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Important Contribution of Bacterial Carbon and Nitrogen to Sinking Particle Export

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Key Points:

- We exploit D-amino acid biomarkers in multi-year deep-sea sediment trap time series to evaluate bacterial contribution to total export
- Bacterial detritus accounts for up to 19 ± 8% of sinking POC and up to 36 ± 14% of PN, making up a large unrecognized part of biological pump
- The relative contribution of bacterial detritus to sinking particles increases with decreased export production

Supporting Information:

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

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Abstract Photosynthesis in the surface ocean converts atmospheric CO_2 into organic particles, with the fraction sinking to depth representing a major part of the ocean's biological pump. Although sinking particles are known to be altered by attached-bacteria during transit, most prior organic geochemical data indicated only minor replacement of plankton-derived particles by bacterial material. We exploit bacteria-specific biomarkers (D-amino acids) in a multi-year sediment trap in the Pacific Ocean (1,200 m) and suggest a different view. Major D-amino acids were consistently measured at abundance demonstrating widespread accumulation of bacterial material in sinking particles. Bacterial detritus was estimated to account for up to 19% of particulate organic carbon and up to 36% of particulate nitrogen, much higher than cell count-based values. The bacterial relative contribution increased with decreasing export production. Our results indicate that bacterial material constitutes an underappreciated component of the biological pump, a role expected to rise as the ocean warms.

Plain Language Summary Phytoplankton photosynthesis in the surface ocean plays a critical role in stabilizing atmospheric CO_2. It converts CO_2 into organic particles that sink and are reworked by colonizing bacteria. Bacteria respire most particles back to CO_2 while also transforming some into their cell components. Although the involvement of bacteria can replace the plankton-derived particles to bacterial material, most past organic geochemical data have suggested that the deep-sea particles are still comprised mainly of plankton remnants. This renders the contribution of bacterial material to total particle export an unresolved and yet important question, because the source and composition of particles are important to their fate in the ocean. Here, we analyzed bacteria-specific molecules in deep-sea sinking particles and found that bacterial organic matter actually made up a large fraction of the particles. In addition, the relative contribution of bacterial material to the sinking particles increased as the total carbon export decreased. This has important implications for the future ocean carbon cycle, because modeling work predicts a scenario of lower carbon export to the deep sea as the ocean warms. In this context, our findings imply a greater importance of bacteria in marine organic matter export and sequestration in a warming ocean.

1. Introduction

A fraction of fixed carbon in the surface ocean sinks to depth as detrital particles containing a mixture of phytodetritus, consumer fecal pellets, and other organic aggregates (Turner, 2015). The downward transit and remineralization of this particulate material play an important role in stabilizing atmospheric carbon dioxide and supporting deep-sea metabolism, together representing a main component of the ocean's biological pump (Arístegui et al., 2009; Herndl & Reinthaler, 2013). The large majority of sinking particulate organic matter (POM) is respired and altered by bacteria during transit to the sea floor (Bidle & Azam, 1999; Smith et al., 1992). The extent to which the particles are altered exerts large scale feedback on global warming and is directly linked to particle source and composition.

Past data based on molecular, isotopic, spectroscopic, and genomic approaches offered varied perceptions on the composition of the deeply exported particles (Wakeham & Lee, 2019). Chemical structures resolved by solid-state ^{13}C NMR and pyrolysis mass spectrometry showed a remarkable compositional similarity between the deeply exported particles and surface phytoplankton, suggesting non-selective preservation of plankton material in sinking particles (Hedges et al., 2001; Minor et al., 2003). Additional insights from the Redfield stoichiometry, confocal microscopy, bulk stable and radioactive isotopes, as well as the emerging compound-specific amino acid stable isotopes have indicated a relatively "fresh" planktonic signature in midwater and deep-sea sinking particles

(Hernes et al., 2001; McCarthy et al., 2007; Robinson et al., 2012; Roland et al., 2008; Shen et al., 2021; Waite et al., 2000). Together, much of this past work has created a paradigm that despite the large degree of bacterial remineralization, the deeply exported particles are composed predominately of leftovers of surface plankton. However, at the same time molecular level characterizations based on conventional hydrolysis and chromatograph approaches have shown a rapid depletion in common biochemicals with depth (e.g., amino acids, carbohydrates, lipids), with varying degrees of changes in molecular composition (Hernes et al., 1996; Lee et al., 2000; Wakeham et al., 1997). These data suggest substantial microbial removal of algal OM along with partial replacement by bacterial remnants. Recent studies based on genomic approaches have also pointed to large presence and activity of diverse groups of colonizing bacteria in the ocean (Boeuf et al., 2019; Johnson et al., 2020; Mestre et al., 2018; Preston et al., 2020; Zhao et al., 2020), implying accumulation of bacterial biomass in particles.

