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Enhanced carbon sequestration in marginal seas through bacterial transformation

Jinqiang Guo^{a,b}, Bu Zhou^{a,b}, Eric P. Achterberg^b, Yuan Shen^d, Jinming Song^{a,c,e,f,*}, Liqin Duan^{a,c,e,f}, Xuegang Li^{a,c,e,f}, Huamao Yuan^{a,c,e,f,*}

^a Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, PR China

^b Marine Biogeochemistry Division, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

^c Laboratory for Marine Ecology and Environmental Sciences, Qingdao Marine Science and Technology Center, Qingdao, PR China

^d State Key Laboratory of Marine Environmental Science & College of Ocean and Earth Sciences, Xiamen University, Xiamen, PR China

^e University of Chinese Academy of Sciences, Beijing, PR China

^f Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao, PR China

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ABSTRACT

Labile organic carbon is a highly dynamic component of the marine carbon pool, traditionally thought to be respired within hours to days into carbon dioxide (CO₂) by bacteria, although there is a paucity of direct observational evidence. Here, we report that a significant portion of labile particulate organic carbon (POC) in marginal seas is converted into bacterial material. By exploiting D/L-amino acids, we trace the origins of labile POC and its transformation into bacterial POC in the marginal seas off Eastern China. Our results indicate that labile POC primarily originates from autochthonous primary production, with bacterial POC fractions closely paralleling those of labile POC. It appears that rapid bacterial POC transformation is driven by enhanced bacterial organic carbon is buried annually in global marginal seas. We estimate that around 0.08 \pm 0.03 Pg of bacterial organic carbon is buried annually in global marginal seas, accounting for ~40 % of total organic carbon burial, thus contributing to long-term carbon sequestration. These findings highlight the critical role of bacterial ransformation in carbon sequestration within marginal seas and provide a potential mechanism for the observed increase in CO₂ uptake in coastal regions.

1. Introduction

Marginal seas account for ~7 % of the global ocean area, but contribute ~30 % of the global marine primary production and ~80 % of organic carbon burial (Bianchi et al., 2018; Liu et al., 2010), hence playing an important role in the global carbon cycle. Extensive research has been conducted in ocean margins, indicating that carbon cycling is highly complex due to the impacts of human activities, climate change, and hydrodynamic processes (Bauer et al., 2013; Regnier et al., 2013; Zhao et al., 2021). The carbon source-sink dynamics in marginal seas are still not well constrained. Recent observations suggest an increase in coastal ocean CO_2 uptake over the past decade (Laruelle et al., 2018). However, the mechanisms driving this trend remain unclear.

Marginal seas are characterized by abundant nutrients and enhanced levels of primary production. The areas of elevated phytoplankton production represent hot spots for labile organic matter production (Shen et al., 2016). Labile organic matter refers to organic material that is readily degraded by microorganisms. It is enriched in bioavailable components such as amino acids and carbohydrates, which can be rapidly utilized by microorganisms within hours to days (Davis and Benner, 2007; Moran et al., 2022). Labile organic matter plays an essential role in supporting heterotrophic metabolism and driving elemental cycles (Zhang et al., 2018), and is generally assumed to be respired primarily to carbon dioxide (CO₂) (Cherrier et al., 1996; Hansell and Carlson, 2015; Hedges et al., 2001). The extent to which the labile organic matter is altered exerts an important impact on atmospheric CO₂ concentrations. In particular, labile organic matter in oligotrophic oceans is considered to be largely removed through respiration to generate energy (del Giorgio et al., 2011; del Giorgio and Cole, 1998; Rivkin and Legendre, 2001). However, recent studies have shown

E-mail addresses: jmsong@qdio.ac.cn (J. Song), yuanhuamao@qdio.ac.cn (H. Yuan).

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^{*} Corresponding authors at: Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, PR China.

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that bacteria in eutrophic marginal seas are able to efficiently convert labile organic matter into bacterial organic matter, thereby facilitating the production of refractory organic matter (Guo et al., 2023a, 2024; Zhu et al., 2014).

