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Interaction Between Organic Carbon Conversion and Microbial Metabolism in Marginal Seas Sediments During Hydrodynamic Sorting Processes

Ziyang Yang[1,2], Lei Xing[1], Yangli Che[1,2], Nan Wang[3], Haiyue Ma[1,2], Siqi Zhao[1,2], Anna Chen[3], Haoshuai Li[1,2], and Rui Bao[1,2]

[1]Frontiers Science Center for Deep Ocean Multispheres and Earth System, and Key Laboratory of Marine Chemistry Theory and Technology, Ministry of Education, Ocean University of China, Qingdao, China, [2]Laboratory for Marine Geology, Qingdao Marine Science and Technology Center, Qingdao, China, [3]Frontiers Science Center for Deep Ocean Multispheres and Earth System, Key Lab of Submarine Geosciences and Prospecting Techniques, Ministry of Education and College of Marine Geosciences, Ocean University of China, Qingdao, China

Abstract Hydrodynamic sorting processes control the transport of marine sediments in benthic environments of marginal seas, affecting the distribution of associated microbes and organic carbon (OC) composition in marine sediments. However, microbial characteristics variations and their impacts on OC stability during hydrodynamic sorting processes remain insufficiently understood. Here, we analyzed the concentrations and carbon isotopes of phospholipid fatty acids (PLFAs), and conducted the thermal stability analysis on OC in grain-size fractionated sediments retrieved along the classical transport pathway from the Yellow River delta to the Yellow Sea. We find that the relative abundance of anaerobic bacterial PLFAs has positive correlations with the proportion of pre-aged OC and negative correlations with the proportion of refractory OC compounds, and bioavailable OC become more limited along the transport pathway. We suggest that the decreasing refractory OC and the increasing pre-aged OC may facilitate the increasing abundance of anaerobic bacteria, and the metabolism of microbes can utilize the refractory OC during resuspension of marine sediments. The metabolism of microbes attached to resuspension sediments may produce by-products including pre-aged OC, which may promote the pre-aged OC burial in benthic environments, with important environmental implications such as carbon sequestration in marginal seas sediments.

Plain Language Summary Organic carbon (OC) burial in marginal seas sediments is regulated by microbial degradation and metabolism. Hydrodynamic processes play a crucial role in driving the transmission of harboring diverse microbes and changing the microbial metabolism, which may impact the burial of OC in marginal seas sediments. In this study, we utilized the phospholipid fatty acids (PLFAs), a specific biomarker, to investigate the abundance and metabolic variations of living microbes. Additionally, we examined the relationship between variations of microbial activity and OC components. Our results suggest that microbes may utilize recalcitrant OC compounds, promoting the burial of unbioavailable OC in marginal seas sediments.

Key Points:

- The abundance of anaerobic bacteria attached on resuspended sediments increases along the transport pathway
- The transition from refractory OC to pre-aged OC is accompanied by and contributes to the increase of anaerobic microbial abundance
- Microbial carbon utilization may enhance the preservation of pre-aged OC in marginal seas sediments

Supporting Information:

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

Correspondence to:

R. Bao,
baorui@ouc.edu.cn

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Author Contributions:

Conceptualization: Ziyang Yang, Yangli Che, Rui Bao
Data curation: Ziyang Yang, Nan Wang, Anna Chen
Formal analysis: Rui Bao
Investigation: Haiyue Ma
Methodology: Ziyang Yang, Yangli Che, Nan Wang, Haiyue Ma, Anna Chen, Rui Bao
Project administration: Rui Bao
Resources: Rui Bao
Visualization: Ziyang Yang, Yangli Che, Siqi Zhao, Rui Bao
Writing – original draft: Ziyang Yang
Writing – review & editing: Ziyang Yang, Lei Xing, Yangli Che, Siqi Zhao, Haoshuai Li, Rui Bao

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1. Introduction

Marginal seas, despite occupying a small portion of the surface area in the ocean, play a significant role in carbon storage of natural environments. It is responsible for burying 90% of organic carbon (OC) in the ocean, making it one of the largest carbon reservoirs on global ecological environments (Ausín et al., 2021; Hedges & Keil, 1995; Yu et al., 2021). The burial and degradation of OC in marginal sediments regulate CO_2 release from marine environments and have an impact on atmospheric CO_2 level (Galy et al., 2008; Hilton & West, 2020; Horan et al., 2019). The dynamic and heterogeneous nature of marine sediments determined by hydrodynamic sorting processes can influence the mechanisms governing degradation and protection of OC, thus affecting the total amount of OC buried in marginal marine sediments (Bao et al., 2016, 2018b; Bianchi et al., 2018). Ausín et al. (2021) demonstrated the significant influence of hydrodynamic sorting processes on the content and composition of OC in a series of continental marginal environments, such as Peruvian margin, Namibian margin, and Northwest African margin. Thus, understanding the mechanisms of OC degradation and protection in benthic environments of marine sediments, and obtaining the information of the fate of buried OC in marine sediments during hydrodynamic sorting is meaningful for assessing and predicting the future reginal CO_2 budget and climate change on a global scale. We need to elucidate the mechanisms that how hydrodynamic sorting processes

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influence the characteristics and preservation of OC in marginal seas sediments, which can get a more accurate assessment of the impact of hydrodynamic sorting processes on aquatic carbon cycle.

The hydrodynamic sorting processes of marine sediments through resuspension and deposition affect the degradation, mineral protection mechanism, and characteristics of OC, and ultimately impacts the burial of OC in marginal marine sediments (Bao et al., 2016; Bröder et al., 2018; Inthorn et al., 2006; Tesi et al., 2016). These impacts of resuspension also differ for marine sediments with varying grain sizes (Amalfitano et al., 2017). It has been observed that the resuspension can change the microbial communities and make different microbial communities' colonization on marine sediments (Che et al., 2024; Kleeberg et al., 2013). The resuspended sediments can serve as "growth sites" for suspended microbes in water, facilitating close interactions between different functional microbial communities (Lyons et al., 2010; Simon et al., 2002; Wotton, 2007). Investigations on microbial composition and metabolism in different grain-size sediments are thus essential for further elucidating the degradation and protection mechanism of OC in resuspended marine sediments and estimating amount of CO_2 release from marine environments during hydrodynamic sorting processes. These investigations will thus provide a potential mechanism for explaining the important role of microbes in the alterations of OC preservation in marginal seas sediments.

The information of microbial composition and metabolism can be deciphered through biomarkers. Phospholipid fatty acids (PLFAs) are important components of cell membranes of almost all microbes and molecular markers of microbes in sedimentary environments (Frostegård et al., 2011; Pond et al., 2014; Whaley-Martin et al., 2016). The PLFAs in the cell membrane are linked to a glycerol molecule through an ester bond, forming a phospholipid molecule with a phosphate group. These molecules further assemble into a phospholipid bilayer of cell membranes (Willers et al., 2015). The PLFAs degrade rapidly after cell death, and the structures of PLFAs differ among different microbial communities, and can indicate specific microbial communities (Hill et al., 2000). These characteristics make it act as a specific biomarker that can be used to quantify the in situ living microbial biomass and characterize their community structures (Dippold & Kuzyakov, 2016; Frostegård et al., 2011; Zhang, Naafs, et al., 2022). Furthermore, stable carbon isotope characteristics of compound-specific PLFAs (δ^{13}C-PLFAs) have been used to distinguish the different utilization and assimilation pathways of carbon sources by microbes to provide information for understanding the microbially mediated carbon cycle (Evershed et al., 2006; Zhang et al., 2004). The values of δ^{13}C-PLFAs are mainly related to the substrates in natural environments and the kinetic isotope fractionation of the microbial assimilation of OC such as heterotrophic and autotrophic pathways (Hayes, 1993, 2001; Pancost & Sinninghe Damsté, 2003). The variation of abundance, composition, and metabolism of microbes can be reflected by PLFAs concentration, species composition, and compound-specific isotope values. Therefore, we can use the information of PLFAs in different grain-size sediments to get the insights into the microbial composition and metabolism variation during hydrodynamic sorting processes.

In contrast to the previous studies, our study emphasizes the dynamic variations of microbial composition during hydrodynamic sorting processes, and elucidates the differences in microbial metabolic utilizations of carbon source substrates via biomarkers and compound-specific carbon isotopes along the sediments transport pathway. While Bao et al. (2016) investigated the changes in the content, δ^{13}C and Δ^{14}C signatures of OC in different grain-size sediments during hydrodynamic sorting processes, this study primarily focused on the composition and source characteristics of OC, overlooking the significant roles in OC characteristics played by microbes. A few laboratory simulation experiments studied the changes of microbial composition and organic geochemical parameters under different shear forces (Che et al., 2024). However, this study only aims to highlight the behavioral characteristics of microbes under varying hydrodynamic conditions, with a focus on the changes in microbial behavior. Previous studies explored microbial composition and organic geochemical parameters separately but lacked of the research on their interaction; we need to integrate microbial and geochemical parameters closely and address gaps in previous studies.