A holistic interpretation of these seemingly inconsistent data types has been unclear, due mainly to the lack of studies that directly quantify the extent of bacterial material input to sinking POM. Early work attempting to estimate bacterial contribution in organic carbon pool has focused mainly on non-sinking POM. Based on measurements of bacterial cell number, a large and variable contribution of bacterial organic carbon to total particulate organic carbon (from <13% to 70%) has been estimated in the upper water column of northeast Pacific Ocean and central north Pacific gyre (Azam et al., 1992; Cho & Azam, 1988; Simon et al., 1990). For sinking POM, the few existing quantitative estimates of bacterial biomass were also based on bacterial cell counts and they indicated only a very small bacterial carbon contribution (1% to ~4%) to the sinking organic carbon in the mesopelagic and deep ocean (Ducklow et al., 1985; Turley & Mackie, 1994). The substantially low bacterial fraction estimated for sinking POM imply that the cell count-based approach may have underestimated bacterial material entrained in sinking particles. Given that the vast majority of organic matter in the ocean is present as nonliving forms (Benner & Kaiser, 2003; Hedges & Keil, 1995), estimates based on intact cell counts would likely provide a lower bound on actual export of bacterial material to the deep sea.

To obtain more accurate estimates of the bacterial material contributions to sinking POM, specific organic tracers for bacteria detritus are needed. Bacteria synthesize a variety of unique molecules ("biomarkers") that can trace the occurrence of bacterially-produced material in natural organic matter mixtures. Such biomarkers include D-enantiomers of amino acids, muramic acid, diaminopimelic acid, and short-chain 3-hydroxy fatty acids (Kaiser & Benner, 2008; Kawasaki & Benner, 2006; Schleifer & Kandler, 1972; Wakeham et al., 2003). Among these, the D-amino acids have been the most extensively studied, and are perhaps the most representative biomarkers of bacterial organic matter given their high abundance and widespread occurrence in diverse bacterial macromolecules (e.g., peptidoglycan, lipopeptides, etc.) (Schleifer & Kandler, 1972). D-amino acids have also been developed as quantitative tracers for estimating the relative bacterial contribution to marine dissolved organic matter (DOM) and suspended POM (Kaiser & Benner, 2008; Kawasaki et al., 2011; Tremblay et al., 2015). Despite the uncertainties associated with the potentially dissimilar reactivities among organic components (e.g., peptidoglycan degrades slower than protein; Nagata et al., 2003), the D-amino acids-based estimates represent one of the few available approaches to quantify bacterial material in natural organic matter. To our knowledge, no published studies have examined D-amino acids in sinking POM.

In this study, we present what we believe to be the first D-amino acid measurements in a long-term sediment trap time series deployed at 1,200 m depth on the California margin. We use these data to evaluate the abundance of bacterial material in deep-sea sinking particles, explore the temporal trends of bacterial material export, and quantify the contribution of bacterial organic carbon and nitrogen to the total sinking particle fluxes. Further, we discuss the implications for carbon export and sequestration in the context of a warming ocean.

2. Materials and Methods

The study region, Monterey Bay, is situated on the central coast of California (Figure S1 in Supporting Information S1) and characterized by a strong seasonality in hydrographic conditions and biological production (Chavez et al., 2017). These factors provide an ideal setting to evaluate bacterial signatures in exported particles under varying conditions (see more information in Supporting Information S1). Sinking particle samples were collected between August 1998 and December 2004 using a Honjo Mark IV sediment trap as described previously (Castro et al., 2018; Shen et al., 2021). The trap was deployed at the M2 mooring station (36.697°N, 122.378°W; Figure S1 in Supporting Information S1) at 1,200 m depth and was pre-programmed to collect sinking particles every 14 days. Samples recovered from the field were wet-sieved (1 mm), rinsed with distilled water, centrifuged, and

then dried at 60°C for 24 hr. Bacterial alteration of the particle samples during the long-term storage was not evident from analytical data in both this and another associated project (see discussion in Supporting Information S1). Approximately 20 mg of dried sample was weighed for measurements of particulate organic carbon (POC) and total particulate nitrogen (PN) using a Carlo-Erba NA-1100 analyzer. Samples for the determination of POC were decarbonated with addition of 15% hydrochloric acid (HCl) prior to analysis. The actual weights of samples were recorded and used to calculate the fluxes of POC and PN.

