

## Geomicrobiological Perspectives in the Role of Picoplankton

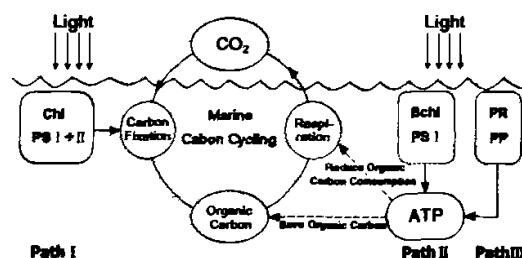
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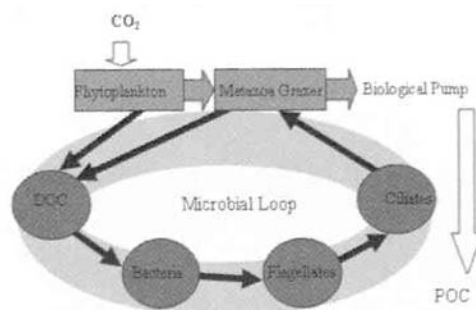
Picoplankton are tiny microorganisms (<2  $\mu\text{m}$ ), that inhabit in the water column of the sea. They are so abundant that one liter of seawater can house as many of them as the total human population on the earth. Picoplankton are indispensable for habitation of mankind on this planet. Cyanobacteria, one of the major component of picoplankton, was the primary contributor turning the ancient reduced atmosphere to oxic so that modern life including human being arose later on. At the present, picoplankton are playing a key role in carbon cycling in the ocean and consequently affecting the global climate. Planktonic bacteria, accounting more than half of picoplankton, is the major driving force for essential biogeochemical cycles of C, O, N, P, or S in the ocean. Picoplankton are extremely versatile, scientists just get started to know their diverse functions.

### BIOLOGICAL UTILIZATION OF LIGHT AND CARBON CYCLING IN SURFACE OCEAN

Photosynthesis in the sea is usually thought to be induced primarily by chlorophylls. However recent studies have revealed that light-harvesting pigments are not only confined to normal chlorophyll, other pigments also contribute substantially to light utilization of the sea, such as divinyl-chlorophyll in *Prochlorococcus* which are extremely abundant in tropical and subtropical oceans; bacterial chlorophyll in aerobic anoxygenic phototrophic bacteria (AAPB) which are newly recognized to be ubiquitous in all marine environments (Beja et al., 2002; Kolber et al., 2001). Furthermore, the breakthrough of environmental genomics of picoplankton has revealed the wide existence of proteorhodopsin (PR) bearing bacteria which account for 13% of the total microorganisms in surface ocean (Sabeji et al., 2005). These new findings bring to light the non-chlorophyll dependent pathways of light utilization contrasting to the well-known chlorophyll-dependent photosynthesis, the new paths are not to be ignored in energy metabolism and carbon cycling in the ocean. Based on the understanding of current literature and our own investigation on *Prochlorococcus*, AAPB and PR in world oceans, we propose a conceptual model of energy flow and carbon cycling driven by both pigment-dependent and -independent biological utilization of light in the ocean (Fig. 1).



**Figure 1.** A model of light bio-utilization and carbon cycling in the ocean. Chl. chlorophyll and divinyl chlorophyll; Bchl. bacteriochlorophyll; PR. proteorhodopsin; PS I, II. photosystems I and II; PP. proton pump (Jiao et al., 2006).



**Figure 2.** A diagram of "microbial loop" picking up DOC from water and transport pico-sized POC to upper trophic levels for sinking biological pump.

### SINKING AND NON-SINKING BIOLOGICAL PUMPS

Particulate organic carbon (POC) formed by organisms in the euphotic zone can sink out of the surface layer and partially down to deep sea, thus keeping away from returning back into atmosphere for hundreds of year (Feely et al., 2001). This process is primarily driven by biota and is thus called "biological pump". In contrast, dissolved organic carbon (DOC) is not sinkable, and thus used to be considered as zero contribution to the "biological pump". Even picoplankton were once thought to be insignificant contributors to the "sinking pump". However, recent studies have revealed that neither DOC nor picoplankton are negligible in terms of carbon sequestration of  $\text{CO}_2$  by the ocean. Labile DOC (LDOC) can be picked up by heterotrophic bacteria and then transported to upper trophic levels through "microbial loop" and

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consequently forming sinking POC (Fig. 2). Picoplankton can even form significant sinking flux by their “aggregation mechanisms” (Richardson and Jackson, 2007).

The fraction of DOC that can not be utilized by bacteria is called refractory DOC (RDOC). Although RDOC can not be transformed to POC by the microbial loop, it is a kind of carbon sequestration as its turnover time in the ocean is approximately 4 000–6 000 years. As RDOC is either produced by biota or left by bacteria, such processes can be called “non-sinking biological pump” (Fig. 3). Since DOC is the largest organic carbon pool in the ocean, and RDOC is the majority of total DOC (Ogawa and Tanoue, 2003), non-sinking biological pump is one of the keys to understanding of carbon sink of the ocean. The accumulation of DOC in the ocean from ancient time to the present has demonstrated its significance.