In natural benthic environments, the degradation of OC is influenced by factors such as microbial characteristics, and is determined by chemical characteristics of OC. Meanwhile, microbial metabolism can alter the chemical properties of OC (Burdige, 2007; Hemingway et al., 2018; Pedler et al., 2014; Schmidt et al., 2011). For example, the microbial metabolism may affect the intrinsic thermal stability of OC (Leifeld & von Lützow, 2014). Therefore, changes in microbial metabolism can impact the molecular structure that governs the OC activation energy (E). The E value is a parameter of the strength of carbon bonds and can serve as an indicator for the thermal stability of OC compositions. Variations in the stability of OC compositions in marine sediments can be studied

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by analyzing the activation energy information (Huang et al., 2023). We can use the *E* value information to investigate the different compositions of OC along the sediments transport pathway and to investigate the relationship between microbial metabolism and the stability of OC compositions, which may be crucial for understanding the microbial influence on OC compositions and burial processes during hydrodynamic sorting processes.

In this study, we collected different grain-size sediments along the classical transport pathway of Shandong Coastal Current (SCC), which is located in the continental margins area controlled by Yellow River and forms strong hydrodynamic sorting processes along the current pathway (Zheng et al., 2021). This facilitates our comprehension of lateral transport and burial mechanisms of OC. Additionally, we assessed the content and stable carbon isotopes of OC and examined the compositions of PLFAs and their compound-specific carbon isotopes to investigate the variations of microbial compositions and metabolism in different grain-size sediments along the sediments transport pathway. These measurements were integrated with activation energy information obtained from ramped pyrolysis/oxidation analysis (RPO) to examine the relationship between the variation of microbial activity and activation energy information, aiming to assess variation of the microbial community induced by the variation of OC compositions and explore the effects of microbial processes on OC burial during hydrodynamic sorting processes in marginal seas sediments.

2. Materials and Methods

2.1. Study Site

In the north of Shandong Peninsula, the Yellow River generates strong hydrodynamic processes that drive the formation of the SCC, promoting the resuspension, lateral transport, and deposition of fluvial sediments. And sediments are carried eastward parallel from the Yellow River estuary to Bohai Sea (Qiao et al., 2017; Yu et al., 2021). A significant fraction of marine sediments in the northern coastal area of Shandong Peninsula is mainly composed of fluvial sediments derived from Yellow River (Bian et al., 2013; Yang & Liu, 2007). The Yellow River, originating on the Qinghai-Tibetan Plateau, traverses the Chinese Loess Plateau in northwestern China before flowing eastward to the Bohai Sea. It carries particulate organic carbon derived from highly erodible loess deposits on the Chinese Loess Plateau (Zhang et al., 2013). In view of these characteristics, we selected three sites strategically positioned at the upstream, midstream, and downstream regions of the classic coastal flow route of the northern Shandong Peninsula, along with the pathway of resuspension, lateral transport, and deposition of fluvial sediments. In addition, this classical transport pathway provides us with natural environments to study the interaction between microbial activity and geochemical parameters during hydrodynamic sorting processes.

2.2. Sample Collection and Preparation

Surface sediments (0–2 cm) were collected from three locations using a box core sampler at the Yellow River estuary and along the pathway of the Shandong Coastal Current during April 2022 (Figure 1). The information of stations and sediments are shown in Table S1 in Supporting Information S1. Samples were collected onboard of *R/V* "Lanhai 101." These stations were chosen to be consistent with the classical hydrodynamic transport pathway. In this region, the distribution of sediments is strongly influenced by hydrodynamic sorting processes, resulting in extensive and intense sediment resuspension, and sediments are transported from the Yellow River estuary to the northeast of Shandong Peninsula along the hydrodynamic transport pathway (Liu et al., 2020). A portion of each sample was subjected to wet sieving using Milli-Q water and passed through a series of stainless steels sieves into three grain-size fractions: >63 μm, 20–63 μm, and <20 μm (Bao et al., 2016). The critical values of 20 and 63 were chosen because the 20–63 μm grain-size fraction can be resuspended at lower shear forces (Bao et al., 2016). Once 20–63 μm grain-size fraction sediments were resuspended, this fraction part may be transported over much greater distances than other fractions, and these three grain-size fractions exhibit different geochemical values during the hydrodynamic sorting processes. The different grain-size fractions were freeze-dried for 48 hr and subsequently ground into a homogeneous powder.

2.3. Analysis of Content, Carbon Isotope, and Activation Energy Information of OC Associated With Grain-Size Fractionated Sediments

Approximately 7–8 mg of each sample fraction was weighed, and inorganic carbon was removed by fumigation with concentrated HCl (37%, 72 hr) and drying over NaOH pellets (72 hr) in a desiccator at 60°C

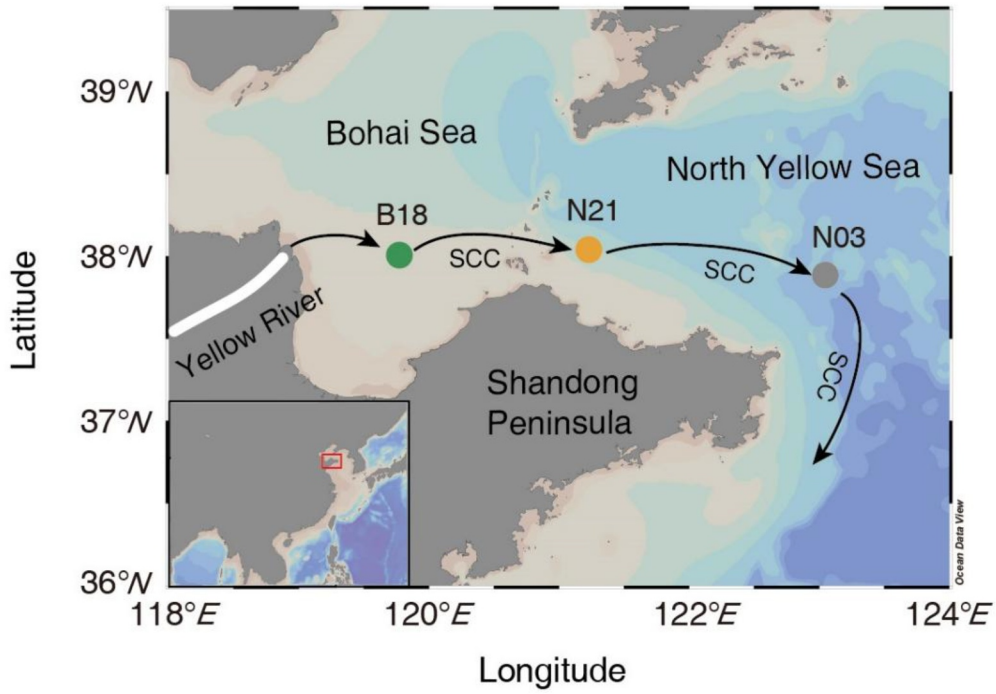

Figure 1. Sampling locations along Shandong Coastal Current (SCC) and the hydrodynamic transport pathway in the Bohai Sea and northern Yellow Sea. Green color corresponds to B18, orange color corresponds to N21, and gray color corresponds to N03.

(Bao, McNichol, et al., 2018). Then, the OC content and OC isotope values, δ^{13}C-OC were analyzed using an EA IsoLink elemental analyzer interfaced with an MAT253 plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Germany). The international reference materials (RMs) were USGS40 (L-glutamic), USGS64 (glycine), and USGS65 (glycine) (all from NIST, US). The δ^{13}C values certified by USGS40, USGS64, and USGS65 as the mean ±95% confidence are −26.39 ± 0.09‰, −40.81 ± 0.04‰, and −20.29 ± 0.04‰, respectively. The detection limit is 0.01% for 10-mg sediment. The accuracy of methods for the determination of carbon content in samples can be estimated to be around 3% RSD. The precision for δ^{13}C is ±0.06‰ (1σ) for 30 μg of carbon (Wang et al., 2021).

Different *E* regions can reflect the different compositions of OC. The *E* information was obtained through RPO analysis. Each sample was treated with 10% HCl (HCl: Milli-Q water = 1: 9, v: v) and then placed in a 60°C water bath (1 hr). Then, HCl that used to remove inorganic carbon was rinsed with Milli-Q water. The samples were filtered onto a GF/F filter (0.7 μm) and freeze-dried. RPO analysis was completed through an OEC approach introduced by Wu et al. (2023). We used standard sucrose solution as external standard to ensure the measurement accuracy. The concentration of the sucrose standard solution prepared is 3.64 μg/μL in this experiment. The accuracy of methods for the determination of carbon content in samples can be estimated to be around 5% RSD. The *E* information was calculated applying the inverse regularization approach performed in the Python programming language v. 3. 6 using the open-source "rampedpyrox" package to further analysis the composition of OC (Hemingway et al., 2018; Wu et al., 2023). We choose the Arrhenius preexponential factor, $\omega = 10^{10}$ s^{-1} for all samples, and determine the *E* distribution, which leads to the thermal profiles, expressed by p (0, *E*) (Hemingway et al., 2018; Wu et al., 2023). The variation of characteristics of chemical bond pyrolysis stability of OC can be reflected by changes in the *E* values of OC in sediments along the hydrodynamic transport pathway (Figures 3 and 4a–4c). The *E* values of 150 kJ/mol and 210 kJ/mol are utilized to distinguish different chemical bond pyrolysis stabilities of OC: modern biospheric OC (low *E*: $E < 150$ kJ/mol, the OC fraction containing low bond energy), pre-aged OC (mid-*E*: 150 kJ/mol $< E <$ 210 kJ/mol, the OC fraction containing medium bond energy), and refractory OC (high *E*: $E > 210$ kJ/mol, the OC fraction containing high bond energy) (Figure 3)

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(Hage et al., 2020; Hemingway et al., 2018; Zhang, Galy, et al., 2022). Our study employs distinct E regions to discern the thermal stability of OC in sediments. The integral proportions, $f_{\text{biospheric OC}}$, $f_{\text{pre-aged OC}}$, and $f_{\text{refractory OC}}$ are calculated to quantify the proportions of different chemical bond pyrolysis stabilities and investigate their variations along hydrodynamic transport pathway.