D- and L-enantiomers of amino acids were determined using an Agilent 1,260 ultrahigh performance liquid chromatography (HPLC) system equipped with a Poroshell 120 EC-C18 column and a fluorescence detector. Approximately 100–200 μg of dried sample (weight recorded) was hydrolyzed in sealed glass vials with 6 mol L^{-1} HCl at 110°C for 20 hr to liberate amino acids. The hydrolyzed samples were dried with N_2 and immediately derivatized with *o*-phthaldialdehyde and *N*-isobutyryl-*L*-cysteine (Shen et al., 2017). A total of eighteen (18) hydrolyzable amino acids were separated, including the non-protein β-alanine and γ-aminobutyric acid. The four D-amino acids commonly found in marine organic matter were reported in this study: D-Asx (asparagine + aspartic acid), D-Glx (glutamine + glutamic acid), D-Ser (serine), and D-Ala (alanine). Acid-catalyzed racemization was corrected according to Kaiser and Benner (2005). The amount of D-amino acids determined was divided by total POC or PN to calculate D-amino acid yield value. This yield value was multiplied by POC or PN flux to calculate the flux of D-amino acids (in units of μmol AA-C m^{-2} d^{-1} or μmol AA-N m^{-2} d^{-1}).

The relative contribution (%) of bacterial carbon and nitrogen to the total POC and PN was estimated from D-amino acids, following the formula and endmembers of Kaiser and Benner (2008):

$$\text{Bacterial C or N contribution (\%)} = \text{D-amino acid yield}_{\text{sample}}/\text{D-amino acid yield}_{\text{bacteria}} \times 100,$$

where D-amino acid $\text{yield}_{\text{sample}}$ and D-amino acid $\text{yield}_{\text{bacteria}}$ are the POC- and PN-normalized values of two D-amino acids (i.e., D-Glx and D-Ala following the choice of Kaiser & Benner, 2008) in sediment trap material and cultured marine bacterial cell, respectively. The D-amino acid yields are reported with units of μmol AA-C mmolPOC^{-1} or μmol AA-N mmolPN^{-1}. The endmember values for D-amino acid $\text{yield}_{\text{bacteria}}$ were obtained from a mixture of 20% autotrophic bacteria and 80% heterotrophic bacteria (Kaiser & Benner, 2008), averaged at 4.7 μmol AA-C mmolPOC^{-1} and 6.0 μmol AA-N mmolPN^{-1}.

3. Results and Discussion

3.1. Flux and Export Pattern of Total Bacterial Material to the Deep Ocean

Sinking particle fluxes measured at 1,200 m of Monterey Bay showed large temporal changes (Figures 1a and 1b; Table S1 in Supporting Information S1), reflecting the pronounced variation in overlying plankton production. Mass fluxes of POC and the total of 18 hydrolyzable amino acids (THAA) during 1998–2004 varied by over an order of magnitude from 1.2 to 11.8 mmol C m^{-2} d^{-1} and from 91 to 1,305 μmol AA-C m^{-2} d^{-1}, respectively. Fluxes of THAA closely followed those of POC (Pearson correlation: $r = 0.84$, $p < 0.001$) and also generally increased during the more productive months (April–August). Fluxes of THAA determined in this study were overall higher and more variable than those measured previously in open ocean deep water (>1,000 m), including the equatorial Pacific Ocean (15–300 μmol AA-C m^{-2} d^{-1}; Gupta & Kawahata, 2002; Lee et al., 2000), north subtropical Pacific Ocean (<1 μmol AA-C m^{-2} d^{-1} at VERTEX IV site; Wakeham & Lee, 1989), and Atlantic Ocean (PAP Site: 10–650 μmol AA-C m^{-2} d^{-1}; Sargasso Sea: 4–55 μmol AA-C m^{-2} d^{-1}; Ittekkot et al., 1984; Salter et al., 2010).

On average, the THAA-carbon accounted for 9 ± 3% (range: 4%–13%) of the total POC (Table S1 in Supporting Information S1). This value was substantially lower than those commonly observed in freshly-produced marine POM (e.g., >50% of POC in the upper equatorial Pacific Ocean), but was ~10-fold higher than that of its dissolved counterparts (i.e., 0.5%–1.0% of DOC in the deep Pacific and Atlantic Oceans; Kaiser & Benner, 2009; Lee et al., 2004). While THAA concentrations in the DOM and POM pools may not be exactly comparable, the relative content of THAA (%OC) has been widely demonstrated to be a fairly universal proxy for relative lability in marine DOM, POM, and sediments (Benner & Amon, 2015; Cowie & Hedges, 1994; Lee et al., 2000). The observed moderate relative abundance of THAA in this study suggests that the particles exported to deep water have been substantially altered by degradation, but were still of relatively high lability compared to ambient deep-sea DOM.

