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Key Points:

- We assess bacterial contributions to suspended particulate organic matter (POM) in the Western Pacific Warm Pool on the basis of D-amino acid biomarkers
- Bacterial organics constitute 27% of surface ocean particulate organic carbon (POC) and 39% of particulate nitrogen (PN), but majority (~87%) is labile or semi-labile
- Rapid cycling of bacterial POM in the upper ocean results in a contribution of only ~8% to refractory POC and ~13% to PN

Supporting Information:

Supporting Information may be found in the online version of this article.

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Rapid Cycling of Bacterial Particulate Organic Matter in the Upper Layer of the Western Pacific Warm Pool

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Abstract Bacterial metabolism largely drives the sequestration of refractory organic matter in the ocean. However, a lack of understanding exists regarding the abundance and reactivity of bacterial particulate organic matter (POM). Here we report the bacterial contributions to suspended POM collected in the oligotrophic Western Pacific Warm Pool (WPWP). Around 27% of particulate organic carbon (POC) and ~39% of particulate nitrogen (PN) in the surface ocean were derived from bacteria. Most of the bacterial POM (~87%) was labile or semi-labile, and ~85% of bacterial POM was removed between depths of ~100–300 m. Bacterial POM constituted only ~8% and ~13% of refractory POC and PN, respectively. The rapid cycling of bacterial POM in upper waters was likely related to oligotrophic conditions and facilitated by higher temperatures in the WPWP. Taken together, these observations indicate that bacterial POM plays a crucial role in supplying energy for bacterial respiration.

Plain Language Summary Bacteria transform a large fraction of the organic matter made by primary producers and contribute to long-term oceanic carbon sequestration with bacterial detritus, thereby contributing to ocean uptake of atmospheric carbon dioxide. The abundance and reactivity of bacterial organic matter are critical to consider in this carbon storage pathway. Here we collected suspended particulate organic matter (POM) in the Western Pacific Warm Pool (WPWP) and assessed the bacterial POM contribution. A substantial proportion of bacterial POM was found in the surface ocean, but most (~85%) was rapidly removed between depths of 100–300 m as particles sink. The high temperature and oligotrophic features of WPWP facilitate the use of bacterial POM as an energy source for bacterial respiration. This rapid turnover of bacterial POM in the upper ocean results in a contribution of only ~8% to long-term carbon sequestration. Our results suggest that bacterial POM exhibits high reactivity and only a small fraction can lead to long-term carbon sequestration.

1. Introduction

The ocean is the largest carbon reservoir of the surface earth system, plays an important role in the global carbon cycle, and has absorbed about one-third of anthropogenic carbon dioxide (CO₂) emissions since the Industrial Revolution (Le Quéré et al., 2016). Sinking of particulate organic matter (POM) links CO₂ fixed through photosynthesis by phytoplankton in the surface ocean with carbon storage in the ocean interior. This pathway has been conceptualized as the biological carbon pump (BCP), and represents a key carbon sequestration mechanism (Llonghurst & Harrison, 1989; Turner, 2015). Bacteria play a crucial role in the efficiency of the BCP since most POM undergoes fast remineralization in the upper ocean and only a small fraction (~10%) is exported to the mesopelagic zone (Buesseler & Boyd, 2009; Le Moigne et al., 2016). Compiled global budgets suggest that bacterial carbon demand in the dark ocean exceeds the influx of sinking POM (Burd et al., 2010). Although the supply of organic substrate is not well constrained, suspended POM is recognized as a potential carbon source for deep ocean metabolic activity (Baltar et al., 2010).