2.4. PLFAs Extractions and Compound-Specific Carbon Isotope Analysis

Lipid extraction followed the modified Bligh and Dyer method (Bligh & Dyer, 1959; Nielsen & Petersen, 2000; Papadopoulou et al., 2011; White et al., 1979; Wu et al., 2009). Briefly, 8 g of freeze-dried sediments were ultrasonically extracted with dichloromethane, methanol, and phosphate buffer (1: 2: 0.8, v: v: v) for 2 hr. Collect the supernatant into a glass bottle, and then add additional dichloromethane and ultrapure water to adjust the ratio of the solvent to 1: 1: 0.9. The suspension was mixed for 2 hr using a shaker and allowed to separate. Then, the lower organic phase (dichloromethane) was collected, and dried under nitrogen flow to obtain the total lipids extract. TLE was fractionated into neutral lipids, glycolipids, and phospholipids through silicic acid column chromatography, using dichloromethane, acetone, and methanol as the respective eluents. The phospholipids were methylated into fatty acid methyl esters (FAMEs) by methanol-toluene (1: 1, v: v) and alkaline methanol solution heated in 37°C water for 20 min. An internal standard of C19 fatty acid was added for quantification. FAMEs were analyzed by gas chromatography-time-of-flight mass spectrometry using an Agilent 8890 gas chromatograph coupled to an Agilent 7250 Q-TOF mass spectrometer equipped with an Agilent DB-5 column (60 × 0.25-mm internal diameter and 0.25-μm film thickness). The GC oven temperature was programmed as follows: the initial temperature at 60°C (3-min hold), increased to 160°C at 10°C/min (10-min hold), then increased to 180°C at 5°C/min (6-min hold), then increased to 200°C at 5°C/min (6-min hold), then increased to 200°C at 5°C/min (6-min hold), then increased to 240°C at 5°C/min (6-min hold), and then increased to 280°C at 10°C/min (20-min hold). Compounds were quantified by comparison with peak areas of the internal standard (C19 fatty acid). Identification was based on 37 FAMEs standard mixture and NIST 17 library searching and some characteristic ion peaks. Quality correction is conducted prior to sample injection to instruments, ensuring mass error being less than 2 ppm. Instrument detection limit is 250 fg. We use octafluoronaphthalene (instrument correction standard) for instrument correction. The accuracy of 1-pg octafluoronaphthalene for the analysis of PLFAs content in samples can be estimated to be less than 8% RSD. Different PLFAs species are assigned and classified into specific microbial species (Table S2 in Supporting Information S1).

PLFAs contents were lower, multiple sediments enrichment extractions were required to test the information of compound-specific carbon isotope, the δ^{13}C-PLFAs values. The PLFAs extracts were enriched from extraction procedures, which were repeated three to four times, and then, δ^{13}C values of PLFAs were measured with GC-C-IRMS (Zhang, Naafs, et al., 2022), a TRACE GC IsoLink II gas chromatograph instrument coupled to an MAT253 plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Germany) equipped with an Agilent DB–5 column (60 × 0.25 mm internal diameter, 0.25 μm film thickness). The GC oven temperature was the same as above. Instrument reliability and stability were verified before and after each sample run using a n-alkanes standard mixture with known δ^{13}C values. To correct for additional methyl carbon introduced during the transesterification, we used the following mass balance equation:

$$\delta^{13}C_{\text{PLFAs}} = \left[(n+1) \times \delta^{13}C_{\text{FAME}} - \delta^{13}C_{\text{methanol}}\right]/n \quad (1)$$

where $\delta^{13}C_{\text{PLFAs}}$ is the δ^{13}C value of the fatty acids, n is the carbon number of the fatty acid, $\delta^{13}C_{\text{FAME}}$ is the measured δ^{13}C value of the fatty acid methyl esters, and $\delta^{13}C_{\text{methanol}}$ is the known δ^{13}C value of the methanol used for the transesterification.

Based on previous studies, common PLFAs are grouped into gram-negative bacteria, gram-positive bacteria, aerobic bacteria, anaerobic bacteria, pseudomonas, and so on. Common PLFAs and their designations are shown in Table S2 in Supporting Information S1 (Bossio & Scow, 1998; Vestal & White, 1989; Zhang et al., 2021). We use multiple regression analysis (stepwise multiple regression analyses) to explore the interaction between microbes and environmental factors, and determine the significant factors influencing various microbial species and various geochemical parameters.

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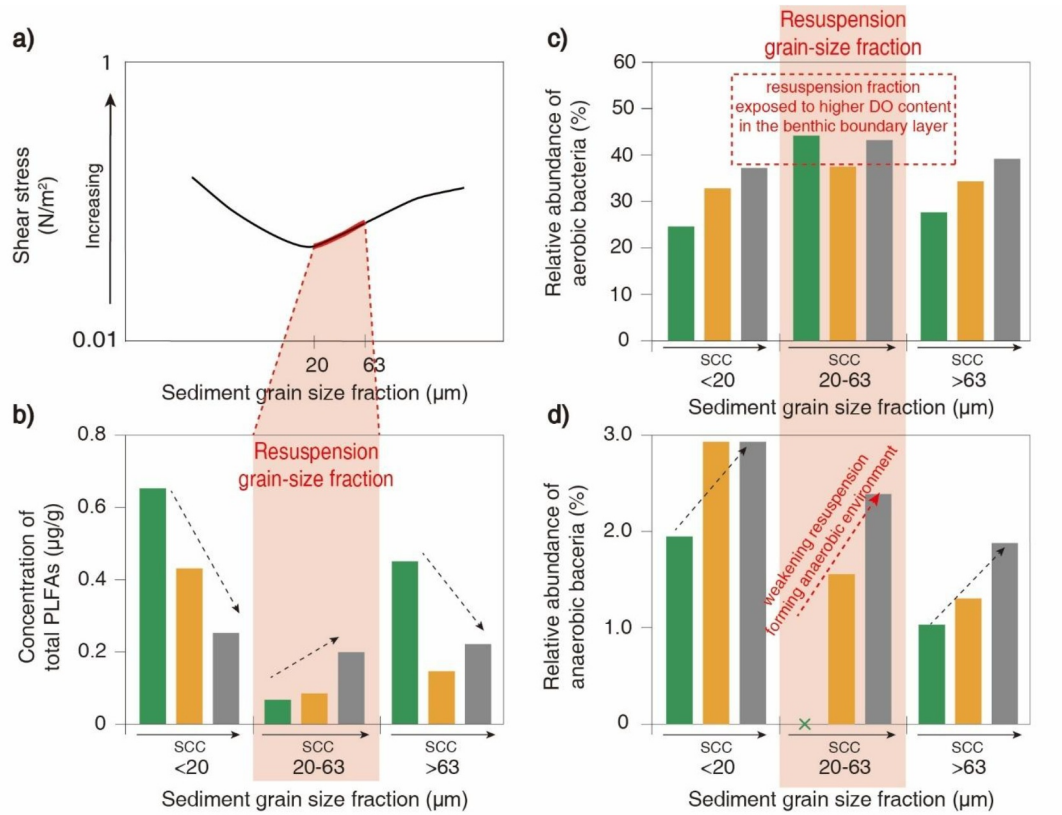

Figure 2. (a) The idealized behavior of bed shear stress as a function of grain size, and the grain sizes range of sediments that is resuspended at critical shear stresses (modified from Bao et al., 2016). (b) Variation of total PLFAs concertation in different grain-size sediments along the Shandong Coastal Current pathway. (c) Variation of relative abundance of aerobic bacteria in total microbial biomass in different grain sizes. (d) Variation of relative abundance of anaerobic bacteria in total microbial biomass in different grain sizes. The resuspension grain-size fraction (red bar) represents 20–63 μm fraction that are susceptible to suspension.