A holistic perception of the fate of labile organic matter in marginal seas requires the characterization of reactive components as well as bacterial organic matter. Incubation experiments are traditionally used to determine the labile fraction of organic matter (Bendtsen et al., 2015; Panagiotopoulos et al., 2002), but this approach changes the environmental conditions and is limited in terms of spatial and temporal coverage. Biomarkers provide a potent tool for addressing these issues. Bioactive molecules, such as amino acids, are preferentially removed during organic matter degradation (Amon et al., 2001; Hedges et al., 1994). The proposed index of carbon normalized yield of amino acids to indicate the bioavailability of organic matter has been validated in incubation experiments (Davis et al., 2009; Lehmann et al., 2020) and is widely applied in diverse aquatic systems (Chapelle et al., 2009; Davis and Benner, 2005; Liang et al., 2023). In addition, d-enantiomers of amino acids are widespread in bacterial macromolecules (e.g., peptidoglycan) and have been used to quantitatively track the relative bacterial contribution to marine organic matter (Guo et al., 2023b; Kaiser and Benner, 2008; Kawasaki et al., 2011).

In this study, we collected suspended particulate organic matter (POM) samples from the Eastern China Marginal Seas to analyze particulate organic carbon (POC) and D/L-amino acids. By assessing the abundance and production of the labile fraction of POC and quantifying the bacterial contribution to POC, we aim to enhance our mechanistic and quantitative understanding of bacterial transformation processes and their implications for carbon sequestration in marginal seas.

2. Materials and methods

2.1. Sample collection

The sampling region is located in the Eastern China Marginal Seas, and includes the South Yellow Sea and East China Sea (Fig. 1). Samples were collected aboard the R/V Kexue 3 during three cruises: April 27 to May 2, 2017; November 14 to December 3, 2019; and August 8 to August 20, 2020. Water samples were obtained within the 100 m isobath on the continental shelf at discrete depths, using a rosette sampler system equipped with 12 L Niskin bottles. Conductivity-Temperature-Depth (CTD; Seabird) sensors were mounted to the sampler system to collect temperature and salinity data. Samples for analyses of POC and total particulate amino acids (TPAA) were filtered over pre-combusted (450 $^{\circ}$ C, 5 h) glass fiber filters (GF/F, 0.7 μ m pore size, Whatman) and stored frozen (-20 °C). The filtrate was collected in acid-cleaned 60 mL high-density polyethylene (HDPE) bottles and stored at -20 °C for laboratory analysis of inorganic nutrients. Water samples for chlorophyll-a (Chl-a) were filtered (GF/F; 0.7 µm pore size; Whatman) immediately following collection and stored frozen (-20 °C) in the dark until analysis.

2.2. Analysis of Chl-a and nutrients

Samples for Chl-a determination were extracted with 10 mL of 90 % acetone for 24 h at 4 $^\circ$ C, centrifuged, and subjected to analysis in a fluorescence spectrophotometer (Hitachi F-4600; excitation: 436 nm; emission: 670 nm).

Concentrations of nitrate (NO₃-N), nitrite (NO₂-N), ammonium (NH₄-N), and phosphate (PO₄-P) were analyzed using an autoanalyzer (Bran-Lubbe Quaatro) (Guo et al., 2020). The limits of quantification were 0.02, 0.02, 0.03, and 0.01 μ mol L⁻¹ for NO₃-N, NO₂-N, NH₄-N and PO₄-P, respectively. The analytical precision among three injections of a given water sample was typically < 3 %. Concentrations of NO₃-N, NO₂-N, and NH₄-N were summed as dissolved inorganic nitrogen (DIN).



Fig. 1. Sampling stations on the shallow (within 100 m of the isobath) continental margin in Eastern China. Suspended particulate organic matter (POM) samples were collected during three cruises: April–May 2017, November–December 2019, and August 2020.

2.3. Chemical characterization of POM

Samples for POC were treated with 10 % hydrochloric acid (HCl) to remove inorganic carbon, oven-dried at 60 °C, and determined using a Flash IsoLink CN elemental analyzer (EA) (Thermo Fisher Scientific, Germany).

Filters for D- and L-amino acid analysis were freeze-dried and then hydrolyzed using 6 M HCl at 110 °C for 24 h. Then, HCl was removed by repeated drying, and the residue was derivatized by o-phthaldialdehyde and N-isobutyryl-l-cysteine. Separation and detection of amino acids were performed using a Thermo Fisher Scientific U3000 ultra high performance liquid chromatography (UHPLC) system equipped with a Poroshell 120 EC-C18 column (4.6 \times 100 mm, 2.7 μ m particles) and a fluorescence detector (excitation: 330 nm; emission: 445 nm) (Shen et al., 2017). The column temperature was 30 °C and the flow rate was 1 mL min⁻¹. A linear binary gradient was used starting with 100 % potassium di-hydrogen phosphate (KH₂PO₄; 48 mmol L^{-1} , pH = 6.25) to 61 % KH₂PO₄ and 39 % methanol: acetonitrile (13:1, v/v) at 22 min, 46 % KH2PO4 at 30 min, 40 % KH2PO4 at 37 min, and 20 % KH2PO4 at 39 min. Amino acids included in the analysis were as follows: aspartic acid + asparagine (Asx), glutamine + glutamic acid (Glx), serine (Ser), histidine (His), glycine (Gly), threonine (Thr), arginine (Arg), alanine (Ala), tyrosine (Tyr), valine (Val), phenylalanine (Phe), isoleucine (Ile), leucine (Leu), and lysine (Lys). Hydrolysis-induced racemization was corrected according to Kaiser and Benner (2005). The relative standard deviation (RSD) among six runs of a given sample was consistently < 5% for individual amino acids.