Heterotrophic bacteria are not only consumers of organic matter but also contributors. Their metabolic activity utilizes a large fraction of the primary production and contributes non-living organic matter to the ocean in the form of bacterial detritus. Kaiser and Benner (2008) found that ~25% of suspended particulate organic carbon (POC) is derived from bacteria. Attached bacteria are more likely to colonize suspended particles compared to sinking

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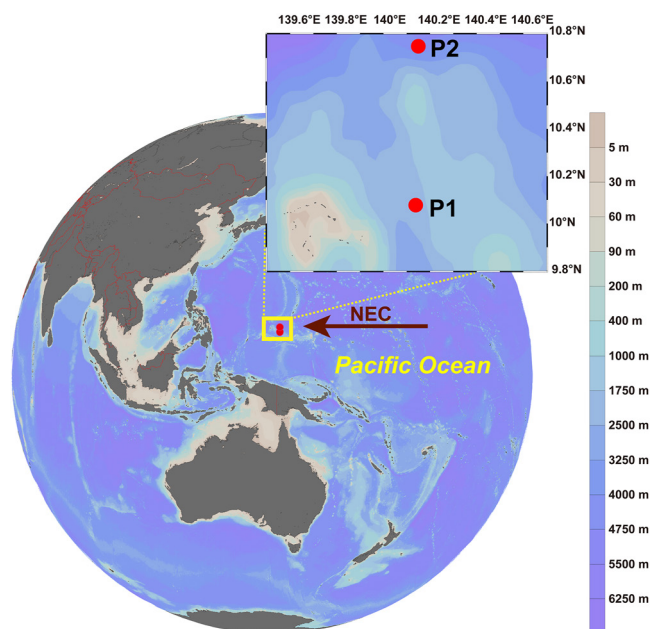


Figure 1. Sampling locations in the Western Pacific Warm Pool. Suspended particle samples were collected at P1 (140.14°E, 10.08°N) and P2 (140.15°E, 10.75°N) stations, respectively. NEC, North Equatorial Current.

particles, and feature a relatively high prokaryotic heterotrophic productivity (Baumas et al., 2021; Karl et al., 1988; Turley & Mackie, 1994). Especially in the deep ocean, bacteria preferentially have a particle-attached lifestyle, thereby regulating the dark end of the BCP (Herndl & Reinthaler, 2013). Heterotrophic bacteria can actively sequester carbon by transforming labile (turnover time: hours to weeks) organic matter into refractory (turnover time: >several decades) bacterial metabolites (Jiao et al., 2010; Ogawa et al., 2001). Despite this, a portion of the bacterial POM may still exhibit labile or semi-labile (turnover time: months to years) reactivities in the upper ocean. In oligotrophic ocean regions, bacterial respiration rates exceed phytoplankton production (del Giorgio et al., 1997), implying that bacterial POM could be a particularly important energy source for heterotrophic metabolism. There have been a range of studies on POM fluxes over the past three decades, revealing the spatial and temporal heterogeneity of BCP efficiency (Honjo et al., 2008; Lee et al., 2000; Nowicki et al., 2022; Wakeham & Canuel, 1988). However, monitoring the reactivity of bacterial POM in the tropical ocean remains challenging, and little is known about how the bacterial POM contributes to BCP carbon sequestration in this ocean region.

Biomarkers provide powerful tools to obtain insight into transformations and bacterial origins of POM. Amino acids are labile organic compounds that are preferentially metabolized during heterotrophy (Amon et al., 2001). Their composition and carbon-normalized yields can effectively indicate the diagenetic state of organic matter (Dauwe et al., 1999; Davis et al., 2009; Le Moigne et al., 2017). Nonprotein amino acids, β -alanine (β -Ala) and γ -aminobutyric acid (γ -Aba), increase in relative abundance with the progression of organic

matter degradation, thereby providing additional insights into POM alterations (Kaiser & Benner, 2009; Shen et al., 2015). In addition, D-enantiomers of amino acids mainly occur in bacterial macromolecules and are useful biomarkers for tracing the bacterial contribution in POM (Kaiser & Benner, 2008).

The Western Pacific Warm Pool (WPWP) is located in a region affected by the North Equatorial Current (NEC) in the equatorial western Pacific and characterized by high surface seawater temperatures (SST > 28°C), exerting a profound role in the global climate system (e.g., ocean-continent moisture transport) (Jian et al., 2022). Strong water column stratification results in the oligotrophic characteristics of the upper WPWP (Radenac et al., 2013), with low primary productivity of $\sim 26.37 \pm 1.09 \text{ mmol C m}^{-2} \text{ day}^{-1}$ (Le Borgne et al., 2002). Higher temperatures drive active heterotrophic respiration, forming biological hotspots that enhance elemental cycling in upper waters (McKinnon et al., 2017; Murray et al., 1994). In the present study, suspended POM samples in two water columns were collected in the core area of the WPWP. Concentrations of amino acid enantiomers were determined and bacterial POM was quantified, with the aim to advance our understanding of POM transformation and bacterial organic matter cycling in an oligotrophic ocean region.

