

SHORT COMMUNICATION

Significant roles of bacteriochlorophylla supplemental to chlorophylla in the ocean

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Bacteriochlorophylla (BChla)-based phototrophy cannot be ignored in understanding of carbon cycle in the ocean. However, the role of BChla relative to chlorophylla (Chla) along environmental gradients remains unclear. On the basis of the investigations in the Pacific, Indian Oceans and the China Seas, we show that the average contribution of BChla relative to Chla is higher in open-ocean compared with shelf environments, the estimated BChla-based phototrophy could reduce respiratory organic carbon consumption of 2.4% and 5.4% of the primary productions in the shelf and oceanic waters, respectively. This suggests that BChla-based phototrophy has an important role supplemental to Chla-based photosynthesis in the ocean's carbon cycle and would be critical for a marine region to be a sink or a source of atmospheric CO₂.

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With bacteriochlorophylla (BChla)-based light utilization function, aerobic anoxygenic phototrophic bacteria (AAPB) are critical to our understanding of carbon and energy cycling in the ocean (Kolber *et al.*, 2001; Eiler, 2006). Recent studies on the dynamics of AAPB in marine environments have suggested that AAPB are more abundant in eutrophic than oligotrophic waters (Jiao *et al.*, 2007). As AAPB are primarily heterotrophic (Yurkov and Beatty, 1998) and their distribution pattern may be more determined by the availability of the dissolved organic carbon than by light (Jiao *et al.*, 2007), we argue that the abundance or biomass of AAPB is primarily determined by heterotrophy and thus is not indicative of their phototrophy, which is critical for understanding of the role of AAPB as a special functional group in the community. At this juncture, the contribution of energy flow through BChla relative to that through chlorophylla (Chla) along large environmental gradients remains to be systematically elucidated.

In this study, simultaneous *in situ* measurements of BChla, Chla, AAPB abundance, photochemical efficiency, relative functional cross-section of photoreaction center and photosynthetic available radiation were carried out (methods given in Supplementary Information) in the Pacific and

Indian Oceans, and the China seas (Figure 1) toward a better understanding of the relative significance of BChla-based phototrophy to Chla-based photosynthesis in shelf and oceanic environments, and possible impacts of BChla-induced solar energy utilization on carbon cycling in the surface ocean.

Bacteriochlorophylla concentrations were distinctly higher in the shelf waters (1.9–25.8 ng l⁻¹) than in the oceanic waters (0.5–4.4 ng l⁻¹) (Figure 1a, Supplementary Figure S1, Supplementary Table S1). Whereas, the proportion of BChla in total photosynthetic pigments (BChla/(BChla + Chla)), ranging from 0.2% to 3.0%, had an opposite distribution pattern (Figure 1b, Supplementary Figure S1, Supplementary Table S1). AAPB abundance increased with increasing Chla concentration as shown by the regression analysis ($r = 0.65$, $n = 201$, $P < 0.01$; Figure 1a inset plot), clearly showing that AAPB abundance was higher in eutrophic waters compared with oligotrophic waters. Interestingly, the BChla proportion increased with decreasing Chla concentrations ($r = 0.55$, $n = 211$, $P < 0.01$; Figure 1b inset plot), suggesting that in the surface layer AAPB contribute relatively more phototrophic energy in oligotrophic oceans, that is, BChla has a more important role when Chla is scarce.

Vertically, BChla was detectable above 100 m on the shelf and 150 m in the oceanic waters. The depth profiles of BChla were significantly less peaked than those of Chla ($n = 207$, $P < 0.01$ for the oceanic water and $n = 420$, $P < 0.01$ for the shelf water; Figures 2a and b), suggesting that BChla is more tolerant to light variation than Chla. At the ocean surface,

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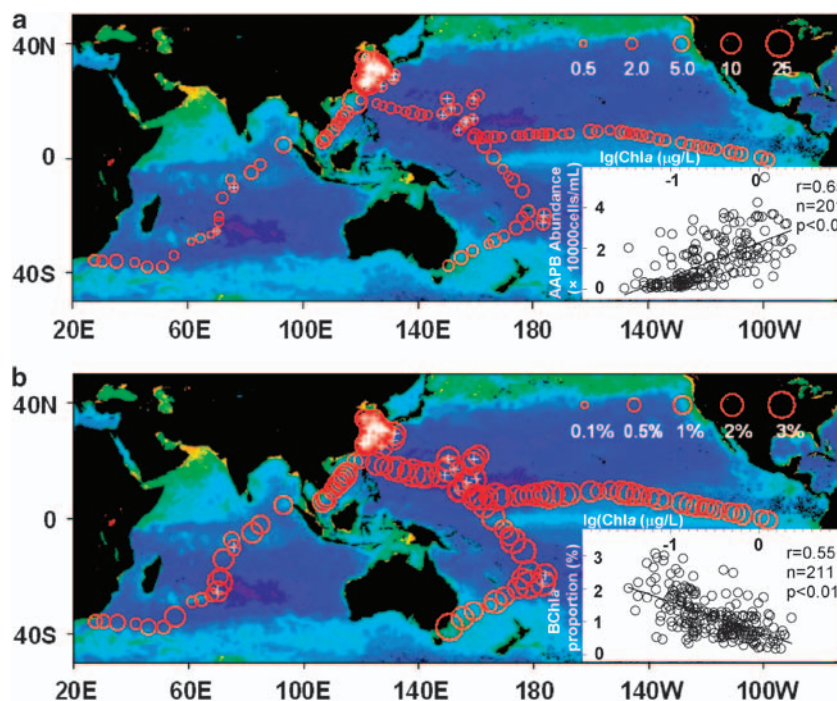


Figure 1 Distribution of bacteriochlorophylla (BChla) concentration (a) and BChla proportion (b) in the Pacific, Indian Oceans and the China seas (Aqua-MODIS remote-sensed chlorophylla (Chla) images were used as the background). Depth profile sites are indicated with white crosses. The inset plots in panels a and b show significant positive or negative correlations between AAPB abundance and BChla proportion with Chla concentration (logarithm transformed), respectively.

