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# Presence of *Prochlorococcus* in the aphotic waters of the western Pacific Ocean

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Abstract

*Prochlorococcus*, the smallest but most abundant marine primary producer, plays an important role in carbon cycling of the global ocean. As a phototroph, *Prochlorococcus* is thought to be confined to the euphotic zone, with commonly observed maximum depths of ~ 150–200 m. But here we show, using flow cytometry and cellular ribosomal content, for the first time the presence of abundant and active *Prochlorococcus* in the dark ocean (“deep *Prochlorococcus*” hereafter). Intensive studies at the Luzon strait in the western Pacific Ocean show that the deep *Prochlorococcus* populations are exported from the euphotic zone. Multiple physical processes including internal solitary waves could be responsible for the transportation. The unexpected abundance of the tiny phototrophs in the dark ocean reveals a novel mechanism for picoplankton carbon export other than the known mechanisms such as sinking of phytodetritus and aggregates or grazing-mediated transportation. Such direct transportation of picoplanktonic phototrophs from surface to deep waters is poorly understood, but could significantly contribute to both the biological pump (through particulate organic carbon) and the microbial carbon pump (through release of dissolved organic carbon from microbial processes) for carbon sequestration in the ocean.

## 1 Introduction

*Prochlorococcus*, the known smallest oxygenic phototroph, is the numerically dominant primary producer (typically  $10^4$ – $10^5$  per mL) between 40° N and 40° S, and contributes significantly to total primary productivity in the vast oligotrophic oceans (Partensky et al., 1999; Coleman and Chisholm, 2007; Partensky and Garczarek, 2010). Unlike other primary producers, *Prochlorococcus* does not sink due to its small size (0.5–0.7  $\mu\text{m}$  in diameter) and neutral buoyancy. Thus, the tremendous amount of carbon fixed by *Prochlorococcus* had been generally regarded to be consumed through the microbial loop and recycled within the euphotic ocean. However, a recent model analysis

BGD

10, 9345–9371, 2013

## Deep *Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



suggested a significant fraction of carbon export may be attributable to the picoplankton despite their lack of direct sinking (Richardson and Jackson, 2007). The known picoplankton export mechanisms include aggregation (Jackson et al., 2005), particle packing through grazing and egestion (Richardson and Jackson, 2007), phytodetritus (Lochte and Turley, 1988) as well as winter ventilation (Vilibić and Šantić, 2008). In practice, the previously observed picoplankton exported to the deep sea are mainly *Synechococcus*, and more rarely picoeukaryotes (Lochte and Turley, 1988; Vanucci et al., 2001; Sohrin et al., 2011). *Synechococcus* are reported to be able to utilize organic substrates (Moore et al., 2002; Glibert et al., 2004), and thus thought to be able to survive in the dark (Cottrell and Kirchman, 2009; Sohrin et al., 2011). In the case of *Prochlorococcus*, although previous molecular analysis revealed the existence of some functional genes of *Prochlorococcus* in aphotic waters in the North Pacific subtropical gyre area (DeLong et al., 2006) and Sargasso Sea (Martinez et al., 2012), abundant *Prochlorococcus* populations are thought to be confined to the euphotic zone (Partensky et al., 1999; Coleman and Chisholm, 2007; Partensky and Garczarek, 2010). Here we report for the first time the presence of abundant *Prochlorococcus* populations in the dark ocean (hereafter “deep *Prochlorococcus*”). During our investigations from 2008 to 2012, we frequently observed *Prochlorococcus* in the mesopelagic waters in the western Pacific Ocean and its marginal seas. Based on biological and physical oceanographic observations and analysis, we propose here a novel mechanism for export of *Prochlorococcus* to the ocean interior, which could contribute to both the particulate organic carbon (POC) based classical biological pump and the newly proposed dissolved organic carbon (DOC) transformation based microbial carbon pump (Jiao et al., 2010). These results shed new light on our understanding of carbon cycling and carbon sequestration in the ocean and point to additional areas where further studies are needed.

**BGD**

10, 9345–9371, 2013

**Deep  
*Prochlorococcus***

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 2 Materials and methods

### 2.1 Cruises and sampling

Seven cruises to the western Pacific Ocean, northern South China Sea, and Luzon Strait were conducted from 2008 to 2012 (Table 1). Water samples were collected at various depths from the surface to 2000 m using 12 L Niskin bottles mounted on a CTD-carousel sampler. Standard sampling procedures were followed (Sohrin et al., 2011) and temperature, salinity and pH of the sampled water in the Niskin bottles were monitored to assure no contaminations from the surface water to the deep water samples. Subsamples (15 mL) were collected immediately for onboard flow cytometry analysis. Aliquot samples were fixed with glutaraldehyde (final concentration 0.5 % v/v), flashly frozen in liquid nitrogen and stored at  $-80^{\circ}\text{C}$  until later flow cytometric analysis in the laboratory.