2. Sampling and Methods

Suspended particles were collected during an expedition on R/V *Kexue* to the Equatorial Northwest Pacific between May and June 2019. The cruise surveyed the region near the M5 seamount in the WPWP and collected samples at two stations: P1 (water depth: 2,307 m) and P2 (water depth: 5,148 m) (Figure 1). Vertical profile samples were obtained using 12-L Niskin bottles mounted on a Seabird Conductivity-Temperature-Depth (CTD) rosette. Deep chlorophyll maxima (DCM) were identified at P1 at 106 m and P2 at 110 m. Suspended POM samples were obtained by filtration of 10–30 L of seawater onto pre-combusted (450°C for 5 hr) Whatman GF/F filters (0.7 μm pore size). The filters were collected in duplicate for analysis of POC, particulate nitrogen (PN) and total particulate amino acids (TPAA). Samples for chlorophyll-*a* (Chl-*a*) were filtered through Whatman cellulose acetate filters (0.45 μm pore size).

Samples for POC and PN were treated with hydrochloric acid (HCl) to remove inorganic carbonates, oven-dried at 60°C, and analyzed using a Flash EA IsoLink CN elemental analyzer (Thermo Fisher Scientific, Germany). D- and L-amino acids were hydrolyzed using 6 M hydrochloric acid and then separated as *o*-phthalaldehyde

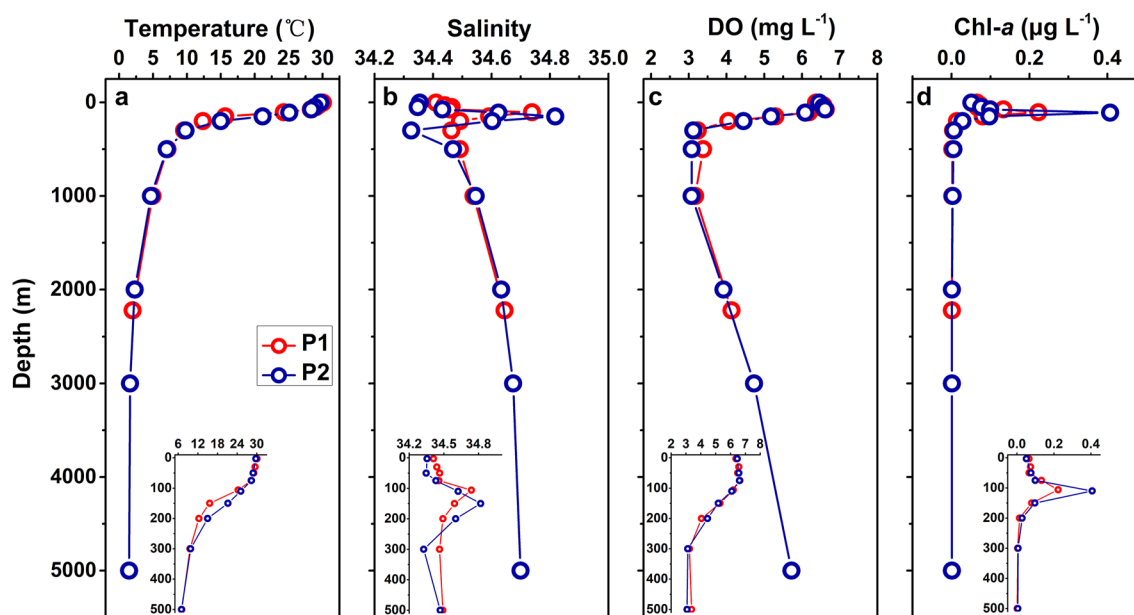


Figure 2. Depth profiles of (a) temperature, (b) salinity, (c) dissolved oxygen concentrations and Chlorophyll-*a* (Chl-*a*) concentrations at P1 and P2 stations. The insets show the vertical distributions in the upper 500 m.