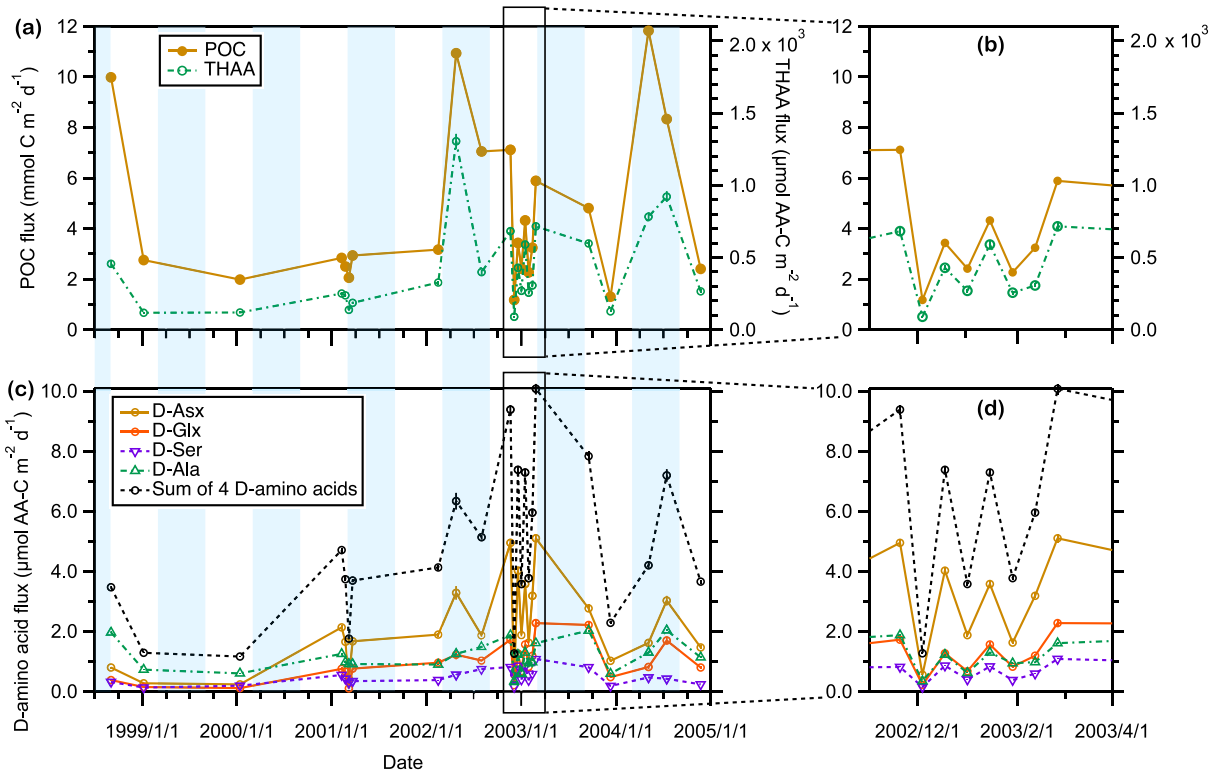

Figure 1. Changes in mass fluxes of (a, b) total particulate organic carbon and total hydrolyzable amino acids (THAA) and (c, d) four major D-amino acids as a function of collection date (shown as the medium date of each deployment). D-Asx: D-asparagine + D-aspartic acid; D-Glx: D-glutamine + D-glutamic acid; D-Ser: D-serine; D-Ala: D-alanine. Upwelling months (March–August) are marked with light blue bands. Errors were determined by propagating uncertainties from amino acid instrumental measurements (the Relative Standard Deviation of replicate injections for single amino acid, i.e., RSD is ~1%) and racemization corrections (Kaiser & Benner, 2005).

The four D-amino acid biomarkers (D-Asx, D-Glx, D-Ser, D-Ala) unique to bacteria were consistently measured in all samples (Figures 1c and 1d; Table S1 in Supporting Information S1), indicating a widespread bacterial imprint of heterotrophic or/and autotrophic bacteria. Mass flux of individual D-amino acids at 1,200 m varied substantially across the 6-yr sampling period (Figures 1c and 1d). The sum of the four D-amino acid fluxes varied from 1.2 to 10.1 μmol AA-C m^{-2} d^{-1} with a flux-weighted average of 5.5 ± 2.4 μmol AA-C m^{-2} d^{-1} (Table S1 in Supporting Information S1). For context, this D-amino acid flux is not trivial, with its magnitude comparable to that of total THAA fluxes measured previously in the deep subtropical Pacific and Atlantic Oceans (<1–55 μmol AA-C m^{-2} d^{-1}; Ittekkot et al., 1984; Wakeham & Lee, 1989). Given that D-amino acids by themselves represent only one kind and also minor component of the many compound classes (e.g., peptidoglycan, lipopeptides, etc.) that constitute the bacterial cells, the observed large flux of D-amino acids alone implies that the export of total bacterial detritus to the mesopelagic and deep ocean is substantial.

Little is known about the temporal export pattern of bacterial material in the ocean. Careful examination of the relationships between D-amino acid flux and the total POC flux revealed a somewhat surprising, but highly consistent, parabolic pattern (quadratic regression: $r^2 = 0.50–0.78$, $p < 0.001$; Figure 2). Bacterial material flux, as indicated by D-amino acid flux, was low when POC flux was the lowest or highest. The highest bacterial material flux was observed when POC flux was intermediate in value (Figure 2). These results suggest that the mass flux of bacterial material is highly variable and is not a simple linear function of the total export production. One major implication is that it is not possible to directly estimate the flux of bacterial material using a single fixed percentage of total export production.