For phylogenetic analysis, 2 L of seawater was filtered onto 0.22  $\mu\text{m}$  pore-size 47 mm diameter polycarbonate filters (Millipore, Bedford, MA, USA) to retrieve the total picoplanktonic population. The filters were stored at  $-80^{\circ}\text{C}$  until genomic DNA extraction. For cellular ribosomal RNA content analysis, 100 mL (depths  $< 200$  m) or 200 mL (depths  $\geq 200$  m) of seawater was filtered onto a 0.22  $\mu\text{m}$  pore-size 25 mm diameter polycarbonate filters under low vacuum ( $> -0.3$  bar). To preserve DNA for qPCR, filters were stored at  $-80^{\circ}\text{C}$  until DNA extraction. To preserve RNA for RT-qPCR, each filter was immersed in 600  $\mu\text{l}$  of RLT solution (Qiagen, Chatsworth, CA, USA) containing 1 %  $\beta$ -mercaptoethanol and stored at  $-80^{\circ}\text{C}$  until RNA extraction.

### 2.2 Flow cytometry analysis

*Prochlorococcus* and other picoplankton (*Synechococcus*, heterotrophic bacteria/archaea, picoeukaryotes and viruses) were analyzed using an onboard FACSaria flow cytometer (Becton, Dickinson and Company, USA) equipped with a 488 nm laser as the excitation light source, following procedures described previously (Marie et al.,

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1999). All onboard observations were confirmed by another flow cytometry analysis (EPICS Altra II; Beckman Coulter, USA) in the laboratory. In both flow cytometry analyses, BD Trucount control beads were used to calibrate the flow rate to achieve accurate enumeration of the cells.

## 2.3 Molecular analysis

Environmental genomic DNA was extracted by using phenol-chloroform method (Fuhrman et al., 1988). The quantity and quality of DNA were evaluated by NanoDrop (Thermo Scientific). Cyanobacterial 16S-ITS-23S rRNA gene (ITS hereafter) fragments were amplified with primers Picocya16S-F (TGGATCACCTCCTAACAGGG) and Picocya23S-R (CCTTCATCGCCTCTGTGTGCC)(Cai et al., 2010). The cycling program included 8 touch-down cycles at 94 °C for 30 s, 58–54 °C for 50 s (–0.5 °C/cycle) and 72 °C for 1 min, 20 normal cycles at 94 °C for 30 s, 55 °C for 50 s and 72 °C for 1 min, and a 7 min extension step. The PCR products were purified using the QIAquick Gel Extraction Kit (QIAGEN, Hilden, Germany), and cloned using the TOPO TA cloning kit (Invitrogen, Carlsbad, CA, USA) following the manufacturer's instructions. All sequences obtained were carefully checked for chimeric artifacts using the BLASTN program (<http://www.ncbi.nlm.nih.gov/BLAST>), and chimeric sequences were excluded. Phylogenetic analysis based on ITS sequences was carried out using MEGA 4 (Tamura et al., 2007) with the inputted alignment created by Clustal X2 (Larkin et al., 2007). The neighbor-joining phylogenetic tree was rooted from an ITS sequence of *Synechococcus* (CC9311) and constructed with representative ITS sequences of major *Prochlorococcus* ecotypes (MIT9515, MED4, MIT9215, MIT9202, MIT9312, MIT9301, AS9601, NATL1A, NATL2A, SS120, MIT9211, MIT9303, MIT9313) as references. The ITS sequences obtained in this study were deposited in the GenBank under accession numbers JN382571–JN383336 and KC770800–KC770987.

We quantitatively assessed the abundances (rDNA) and activities (rRNA/rDNA ratio) of two ecotypes of *Prochlorococcus* (high-light (HL)-adapted ecotype II and low-light (LL)-adapted ecotype IV). These two ecotypes numerically dominate the upper

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and lower euphotic zone, respectively, in low- and mid-latitude waters (Johnson et al., 2006). Ecotype abundance was estimated using DNA based qPCR assay as described previously (Zinser et al., 2006) with 23S rRNA primers targeting HLII (Ahlgren et al., 2006) and LLIV (Hunt et al., 2013). Ecotype specific rRNA concentration was measured by a RT-qPCR assay as described previously (Lin et al., 2013). Briefly, after bead-beating cell lysate was diluted 1 : 100 in RNase-free water and directly used as template for cDNA synthesis (iScript, Bio-Rad, Hercules, CA). The rDNA concentration, which was estimated from qPCR assay, was subtracted from the RT-qPCR results to obtain rRNA concentration.

## 2.4 Physical oceanographic observation and analysis

In order to explore mechanisms responsible for the presence of *Prochlorococcus* in the aphotic deep waters, we focused on the Luzon Strait where general physical processes including solitary waves, meso-scale eddies, interfacial Ekman transport, and turbulent mixing have been extensively investigated (Jackson and Apel, 2002; Yuan, 2002; Jia and Liu, 2004; Zhao et al., 2004b; Tian et al., 2006, 2009; Zhao and Alford, 2006; Yuan et al., 2007; Jan et al., 2007; Laurent, 2008; Jan and Chen, 2009; Alford et al., 2010). In our study, 75 kHz Acoustic Doppler Current Profilers (ADCP) were deployed to monitor internal solitary waves in the western side of the Luzon Strait (21°00' N, 118°00'–120°00' E) (Fig. S1). Sea level anomalies (SLA) were also observed by satellite altimeters (Su, 2004) The turbulent dissipation rate  $\varepsilon$  and mixing rate  $K$  are derived by applying “Thorpe scale” analysis to CTD data. The root mean square Thorpe displacement  $L_{th}$  for an actively mixing patch is given by  $L_{th} \approx 0.8^{-1} L_o$ , where  $L_o = (\varepsilon/N^3)^{1/2}$  is the Ozmidov length scale (Dillon, 1982).  $L_{th}$  can be calculated by reordering the density profile into a monotonic gravitationally stable profile. Each sample  $\rho_n$  within the original profile is associated with a depth  $z_n$  and in the reordered profile with a depth  $z_m$ .  $L_{th}$  is defined as  $L_{th} = (\overline{d'^2})^{1/2}$ , where  $d'_n = z_n - z_m$ . After  $\varepsilon$  has been estimated from

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



measured  $L_{th}$  via these relationships, the mixing rates can be obtained as  $K = \Gamma \varepsilon / N^2$ , where a typical value of the mixing efficiency  $\Gamma$  is 0.2 (Finnigan et al., 2002).