and *N*-isobutryl-L-cysteine derivatives using a Thermo Fisher Scientific U3000 ultrahigh performance liquid chromatography (UPLC) system equipped with a Poroshell 120 EC-C18 column (4.6 × 100 mm, 2.7 μm particles) (Kaiser & Benner, 2005; Shen et al., 2017). Further information is provided in Text S1 in Supporting Information S1. POC- and PN normalized yields of TPAA, that is, TPAA (%POC) and TPAA (%PN) were calculated as the percentage contributions of amino acid carbon and nitrogen (except the nonprotein amino acids β-Ala and γ-Aba) to the total suspended POC and PN concentrations, respectively.

The bacterial contributions to suspended POC and PN were estimated based on D-alanine (D-Ala) and D-glutamine + glutamic acid (D-Glx) (Kaiser & Benner, 2008), using Equation 1:

$$\text{Bacterial OM (\%)} = \frac{\text{Biomarker}_{\text{OM}}}{\text{Biomarker}_{\text{bacterialOM}}} \times 100 \quad (1)$$

where Biomarker_{OM} and Biomarker_{bacterialOM} are the carbon- or nitrogen-normalized yields of D-Ala or D-Glx in marine POM and bacteria, respectively. Biomarker_{OM} was measured in this study, while Biomarker_{bacterialOM} was obtained from culture experiments performed by Kaiser and Benner (2008). For the DCM and shallower waters, the Biomarker_{bacterialOM} values used in the calculation were 50.3 nmol mg C⁻¹ and 215 nmol mg N⁻¹ for D-Ala, 48.3 nmol mg C⁻¹ and 206.7 nmol mg N⁻¹ for D-Glx, assuming a mixture of 80% heterotrophic bacteria and 20% phototrophic bacteria (Kaiser & Benner, 2008). Below DCM, the Biomarker_{bacterialOM} values used were 58.9 nmol mg C⁻¹ and 248.5 nmol mg N⁻¹ for D-Ala, 56.4 nmol mg C⁻¹ and 238.2 nmol mg N⁻¹ for D-Glx based on the assumption of 100% heterotrophic bacteria (Kaiser & Benner, 2008).

3. Results and Discussion

The warm waters carried by the NEC flow from east to west and accumulate in the western Pacific as a warm pool, with a SST between 3°C and 9°C higher than waters in the eastern Pacific. The two sampling stations were located in the central WPWP with similar SST (30.1°C and 29.7°C for P1 and P2, respectively). The temperature decreased with depth to <10°C at 300 m (Figure 2a). In comparison, salinity profiles varied little (Figure 2b). The strong thermocline hampered upward supply of nutrients (Ma, Song, Li, Wang, Sun, et al., 2021), and nitrogen fixation was limited by low iron supply (Wen et al., 2022), resulting in low productivity (~26.37 ± 1.09 mmol C m⁻² day⁻¹) in this oligotrophic region (Le Borgne et al., 2002). Low Chl-*a* concentrations were observed in the DCM layer, with 0.22 and 0.41 μg L⁻¹ at P1 and P2, respectively (Figure 2d).

