Microbial Extracellular Alkaline Phosphatase Revealed the Linkage Between Carbon and Phosphorus Cycles in the Deepest Ocean

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Abstract

We present the first dataset of microbial extracellular alkaline phosphatase activities (APA) and community compositions measured in the entire water column of the Challenger Deep (CD), Mariana Trench. We show that there existed two distinct P-APA regimes in the CD water column, reflecting different nutrient use strategies of the microbes; that in surface water (50 m) where microorganisms were P-limited (110 nmol L^{-1}) and expressed extremely high APA (average 23.8 nmol h^{-1}) for generating inorganic P, and that in the deep waters (1,000–10,918 m) which were P-replete (average 2.2 mmol L^{-1}), yet microorganisms were carbon-starved and also expressed high levels of APA (average 17.0 nmol h^{-1}). We suggest that microorganisms in the deep waters likely utilized a piggyback strategy to satisfy carbon requirements by expressing elevated APA to decompose dissolved organic phosphorus and concurrently, leading to high concentrations of P in the deep. Our results implicate the intimate connection and coupling between P- and C-cycling mediated by microbes in the hadal biosphere.

Introduction

Phosphorus (P) is an essential nutrient for life and central to the structuring of cell membranes, genetic materials, energy transporters, and metabolic signaling[1-3]. Previous studies have revealed the dynamic nature of P cycle in the global ocean, showing that phosphorus is the ultimate limiting nutrient in the ocean, from coastal areas to the open ocean, and from surface water to the deep sea[3-8].

Phosphorus is present in the ocean as dissolved inorganic (DIP) and organic form (DOP). DIP is the most bioavailable form and can be taken up directly by microorganisms. DOP is considered as the main phosphorus reservoir in the ocean[9]. As there is no atmospheric input of phosphorus like nitrogen, regeneration of phosphorus from DOP by alkaline phosphatase (AP) in the water column is crucially important in supplying P to microbial metabolism on a global scale[10]. P regeneration is largely an extracellular process as most phosphorylated compounds do not cross cytoplasmic membranes[11,12]. As such this process is catalyzed by microbial extracellular alkaline phosphatase (AP).

Hadal trenches are the deepest ocean with depth from 6,000 to 11,000 m. Due to their unique tectonics, topography, bathymetry, hydrography, and microbiology, the trenches constitute the so-called hadal biosphere[13-15]. Despite their remoteness, horizontally (distant from continents) and vertically (far from the euphotic zone), the hadal biosphere exhibited unexpected endemic life and high microbial activities in the water column and sediment[13,14,16]. It has been shown that the trenches are depocenters for organic matter, and compared to the adjacent abyssal plains, exhibited elevated microbial activities and respiration rates[16-18]. On the other hand, the trench water column typically exhibited stratified microbial community structure[14,19]. These previous studies undoubtedly provided new insight into microbial components and processes in hadal trenches. However, there are significant gaps in our understanding of the connections among the various components and processes in the hadal biosphere. There have been abundant studies on alkaline phosphatase activities (APA) in marine systems, yet there have been no

reported studies examining APA in hadal waters. Liu Q. et al. (2018)[15] was the only study that examined microbial extracellular enzymes (protease and aminopeptidase) in a trench water column (the New Britain Trench), from sea surface to the depth of 6,000 m.

Microbial extracellular alkaline phosphatases appear to be the connector of hadal microbial components and processes as phosphorus plays a central role in microbial energy transactions and metabolism[1,3,6,20,21]. As such, microbial extracellular AP would provide insights on linkage between P and C cycling in the ocean. In this study, we measured concentrations of dissolved organic and inorganic phosphorus, APA, and compositions of microbial communities in the water column of the Challenger Deep (CD), Mariana Trench. Our goals were to characterize microbial extracellular alkaline phosphatase activities (APA) and explore the linkage between P- and C-cycles in the water column of the Challenger Deep, the deepest ocean on earth.