### 3 Results and discussion

#### 3.1 Abundance and phylogeny of deep *Prochlorococcus* in the western Pacific and its marginal seas

Onboard flow cytometry analysis showed that *Prochlorococcus* was frequently present in the mesopelagic waters of the western Pacific Ocean, the Luzon Strait and the South China Sea. The flow-cytometrically characterized populations of *Prochlorococcus* were well defined indicating coherent and possibly active populations (Fig. 1). In the western Pacific tropical and subtropical areas, deep *Prochlorococcus* populations were often found at depths > 1,000 m, while in the Luzon Strait and South China Sea, deep *Prochlorococcus* populations were mostly observed at shallower aphotic waters from 300 m to 500 m (Table 1). Taking the case of the Luzon Strait as an example for more details, the abundances of *Prochlorococcus* were variable with depths, ranging from  $10^4$  to  $10^5$  cells mL<sup>-1</sup> in the euphotic zone and from  $\sim 10^2$  to  $10^4$  cells mL<sup>-1</sup> in the aphotic zone (Fig. 2). The maximum abundances usually occurred at around 100 m, and the lowest abundances within the euphotic zone were often found at 200 m. In the dark waters below 200 m, the abundances of *Prochlorococcus* were not evenly distributed and generally decreased with depth (Fig. 2). In addition to flow cytometry enumeration, the abundances of major *Prochlorococcus* ecotypes (HLII and LLIV) at St. DC01 were also determined by qPCR which showed that the sums of the two ecotypes were comparable to the flow cytometry results (Figs. 2 and 3a).

Phylogenetic analysis of the deep *Prochlorococcus* samples from the western Pacific Ocean (St. N8-12) and the Luzon Strait (St. DC01) showed that both the high-light and low-light adapted *Prochlorococcus* ITS sequences were present in all the water depths (Fig. 4). The high-light adapted *Prochlorococcus* were clustered in the HLII,

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



while diverse low-light lineages were observed, which can be affiliated into LLI-VI and NC1 clades. No distinct phylogenetic differences of cyanobacterial ITS sequences were observed between samples from the euphotic and the aphotic zones (Fig. 4). These results suggest a euphotic zone source for these deep *Prochlorococcus* populations rather than a population unique to the aphotic environment.

### 3.2 Activity of *Prochlorococcus* in the dark ocean

Flow cytometry fluorescence signals can be used as indicators of cellular pigment contents (Six et al., 2004). In the Luzon Strait area, the red fluorescence signals of the *Prochlorococcus* cells increased with increasing water depth until the bottom of the euphotic zone (150–200 m) and then declined a bit below, but were still comparable to the maximum (~ 80 % of the maximum). Except for the cases of 700 m and 800 m, the cellular fluorescence signals of the *Prochlorococcus* cells at the aphotic depths were much higher than that in the upper euphotic zone (mostly 5–20 % of the maximum) (Fig. 5).

At St. DC01 in the Luzon Strait, we quantified the 23S rRNA contents of two dominant *Prochlorococcus* ecotypes (HLII and LLIV) using a RT-qPCR approach to assess their in situ activity. As illustrated by Fig. 3b, the estimated cellular rRNA contents were 150–270 copies cell<sup>-1</sup> for HLII, and 500 copies cell<sup>-1</sup> for LLIV. Within the euphotic zone, both LLIV and HLII exhibited increasing cellular rRNA with depth (maximum at 150 m), perhaps reflective of cell size increase, while below the euphotic zone, HLII maintained significant amount of rRNA at 300 m (~ 150 copies cell<sup>-1</sup>) and LLIV cellular rRNA was below the limit of detection. This suggests that those high-light adapted *Prochlorococcus* cells were still viable in the dark.

Flow cytometry side light scatter signals can be used as indices of cell size and cell density for picoplankton (Wittrup et al., 1988; Jochem, 2000). In the Luzon Strait, the side light scatter signals of the *Prochlorococcus* cells typically increased to their maximum values at the bottom of the euphotic zone (150–200 m) and then decreased gradually when depth further increased (Fig. 6), suggesting a shrinking of the cell size

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and density downward. Such shrinking could be due to consumption of cellular storage for their prolonged survival in the extended darkness.