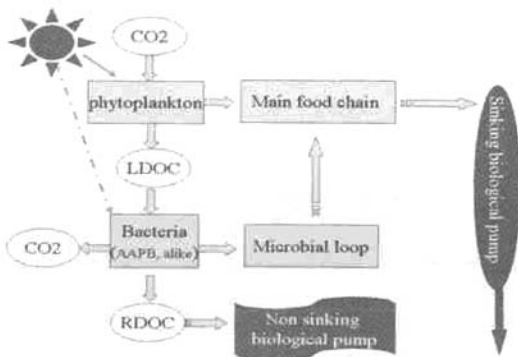


Figure 3. A diagram of “non-sinking biological pump” vs sinking “biological pump” (Jiao, 2006).

#### LINK THE PRESENT WITH THE ANCIENT THROUGH PICOPLANKTON

Picoplankton are usually ignored in deep sea paleogeological record because of their “non-sinking” property. This common sense turns out to be not really true. As mentioned above they do sink through “aggregation” or “trophic transformation” mechanisms. Although they are invisible in the sediment sample, they may have molecular markers there or even in the water column. The key to pick up their records is to identify corresponding molecular markers or fingerprints. On the other hand, we should try to understand the ancient from the current observations. Looking at the ecological patterns of *Prochlorococcus* or AAPB in the present oceans, their favorite habitats would set people thinking. The environments they like are not what we think they would like. For *Prochlorococcus*, the favorite environmental conditions are high temperature, low light, low nutrients. What more surprising are their molecular features: unique photosynthesis pigment of divinyl-chlorophyll and lack of nitrate reductase encoding genes. Checking on the history of the earth, one will find such an environment in the ancient time when the planet was covered with thick green house gasses ( $\text{CO}_2$ ,  $\text{CH}_4$  etc), and

therefore surface temperature was high and irradiation was low (Fig. 4). There was obviously no nitrate in the ocean due to the reduced atmosphere at that time. Could that be the time when *Prochlorococcus* arose? For the case of AAPB, its diversity decreased with increasing trophic gradients in the current global oceans (Jiao et al., 2007). Compared with other bacteria, AAPB have less versatility in their diet of DOC and have a closer tie with cyanobacteria. These observations together with other features of AAPB such as moderate requirements for light and oxygen (Ogawa and Tanoue, 2003), suggest that AAPB could arise during the long reign of cyanobacteria in the Mesoproterozoic when oceans were primarily anoxic but moderately oxic at the surface (Anbar and Knoll, 2002; Kerr, 2002). At that time, DOC in the oceans were mainly contributed by cyanobacteria and are much less complex compared to today’s ocean. With increasing organic matters and oxygen in the ocean later on, particularly after the emergence and evolution of plants, some original AAPB species might have consequently lost their photosynthesis genes and become non-AAPB. Our observations demonstrate a scenario in the present ocean to explore co-evolution of life and the earth as seen from AAPB/*Prochlorococcus* along the environmental gradients from the Pacific Warm Pool to the marginal seas.

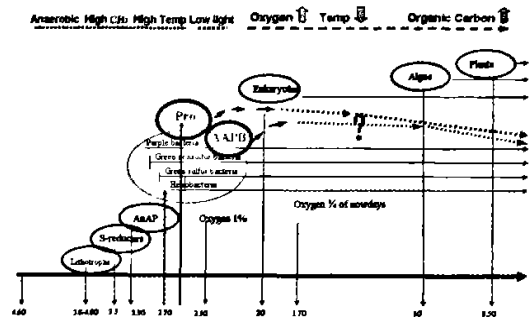


Figure 4. A putative chart of co-evolution of life and the earth as seen from current molecular ecological processes of *Prochlorococcus* and AAPB (Jiao et al., 2007).

**KEY WORDS:** picoplankton, *Prochlorococcus*, aerobic anoxygenic phototrophic bacteria (AAPB), proteorhodopsin (PR), bacterial chlorophyll, non-sinking biological pump, evolution.

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## Microbial Effects in Biomineralization and Weathering

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The interface between biological and geological world is epitomized by two important but not-well-understood processes, namely biomineralization and bio-promoted weathering. Here, we report two case studies: one concerns microbial formation of carbonate minerals mediated by a strain of soil bacteria isolated from Chinese loess, and the other explores the roles of a strain of thermophilic fungi in solubilizing potassium from K-bearing aluminosilicate minerals. For biomineralization study, we found that calcite was the dominant mineral phase formed when the bacteria are present. However a significant portion of vaterite was also precipitated in cultures where the cells were filtered out. We also noticed that the bacteria had a strong tendency to colonize the center area of the calcite {10 $\bar{1}$ 4} faces to promote the growth normal to each individual faces when the cell concentration was high, but may retard it or even cause dissolution of the immediate substrate surfaces when the concentration is low.  $\delta^{13}\text{C}$  measurements proved that the crystals were further enriched in heavier isotope, implying

that the bacterial metabolism may not be the carbon sources for mineralization. For weathering study, measurements over a period of 30 days showed that the concentrations of free K in the fungus growth cultures were up to 30 times higher than those in control experiments without living organism. Kinetic analysis indicated that the potassium solubilization rate showed a positive dependence upon pH when the fungi and minerals were mixed, and exhibited no correlations with solution acidity when the cells and rock grains were separated, sharply contrasting to the inverse relationship between rate and pH known for inorganic weathering, indicating that proton catalyzed surface process may be secondary in this case. Based upon these observations, we proposed mechanism to interpret the involvement of biological effect to mineral formation and dissolution.

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