Results And Discussion

Seawater samples were collected at 7 depths (from 50 to 10,918 m) of the CD (Table 1). Our results show that DIP concentration was relatively low (0.11 μmol L^{-1}) in surface water (50 m). This concentration is comparable to those reported for surface waters in the Pacific subtropic gyres[6], the HOT station[2], and the Arabian Sea [5], but higher than those in central, eastern parts of the North Atlantic Gyre[22]. However, DIP concentrations were rather uniformly significantly higher in the deep waters (1,000–10,918 m), ranging between 2.22 and 2.91 μmol L^{-1} and averaging 2.49 ± 0.25 μmol L^{-1}. These results are comparable to those for the Mariana Trench reported in an early study[13].

Different than DIP distribution, dissolved organic P showed a stratified pattern of distribution in the CD water column, with high and low concentrations alternating between successive sampling depths (Fig. 1). DOP concentrations varied from 79 to 463 nmol L^{-1} (averaging 214.0 ± 152.3 nmol L^{-1}) and differed between consecutive depths by up to one order of magnitude. Furthermore, DOP concentrations were 1–2 orders of magnitude lower than DIP, opposite to that commonly observed in non-trench waters[23]. Notably, DOP represented on average 46.1% of the total dissolved phosphorus (TDP) in surface water and only 8.4% in the deep waters (Table S1), much lower than those (55–92%) reported for non-trench waters in the Pacific and Atlantic oceans[6,24]. Furthermore, the turnover time of the DOP pool was 13.0 months in surface water and from 5.1 to 6.9 months in the deep waters (Table S1), much less than those previously reported for the Atlantic Ocean[25].

We measured the potential activity of alkaline phosphatase using fluorogenic substrate 4-methylumbelliferyl-phosphate, extending our previous work to the full ocean depth[15]. The most striking observation was the contrasting patterns in DIP and APA between surface water and deep waters. The CD surface water had the highest APA with the lowest measured DIP and DOP concentrations (Fig. 1). On the contrary, the CD deep waters had high concentrations of DIP and concurrently, elevated levels of APA. APA averaged 17.0 ± 1.1 nmol h^{-1}, which is 2–3 orders of magnitude higher than those reported for non-

trench waters in the Pacific Ocean[4]. Similarly, exceptionally high K_m values (60.3–221.6 mmol, averaging 71.7 mmol) were measured in the water column, suggesting that the CD microbial communities had great potential to maximize APA for utilizing DOP. Thus, our results showed that two distinct P-APA regimes existed in the CD water column, one in the surface water having low DIP and high APA, and the other in the deep waters with high DIP and elevated APA (Fig. 1).

Alkaline phosphatase, which releases P bound in DOP, is a large group of phosphomonoesterases with a relaxed substrate specificity [2]. APA can be induced by DIP-stressed or -limited microbial communities in environments where DIP concentrations are low[25,26]. Therefore, APA is commonly used as an indicator for P-limit conditions in the aquatic system. The detection of elevated concentrations of DIP in the deep waters (Fig. 1) of the Challenger Deep suggests that microbial communities in the deep waters of the trench were not P-limited. However, different from the non-trench deep waters, e.g., the central Pacific Ocean[4] and central Atlantic Ocean[27], the CD deep waters retained both elevated concentrations of DIP and exceptionally high levels of APA. The measured APA were orders of magnitude higher than those measured in other oceans, like the Atlantic Ocean[27,28], the Mediterranean Sea[29], and the Tyrrhenian Sea[30].