3. Results and Discussion

3.1. Selective Adsorption of Microbes During Hydrodynamic Sorting Processes of Sediments

Our study examines the species and concentrations of PLFAs to explore the variations of microbial biomass and compositions in the surface marine sediments along the hydrodynamic transport pathway from B18 to N03. We find obvious variations in microbial PLFAs among different grain-size fractions of the marine sediments (Figure 2; Tables S1, S3, and S4 in Supporting Information S1). In the red bar (corresponding to 20–63 μm grain-sizes sediments) of Figure 2, the total PLFAs contents, the relative abundance of aerobic and anaerobic bacteria exhibited markedly distinct trends. These differences may be due to the effects of the hydrodynamic sorting processes on different grain-size fractions of sediments (Che et al., 2024; Chen et al., 2022; Xu et al., 2021). Different grain-size fractions of sediments also exhibit distinct responses to the hydrodynamic sorting processes. Resuspension, one of the hydrodynamic processes, occurs when a critical shear velocity is reached, causing marine sediments erosion and transport (Che et al., 2024; Luo et al., 2022). The 20–63 μm fraction is particularly prone to resuspension under low shear velocities, exhibiting distinct PLFAs variations compared with other grain-size sediments (the resuspension grain-size fraction (red bar) in Figure 2). Different species of PLFAs can indicate different microbial community structures (Table S2 in Supporting Information S1), for example, monounsaturated PLFAs (16:1ω7, 18:1ω7 and 18:1ω9) correspond to the aerobic bacterial community, while cyclopropyl PLFAs (cy17:0) correspond to the anaerobic bacterial community (Vestal & White, 1989; Zhang et al., 2021). Polyunsaturated PLFAs (16: 3, 18: 3, and 20: 5) correspond to algae (Jonasdottir, 2019; Lammers et al., 2017). Although marine algae can synthesize these fatty acids, they may degrade during the algae's decay upon settling. Algal PLFAs

16: 3, 18: 3, and 20: 5 may have undergone significant degradation when settling into marine sediments in marine sediments, rendering their contribution negligible. In Table S2 in Supporting Information S1, although microbial communities identified by PLFAs exhibit partial overlap and PLFAs offer limited specificity for distinguishing certain microbial communities, the listed PLFAs are still predominantly and characteristically associated with the corresponding microbial species (Willers et al., 2015). The PLFAs remain effective in indicating variations in the abundance and metabolic activities of most bacterial species. Our study finds that the average relative abundance of PLFAs associated with aerobic bacteria is the highest in the 20–63 μm fraction, 37.46%–44.08% (the values in the resuspension grain-size fraction of Figure 2c), suggesting a preference of aerobic bacteria for specific grain-size sediments, which is susceptible to resuspension that may provide aerobic environmental conditions conducive to aerobic bacterial settlement and reproduction. Marine sediments undergoing prolonged resuspension are likely exposed to environments with higher dissolved oxygen content in the benthic boundary layer (BBL) containing the overlying water, likely stimulating the adsorption of free aerobic bacteria onto resuspended sediments (Bianucci et al., 2018; Che et al., 2024). The exchange of oxygen between water and sediments often occurs through the BBL, increasing the dissolved oxygen content in the boundary layer from sediments to water (Jørgensen et al., 2022), promoting the adsorption of aerobic bacteria onto the 20–63 μm fraction during the resuspension process. Our findings suggest the sediments undergoing frequent resuspension will selectively adsorb more of the free microbes in the water, depending on various environmental conditions and dissolved oxygen contents, such as aerobic bacteria in this study. Subsequently, it is necessary to investigate the alterations in other microbial species and metabolism under diverse environments factors.

The microbial composition and adsorption in the sediments are also influenced by environmental conditions induced by hydrodynamic processes (Che et al., 2024; Risse-Buhl et al., 2017). When sediments are resuspended, the sediments are carried along the Shandong Coastal Current, potentially with decreasing resuspension intensity (Wang et al., 2011; Yang et al., 2011). In this study, sampling stations from B18 to N03 are strategically located along this transport pathway. The decrease in turbidity values (from approximately 21 mg/L at B18 to 8 mg/L at N21) indicates a gradual reduction in resuspension intensity along the transport routes (Liu et al., 2020; Martin et al., 1993), consistent with the decrease in resuspension shear stress (Wang et al., 2016; Yang & Liu, 2007). The reduction in resuspension intensity of marine sediments leads to a decreased interaction between sediments and dissolved oxygen in the overlying water, resulting in a gradual transition toward anaerobic conditions, which promotes the selective adsorption of anaerobic bacteria. Indeed, our findings show that the relative abundance of anaerobic bacteria increases in marine sediments along the transport routes from B18 to N03 (Figure 2d). Particularly, in the 20–63-μm fraction, the relative abundance of anaerobic bacteria increases from being undetectable at B18 to 2.39% at N03 (the values in the resuspension grain-size fraction (red bar) of Figure 2d; Table S3 in Supporting Information S1). This result shows a more significant increase compared to other grain-size fractions, where the relative abundance increases from 1.97% to 2.95% in the <20 μm fraction, and from 1.03% to 1.88% in the >63 μm fraction (Figure 2d; Table S3 in Supporting Information S1). Due to the weakening of the resuspension intensity, the sediments in the resuspension grain-size fraction (red bar) of Figure 2 exhibited a reduced state of disturbance of resuspension, resulting in a shift in microbial characteristics, transitioning from dynamic conditions to stable conditions dominated by anaerobic bacteria. These results suggest that the transition toward anaerobic conditions promotes the adsorption of anaerobic bacteria. The decrease in resuspension intensity, leading to the formation of anaerobic environments, enhances the adsorption of anaerobic bacteria on the marine sediments. We need to further explore the variations of total microbial biomass and its correlations with the environments along the hydrodynamic transport pathway.

The concentrations of total PLFAs, which represent total microbial biomass (Frostegrd & Bth, 1996; Halász et al., 2022), increase in the 20–63 μm fraction along the hydrodynamic transport pathway from B18 to N03 (the values in the resuspension grain-size fraction of Figure 2b). This increase suggests that the total biomass of microbes adhering to the 20–63 μm fraction of marine sediments increases during the hydrodynamic sorting processes. The observed increase corresponds with the rise in OC content from 0.12% to 0.20% in the 20–63 μm fraction (Table S1 in Supporting Information S1). The enhanced supply of OC in the sortable silt fraction may facilitate the selective adsorption and colonization of microbes during the hydrodynamic sorting processes. And as the sediments are transported further downstream, the sediments undergoing resuspension and deposition may also adsorb more microbes, leading to an increase in microbial abundance during hydrodynamic sorting processes. Through the PLFAs analysis, we can gain insights into the changes in abundance characteristics of microbes across different grain-sizes sediments during hydrodynamic sorting processes. In addition, we need to

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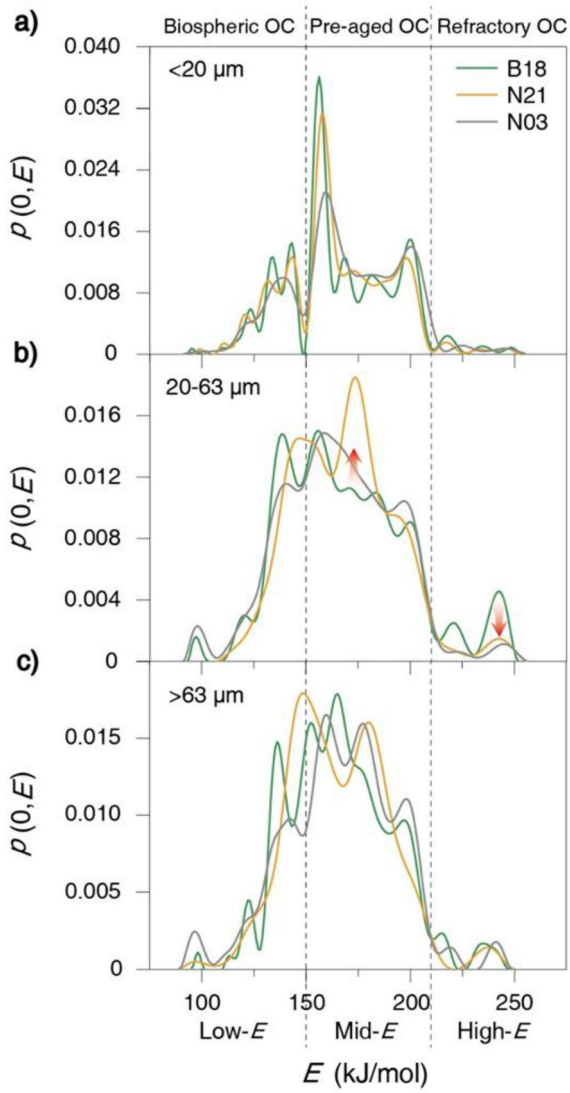

Figure 3. Activation energy (E) distribution of different grain-size sediments along Shandong Coastal Current stations, (a) <20 μm, (b) 20–63 μm, and (c) >63 μm. The OC in Yellow River estuary sediments is divided into three regions using dashed lines, with intervals E value of 150 kJ/mol and 210 kJ/mol. The percentages of biospheric OC from marine primary production (low-E, E < 150 kJ/mol), and pre-aged OC from aged terrestrial soil (mid-E, 150 < E < 210 kJ/mol) and refractory OC from eroded rocks (high-E, E > 210 kJ/mol) fractions are determined by calculating the integral area of every E region in the Yellow River estuary and marginal seas sediments.

investigate the variations in OC composition characteristics across different grain-sizes sediments, thereby elucidating the relationship between shifts in microbial properties and OC composition, as well as the influence of microbial activity on OC burial.