Labile POC was calculated as the percentage contributions of amino acid carbon to the total POC using the following equation:

Labile POC (%) =
$$\frac{\text{TPAA} - \text{C}}{\text{POC}} \times 100$$
 (1)

where POC and TPAA-C represent the concentrations of bulk POC and

the carbon measured in TPAA, respectively.

2.4. Bacterial contributions to POC

The relative contribution of bacterial organic carbon to POC was estimated following the method of Kaiser and Benner (2008):

Bacterial POC (%) =
$$\frac{D - amino acid_{sample}}{D - amino acid_{bacteria}} \times 100$$
 (2)

where D-amino acid_{sample} and D-amino acid_{bacteria} are the carbonnormalized yields of two D-amino acids (i.e., D-Ala and D-Glx) in suspended POM and bacteria, respectively. The end-member values for Damino acid_{bacteria} employed in the calculation were 50.3 nmol mg C⁻¹ for D-Ala and 48.3 nmol mg C⁻¹ for D-Glx, as outlined by Kaiser and Benner (2008). These values were derived from a mixture comprising 20 % autotrophic and 80 % heterotrophic bacteria.

3. Results and discussion

3.1. Production of labile POM

Labile organic matter primarily comprises bioactive compounds such as amino acids, carbohydrates, and nucleic acids (Amon et al., 2001; LaRowe and Van Cappellen, 2011; Moran et al., 2022). Among these, amino acids are particularly abundant in labile POM, while other reactive components like neutral sugars and nucleic acids constitute a relatively low proportion (<10 %) of fresh algal organic carbon (Whitehead et al., 2008). In this study, we used carbon content of amino acids to represent labile POC (Kang et al., 2021). Concentrations of labile POC in the shallow Eastern China Marginal Seas ranged from 0.9 to 30.7 μ mol L⁻¹ (Fig. 2a). This approach possibly underestimates the concentration of labile POC, but the results of incubation experiments indicated that changes in amino acid yield were consistent with the labile organic carbon fraction (Lehmann et al., 2020; Shen et al., 2015).

Labile POC is strongly linked to primary production. The Eastern China Marginal Sea, receiving substantial nutrient inputs from rivers such as the Changjiang River and the intrusion of Kuroshio subsurface water (Chen, 1996), is recognized globally as one of the most productive ocean margins (> 400 gC m⁻² yr⁻¹) (Tan and Shi, 2006). Phytoplankton production peaks in regions with moderate salinity, where lower levels of suspended particulate matter and elevated nutrient concentrations are observed (Dagg et al., 2004). In summer, Chl-a concentrations can exceed 20 µg L⁻¹ (Fig. S1). The strong relationship between labile POC and Chl-a (R² = 0.81, p < 0.01; Fig. 2b) suggests that the production. Amino acid composition provides additional insights into the

contribution of phytoplankton to POM. For instance, diatoms are characterized by a higher molar percentage of Ser + Thr (16.9 %) and a lower Asx to Gly ratio (0.62), whereas coccolithophores exhibit the opposite pattern (mol % Ser + Thr: 9.0 %; Asx/Gly: 1.88) (Dittmar et al., 2001). In our sampling region, the average mol % Ser + Thr and Asx/Gly ratio were 13.0 \pm 1.7 % and 0.7 \pm 0.1, respectively (Fig. S2). These findings suggest that diatoms significantly contribute to POM, aligning with the reported dominance of diatoms in the Eastern China Marginal Seas (Guo et al., 2014). Although the Changjiang River transports ~1.5 \times 10¹² g of POC per year, terrestrial inputs are not a major source of labile POC (Liang et al., 2023; Wang et al., 2012). Previous studies based on isotopes and biomarkers have shown that organic matter in Changjiang River is bio-refractory and mainly derived from highly degraded soil organic matter (Wu et al., 2007; Zhu et al., 2014). Furthermore, a significant portion of terrestrial organic matter is rapidly removed through biotic and abiotic processes in the low salinity (0-20) zone (Bianchi, 2011; Liang et al., 2023).