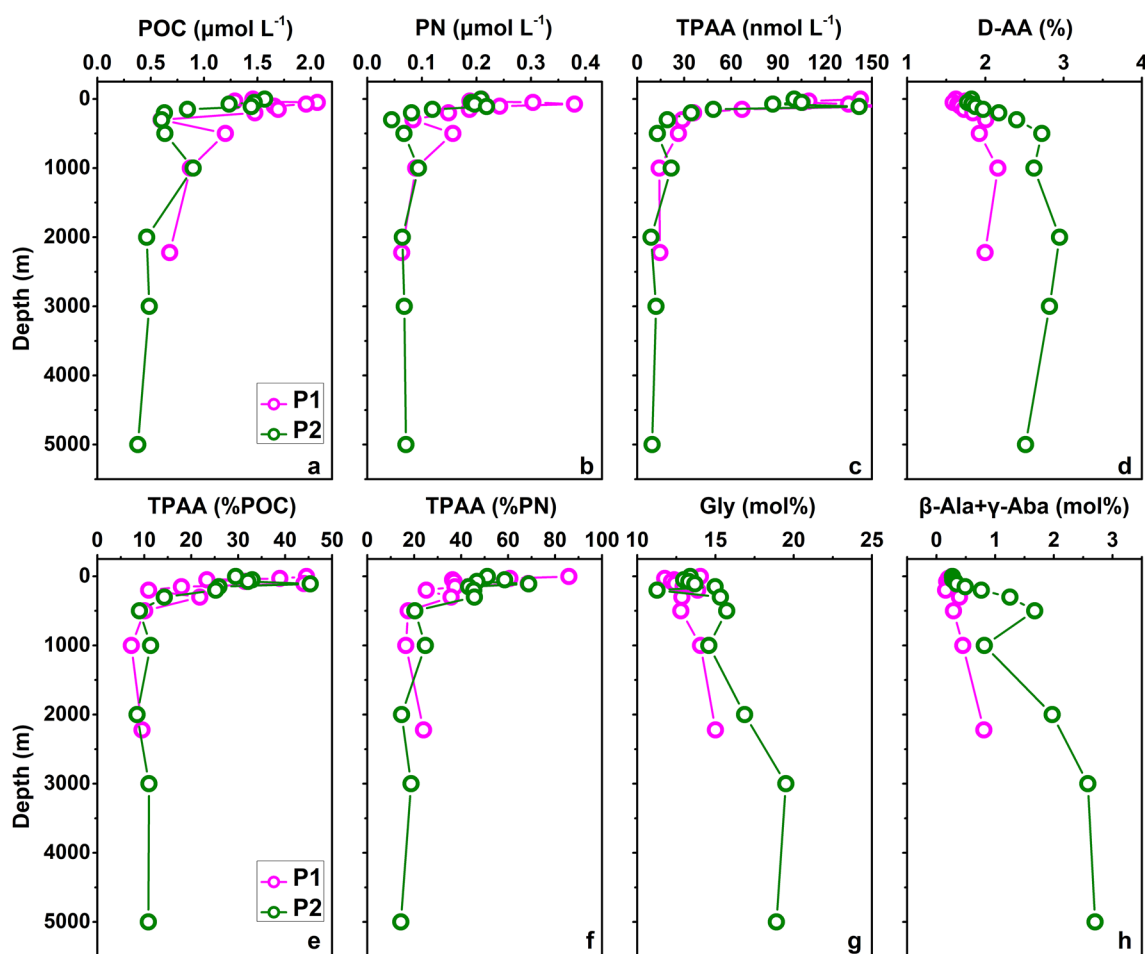


Figure 3. Vertical distributions of (a) particulate organic carbon (POC), (b) particulate nitrogen (PN), (c) total particulate amino acids (TPAA), (d) percentages of D-enantiomers of amino acids, (e) POC-normalized yields of TPAA, (f) PN-normalized yields of TPAA, (g) mole percentages of glycine and (h) mole percentages of two nonprotein amino acids: γ -alanine (γ -Ala) and β -aminobutyric acid (β -Aba) at P1 and P2 stations.

3.1. Depth Variations of Suspended POM

Concentrations of POC and PN decreased with depth and varied from 0.38 to $2.06 \mu\text{mol L}^{-1}$ and from 0.04 to $0.38 \mu\text{mol L}^{-1}$ at stations P1 and P2, respectively (Figures 3a and 3b). These results are comparable to those reported for the Northeast Pacific (Dong et al., 2022). Above the DCM layer, POC and PN concentrations were enhanced, but their maximum values did not coincide with the DCM. Below the DCM to 300 m, POC and PN declined sharply. About 64% of POC and ~67% of PN were removed at station P1 over this depth range, while ~58% and ~82% were removed at station P2. Below 500 m, POC and PN concentrations remained relatively constant with depth. Typically, POC and PN concentrations in the oligotrophic ocean are low ($<2 \mu\text{mol L}^{-1}$) due to low primary productivity and rapid decomposition. Kaiser and Benner (2009) found that POC only accounted for ~3% of organic carbon pool. Vertical distributions of TPAA showed a similar pattern to POC and PN (Figure 3c). Rapid declines were observed from the DCM to 300 m, and ~82% and ~86% of TPAA were removed over this depth range at stations P1 and P2, respectively. The higher TPAA removal compared to POC and PN demonstrates that amino acids are preferentially utilized over bulk POM. Unlike POC and PN, the maximum concentration of TPAA matched well with the position of the DCM, indicating that phytoplankton were important TPAA sources.