3.2. The Correlation Between the Relative Abundance of Different Microbial Communities and Environmental Factors

The adsorption behavior of microbes on marine sediments can induce alterations in the metabolic reactions, such as OC remineralization, further causing the variation of OC characteristics, including composition and chemical bond pyrolysis stability (Ahmerkamp et al., 2020; Kleber et al., 2021). The average $f_{\text{refractory OC}}$ of three grain-size sediments decreases along the transport pathway, while the average $f_{\text{pre-aged OC}}$ increases, most notably in the 20–63 μm fraction (Figures 3b, 4b, and 4c), which is susceptible to sediment resuspension. These results show that the proportion of refractory OC gradually decreases, while the proportion of pre-aged OC increases during sediments sorting and resuspension in benthic environments.

The variation trends of different proportions of OC with various chemical bond pyrolysis stabilities may be attributed to their OC sources and reaction mechanisms during hydrodynamic sorting processes. The increasing proportion of $f_{\text{pre-aged OC}}$ could originate from diverse sources, including OC within terrestrial and marine characteristics. The settling particulate matter mainly originates from marine primary productivity of algal contribution, and the δ^{13}C-OC values are characterized by marine OC (from −21.9‰ to −18.6‰, −20.3‰ is chosen as the marine end-member, $\delta^{13}C_{\text{marine}}$, in this study) (Lin et al., 2023; Liu et al., 2015). We estimate the relative proportion of terrestrial and marine OC in the sediments with the end-member mixing model that previous studies used (Liu et al., 2015; Shultz & Calder, 1976). Based on the δ^{13}C value of C3 plants that predominantly occur in the northern China, the value of −27.0‰ is chosen as the terrestrial end-member, $\delta^{13}C_{\text{terrestrial}}$ (Guo et al., 2006). The relative contribution of the terrestrial-derived OC ($f_{\text{terrestrial OC}}$) and algal-derived OC ($f_{\text{algal OC}}$) are calculated as follows:

$$f_{\text{terrestrial OC}}\,(\%) = \frac{\delta^{13}C_{\text{marine}} - \delta^{13}C_{\text{sediment}}}{\delta^{13}C_{\text{marine}} - \delta^{13}C_{\text{terrestrial}}} \times 100 \quad (2)$$

$$f_{\text{algal OC}}\,(\%) = 1 - f_{\text{terrestrial OC}} \quad (3)$$

The highest proportion of algal contribution is observed in <20 μm fraction sediments (57.96%–64.70%), indicating that a significant portion of marine-derived OC is predominantly concentrated in the fine grain-size fraction. Based on previous Δ^{14}C data analysis, it appears that OC produced from marine primary production may predominantly consist of biospheric OC (Zhang, Galy, et al., 2022). The average contribution of algal OC diminishes along the hydrodynamic transport pathway (average $f_{\text{algal OC}}$ decreases from 55.13% to 43.66%, Figure 4h), suggesting a reduced significance of algal OC in the overall OC composition.

Meanwhile, the δ^{13}C-OC values show a negative variation trend (Figure 4e; Table S1 in Supporting Information S1), indicating that the OC characteristic is gradually transformed into terrigenous characteristics, and the proportion of OC with marine characteristics decreases. However, algal OC is primarily generated in the euphotic zone of aquatic environments (Polimene et al., 2016). During the process of sedimentation, the algal OC, which is composed of biospheric OC, undergoes degradation and utilization by aquatic microbes. The bioavailable biospheric OC may be converted into pre-aged OC components following degradation and utilization, which may

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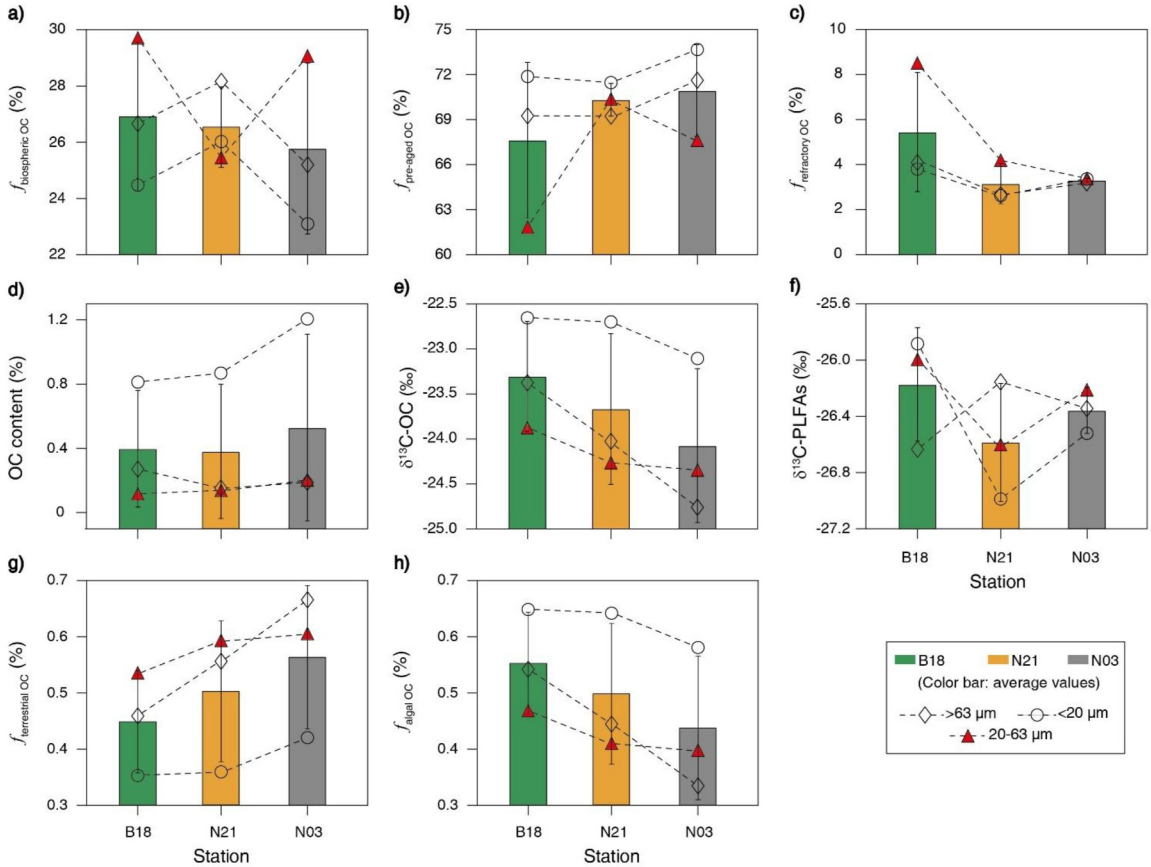

Figure 4. Variations in panel (a) $f_{\text{biospheric OC}}$, (b) $f_{\text{pre-aged OC}}$, (c) $f_{\text{refractory OC}}$, (d) OC content, (e) δ^{13}C values of OC, (f) weighted average δ^{13}C values of PLFAs, (g) the proportion of terrestrial OC ($f_{\text{terrestrial OC}}$), and (h) the proportion of algal OC ($f_{\text{algal OC}}$) in different grain-size sediments along the Shandong Coastal Current pathway.

also result in the increasing proportion of pre-aged OC in sediments. Therefore, a minor portion of the metabolized algal OC may also consist of pre-aged OC composition.

In the marine sediments of the Yellow River estuary, refractory OC is primarily derived from the erosion of terrigenous rock (Zhang, Galy, et al., 2022). The refractory OC and pre-aged OC exhibit opposite trends, with the $f_{\text{pre-aged OC}}$ showing an increase while the $f_{\text{refractory OC}}$ expresses a decrease. Therefore, the observed increase in pre-aged OC is likely predominantly attributed to the OC with terrigenous characteristics. We speculate that the increasing proportions of $f_{\text{pre-aged OC}}$ may also come from the by-products generated by microbes through utilization of refractory OC containing terrigenous material.

Our study investigates the relationship between various environmental factors (including OC content, δ^{13}C-OC, C/N, $f_{\text{algal OC}}$, and so on) and the relative abundance of different microbial communities (indicated by different species of PLFAs) to explore the metabolic contribution of microbes to the alterations of OC composition, and microbial response to environmental factor alterations. We find a significant negative correlation between the relative abundance of aerobic bacteria and both δ^{13}C-OC and $f_{\text{algal OC}}$, indicating that aerobic bacteria may be influenced by the sources of OC. Along the sediments transport pathway, the relative abundance of aerobic bacteria increases while the contribution of algal OC concurrently diminishes, which suggests that the degradation and utilization of algae OC may facilitate the proliferation of aerobic bacteria. Aerobic bacteria may preferentially degrade algal OC (Ding & Sun, 2005; Wetz et al., 2008), with algal OC serving as the preferred electron donor for aerobic bacteria in redox reactions. There are significant correlations between the relative abundance of *Desulfovibrio* and the OC content, δ^{13}C-OC, as well as $f_{\text{terrestrial OC}}$ and $f_{\text{algal OC}}$, which suggests that variations in OC content and sources influence the relative abundance of *Desulfovibrio*. In contrast to aerobic bacteria, *Desulfovibrio* may exhibit a preferential degradation of terrestrial OC. Most significantly, we mainly find a positive relationship between anaerobic bacteria and $f_{\text{pre-aged}}$ OC, and a negative relationship between