The weak relationship between bulk POC and labile POC ($R^2 = 0.28$, p < 0.01) indicates that labile POC has distinct turnover properties, highlighting the need to classify organic matter based on turnover time. The distribution of labile POM reflects the balance between production and consumption. Whilst labile POC is rapidly utilized, its production can exceed consumption in highly productive marginal seas. The notable concentrations of labile POC observed in this study suggest the accumulation of bioavailable POM in the marginal seas. Likewise, Shen et al. (2012) found a substantial accumulation of amino acid-rich dissolved organic matter (DOM) in the productive Chukchi Sea. The accumulated labile organic matter could fuel heterotrophic metabolism in both benthic and open ocean environments through vertical and cross-shelf transfer (Lønborg and Álvarez-Salgado, 2012).

3.2. Rapid bacterial transformation of labile POM

Labile organic matter can stimulate rapid responses from microorganisms, facilitating biogeochemical processes and the formation of biological hot spots (McClain et al., 2003; Shen et al., 2016; Stocker et al., 2008). The relationships between bacterial metabolism and environmental factors are complex, but several studies have shown that the supply of bioavailable organic matter leads to significant increases in bacterial biomass (Lønborg et al., 2022; Obernosterer et al., 2008). In the present study, we found a significant positive correlation between d-amino acids and labile POC ($R^2 = 0.82$, p < 0.01; Fig. S3), suggesting that labile organic matter promotes rapid bacterial growth. This finding aligns with previous work reporting high heterotrophic bacterial abundance in regions with elevated bioavailable POM (Guo et al., 2024). Rapid transformation of labile POC into bacterial organic carbon was



Fig. 2. Plots of labile particulate organic carbon (POC) against (a) salinity and (b) chlorophyll-a (Chl-a). The gray band represents the 95 % confidence interval.

observed in the Eastern China Marginal Seas. The functioning of heterotrophic bacteria relies on the supply of bioavailable organic carbon. Some of this labile organic carbon is converted into CO₂ by respiration and provides energy to the bacteria, while another fraction is assimilated into bacterial material. Bacteria-specific biomarkers (e.g., d-amino acids) enable the tracking of bacterial organic carbon (Kaiser and Benner, 2008; McCarthy et al., 1998). In our study region, bacterial contributions to POC varied from 6.0 % to 52.9 % (mean: 23.2 \pm 7.7 %). Moreover, a strong positive relationship was found between bacterial contributions and labile POC fractions ($R^2 = 0.42, p < 0.01$; Fig. 3). Both autotrophic and heterotrophic bacteria contribute to bacterial organic carbon. The primary origin of autotrophic bacterial organic carbon in the oceans is cyanobacteria, particularly Synechococcus (Kaiser and Benner, 2008; Zhu et al., 2014). However, the relative abundance of autotrophic bacteria is low in the eutrophic marginal sea. Prior work based on 16S rDNA sequencing found that phototrophs constituted only 14 % of the bacterial community in the Eastern China Marginal Seas (Guo et al., 2024), suggesting that heterotrophic bacteria dominate bacterial organic carbon. These findings collectively indicate that bioavailable POC can be rapidly transformed into bacterial organic carbon.

We identified two distinct patterns in bacterial POC response to labile POC changes: Pattern 1 with a sharp increase in bacterial POC with increasing labile POC, and Pattern 2 with a less steep increase in bacterial POC with increasing labile POC (Fig. 4). These patterns likely reflect differences in bacterial growth efficiency (BGE, the ratio of assimilated organic carbon converted into bacterial biomass), with Pattern 1 representing higher BGE and Pattern 2 representing lower BGE. The BGE values can vary significantly in natural aquatic ecosystems, ranging from 0.01 to 0.63 (Alonso-Sáez et al., 2007; Anderson and Turley, 2003; del Giorgio, 2000). A range of factors determine the BGE, but it has been reported that BGE varies systematically with nutrient status of ecosystems (Berggren et al., 2023; Biddanda et al., 2001; del Giorgio and Cole, 1998). In oligotrophic systems, BGE can be as low as 0.01, while in eutrophic systems, it can reach up to 0.5 (del Giorgio and Cole, 1998). Incubation experiments have shown that BGE increases significantly with higher DIN concentrations (Lønborg et al., 2011). The BGE values in the Eastern China Marginal Seas have rarely been documented, but the elevated DIN concentrations (average: 7.7 μ mol L⁻¹; Fig. S1) suggest the potential for enhanced BGE in this region. Our data revealed a significant positive correlation between DIN and bacterial organic carbon (r = 0.43, p < 0.01), supporting the role of DIN in enhancing bacterial production. Despite the absence of a significant positive correlation between PO₄-P and bacterial POC, we observed a major difference in PO₄-P concentration between the two patterns. Pattern 1 showed high concentrations of both DIN and PO₄-P, while Pattern 2 exhibited high DIN but low PO₄-P levels (Fig. 4). This indicates