3.2. Reactivity and Removal of Suspended POM

Amino acids form an important component of POM. In the surface waters of station P1, amino acids contributed 44.6% of POC and 85.9% of PN, whereas at station P2, they contributed 29.5% and 51.2% (Figures 3e and 3f).

The comparatively high TPAA fraction at P1 station likely relates to the close proximity to seamounts. Seamounts can facilitate enhanced phytoplankton production due to increased subsurface nutrient supply by water column mixing processes (Turnewitsch et al., 2016). The fresh organic matter thus produced may be transported to the surface layer of station P1 through advection (Shi et al., 2021). By comparison, the amino acid fractions of dissolved organic matter (DOM) are extremely low (<1%) (Kaiser & Benner, 2009), implying that POM is fresher than DOM. A sharp decrease with depth was observed for TPAA (%POC) and TPAA (%PN) (Figures 3e and 3f). In particular, amino acids were rapidly removed relative to bulk POM in the upper 300 m, suggesting efficient remineralization in the surface ocean. Nevertheless, the contributions of TPAA to POC (~10%) and PN (~19%) were relatively constant below 500 m. The sinking of particles from the surface to the deep ocean with exponential attenuation of flux reflects a spectrum of organic matter reactivity from labile to refractory (Marsay et al., 2015). During the transformation, the composition of POM becomes more complex. In contrast to fresh POM, only a small fraction of refractory POM can be identified at the molecular level (Lee et al., 2000; Wakeham & Canuel, 1988). Compared to the TPAA fractions, mole percentages of D-amino acids (Figure 3d), glycine (Figure 3g) and nonprotein amino acids (β -Ala + γ -Aba) (Figure 3h) increased with depth. Concentrations of POM and TPAA (%POM) indicated similar POM qualities at the two stations, but individual amino acids revealed distinct intrinsic properties. Cowie and Hedges (1994) found that no single index can represent the full continuum of organic matter diagenesis, but rather each index is sensitive to a specific stage of diagenesis. Davis et al. (2009) concluded that carbon-normalized amino acid yields are good indicators during early diagenesis, and relative abundances of amino acids are effective indicators of intermediate stages of diagenesis, while the mol% of nonprotein amino acids is most sensitive in later diagenesis. The residence time of deep waters (>1,000 m) in the Pacific is over 800 years (Kawasaki et al., 2022; Matsumoto, 2007). In this scenario, the relatively high molar ratio of nonprotein amino acids and glycine indicates a more recalcitrant POM at the deep P2 site. North Pacific Intermediate Water and North Pacific Deep Water are found below 500 m in the WPWP (Wijffels et al., 1996). Stations P1 and P2 are located on either side of the seamount. The longer deep circulation age at station P2 may account for the more refractory nature of the POM (Matsumoto, 2007).

The pronounced vertical gradient of POM suggested a rapid cycling in the upper ocean (<300 m). Net removal rates for suspended POM were estimated by comparing concentration changes over the depth intervals (DCM layer to 300 m) to chlorofluorocarbon (CFC)-derived ventilation ages. In the DCM layer (~110 m depth), the ventilation age was ~9 years, and ~17.5 years at 300 m (Fine et al., 2001; Wijffels et al., 1996). The net removal rates of POC, PN, and TPAA were 0.125, 0.019, and 0.015 $\mu\text{mol L}^{-1} \text{yr}^{-1}$ at the station P1, and 0.099, 0.021, and 0.014 $\mu\text{mol L}^{-1} \text{yr}^{-1}$ at station P2. By comparison, the net removal rates of POC and PN in the WPWP were lower than those reported for the shallow isopycnals (110–150 m) at station ALOHA (0.24–0.67 $\mu\text{mol L}^{-1} \text{yr}^{-1}$ for POC and 0.03–0.06 $\mu\text{mol L}^{-1} \text{yr}^{-1}$ for PN) (Kaiser & Benner, 2012). The suspended particles collected in this study may incorporate some sinking particles with faster settling rate, but their effect on suspended POM removal is likely small. In the oligotrophic ocean, concentrations of suspended POM account for more than 80% of the total POM (Lam et al., 2018). In addition, the fragmentation of sinking particles exerts a major control on their flux attenuation, contributing to >50% of flux loss in the upper mesopelagic layer (Briggs et al., 2020).