The exceedingly high concentrations of DIP with concurrent high levels of APA in the CD deep waters contradicts with the common notion that high abundances of DIP repress microbial synthesis of AP[9,26,31,32]. We further examined the nutrient chemistry of the water column, showing that the CD microorganisms were periodically carbon-starved. This is evidenced by the depth-alternating C/P ratios in the water column (Table 1). The surface water had a C/P ratio of 603:1, much higher than the canonical Redfield ratio, whereas the deep waters exhibited alternating low and high C/P ratios, which were, respectively, lower and higher than the Redfield ratio (Table 1). Thus, the two P-APA regimes in the CD water column exhibited different patterns in distribution of DIP, DOP, APA, Km and microbial community compositions (described below), reflecting the different nutrient utilization strategies of the microorganisms in the CD water column. Specifically, microorganisms in the surface-water regime produced APA in response to P-stress, whereas those in the deep-water regime responded in an adaptive manner to C-limitation, implicating the intimate linkage between P cycle and C cycle in the trench waters. We posit that the deep-water microbes likely utilized a piggyback strategy to liberate organic carbon (OC) from breaking DOP by expressing high levels of APA, concurrently leading to high abundances of DIP in the deep[33,34]. In fact, the proportions of the regenerated DIP (surface water, 92.2%; deep waters, average 65.2%) from DOP breakdown in the CD water column were much higher than the global average (36%; Table S1)[35]. Microbial expression of enhanced AP activity in the deep waters represents a strategy for microbial liberation and consumption of organic moieties derived from DOP, irrespective of P availability in the environment[26,36]. We interpret the contrasting patterns of APA, DIP and DOP in the surface water and deep waters reflecting microbial niche partitioning and adaptation to the two different P-APA regimes in the water column. This argument is also supported by the calculated potential in situ hydrolysis rate of DOP (V_{DOP})[6], which showed a strong linear relationship with DOP ($R^2 = 0.983$; $p < 0.003$, data not shown).

Viewed together, these results demonstrated that microbial APA in the CD deep waters was responding to carbon starvation and access to OC, rather than to phosphorus depletion.

It appears that input of AP-hydrolyzable DOP to the deep trench water was in a pulsed mode, the dynamics of which are well illustrated by the pattern of alternating high and low values of DOP, C/P ratio, and V_{DOP} (Fig. S1). Additionally, the measured K_m values were 2–3 orders of magnitude higher than the measured DOP concentrations, implying that the CD microorganisms must be adapted to use the pulsed AP-hydrolyzable DOP in the water column as microorganisms can adjust their utilization of available DOP in the environment[6]. Thus, we hypothesize that the intermittent pulse inputs of DOP from the surface to the deep water provided a mechanism of P and C supply and the resultant APA impulses for regeneration of DIP and DOC. Consequently, the deep trench waters exhibited high levels of APA and the accumulated DIP, which correspondingly resulted in alternating high and low C/P ratios and DOC concentrations. Our results further suggest that cautions must be exercised in using APA as an indicator of P stress or limitation in ecological interpretations[4–6, 37]. High APA values may not necessarily reflect a P-limiting or -stressed condition to the microbial community[2].

We used 16S rDNA and rRNA to determine, respectively, the compositions of bulk and active assemblages of the resident microbial communities in the CD water column. Microbial communities consisted of taxa from 21 dominant classes in 16 phyla, among which 19 classes were bacteria and 2 archaea (Marine Group I and Thermoplasmata) (Fig. S2). Notably, microbial communities in the CD water column were dominated by lineages that had been shown in actively producing AP and utilizing both DIP and DOP, including the oligotrophs SAR11 clade, mixotrophs cyanobacteria like *Procholorcoccus*, and oppotunitrophs like Gammaproteobacteria (mainly *Alteromonas*) (Fig. 2). Our results showed that the SAR11 clade accounted for 48.5% (32.0%) of bulk (active) bacterial OTUs in surface water, 31.3% (12.4%) and 68.2% (8.9%) at 7,000 and 10,918 m, respectively. The SAR11 clade is the dominant chemoheterotrophic bacteria and efficient competitors for nutrient resources in the global oceans[38,39]. Members of the SAR11 clade are frugal and typically have low P requirements[40]. The capacity of taking up DIP and DOP has been demonstrated experimentally[22,40,41]. Given the exceptionally high DIP concentrations in the CD deep waters, it is reasonable to posit that SAR11 used DOP for producing organic carbon (OC), rather than for DIP.