All these above observations suggest that the *Prochlorococcus* we observed in the aphotic waters was active and still viable in the dark. Molecular analysis of functional genes has shown that photoautotrophs in twilight waters are highly adaptive to poor light conditions and are functionally active (Gao et al., 2011). Cell digestion assay has shown that *Prochlorococcus* have higher capacity to survive at low irradiance than *Synechococcus* (Agustí, 2004). In terms of heterotrophic potentials, although *Prochlorococcus* are not as well documented as *Synechococcus* strains that are believed to have ectoproteolytic activities (Martinez and Azam, 1993; Moore et al., 2002; Cottrell and Kirchman, 2009), it has been reported that *Prochlorococcus* can incorporate exogenous organic nutrients (Moore et al., 2002; Zubkov et al., 2003; Zubkov and Tarran, 2005; Martinez et al., 2012) and oligopeptide transporters are found in the genomes of *Prochlorococcus* strains (Rocap et al., 2003). However, there has been no direct evidence for complete heterotrophic growth of *Prochlorococcus* and the genomic analysis did not reveal known pathways that would allow complete heterotrophy (Johnson et al., 1999; Rocap et al., 2003). Particularly, in the deep waters, exogenous organic compounds are unlikely to meet the energy and carbon demands of deep *Prochlorococcus* due to the restricted availability of labile dissolved organic matters, as most of the dissolved organic matters in the deep sea are refractory (Hansell et al., 2009; Jiao et al., 2010). Therefore catabolizing cellular storage of endogenous carbon sources such as carbohydrates, lipids would likely to be a more possible mechanism for the deep *Prochlorococcus* to keep prolonged survival in the dark, as have reported on other cyanobacteria (Osanai et al., 2005; Montechiaro et al., 2006).

### 3.3 Possible mechanisms for the transportation of the deep *Prochlorococcus* in the Luzon Strait

Previous studies have observed the presence of cyanobacterial cells or aggregates in the deep seas, which are usually attributed to sinking processes through phytodetritus,

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



aggregation, and mesozooplankton grazing (Lochte and Turley, 1988; Richardson and Jackson, 2007). Some occasional observations of cyanobacteria in mesopelagic waters are attributed to winter deep convection (Vilibić and Šantić, 2008). Obviously all the above mechanisms cannot be simply applied to our case of abundant *Prochlorococcus* viable cells in the dark ocean. Active physical transportation is most likely to be responsible for such case. It is known that meso-scale eddies are present in the Luzon Strait area year-round (Yuan, 2002; Yuan et al., 2007). As seen from sea level anomalies (SLA) observed by satellite altimeters, strong cyclonic and anticyclonic eddies are present in the study area year-round (Su, 2004; Yuan et al., 2006). During the study period from 21 March 2010 to 10 July 2011, the standard deviation of the weekly Aviso altimeter SLA averaged in the central Luzon area (19°00′–21°00′ N, 119°30′–121°30′ E) was 8.7 cm (Fig. S2 shows a case of SLA on 21 April 2010). In addition to anticyclonic eddies leading to downwelling transport at the center of the eddies, cyclonic eddies can induce much stronger vertical transport by the interfacial Ekman transport along isopycnal surfaces at their rims. According to the classical Ekman theory, the average velocity across the Ekman layer thickness (1/2 of the horizontal geostrophic velocity) was frequently above  $0.5 \text{ ms}^{-1}$  at the rims of the eddies, which is high enough to induce strong interfacial Ekman transport (Yuan et al., 2007). For an isopycnal with a slope of  $10^{-2}$ , the descending of surface water parcels across the depth of  $\sim 1000 \text{ m}$  via the interfacial Ekman transport can be achieved within a few days (Dillon, 1982). Diapycnal mixing associated with internal waves, tides, meso-scale eddies and other processes play a significant role in exchanging materials between the upper and lower layers (Yuan, 2002; Tian et al., 2009). In particular, a special type of internal waves called soliton can induce rapid vertical water movement and exchange (Jackson and Apel, 2002). Solitons occurred almost daily in the Luzon Strait area (particularly in the west side). For example, 384 internal solitons were observed during the period from 21 March 2010 to 20 April 2011 by an ADCP deployed at 21°00′ N, 119°00′ E (Fig. S1). The amplitudes of some of the observed thermocline depressions of the internal solitons were as large as 170 m. The recorded vertical velocity at 550 m has reached

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



0.25 ms<sup>-1</sup> (at 21°00' N, 119°00' E; Fig. 7a). Combined with the large vertical diffusivity in the area, the solitons could induce deep mixing overcoming the thermocline barriers at about 100 m depth (e.g. Fig. 7b). Thus the rapid vertical water movements could effectively push *Prochlorococcus* cells down and turbulence then acts to keep some of the cells in the deep water.

Unlike the common water column mixing processes that usually reduce the populations of *Prochlorococcus* in the euphotic zone (Post, 2006), the reciprocating depression- and elevation-waves of the internal solitons (Zhao et al., 2004a) mainly took place in the lower euphotic zone and below, with each cycle lasting for a short time (about 30 min for the main pulse and 2 h for the following associates) in the case of Luzon Strait (Fig. 7 and S3). The rapid vertical water movements could regularly transport certain amount of *Prochlorococcus* cells from nutrient-depleted euphotic waters to nutrient-replete deep waters, allowing the cells to access sufficient inorganic nutrients, and subsequently bring a fraction of the cells back to the euphotic zone for efficient photosynthesis and carbon fixation. This could provide the *Prochlorococcus* cells with opportunities to access temporally and spatially alternating light and nutrient conditions, overall supporting higher production in the euphotic zone (up to 10<sup>5</sup> cells mL<sup>-1</sup>) and longer survival of the *Prochlorococcus* cells in the aphotic waters (so as to be observable). Meanwhile, each solitary wave cycle releases certain portion of the *Prochlorococcus* cells into the dark ocean, acting as a vertical conveyer belt for picoplankton export (Fig. S3). Other phytoplankton may also be transported, but *Prochlorococcus* would be the mostly influenced, given that they are naturally dominating in the lower euphotic zone where the momentum of internal solitary waves is the maximum.