This unexpected export pattern could be explained by the variable relative proportion of bacterial material in bulk particles that ultimately leads to the observed parabolic pattern of bacterial material flux (Figure S2 in Supporting Information S1). The relative proportion of bacterial material in sinking particles varied in an opposite direction to the total particle flux (Figure S3 in Supporting Information S1), a feature that appears to be related to particle

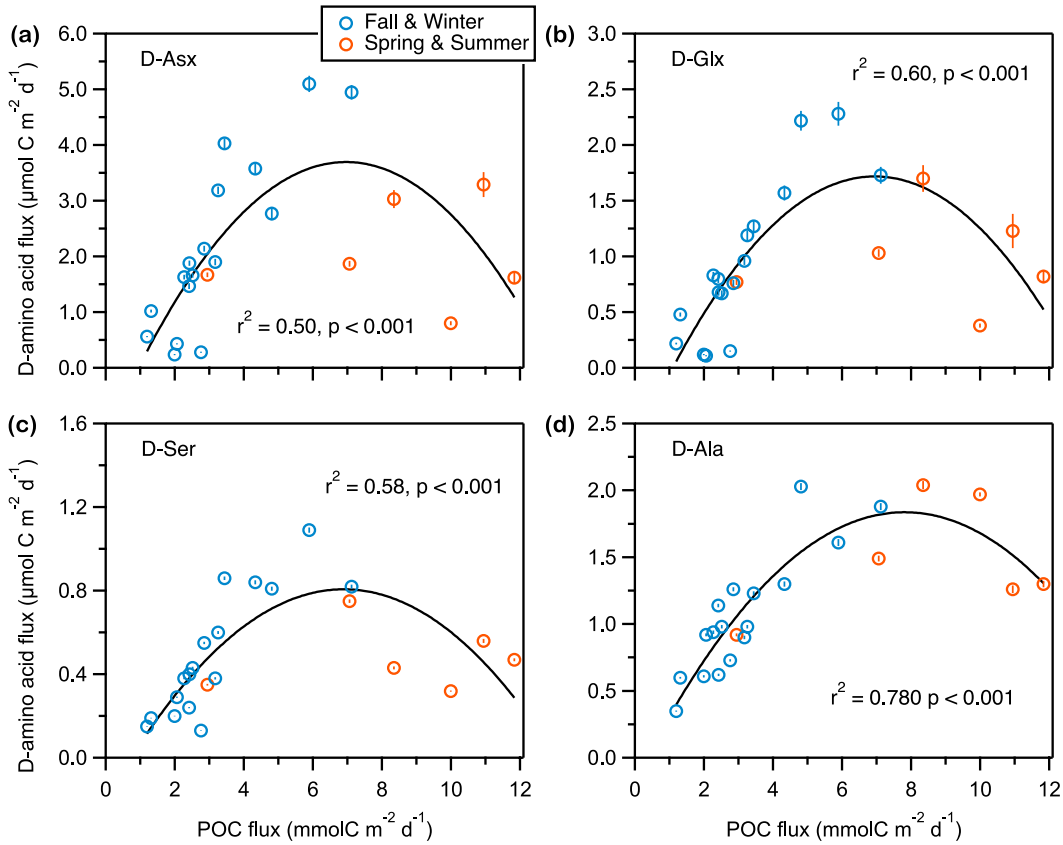

Figure 2. Changes in D-amino acid mass flux as a function of particulate organic carbon (POC) flux. The black solid curves represent the quadratic polynomial fits. Blue circles: samples collected during fall and winter; Orange circles: samples collected during spring and summer. Errors were determined in the same way as those in Figure 1.

properties and overlying plankton dynamics. Lower primary productivity periods dominated by small phytoplankton (e.g., cyanobacteria) tend to produce particles with smaller size, higher porosity and lower sinking rate, which extends the transit time of particles and presumably facilitates heterotrophic bacterial growth and transformation (Goutx et al., 2007; McDonnell et al., 2015; Spilling et al., 2023). Occurrence of cyanobacteria may themselves also contribute D-amino acids (D-Glx, D-Ala). In contrast, higher primary production periods dominated by large phytoplankton tend to produce larger particles with smaller relative bacterial contributions (Figure S4 in Supporting Information S1).

