an infrared-sensitive charge-coupled device (CCD) camera (SPOT Diagnostic Instruments) on an epifluorescence microscope with a 50 W mercury lamp (Carl Zeiss Light Microscopy AXIOSKOP 40). DAPI-stained images (DAPI image), cyanobacterial images (Cyano image) and infrared images (IR images) were acquired for each microscopic view field using a 100× oil immersion objective. All images were captured using automatic exposure with a gain limit of 8. Time-series images of DAPI, Cyano and IR images were obtained for 10–15 min at intervals of 60 s from the start of the exposure. Images analysis was conducted to get three dynamic curves of IR, Cyano and DAPI counts from each microscopic view field. The accurate estimation of AAPB was calculated from the formula: [AAPB counts] = [plateau count of cyanobacterial cells] – [plateau count of cyanobacterial cells] (Jiao et al., 2006). Thirty microscopic fields of each sample were viewed (at least 300 cells could be detected each sample), and the means were multiplied by appropriate factors to yield cell concentrations in the original samples.

**Determination of picoplankton abundance and environmental variables**

Abundances of total heterotrophic bacteria, *Synechococcus, Prochlorococcus*, were determined by flow cytometry (Jiao et al., 2002) on an Epics Altra II (Beckman Coulter, USA) flow
cytometer, equipped with a 306C-5 argon laser (Coherent, USA). Abundance of non-AABP was obtained by subtracting abundance of AAPB from that of total heterotrophic bacteria. Carbon biomass was calculated using carbon conversion factors of 250, 53 fg C cell−1 for Synechococcus and Prochlorococcus respectively (Kana and Glibert, 1987; Campbell et al., 1994).

Seawater temperature was measured with a SeaBird CTD (SBE 9/11 plus, SeaBird, USA). Water samples for Chl. a analysis were immediately filtered through GF/F filter (Whatman, 47 mm) under dim condition and stored at −20°C for later analysis. The Chl. a was determined fluorometrically (Parsons et al., 1984) with a Turner- Designs Model 10 fluorometer (Sigma, USA).

AAPB diversity revealed by pufM gene sequence analysis

Surface water samples (3–5 l) were pre-filtered through 200 μm mesh and subsequently filtered onto a 0.22 μm pore-size filter (Pall, Gelman Sciences). Filter samples were stored in liquid nitrogen until analysis. Community DNA was extracted using the previously reported protocol (Schwalbach and Fuhrman, 2005). The partial pufM gene sequences were amplified on a T3 thermocycler (Biometra, Germany) using the primers pufMF (TAC GGS AAC CTG TWC TAC) and pufMR (CCA TSG TCC AGC GCC AGA A). The reaction mixture and cycle parameters were as previously described (Beja et al., 2002). The PCR products were subsequently cloned into pMD18-T vector (TaKaRa). Fifty clones from each library were randomly selected and the recombinant plasmid DNA was extracted and sequenced on ABI 377A automated sequencer (Applied Biosystems). Sequences obtained and those from cultures deposited in the NCBI database were aligned using the program CLUSTALX 1.81 and edited manually. A common region of c. 193 bp length was obtained and used for the phylogenetic tree inference. To obtain a compact tree, pufM sequences were combined into groups based on 3% sequence difference prior to tree construction. One sequence from each group was then selected as representative for phylogenetic analysis. The neighbour-joining tree was constructed with the program PHYLIP 3.63 (http://evolution.genetics.washington.edu/phylip.html) with bootstrap value of 100. The nomenclature of clusters in the phylogenetic tree was made according to Yutin and colleagues (2005), using the suffix ‘-like’ to indicate the most possible affiliation. To evaluate the diversity of AAPB in each library, all the pufM sequences were grouped through the program DOTUR using the distance 0.05 as species level for functional gene (Schloss and Handelsman, 2005). The Shannon diversity index in each clone library was then calculated using the program PAST (http://folk.uio.no/ohammer/past). The sequences reported in this article have been deposited in the GenBank database (Accession No. AY731094–AY731136, AY640296–AY640252, AY731137–AY731168, AY652818–AY652839, AY652806–AY652817, DQ093226–DQ093270).

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