### 3.4 Contribution of deep *Prochlorococcus* to carbon cycling in the ocean

In our observations, the abundance of the deep *Prochlorococcus* are typically about one to two orders of magnitude lower than the maximum abundance (i.e. lower euphotic

BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



zone) but are comparable to the abundance in the upper part of the euphotic zone in the Luzon Strait areas. If such distribution pattern of *Prochlorococcus* is in normal balanced status, that is, the total number of the observed deep *Prochlorococcus* cells in the 200–800 m water layer would count for about 15% of the total *Prochlorococcus* cells in the upper 200 m layer. This percent is comparable to the level of new production or the  $f$  ratio in general (Yool et al., 2007). Given that the dead cells may not have been included in the observation, the real export rate of *Prochlorococcus* could be even higher. Transportation of *Prochlorococcus* and other microbes from the surface to deeper waters constitutes a vertical carbon flux. It has been reported that the concentrations of total organic carbon in the intermediate waters of the South China Sea (most profiles from sites close to the Luzon Strait) are higher than those in the north-western Pacific Ocean, suggesting higher export of organic carbon in the former (Dai et al., 2009). The vertical carbon transportation indicated by our observation might contribute to this relatively high organic carbon pool in intermediate waters. On the other hand, modeling with inverse analysis and network analysis suggests that picoplankton can make large contribution to carbon export from surface water through sinking of phytodetritus and aggregates or grazing-mediated transportation (Richardson and Jackson, 2007). Our finding of abundant intact *Prochlorococcus* cells in the dark ocean suggests a novel mechanism for rapid vertical transportation of picoplankton carbon other than previously reported mechanisms (Lochte and Turley, 1988; Richardson and Jackson, 2007; Vilibić and Šantić, 2008). In addition to the direct transportation of cells that are particulate organic carbon, dissolved organic carbon left over in the deep sea is an important mechanism to store the carbon in the ocean interior. Not only the dead cells passive leaks but also the viral lysis of alive cells release dissolved organic carbon into the water (Suttle, 2005). Heterotrophic bacteria and archaea would consequently take up the labile DOC and transform part of it to refractory DOC through the microbial carbon pump, constituting long-term carbon storage in the ocean (Jiao et al., 2010). Previous studies on sediment traps and integrated biomass estimations of whole water columns in the West Pacific Ocean have indicated that biological pump in tropical

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and subtropical regions are weaker than in subarctic regions (Yamaguchi et al., 2002, 2004; Honda et al., 2002), while the microbial carbon pump is more active in tropical and subtropical regions (Jiao et al., 2010, 2011). The presence of abundant deep *Prochlorococcus* suggests an even more important role of the microbial carbon pump in the study area (subtropical). Our findings also raise fundamental questions about the ecology and biogeochemistry of *Prochlorococcus* for future studies, such as, how long can *Prochlorococcus* cells survive in the dark ocean where nutrients are replete but temperatures are low? are there any gene mutation, regulation of gene expression or physiological adaptation existing in the dark ocean (given that the physical transportation is successively occurring)? and what are the fates of these *Prochlorococcus* cells and the ecological consequences (food web dynamics, grazing, viral lysis, and their impacts on carbon export)? etc. The presence of abundant *Prochlorococcus* in the dark ocean reported here and the proposed mechanisms bring new insights in, and call further studies on mechanisms of carbon cycling and carbon sequestration in the ocean.

**Supplementary material related to this article is available online at:**  
**[http://www.biogeosciences-discuss.net/10/9345/2013/  
bgd-10-9345-2013-supplement.zip](http://www.biogeosciences-discuss.net/10/9345/2013/bgd-10-9345-2013-supplement.zip)**

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BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## References

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BGD

10, 9345–9371, 2013

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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- 30

Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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## Deep Prochlorococcus

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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**BGD**

10, 9345–9371, 2013

**Deep  
*Prochlorococcus***

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Deep  
*Prochlorococcus*

N. Jiao et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

I ◀

▶ I

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

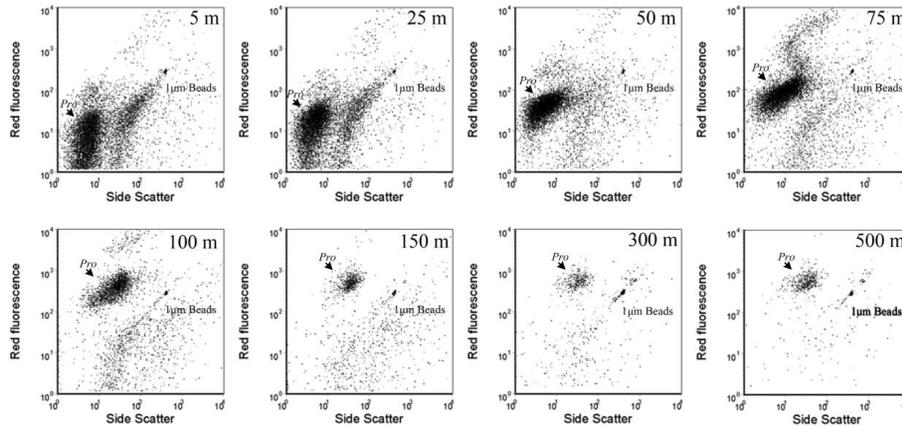


**Table 1.** Locations and water depths where deep *Prochlorococcus* were observed in the western Pacific Ocean, northern South China Sea, and Luzon Strait.