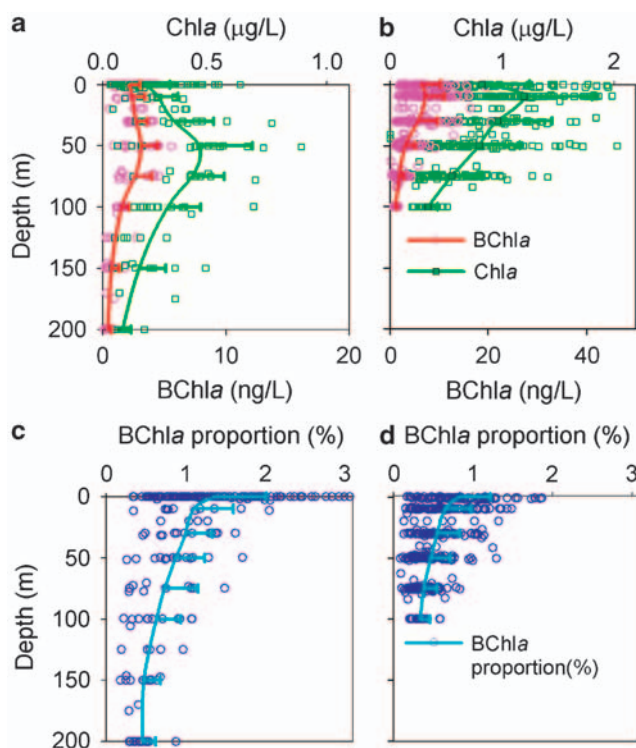


Figure 2 Depth profiles of bacteriochlorophylla (BChla), chlorophylla (Chla) concentrations and BChla proportion in the oceanic (a, c) and shelf waters (b, d).

light intensity often exceeds the demand of Chla-based photosynthesis resulting in photoinhibition. Cellular Chla content could be then reduced as

a result of photoacclimation. Below the surface, however, Chla increased abruptly because of the removal of photoinhibition and higher availability of nutrients. In contrast, being anoxygenic, AAPB are not suffered from such photoinhibition (Koblížek *et al.*, 2007), and have a less curved depth profile of BChla compared with Chla. The depth profiles of BChla proportion always peaked at the surface, with averaged maximum values of 1.40% in the oceanic waters and 0.82% in the shelf seas (Figures 2c and d and Supplementary Figure S1). The high surface values of BChla proportion indicates that BChla contributes more (relative to lower depths in the euphotic zone) to the phototrophic energy flux in the surface, where Chla concentration is low because of photoacclimation and Chla-based photosynthesis is often photoinhibited.

To make a direct comparison between the phototrophic energy fluxes induced by BChla and by Chla, photosynthetic electron transport rates were estimated from the photochemical efficiency (F_v/F_m), relative functional cross-section of the reaction center (σ_{RC}) (Supplementary Table S2) (Gorbunov and Falkowski, 2004) (methods given in Supplementary Information). The averaged surface BChla phototrophic energies were 11.2 and 4.5 $J m^{-3} day^{-1}$ in the shelf waters and oligotrophic oceans, respectively, which contribute approximately 2.0% and 5.7% of total phototrophic energy flows in the corresponding regimes (Supplementary Table S3). This result suggests a compensational role of BChla to Chla, especially in the vast oceans.

The ocean is the largest dynamic carbon pool on the Earth, a region of the ocean can be either a sink or a source of atmospheric CO₂ depending on the balance between photosynthetic carbon fixation and heterotrophic respiration. Different from ordinary heterotrophic bacteria that rely solely on organic carbon respiration for energy, AAPB, with BChla, can use solar energy, which can reduce the demand for organic carbon consumption and consequently impact carbon cycling in the ocean (Eiler, 2006; Moran and Miller, 2007). The observations in this work support the role of BChla in compensating Chla-based photosynthesis in terms of solar energy utilization, particularly in oligotrophic waters and at the ocean surface. When the BChla-based phototrophic energy is converted to carbon respiration consumption using a factor of $5 \times 10^5 \text{ J mol}^{-1} \text{ C}$ (Kolber *et al.*, 2001), the BChla-based phototrophy reduced consumption of organic carbon in the surface water was estimated to be $0.27 \text{ mgCm}^{-3} \text{ day}^{-1}$ in the shelf seas and $0.11 \text{ mgCm}^{-3} \text{ day}^{-1}$ in the oceanic waters, respectively, which could be equivalent to $\sim 2.4\%$ and 5.4% of the respective primary production in the corresponding waters (Barber *et al.*, 1996; Gong *et al.*, 2003). This work also shed light on the following speculation: Given that the overall difference between CO₂ input to and output from the ocean is about 2% (Prentice *et al.*, 2001), these small percentages contributed by BChla-based phototrophy could be big enough to alter a marine region from a sink to a source of atmospheric CO₂ if the energy generated by BChla-based phototrophy were otherwise produced by heterotrophic respiration, which results in an increase of CO₂ output from the ocean. Furthermore, global warming will strengthen ocean stratification, decrease nutrient supply to the euphotic zone, making the surface layer more oligotrophic (Joos *et al.*, 1999). In such scenario, the overall supplemental role of BChla to Chla could be further enhanced.

Conflict of interest

The authors declare no conflict of interest.

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