Strikingly, active cyanobacteria were detected in the whole water column, with high abundances in surface water and in the hadal waters (7,000 and 10,918 m) (Fig. 2). In particularly, *Prochlorococcus* comprised 53.4% of the bacterial OTUs in surface water, 30.6% and 9.1% in 7,000 and 10,918 m deep waters, respectively. Many cyanobacteria are mixotrophs and good competitors of heterotrophic bacteria for DOP [42,43]. Previous studies have shown that cyanobacteria were able to mineralize DOP by producing alkaline phosphatases[44]. Another study revealed that *Prochlorococcus* and *Pelagibacterales* bacteria together accounted for ca. 90% of P uptake in the North Atlantic Ocean[22]. Taken together, our results suggest that these microorganisms likely utilized DOP as a source for producing organic moieties for

sufficing the carbon requirements, especially in the hadal waters where organic matter may be more refractory and less abundant.

Microbial dichotomy in the ocean has been well studied. Our results showed that particle-associated microbial AP probably have played a more important role than the free-living AP in P cycling in the trench. This is evidenced by the observed higher particle-associated APA ($Vmax\text{-}_{PA}$) and higher Vmax/Km ratios than the corresponding values for free-living AP (Table 1; Table S1). The entire water column exhibited a high proportion of cell-associated APA (averaging 60.7% of the total APA) and higher APA_{PA}/K_{m-PA} (0.47) than APA_{FL}/K_{m-FL} (0.13) (Table S1). This conclusion is also supported by the calculated V_{DOP}. V_{DOP} for APA_{PA} is on average 1.7 times greater than APA_{FL} (Table S1), indicating a greater role of APA_{PA} in producing DIP from DOP. This finding is also in accordance with those reported by Malfatti et al. (2014)[45] and Davis and Mahaffey (2017)[46], in contrast to findings of Thomson et al. (2019)[32] and others.

We developed a priori model using path analysis modeling, to test our hypothesized relationships among APA, K_m, DOC, DIP, and active microbial communities in the water column. The model showed a very good fit with our data and explained 90% of DOC variability in the CD waters (Fig. 3). Both K_m and V_{max} contributed directly to the increases in DOC, and a significant positive correlation ($R^2 = 0.976$) was observed between K_m and DOC (data not shown). These results revealed that microbial alkaline phosphatase-induced enzymatic decomposition of DOP provided microorganisms with both P and OC in the trench waters.

In summary, our results represent the first dataset of microbial alkaline phosphatase activities, and provide a direct observational basis for understanding of microbial strategies for resource utilization and linking microbial-mediated P cycle and C cycle in the deepest ocean. Our findings show that carbon cycle in the deep ocean is intricately tied to cycles of nutrients, particularly that of phosphorus.

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Table

Table 1 Sample depths and the concentrations of DOC, DOP, C/P ratios, and kinetic parameters of alkaline phosphatase in the CD water samples.

Depth (m)	DOC (mM)	DOP (mM)	C/P	APA_{PA}[a] ($nM\ h^{-1}$)	APA_{FL}[b] ($nM\ h^{-1}$)	$K_{m\text{-}PA}$[c] (mM)	$K_{m\text{-}FL}$[d] (mM)
50	56.67	0.20	603:1	0.01	0.22	221.62	144.05
1,000	35.00	2.68	76:1	0.10	0.11	80.51	65.06
2,000	37.50	3.01	379:1	0.02	0.02	75.88	60.11
3,000	33.33	3.08	87:1	0.09	0.08	76.03	40.16
4,200	35.83	2.79	230:1	0.03	0.03	78.57	48.16
7,000	35.00	2.64	155:1	0.06	0.06	58.76	37.06
10,918	35.83	2.48	454:1	0.02	0.02	60.29	49.43

[a, b]Particle-associated and free-living alkaline phosphatase activity, respectively.

[c, d]Particle-associated and free-living half-saturation constant, respectively.