Region	Date	Station	Longitude	Latitude	Deep <i>Prochlorococcus</i> depth (m)
<b>Luzon Strait and South China Sea</b>					
	Aug 2008	E05	121°00′ E	20°00′ N	300, 400, 600
	Aug 2008	E04	121°00′ E	20°15′ N	1500
	Mar 2010	LX02	119°21′ E	21°02′ N	300, 400, 500
	Apr 2011	LX01	117°51′ E	21°06′ N	300, 400, 500, 700
	Jul 2011	C0	122°18′ E	19°15′ N	1000, 1200, 1500
	Jul 2011	C01	121°02′ E	19°32′ N	300
	Jul 2011	C02	121°00′ E	20°00′ N	300, 500, 800
	Jul 2011	C03	123°28′ E	20°00′ N	300, 1000
	Jul 2011	N22-1	122°00′ E	22°00′ N	1000
	Jul 2011	N22-4	124°33′ E	22°00′ N	1000, 1500
	Apr 2012	DC01	121°42′ E	21°08′ N	300
<b>Western Pacific Ocean</b>					
	Dec 2008	KX08-97322	145°00′ E	7°00′ N	800, 1500
	Dec 2010	N8-12	133°42′ E	6°22′ N	800, 1000, 1500
	Dec 2010	P7	129°59′ E	9°00′ N	500, 800, 1000, 1500, 2000
	Jul 2011	N5-132	132°04′ E	4°56′ N	600, 800, 1000, 1200
	Jul 2011	N5-133	133°00′ E	5°00′ N	300, 500, 800, 1000
	Jul 2011	N5-134	134°00′ E	5°00′ N	500, 800
	Jul 2011	N7-134	134°00′ E	7°00′ N	300, 500, 800, 1000, 1500
	Jul 2011	N8-6	129°00′ E	8°00′ N	1200
	Jul 2011	P9	130°00′ E	6°30′ N	300, 500, 800, 1000
	Jul 2011	P10	130°04′ E	5°01′ N	1000, 1500

Deep  
*Prochlorococcus*

N. Jiao et al.



**Fig. 1.** Flow cytograms of *Prochlorococcus* samples at different water depths from the Luzon Strait (St. LX02) demonstrating the status of the *Prochlorococcus* populations along the water depth.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

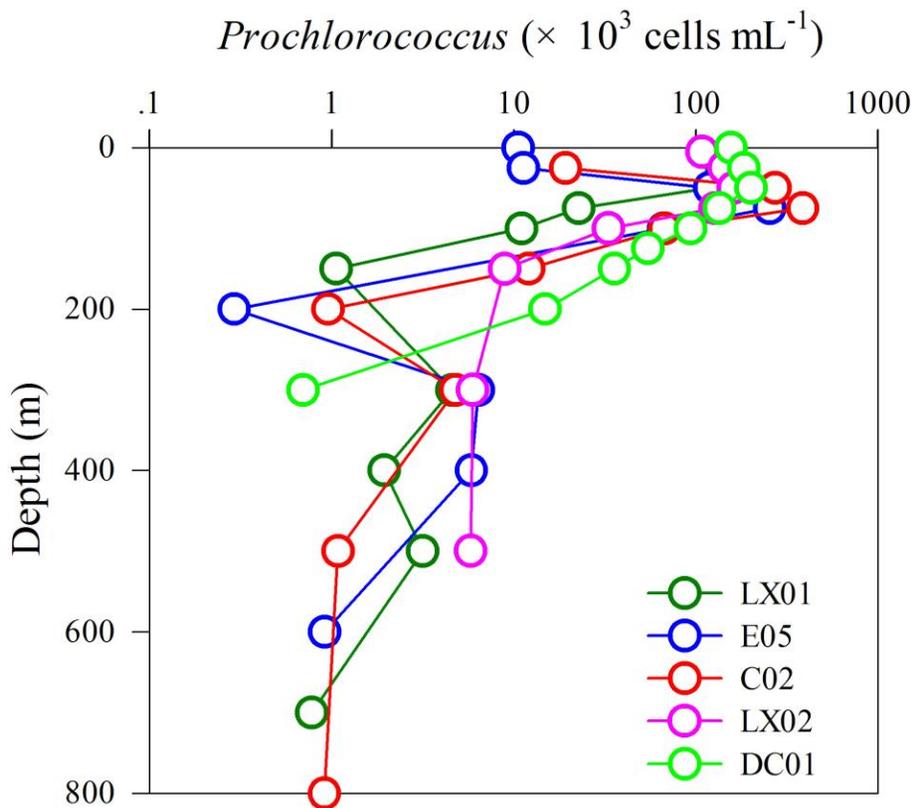
Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 2.** Depth profile of abundance of *Prochlorococcus* in the Luzon Strait area, showing the presence of *Prochlorococcus* ( $10^2$ – $10^4$  cells mL<sup>-1</sup>) in the aphotic waters (below 200 m).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