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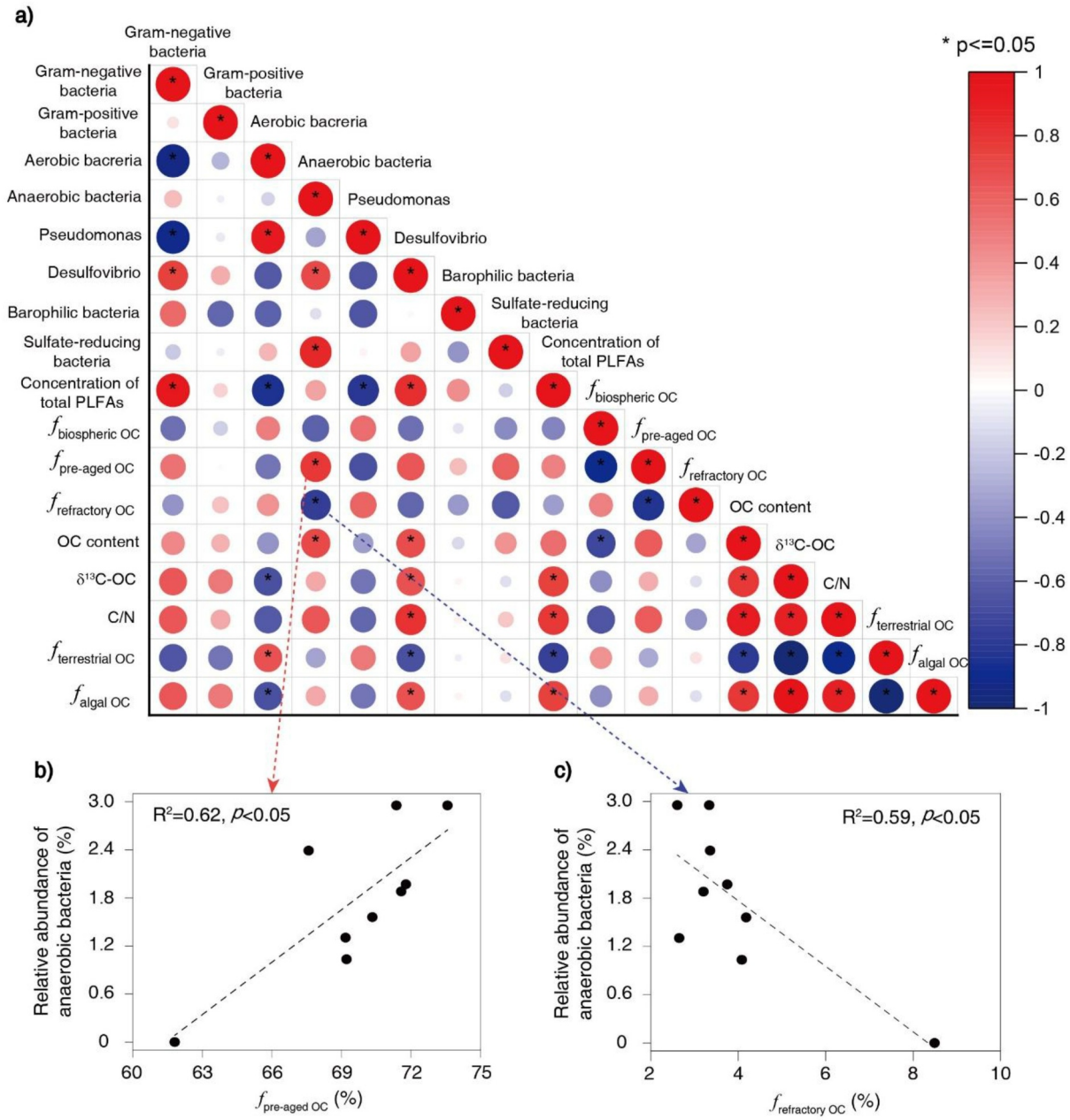

Figure 5. (a) The heatmap of correlation between percentages of different activation energies ($f_{biospheric\ OC}$, $f_{pre\text{-}aged\ OC}$, and $f_{refractory\ OC}$) and the relative abundance of different microbial communities (total microbial biomass described as total PLFAs, the relative abundance of aerobic bacteria, the relative abundance of anaerobic bacteria, and so on). (b) Shows the linear relationships between $f_{pre\text{-}aged\ OC}$ and the relative abundance of anaerobic bacterial PLFAs in total microbial biomass, and (c) shows the linear relationships between $f_{refractory\ OC}$ and the relative abundance of anaerobic bacterial PLFAs in total microbial biomass.

anaerobic bacteria and $f_{refractory\ OC}$ ($R^2 = 0.62$, $p < 0.05$; $R^2 = 0.59$, $p < 0.05$) (Figures 5b and 5c). The relative abundance of anaerobic bacteria in the 20–63 μm fraction exhibits increase; meanwhile, there is also a notable decrease in $f_{refractory\ OC}$ and an increase in $f_{pre\text{-}aged\ OC}$ within the same fraction along the sediments transport pathway (Figures 4b and 4c). These relationships and variation trends suggest that the increasing of pre-aged OC and the decreasing refractory OC are closely associated with the increasing anaerobic microbial OC during sediments resuspension. The activity of anaerobic microbes may influence and promote the increase of pre-aged OC and the decrease of refractory OC. In addition, in Section 3.1, we discuss that the formation of anaerobic environments in sediments results in the increasing relative abundance of anaerobic bacteria through enhanced adsorption. Conversely, the anaerobic condition may lead to a reduction in the activity of oxygen-utilizing

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Table 1
Stepwise Multiple Regression Analysis Between Various Environmental Factors and the Relative Abundance of Different Microbial Communities

Dependentvariables	Independentvariables	Coefficient	Adjusted R^2	*P* value
$f_{\text{pre-aged OC}}$	anaerobic bacteria	0.786	0.562	$P < 0.05$
$f_{\text{refractory OC}}$	anaerobic bacteria	0.768	0.53	$P < 0.05$
OC content	anaerobic bacteria	0.713	0.438	$P < 0.05$
δ^{13}C-OC	aerobic bacteria	0.68	0.385	$P < 0.05$
C/N	Desulfovibrio	0.807	0.602	$P < 0.05$
TN content	anaerobic bacteria	0.729	0.465	$P < 0.05$
aerobic bacteria	δ^{13}C-OC	0.68	0.385	$P < 0.05$
anaerobic bacteria	$f_{\text{pre-aged OC}}$	0.786	0.562	$P < 0.05$
Desulfovibrio	C/N	0.807	0.602	$P < 0.05$

bacteria, such as aerobic bacteria. Given that aerobic bacteria preferentially utilize algal OC for degradation, a reduction in aerobic bacterial activity would result in the accumulation of algal OC in sedimentary environments. The accumulated algal OC deposited in sediment may have already undergone degradation by microbes within the water column, and could contain pre-aged OC, ultimately contributing to an increase in pre-aged OC derived from algae. This possibility could potentially explain the observed correlation (Figure 5) between an increased proportion of pre-aged OC and the relative abundance of anaerobic bacteria.

3.3. Microbial-Mediated Utilization of Refractory OC Compositions

We use multiple regression analysis to determine the main factors influencing the relative abundance of microbial communities and geochemical parameters. The results of a stepwise multiple regression analysis show that δ^{13}C-OC is the main influencing factor of the relative abundance of aerobic bacteria, and C/N is the main influencing factor of the relative abundance of *Desulfovibrio* (Table 1). This suggests that the source characteristics of OC may affect microbial communities. Furthermore, the proportion of $f_{\text{pre-aged OC}}$ is the main geochemical parameter affecting anaerobic bacteria. Meanwhile, anaerobic bacteria may also affect the proportion of $f_{\text{pre-aged OC}}$, $f_{\text{refractory OC}}$, and OC content (Table 1). Both correlation analysis and stepwise multiple regression analysis show the relationship between the relative abundance of anaerobic bacteria and the proportion of $f_{\text{pre-aged OC}}$. These results highlight the interaction between microbial composition and OC stability, and suggest that the proportion of $f_{\text{pre-aged OC}}$ promotes the growth of anaerobic bacteria, and the activity of anaerobic bacteria also dominated the variational proportion of $f_{\text{pre-aged OC}}$ and $f_{\text{refractory OC}}$.