3.2. Contribution of Bacterial Material to Marine Particle Export

We compared D-amino acids yields with values measured previously in pure marine bacterial cultures to evaluate the relative contribution (%) of total bacterial material to sinking particles. Estimation based on this approach in principle includes both autotrophic and heterotrophic bacteria, but as discussed below, multiple lines of evidence indicate heterotrophic bacteria as the dominant source. The calculations suggested that bacterially-derived organic carbon and nitrogen accounted for 4 ± 2% to 19 ± 8% of the total sinking POC and 7 ± 3% to 36 ± 14% of total PN, respectively, with the bacterial contribution increasing with declining POC and PN fluxes (Figure 3). As discussed below, these estimates likely represent an upper bound on the bacterial contribution.

These first geochemical estimates of total bacterial organic matter in sinking POM are far higher than previous estimates based on cell counts, and yet seem to fall within a reasonable range. Regressing %bacterial contribution to the total POC and PN fluxes returned relatively high *y*-intercept values (C: ~16%; N: ~31%) at zero flux (Figure 3). The intercepts predict the theoretical average %bacterial contribution for scenarios of no net export of sinking organic matter. These theoretical values were comparable to those estimated for non-sinking marine

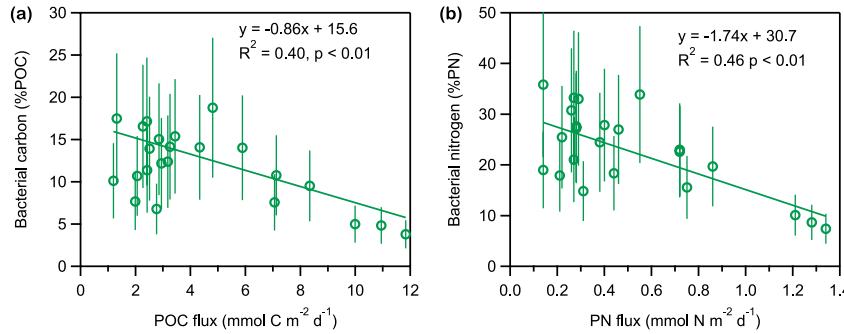

Figure 3. Estimated contributions (%) of bacterial carbon and nitrogen to the total sinking particulate organic carbon (POC) and particulate nitrogen (PN) and their relationships with POC and PN fluxes. Errors were determined by propagating uncertainties from the following sources: D-amino acid instrumental measurements (RSD ~1%), racemization corrections (Kaiser & Benner, 2005), and bacterial D-amino acid endmembers (Kaiser & Benner, 2008).

DOM and suspended POM (C: ~25%, N: ~50%; Kaiser & Benner, 2008; Kawasaki et al., 2011; Tremblay et al., 2015). Importantly, our values were about one order of magnitude higher than the previous cell-count-dependent estimates in sinking POC (1%–4%; Ducklow et al., 1985; Turley & Mackie, 1994). Our estimates suggest that bacterial detritus represents a large fraction of the deeply exported organic matter, substantially beyond that indicated by prior quantitative estimates.

This biomarker-based approach has been broadly applied in organic geochemical literature (Kaiser & Benner, 2008; Kawasaki et al., 2011; Lehmann et al., 2020; Tremblay et al., 2015). However, it is important to note that there are important uncertainties associated with such estimates. It first assumes that D-amino acids track all of bacterial biomass including cell walls and intracellular components. D-amino acids are known to occur in various components of the bacterial cell wall (e.g., peptidoglycan, siderophores, lipopolysaccharides, lipopeptides; Kaiser & Benner, 2008; Schleifer & Kandler, 1972), and thus would most directly trace cell wall components. Previous experiments measuring the hydrolysis and remineralization rates of bacterial cell wall components have suggested that peptidoglycan is more resistant to biodegradation than protein (Nagata et al., 2003). As such, endmember values of D-amino acid yields determined in bacterial cultures (mostly whole cells) are likely lower than those in detrital cells. Therefore, our estimates based on fresh cells might provide an upper bound on the bacterial contribution. A second assumption is that bacterial species used to establish endmembers match those present in the field. This is currently difficult to assess because marine natural bacterial species are poorly constrained, and the majority cannot be cultured. Nevertheless, nearly all the bacterial species used as endmembers for this study are found in the study region (e.g., autotrophs: *Synechococcus* sp., *Trichodesmium*; heterotrophs: *Alteromonas* sp., *Cytophaga* sp., *Roseobacter litoralis*, *Pseudomonas* sp.; Farnelid et al., 2016; Suzuki et al., 2001). The variants of these same caveats, while not aways directly discussed, are inherent in essentially all organic biomarker-based estimations about source of detrital organic matter.

Regarding the specific sources of D-amino acids measured in sinking particles, they could be derived from heterotrophic bacteria or/and autotrophic bacteria. The two D-amino acids that are unique to heterotrophic bacteria (D-Asx and D-Ser) were consistently measured (Figure 1). The D/L ratios of Asx and Ser were many-fold higher than the levels found in fresh heterotrophic bacterial POM (Figure S5 in Supporting Information S1), indicating extensive heterotrophic degradation which leads to preferential removal of L-amino acids over that of D-amino acids (see Section IV in Supporting Information S1). Overall, the specific D/L amino acid signatures suggest that the majority of bacterial material observed in sinking particles was most likely derived from heterotrophic bacteria.