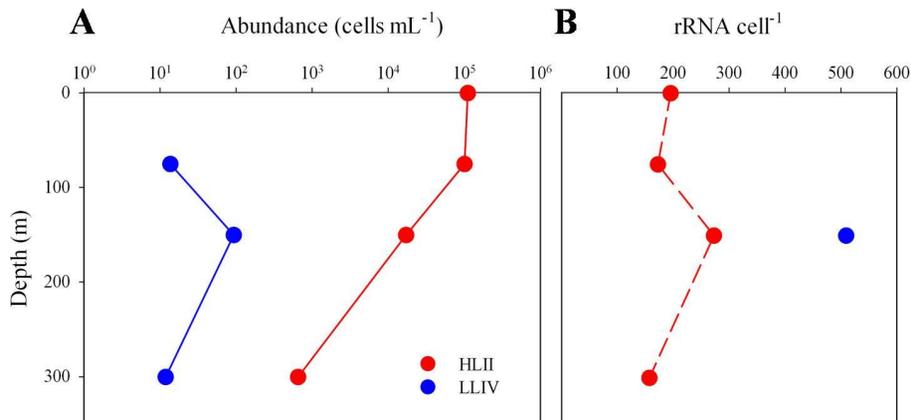
Close

Full Screen / Esc

Printer-friendly Version

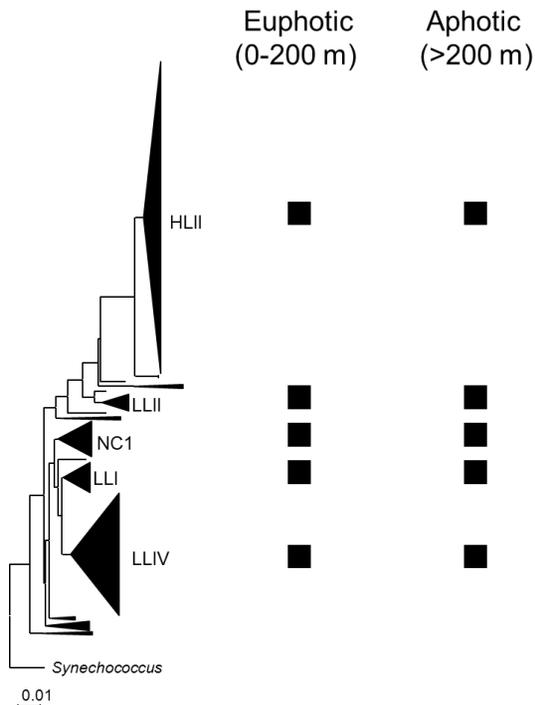
Interactive Discussion





**Fig. 3.** Vertical profiles of **(A)** the abundance and **(B)** cell specific rRNA content of two dominant *Prochlorococcus* ecotype in the Luzon Strait area (St. DC1). Red, *Prochlorococcus* ecotype HLII; Blue, *Prochlorococcus* ecotypes LLIV.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[I◀](#)
[▶I](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

**Fig. 4.** Neighbor-joining phylogenetic tree based on cyanobacterial ITS sequences from the Western Pacific Ocean (St. N8-12) showing that both high-light- and low-light-ecotypes of *Prochlorococcus* were present in samples from the aphotic waters. The distribution of *Prochlorococcus* ecotypes in euphotic or aphotic waters is indicated by solid squares. Scale bar: 0.01 substitutions per position.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

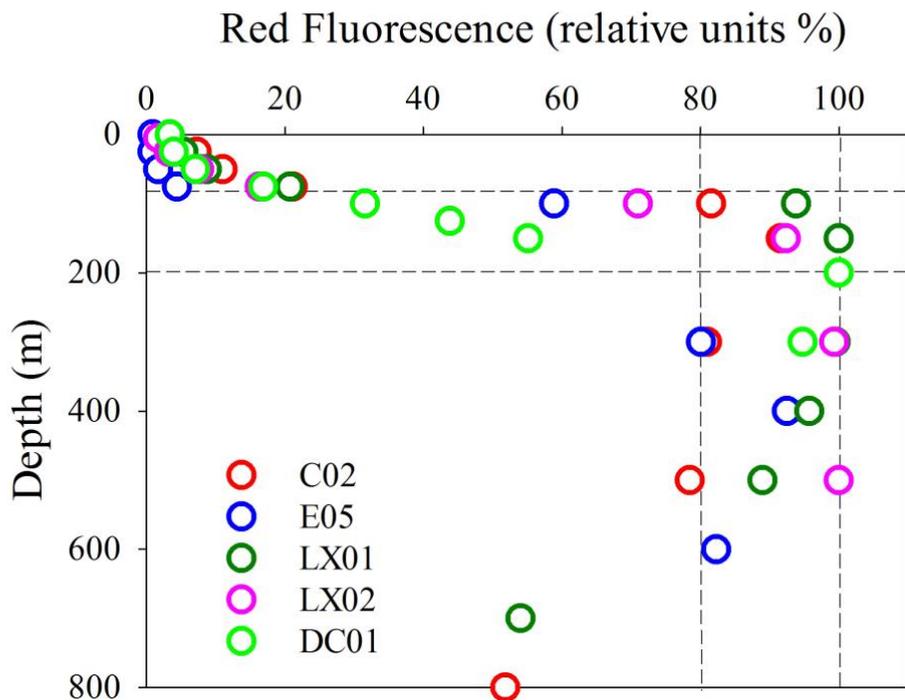
Printer-friendly Version

Interactive Discussion



Deep  
*Prochlorococcus*

N. Jiao et al.



**Fig. 5.** Flow cytometry cellular fluorescence of *Prochlorococcus* from different depths in the Luzon Strait area (dash lines as reference for comparison).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