that the lower bacterial transformation observed in Pattern 2 was likely limited by PO₄-P, underscoring the crucial role of PO₄-P in regulating bacterial transformation efficiency (Kritzberg et al., 2010). Additionally, the carbon to nitrogen (C/N) ratio of the bioavailable substrate is considered to influence the BGE. When the C/N ratio substrate is higher, the bacterial community requires more energy to assimilate inorganic nutrients, consequently leading to lower BGE (Lønborg et al., 2011; Rivkin and Anderson, 1997). The C/N ratio of the labile POM is approximately 4. Such a low C/N ratio further promotes bacterial assimilation of organic carbon. Overall, the abundant nutrients coupled with the low C/N ratio of substrate in the marginal sea primarily drive the rapid bacterial transformation of labile organic matter.

3.3. Bacterial transformation drives carbon sequestration in marginal seas

The efficient bacterial transformation of labile POM observed in this study suggests that biological hot spots represent important sites for carbon sequestration. Bacterial metabolism can contribute to long-term carbon sequestration by converting labile dissolved organic carbon into refractory organic carbon. This process has been conceptualized as the microbial carbon pump (MCP) and is widely used in investigations of the DOM pool (Jiao et al., 2010). Recent work proposes that analogous carbon sequestration processes associated with heterotrophic transformation could also take place in the POM pool, as indicated by the similar D/L-amino acid distribution patterns in both DOM and POM (Shen et al., 2023). Our recent study assessed the bacterial organic carbon content of POM in the Eastern China Marginal Seas using bacterial biomarkers and bacterial cell counts (Guo et al., 2024). We found that < 1/3 of the POC originated from living bacteria, with the majority $(\sim 2/3)$ of bacterial organic matter existing in the form of bacterial detritus. Similar results were observed in DOM and sinking POM (Kaiser and Benner, 2008; Shen et al., 2023). Importantly, bacterial detritus is more resistant to degradation than intact cells and planktonic organic matter (Lehmann et al., 2020; Nagata et al., 2003). These findings underscore the crucial role of bacterial transformation on particles in carbon sequestration by converting labile phytoplankton carbon into bio-resistant bacterial carbon.

Marginal seas are characterized by high sedimentation rates of organic carbon, thus serving as hot spots for carbon burial. Since a portion of bacterial organic carbon is resistant to degradation, the extent of the bacterial contribution to buried organic carbon has important implications for long-term ocean carbon sequestration. Previous work has shown that the annual sinking flux of POC to the seafloor in marginal seas is 0.52 ± 0.20 Pg (Dunne et al., 2007). In the Eastern China Marginal Seas, the bacterial contribution to bottom water POC averaged 22.14 \pm 6.02 %. Extrapolating this proportion to global marginal seas, the sinking flux of bacterial organic carbon to the seafloor would be approximately 0.12 \pm 0.05 Pg yr $^{-1}$, with at least 0.08 \pm 0.03 Pg yr $^{-1}$ $(\sim 2/3)$ derived from bacterial detritus. This recalcitrant detrital carbon is likely to be buried in the sediments, contributing to 42 \pm 33 % of the total organic carbon burial (0.19 \pm 0.13 Pg) (Dunne et al., 2007) (Fig. 5). However, it is important to acknowledge that such estimates of bacterial organic carbon burial involve several uncertainties. Sediment resuspension is prevalent in marginal seas, and the resuspension of degraded organic carbon potentially underestimates bacterial contribution to bottom POC (Guo et al., 2023a). While bacterial detritus generally exhibits low reactivity, it can still undergo degradation during burial in sediments, possibly leading to an overestimation of bacterial organic carbon burial. Furthermore, the highly dynamic physicochemical environments in global marginal seas, driven by hydrodynamic processes such as current interactions and upwelling, could result in substantial variability in bacterial contributions to POC. These processes significantly influence nutrient availability, organic matter composition, and bacterial community structure (Guo et al., 2024, 2018; Sun et al., 2020), thereby modulating bacterial transformation of organic matter.