Figures

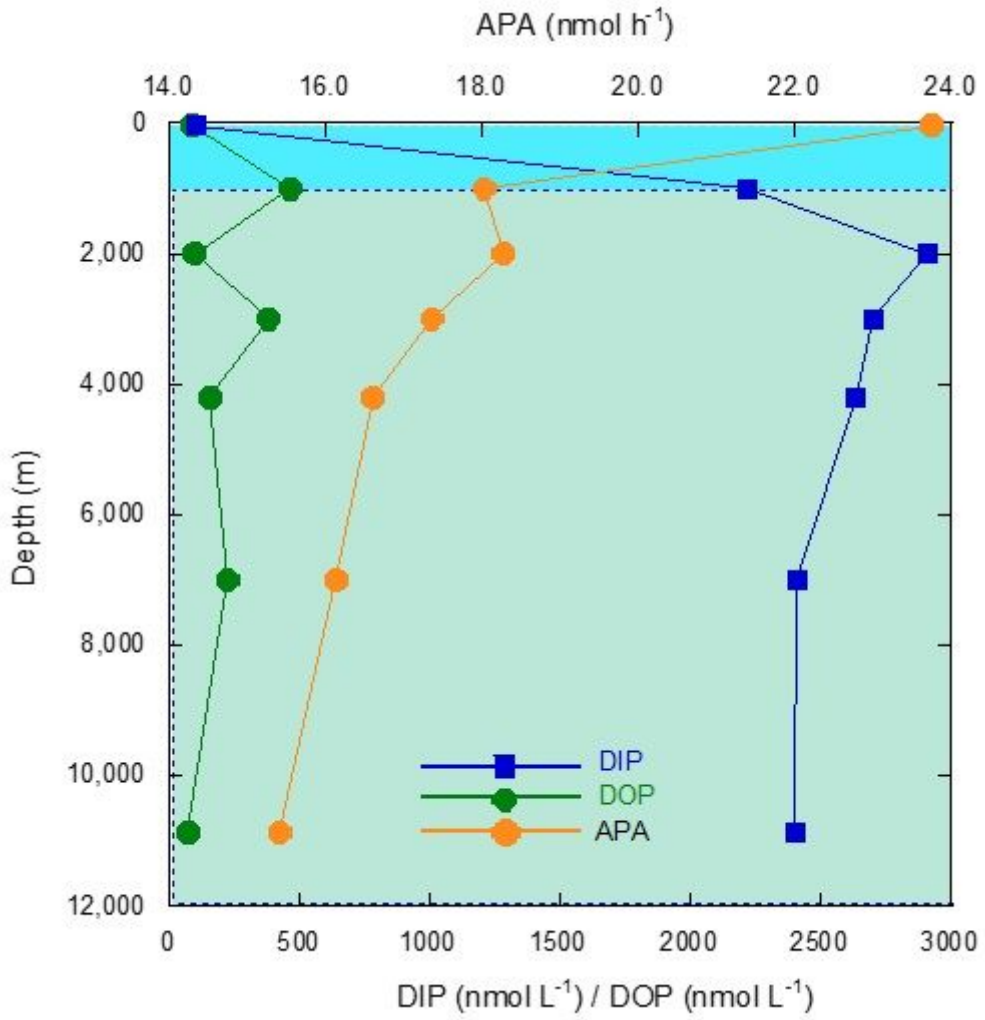

Figure 1

The concentrations of dissolved organic (DOP, nmol L^{-1}) and inorganic phosphorus (DIP, nmol L^{-1}), and alkaline phosphatase activity (APA, nmol h^{-1}) measured in water samples of the Challenger Deep, Mariana Trench.