Because the decreasing resuspension intensity and conversion of OC in benthic environment can enhance the adsorption and formation of anaerobic bacteria (Sections 3.1 and 3.2), microbial activities under different resuspension intensities exert an influence on pyrolysis stability of OC composition in natural environments (Che et al., 2024). Resuspension of marine sediments increases its permeability and facilitates the colonization of anaerobic bacteria after deposition (Amalfitano et al., 2017; Huettel et al., 2014). The resuspension and settling processes allow marine sediments in benthic environment to adsorb and host more anaerobic bacteria, which have the potential to produce catalytic enzymes that metabolize refractory OC (Leifeld & von Lützow, 2014). The complexity of enzymatic reactions driven by microbes may be positively correlated with OC degradation through affecting the stability of OC (Leifeld & von Lützow, 2014). Some studies have shown that anaerobic bacterial community can assimilate and metabolize petrogenic OC with high stability for the synthesis of their own fatty acids, increasing bioavailability of petrogenic OC (Ruben et al., 2023; Vishnupriya et al., 2021). Additionally, microbes can oxidize refractory OC, which belongs to rock-derived OC from the water erosion of mountain bedrock (Hemingway et al., 2018; Ruben et al., 2023). These studies imply that anaerobic bacteria present in sediments have the capability to metabolize refractory OC. Combining with the results of a stepwise multiple regression analysis, which expresses the relations between the relative abundance of anaerobic and $f_{\text{pre-aged OC}}$ (Table 1), our findings suggest that the increasing abundance of anaerobic bacteria along transport pathways may enhance the bioavailability of refractory OC, and the microbes may produce microbial by-products, including pre-aged OC compositions, during the hydrodynamic sorting processes in marginal seas sediments. This observation

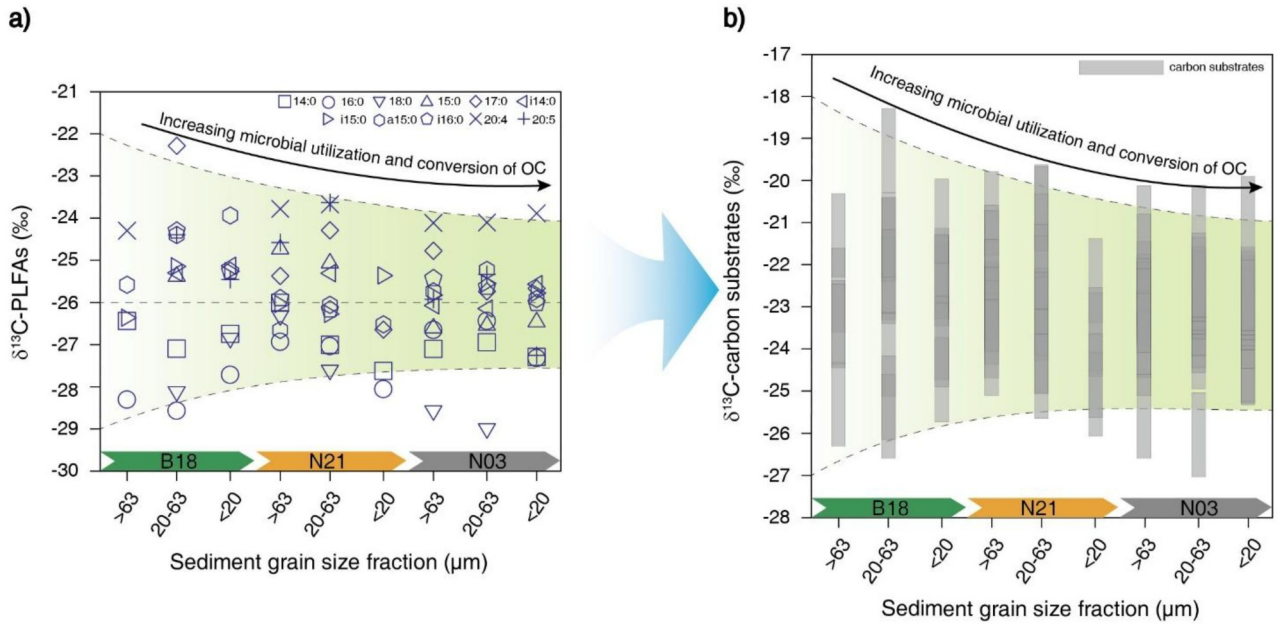

Figure 6. (a) The variations of δ^{13}C-PLFAs in different grain-size sediments (>63 μm, 20–63 μm, and <20 μm) along Shandong Coastal Current pathway. (b) The variation of δ^{13}C-carbon substrates deduced from the values of δ^{13}C-PLFAs. The green color gradient in the figures shows the transition from a broad to a narrow range of δ^{13}C-PLFAs and δ^{13}C-carbon substrates' values.

may provide an additional explanation for the observed correlation between the rising relative abundance of anaerobic bacteria and the decreasing of refractory OC, as well as the increasing of pre-aged OC.

We investigate the utilization of refractory OC by microbes through analyzing the δ^{13}C values of PLFAs. The δ^{13}C values of PLFAs offer insights into the microbial utilization of OC (Boschker, 2002; Temperoni et al., 2018). We examine the variations in δ^{13}C values of specific PLFAs to study the microbial metabolic utilization of OC substrates along hydrodynamic transport pathway. Our findings show that the δ^{13}C values of PLFAs in sediments near the Yellow River estuary exhibit a wide range (approximately from −29.0‰ to −22.0‰, 7‰ offset, Figure 6a; Table S5 in Supporting Information S1). However, the downstream results show a narrower range of δ^{13}C-PLFAs values (approximately from −27.5‰ to −24.0‰, 3.5‰ offset, Figure 6a; Table S5 in Supporting Information S1). Because heterotrophic bacterial PLFAs typically exhibit a carbon isotope fractionation of 2–4‰ depletion compared with carbon substrates in natural environments (Zhang et al., 2019), we deduce the variations of microbial carbon substrates based on the δ^{13}C-PLFAs values. The δ^{13}C-PLFAs and δ^{13}C-carbon substrates exhibit similar variation trends, which are consistent with previous studies (Bouillon et al., 2011). Similarly, we also find that the δ^{13}C values of carbon substrates near the Yellow River estuary exhibit a wide range (approximately from −27.0‰ to −18.0‰, 9‰ offset, Figure 6b), indicating the utilization of OC substrates in natural environments from diverse sources, including both marine and terrestrial characteristics. But downstream δ^{13}C-carbon substrates' values vary approximately from −25.5‰ to −21.0‰ (4.5‰ offset, Figure 6b), suggesting that the sources of carbon substrates available to microbes are limited, and microbes have to utilize fewer types of OC sources. This shift in microbial utilization of OC sources from marine and terrestrial characteristics separately to a mixture may be attributed to metabolic transformations of microbes. These findings suggest that as sediments move downstream, the availability of different OC sources decreases, leading microbes to rely on the remaining OC, implying that OC can be utilized by microbes during hydrodynamic sorting processes.

Along the hydrodynamic transport pathway, the weighted averages of δ^{13}C-PLFAs in the 20–63 μm fraction gradually decrease from −26.00‰ at B18 to −26.20‰ at N03 (Figure 4f; Table S1 in Supporting Information S1). Heterotrophic bacterial PLFAs typically exhibit a carbon isotope fractionation of 2–4‰ depletion compared with carbon substrates in natural environments (Zhang et al., 2019). The δ^{13}C values of OC utilized by microbes gradually shift toward the values characteristic of terrigenous OC derived from refractory OC along the marine sediments transport pathway, approximately from −22.0‰ to −24.2‰ (Hemingway et al., 2018; Tao et al., 2015).

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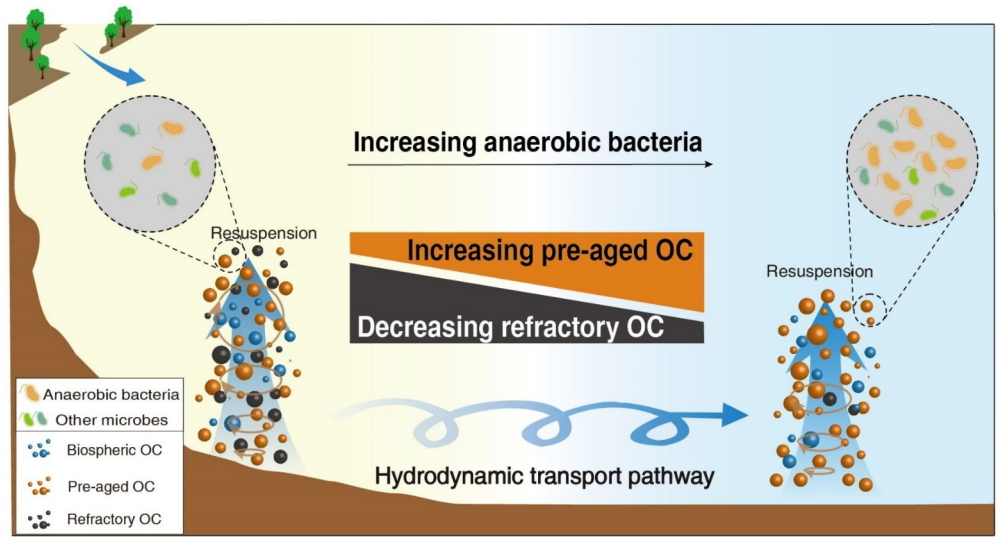

Figure 7. Schematic diagram shows the OC conversion and microbial dynamics along the sediments transport pathway. The yellow bacteria in the circle signify the alteration in the relative abundance of anaerobic bacteria; we can see the increasing abundance of anaerobic bacteria along the transport pathway. The width of the central rectangle represents the variation in the relative proportions of different OC compositions, with orange denoting pre-aged OC variation and gray indicating refractory OC variation. We can see the increasing proportion of pre-aged OC, and the decreasing proportion of refractory OC along the hydrodynamic transport pathway. The decreasing refractory OC and the increasing pre-aged OC are accompanied by, and contribute to the increase of anaerobic microbial abundance along the sediments transport pathway.