There are multiple possible sources for the heterotrophic bacterial material detected in sinking particles, including heterotrophic bacteria that reside in the surface ocean, bacterial growth on particles during sinking, bacteria from zooplankton guts, or aggregation of bacterial detritus. The relative contribution of these sources is difficult to resolve with our current data set. Nevertheless, of these, bacteria from guts of grazers are likely not a major contributor, as suggested by the paired analysis of trophic position (as a rough proxy of the contribution of grazers; Shen et al., 2021) that showed almost no relationship between D-amino acid export and particle trophic position (Figure S6 in Supporting Information S1).

Based on recent studies, we propose that the most likely source is heterotrophic bacteria "growing in" and transforming plankton-derived particles into bacterial material during the long transit (weeks to months), producing most of the bacterial organic matter detected. This might represent the most parsimonious interpretation in light of recent work that reveal rapid bacterial growth and production upon addition of sinking particles (Church et al., 2021), predominant particle-associated lifestyle of deep-sea microorganisms (Zhao et al., 2020), and intimate relationships between bacterial community dynamics (e.g., richness, population density) and rates of particle remineralization (Baumas et al., 2021; Nguyen et al., 2022). Incubation studies in both DOM and POM have shown that fresh algal organic matter is remarkably degraded on short timescales, with bacteria rapidly consuming eukaryotic algal material and producing refractory bacterial material on a scale of days to weeks (Calleja et al., 2013; Lehmann et al., 2020; Shen & Benner, 2020). Finally, the inverse relationships observed between D-amino acid yields (as a proxy of relative bacterial contribution) and surface water Chl-a and phytoplankton biomass in the study region are also consistent with the expectation of more bacterial material "growing" in with slower sinking rates (see Figure S4 and Text in Supporting Information S1).

3.3. Implications for Carbon Export and Sequestration in the Deep Ocean

An outstanding observation in this study is the widespread imprint of bacterial material in sinking particles, with nearly one order of magnitude greater bacterial contribution being suggested compared to the past cell count-based estimates. These findings suggest that the bacterially-derived material play a far more important role in marine carbon export and sequestration than past organic geochemical data would suggest. Importantly, residual bacterial organic matter is generally found to be more resistant to degradation than planktonic organic matter (Amon et al., 2001; Lehmann et al., 2020; Nagata et al., 2003). Therefore, while heterotrophic bacterial biomass synthesized in sinking particles is ultimately derived from surface phytoplankton, the bacterial activity on particles could represent an important unappreciated factor in carbon sequestration by converting labile phytoplankton carbon into bioresistant bacterial carbon. This process conceptually resembles that of microbial carbon pump (MCP), which suggests bacterial growth in the water column can rapidly transform labile substrates into refractory dissolved molecules that contribute to the millennia-year old DOC pool (Jiao et al., 2010; Lechtenfeld et al., 2015; Ogawa et al., 2001). The MCP concept has up to now only been used for the DOM pool and free-living bacteria, and we suggest that similar carbon sequestration processes linked to heterotrophic transformation could also occur in the POM pool. This idea is supported by the remarkable similarity in D/L distribution patterns between sinking particles (i.e., D/L ratio values: Asx > Glx ≈ Ser < Ala) and those observed in suspended POM, as well as DOM from various oceanic regions (Figure S7 in Supporting Information S1).

Building upon the present work on POM and prior studies on DOM, we propose that bacteria colonizing on particles have the potential to mediate at least three different pathways that assist carbon sequestration in the ocean (Figure 4). The first is via the transformation of plankton-derived organic matter into bacterial cell components with reduced reactivity (e.g., peptidoglycan; Nagata et al., 2003). Data from this study suggest that this pathway in fact represents an appreciable fraction of the total carbon export, which has not previously been widely recognized. A second pathway is through the extracellular release of bioresistant dissolved molecules to ambient water during the growth of particle-attached bacteria. Previous bioassay experiments found that bacteria could release a myriad of structurally complex metabolites during growth, and many of these metabolites are resistant to degradation (e.g., carboxyl-rich alicyclic molecules, D-amino acids, and numerous structurally-uncharacterized low-molecular-weight compounds; Gruber et al., 2006; Kawasaki & Benner, 2006; Lechtenfeld et al., 2015). The third is through the support of deep-sea free-living microbial communities. Particle-attached bacteria may solubilize substantially more POM than needed for respiration (Smith et al., 1992). The excess hydrolysates support free-living heterotrophs and likely chemoautotrophs as well (e.g., ammonia oxidizers) in the dark ocean (Hansman et al., 2009; Nagata et al., 2000), offering an additional channel for the production of potentially refractory DOM via the microbial carbon pump (Bayer et al., 2019; Jiao et al., 2010). While the magnitude of the last two pathways cannot be constrained with our data, they likely operate in diverse bacterial groups with varied utilization strategies (e.g., external hydrolysis, selfish uptake, passive scavenging; Arnosti et al., 2021). Overall, we suggest that in the context of accumulating evidence that carbon sequestration in the global ocean is largely mediated by bacteria, it may in fact be linked more strongly to the particle-associated bacteria and be more complex than previously thought.