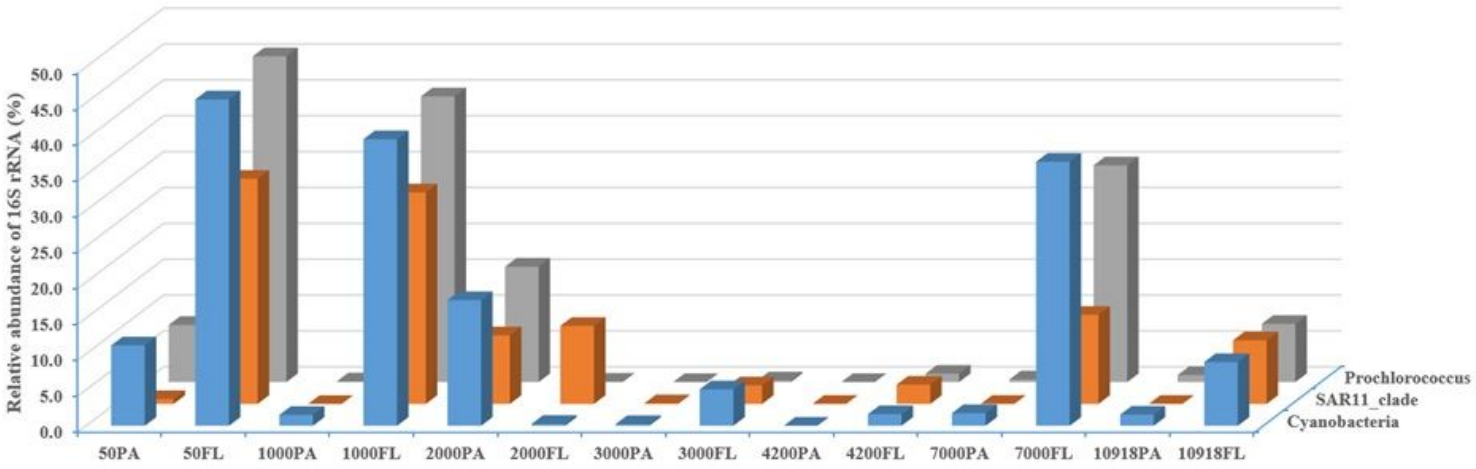

Figure 2

Relative abundance of active particle-associated (PA) and free-living (FL) SAR11 clade, Prochlorococcus, and cyanobacteria in bacterial communities at different depths of the Challenger Deep, Mariana Trench.

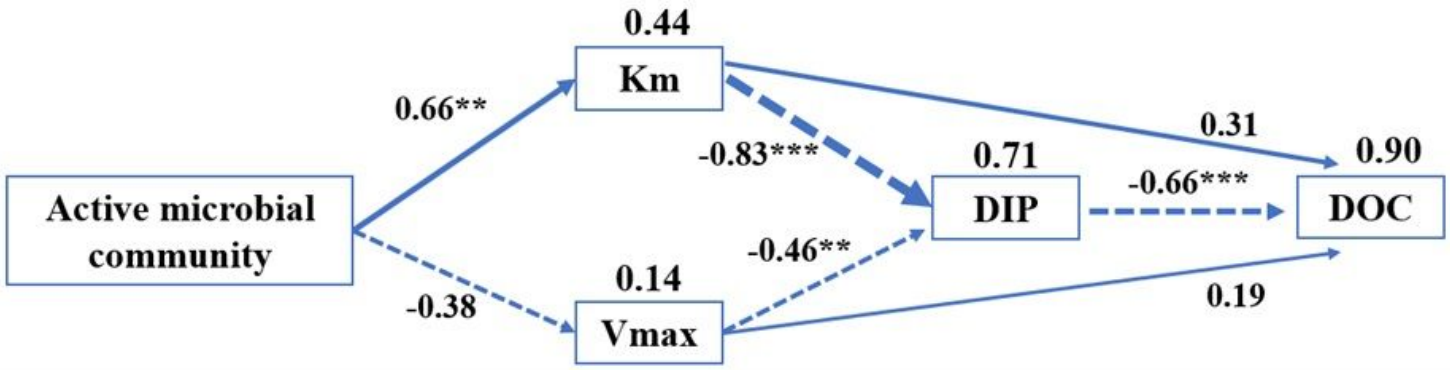

Figure 3

Path analysis model of the hypothesized causal relationships among active microbial communities, V_{max}, K_m, DIP, and DOC in water samples of the Challenger Deep. Arrow thickness indicates the magnitude of the path coefficient. Solid and dashed lines indicate positive and negative path coefficient, respectively. R^2 values indicate the proportion of variance explained by each variable in the model. **: $p < 0.01$; ***: $p < 0.001$.

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