3.3. Abundance and Cycling of Bacterial POM

Accurate tracking of bacterial POM requires knowledge of the biological origin of D-amino acids. Although D-amino acids are a major component of bacterial cell wall complexes, there is evidence that D-amino acids also occur in archaea (Nagata et al., 1998, 1999). Free D-amino acids are the most common form of D-amino acids in archaea, and analysis of trace amounts of bound D-amino acids is challenging. Kaiser and Benner (2008) did not find significant differences between bacterial POM based on muramic acid (exclusively derived from bacteria) and D-amino acid estimates, suggesting that archaea are unlikely to be major sources of particulate D-amino acids. Abiotic equilibrium is a well-known source of D-amino acids (Ritz-Timme et al., 2003), but the rate of stereochemical reversal at ocean temperatures should be far too low (million-year time scale) to compensate for the appreciable racemization that has occurred in the deep ocean over thousands of years (Bada & Man, 1980; Lee & Bada, 1977).

Bacterial POM makes an important contribution to suspended POM in the upper ocean. Above the DCM, ~27% of POC and ~36% of PN were derived from bacteria (Figures 4a and 4b). Our results agreed with those for surface waters at station ALOHA (20% for POC and 33% for PN). Maximum bacterial contributions occurred in the

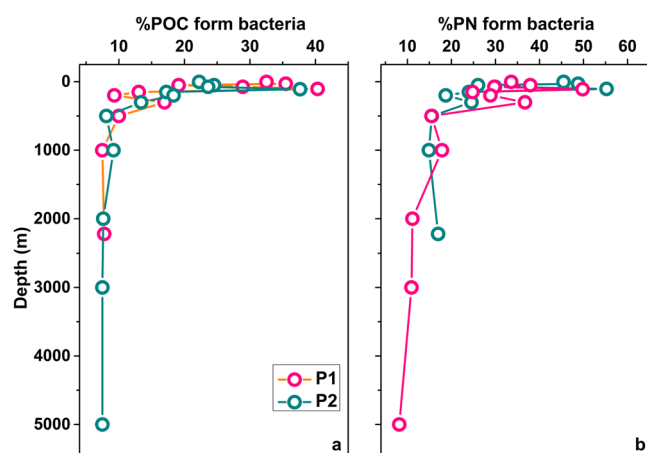


Figure 4. Bacterial contributions to (a) particulate organic carbon and (b) particulate nitrogen versus depth.

DCM, where up to 40% of POC and 55% of PN at station P1, and 38% of POC and 50% of PN at station P2 were of bacterial origin. The enhanced bacterial contributions in the DCM suggest that labile substrates stimulate bacterial growth (Lønborg et al., 2022; Obernosterer et al., 2008). However, below the DCM to a depth of 500 m, the bacterial contribution decreased pronouncedly and then remained largely unchanged at greater depths. Approximately 85% of bacterial POM was removed in the depth interval between the DCM and 300 m. We also estimated the net removal rates of bacterial POM based on the ventilation ages at the DCM and 300 m. At station P1, the removal rates of bacterial POC and PN were 0.067 and 0.013 $\mu\text{mol L}^{-1} \text{yr}^{-1}$, respectively, and 0.054 and 0.011 $\mu\text{mol L}^{-1} \text{yr}^{-1}$ at P2 station. The rapid removal of bacterial POM in the upper ocean indicates its high reactivity. Assuming that the bacterial POM at 2,000 m represents refractory bacterial POM, ~87% of bacterial POC and PN were characterized to be labile or semi-labile in surface waters. A large percentage (70%–90%) of the bacteria-specific D-amino acids was associated with living bacteria in surface waters at station ALOHA (Kawasaki et al., 2011), supporting the idea that the majority of the upper ocean bacterial POM is bioavailable. This indicates that bacterial POM is of higher bioavailability than bulk POC (~62%). Furthermore, bacterial