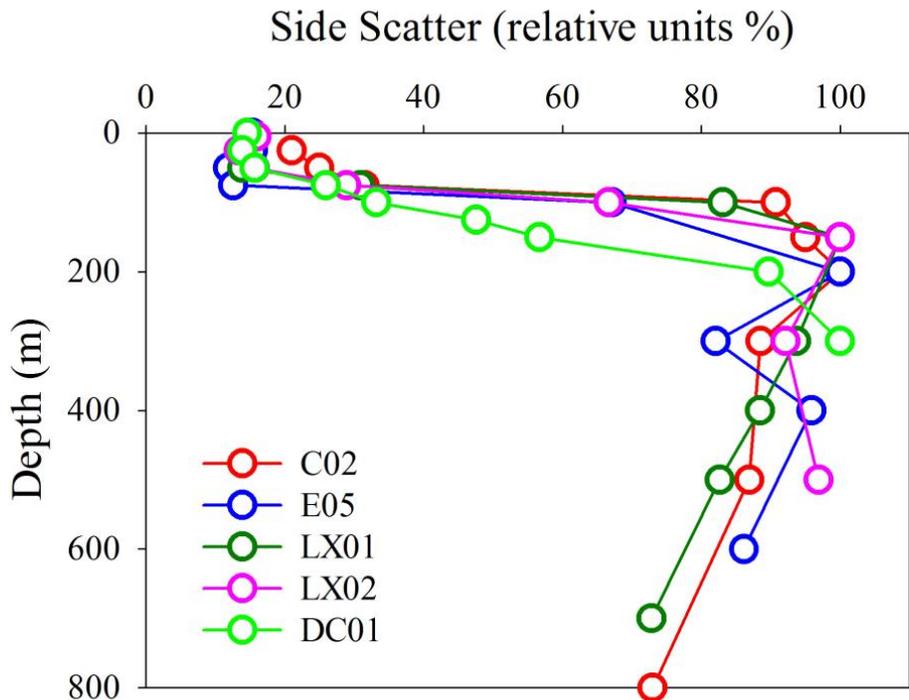
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Full Screen / Esc

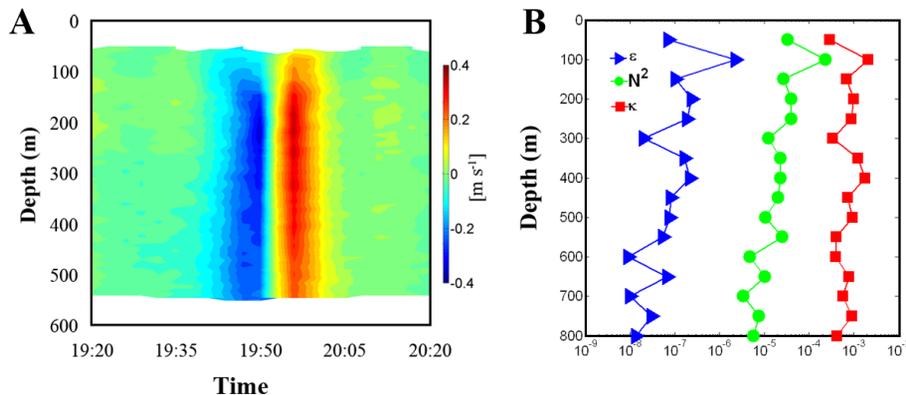
Printer-friendly Version

Interactive Discussion





**Fig. 6.** Depth profiles of flow cytometric side light scatter of *Prochlorococcus* in the Luzon Strait area, indicating the declining of cell sizes and cellular contents of *Prochlorococcus* cells in the aphotic waters (below 200 m).



**Fig. 7.** Physical transportation mechanisms of *Prochlorococcus* in the Luzon Strait. **(A)** A case (31 March 2010) of the 384 solitons observed from 21 March 2010 to 20 April 2011 at  $21^{\circ}00' \text{ N}$ ,  $119^{\circ}00' \text{ E}$ , showing the distribution of the vertical movement. **(B)** A case (28 March 2010) of the observed water column mixing at  $21^{\circ}02' \text{ N}$ ,  $119^{\circ}21' \text{ E}$ .  $\varepsilon$  indicates the dissipation rate of turbulent kinetic energy ( $\text{W kg}^{-1}$ ),  $N^2$  buoyancy frequency square ( $\text{s}^{-2}$ ), and  $\kappa$  mixing rate ( $\text{m}^2 \text{s}^{-1}$ ), at around  $10^{-3} \text{ m}^2 \text{ s}^{-1}$ , 100 fold the oceanic background mixing).

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)