Fig. 4. Relationship between bacterial and labile particulate organic carbon (POC) concentrations.



Fig. 5. Conceptual diagram illustrating the bacterial transformation of labile particulate organic matter (POM) and contribution to carbon sequestration in the marginal sea. The data on total organic carbon burial flux in global marginal seas are derived from Dunne et al. (2007). The bacterial POC sinking flux to the seafloor in global marginal seas accounts for 22.14 \pm 6.02 % of the total POC sinking flux to the seafloor (0.52 \pm 0.20 Pg yr⁻¹) (Dunne et al., 2007). This ratio is based on observations of bacterial contributions to bottom POC in the Eastern China Marginal Seas and is assumed to be representative of global marginal seas. The burial flux of bacterial organic carbon within the bottom bacterial POC can be buried in sediments (Guo et al., 2024). The uncertainty calculations are based on error propagation using the first-order Taylor expansion (Taylor, 1997).

To date, studies on the bacterial contribution to POC in marginal seas remain limited. However, existing studies in the St. Lawrence Estuary (Bourgoin and Tremblay, 2010) and the Mandovi Estuary (Khodse and Bhosle, 2013) have reported bacterial contributions of 20 % to 30 %, consistent with our findings. Further data are needed to refine the estimates of bacterial contributions to organic carbon burial in marginal seas.

Reconstruction of the global ocean CO_2 partial pressure suggests that CO_2 uptake in both the open and coastal ocean has been increasing in recent decades, with a more rapid rise in the coastal ocean-atmosphere partial pressure gradient (Laruelle et al., 2018). This enhanced coastal

 CO_2 uptake is thought to be primarily driven by biological carbon fixation (Mathis et al., 2024), although the specific pathways remain unclear. Our findings indicate that the rapid bacterial transformation of phytoplankton-derived labile organic carbon plays a crucial role in this process. In particular, the substantial contribution of bacterial organic carbon to total organic carbon burial highlights the significant role of bacterial transformation in coastal carbon sequestration.

Although the efficiency of bacterial transformation remains unknown, our results underscore that a significant portion of labile POC in the marginal sea undergoes transformation rather than respiration by bacteria. The observed rapid bacterial transformation of labile POM suggests that, against the backdrop of global change, marginal seas are becoming increasingly important in carbon sequestration. Ongoing global warming is leading to intensified water column stratification in the open ocean, reducing the supply of nutrients from subsurface to surface waters, and it is anticipated that primary productivity and carbon export from the euphotic zone will decrease (Behrenfeld et al., 2006; Wang et al., 2023). In contrast, in shallow marginal seas, human-induced eutrophication is increasing, further enhancing bacterial production. Given that these trends are expected to persist and accelerate, the role of marginal seas in oceanic carbon sinks is projected to become increasingly important.

4. Conclusions

This study highlights the significant role of bacterial transformation in enhancing carbon sequestration in marginal seas. By tracking D/Lamino acids, we demonstrated that a substantial portion of labile POC is rapidly converted into bacterial organic carbon, driven by high nutrient availability. A significant fraction of this bacterial carbon forms recalcitrant detritus, which is more resistant to degradation and likely to be buried in sediments.

Our estimate indicates that approximately 0.08 ± 0.03 Pg of bacterial organic carbon is buried annually in global marginal seas, representing ${\sim}40$ % of the total organic carbon burial. These findings provide a potential mechanistic explanation for enhanced coastal CO₂ uptake and emphasize the importance of bacterial processes in global carbon cycling. Given ongoing eutrophication and climate change, marginal seas are expected to play an increasingly critical role in carbon sequestration.

CRediT authorship contribution statement

Jinqiang Guo: Writing – original draft, Investigation, Formal analysis, Conceptualization. Bu Zhou: Writing – review & editing, Methodology, Investigation. Eric P. Achterberg: Writing – review & editing, Resources. Yuan Shen: Writing – review & editing, Formal analysis. Jinming Song: Writing – review & editing, Supervision, Funding acquisition. Liqin Duan: Writing – review & editing, Methodology. Xuegang Li: Writing – review & editing, Methodology. Huamao Yuan: Writing – review & editing, Formal analysis, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2025.123595.

Data availability

Data will be made available on request.

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