POM in surface waters is more bioavailable than bacterial DOM (~65%) (Kaiser & Benner, 2008). In contrast to the surface ocean, most of the bacterial POM exists in the deeper layers as detritus. Only <10% of biomarkers below 1,000 m were associated with living bacteria (Kawasaki et al., 2011). Similar results were reported in a previous study at station ALOHA, where researchers found that the ratio of bacterial detritus carbon to living carbon increased substantially with depth (Benner & Kaiser, 2003). Thus, the bacterial contribution based on biomarkers was generally higher than that based on intact cell counts.

The prevalence of labile and semi-labile bacterial POM in the upper layers (<300 m) suggests that these fractions may play an important role in metabolic energy supply of bacteria. Fresh organic matter released from plankton production facilitates microbial growth and respiration, leading to the development of biological hotspots (McClain et al., 2003). Heterotrophic bacteria are present in a high abundance in the upper ~100 m with a sharp decrease with depth (Ma, Song, Li, Wang, Sun, et al., 2021). In oligotrophic ocean regions, rapid organic matter remineralization maintains elemental cycles in the upper layers, thereby supporting phytoplankton production. Below the DCM, bacterial consumption of organic matter exceeds production. However, under the nutrient limiting conditions above 200 m (Ma, Song, Li, Wang, Yuan, et al., 2021), most of the degraded organic matter is used for energy supply (i.e., respiration) rather than biomass growth (del Giorgio & Cole, 1998). Increasing temperatures can raise the respiration rates of bacteria (Lønborg et al., 2022; Rivkin & Legendre, 2001). Thus, high temperatures in the WPWP further promote bacterial POM degradation (Marsay et al., 2015). Large areas of the ocean surface (~60%) are characterized by low concentrations of inorganic nutrients, with nutrients occurring largely in organic forms. Given the large bacterial contribution to surface ocean POC and PN, the cycling of bacterial POM appears to tightly link primary production and regeneration processes.

3.4. Implications for BCP Carbon Sequestration

Bacterial POM may make a relatively small contribution to oceanic organic carbon sequestration, based on the rapid cycling of bacterial POM in the upper ocean. The heterotrophic metabolism can transform labile DOM into refractory DOM, thereby facilitating long-term carbon sequestration. This framework has been defined as the microbial carbon pump (MCP) (Jiao et al., 2010). Our results show that the bacterial contribution remained rather constant (~8% and ~13% for POC and PN respectively) below 500 m, suggesting that bacterial POM does not accumulate as refractory POM. Even though molecular indicators (e.g., mole percentages of nonprotein amino acids) showed that the deep POM at station P2 was more recalcitrant than at station P1, the percentage of bacterial POC did not differ significantly. A study using solid-state ^{13}C NMR spectroscopy also showed that only a minor amount of POM was replaced by bacterial remnants during particle sinking (Hedges et al., 2001). These observations imply that bacterial POM does not constitute a substantial component of the BCP. Alternatively, bacterial POM is converted into recalcitrant substances that are not identified by D-amino acids (Kaiser & Benner, 2008). The present study primarily focused on suspended POM, but recent work has shown apparent differences in

bacteria attached to sinking versus suspended POM (e.g., community structure, heterotrophic production rates) (Baumas et al., 2021). Further studies on the chemical composition of POM in different size fractions are needed to enhance our understanding of the role of bacteria in the BCP.

Overall, this study illustrates that bacteria are a major source of suspended POM in the oligotrophic tropical surface ocean. The rapid turnover of bacterial POM underscores the importance of the bacterial detritus as part of the organic matter cycle and energy flow.

Data Availability Statement

Research Data associated with this article can be accessed at <https://figshare.com/s/e687343342ac2b96ed8b>.

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