Finally, the observed inverse relationship between bacterial contribution and export production (Figure 3) predicts an increasingly important role of bacteria in the carbon export and sequestration in a warming climate. Ongoing

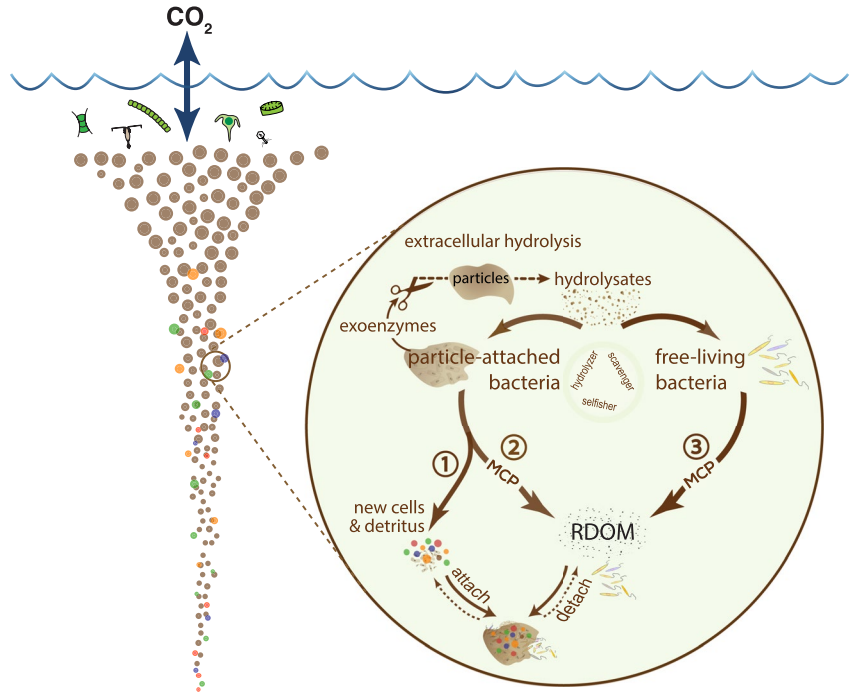

Figure 4. Conceptual diagram illustrating three potential carbon sequestration pathways mediated by particle-associated bacteria in the ocean. Bacteria attached to particles release exoenzymes that cleave large particles into small organic molecules. These hydrolyzed organics support the growth of attached bacteria, which synthesize new bacterial cell components that are incorporated into the sinking particles (pathway 1). As part of their metabolisms, the attached bacteria release numerous structurally complex exometabolites, including refractory dissolved organic molecules (RDOM) (e.g., carboxyl-rich alicyclic molecules) (pathway 2). The excess hydrolytes taken up by free-living bacteria can be transformed into RDOM via the classic microbial carbon pump (MCP) (pathway 3). Some of the newly synthesized cells and detritus (via pathway 1) as well as RDOM (via pathways 2 and 3) can be exchanged with particles through processes of attachment and detachment.

ocean warming, with associated intensified water stratification and nutrient stress, has been implicated in observed large-scale decreases in phytoplankton size, biomass, and productivity in the surface ocean (Behrenfeld et al., 2006; Daufresne et al., 2009). Export production as a result of these shifts is expected to decrease and be increasingly dominated by small particles (Bopp et al., 2005; Close et al., 2013; Henson et al., 2021; Richardson & Jackson, 2007). Smaller and slower-sinking particles would benefit the growth of particle-attached bacteria (McDonnell et al., 2015; Spilling et al., 2023) and thereby their production of refractory DOM and POM (Figure 4), beyond what would be predicted by export production changes alone. As a result, the production and export of refractory bacterial organic matter are expected to rise as the ocean warms, which in turn may represent a novel negative feedback to rising atmospheric carbon dioxide. As these trends are projected to continue and accelerate (Steinacher et al., 2010), the role of bacteria in marine carbon export and sequestration is expected to become increasingly important.

Data Availability Statement

Research data used in this study are presented in Table S1 in Supporting Information S1.

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Erratum

In the originally published version of this article, Figure 4 was missing a blue wave at the top that indicates surface ocean, due to a typesetting error. The figure has been corrected, and this may be considered the authoritative version of record.