This observation indicates a transition in the carbon substrates utilized by microbes, with an increasing utilization of refractory OC, indirectly suggesting that refractory OC is utilized by microbes.

The changes in δ^{13}C-PLFAs values demonstrate the utilization of refractory OC by microbes during hydrodynamic sorting processes. During transportation, the selective adsorption leads to an increasing abundance of anaerobic bacteria (Figure 2d), and the rise in the relative abundance of anaerobic bacteria shows a significant correlation with the increasing fraction of pre-aged OC and the decreasing fraction of refractory OC (Figures 5 and 7, Table 1) in sediments along the hydrodynamic transport pathway. And anaerobic bacteria have the potential to metabolize and utilize refractory OC with higher stability (Ruben et al., 2023; Vishnupriya et al., 2021). Microbes can stimulate the production of OC (such as pre-aged OC in this study) by increasing microbial biomass and accumulating microbial metabolites (Tao et al., 2023). Given the behavioral characteristics of anaerobic bacteria, they may possess the ability to utilize refractory OC. These findings suggest that the utilization and metabolism of microbes may produce pre-aged OC derived from microbial by-products. This process could increase the proportion of pre-aged OC that is buried in sediments, particularly during hydrodynamic sorting in benthic environments. This provides a novel mechanistic perspective for understanding the enhanced burial of pre-aged OC and contributes to a deeper understanding of carbon reservoirs in the sediments of marginal seas.

4. Conclusions

This study aims to analyze the distribution patterns of microbial biomass and the relationship between microbial compositions and OC characteristics across different grain-size sediments along the classical transport pathway, and assess the impact of OC conversion on the burial of OC in marginal seas sediments. Our results show that the relative abundance of anaerobic bacteria increases during hydrodynamic sorting processes, which may be attributed not only to enhanced selective adsorption but also to the utilization of refractory OC. The utilization of refractory OC and the production of pre-aged OC are accompanied by and contribute to the increase of anaerobic microbial abundance along the sediments transport pathway. During marine sediments transport, microbes may utilize and metabolize refractory OC to reproduce and enhance the biomass of bacteria. The microbial utilization of refractory OC may result in the production of metabolites, including by-products and necromass, which can be classified as pre-aged OC. Furthermore, alterations in the sedimentary environment may diminish the activity of aerobic bacteria, potentially leading to an increased accumulation of algal-derived OC, which may also contain

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pre-aged OC. Consequently, the role of microbes in the utilization of various compositions of OC during sediment resuspension can enhance the burial of pre-aged OC. These findings offer further insights into the mechanisms underlying the burial of OC in marine sediments of marginal seas.

Data Availability Statement

Data of parameters values, PLFAs concentration, and δ^{13}C-PLFAs values are available in figshare at https://doi.org/10.6084/m9.figshare.25859845.v1.

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References

Ahmerkamp, S., Marchant, H. K., Peng, C., Probandt, D., Littmann, S., Kuypers, M. M. M., & Holtappels, M. (2020). The effect of sediment grain properties and porewater flow on microbial abundance and respiration in permeable sediments. *Scientific Reports*, *10*(1), 3573. https://doi.org/10.1038/s41598-020-60557-7

Amalfitano, S., Corno, G., Eckert, E., Fazi, S., Ninio, S., Callieri, C., et al. (2017). Tracing particulate matter and associated microorganisms in freshwaters. *Hydrobiologia*, *800*(1), 145–154. https://doi.org/10.1007/s10750-017-3260-x

Ausín, B., Bruni, E., Haghipour, N., Welte, C., Bernasconi, S. M., & Eglinton, T. I. (2021). Controls on the abundance, provenance and age of organic carbon buried in continental margin sediments. *Earth and Planetary Science Letters*, *558*, 116759. https://doi.org/10.1016/j.epsl.2021.116759

Bao, R., McIntyre, C., Zhao, M., Zhu, C., Kao, S.-J., & Eglinton, T. I. (2016). Widespread dispersal and aging of organic carbon in shallow marginal seas. *Geology*, *44*(10), 791–794. https://doi.org/10.1130/g37948.1

Bao, R., McNichol, A. P., McIntyre, C. P., Xu, L., & Eglinton, T. I. (2018). Dimensions of radiocarbon variability within sedimentary organic matter. *Radiocarbon*, *60*(3), 775–790. https://doi.org/10.1017/rdc.2018.22

Bao, R., van der Voort, T. S., Zhao, M., Guo, X., Montluçon, D. B., McIntyre, C., & Eglinton, T. I. (2018). Influence of hydrodynamic processes on the fate of sedimentary organic matter on continental margins. *Global Biogeochemical Cycles*, *32*(9), 1420–1432. https://doi.org/10.1029/2018gb005921

Bian, C., Jiang, W., & Greatbatch, R. J. (2013). An exploratory model study of sediment transport sources and deposits in the Bohai Sea, Yellow Sea, and East China Sea. *Journal of Geophysical Research: Oceans*, *118*(11), 5908–5923. https://doi.org/10.1002/2013jc009116

Bianchi, T. S., Cui, X., Blair, N. E., Burdige, D. J., Eglinton, T. I., & Galy, V. (2018). Centers of organic carbon burial and oxidation at the land-ocean interface. *Organic Geochemistry*, *115*, 138–155. https://doi.org/10.1016/j.orggeochem.2017.09.008

Bianucci, L., Balaguru, K., Smith, R. W., Leung, L. R., & Moriarty, J. M. (2018). Contribution of hurricane-induced sediment resuspension to coastal oxygen dynamics. *Scientific Reports*, *8*(1), 15740. https://doi.org/10.1038/s41598-018-33640-3

Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, *37*(8), 911–917. https://doi.org/10.1139/o59-099

Boschker, H., & Middelburg, J. (2002). Stable isotopes and biomarkers in microbial ecology. *FEMS Microbiology Ecology*, *40*(2), 85–95. https://doi.org/10.1111/j.1574-6941.2002.tb00940.x

Bossio, D. A., & Scow, K. M. (1998). Impacts of carbon and flooding on soil microbial communities: Phospholipid fatty acid profiles and substrate utilization patterns. *Microbial Ecology*, *35*(3), 265–278. https://doi.org/10.1007/s002489900082

Bouillon, S., Connolly, R. M., & Gillikin, D. P., (2011). Use of stable isotopes to understand food webs and ecosystem functioning in estuaries. *Treatise on Estuarine and Coastal Science*, *7*, 143–173.

Bröder, L., Tesi, T., Andersson, A., Semiletov, I., & Gustafsson, Ö. (2018). Bounding cross-shelf transport time and degradation in Siberian-Arctic land-ocean carbon transfer. *Nature Communications*, *9*(1), 806. https://doi.org/10.1038/s41467-018-03192-1

Burdige, D. J. (2007). Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *ChemInform*, *107*(2), 467–485. https://doi.org/10.1021/cr050347q

Che, Y., Lin, C., Li, S., Liu, J., Zhu, L., Yu, S., et al. (2024). Influences of hydrodynamics on microbial community assembly and organic carbon composition of resuspended sediments in shallow marginal seas. *Water Research*, *248*, 120882. https://doi.org/10.1016/j.watres.2023.120882

Chen, Y. J., Leung, P. M., Cook, P. L. M., Wong, W. W., Hutchinson, T., Eate, V., et al. (2022). Hydrodynamic disturbance controls microbial community assembly and biogeochemical processes in coastal sediments. *The ISME Journal*, *16*(3), 750–763. https://doi.org/10.1038/s41396-021-01111-9

Ding, H., & Sun, M. Y. (2005). Biochemical degradation of algal fatty acids in oxic and anoxic sediment–seawater interface systems: Effects of structural association and relative roles of aerobic and anaerobic bacteria. *Marine Chemistry*, *93*, 1–19. https://doi.org/10.1016/j.marchem.2004.04.004

Dippold, M. A., & Kuzyakov, Y. (2016). Direct incorporation of fatty acids into microbial phospholipids in soils: Position-specific labeling tells the story. *Geochimica et Cosmochimica Acta*, *174*, 211–221. https://doi.org/10.1016/j.gca.2015.10.032

Evershed, R. P., Crossman, Z. M., Bull, I. D., Mottram, H., Dungait, J. A. J., Maxfield, P. J., & Brennand, E. L. (2006). ^{13}C-Labelling of lipids to investigate microbial communities in the environment. *Current Opinion in Biotechnology*, *17*(1), 72–82. https://doi.org/10.1016/j.copbio.2006.01.003

Frostegård, Å., Tunlid, A., & Bååth, E. (2011). Use and misuse of PLFA measurements in soils. *Soil Biology and Biochemistry*, *43*(8), 1621–1625. https://doi.org/10.1016/j.soilbio.2010.11.021

Frostegrd, A., & Bth, E. (1996). The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils*, *22*(1–2), 59–65. https://doi.org/10.1007/bf00384433

Galy, V., Beyssac, O., France-Lanord, C., & Eglinton, T. (2008). Recycling of graphite during Himalayan erosion: A geological stabilization of carbon in the crust. *Science*, *322*(5903), 943–945. https://doi.org/10.1126/science.1161408

Guo, Z., Li, J., Feng, J., Fang, M., & Yang, Z. (2006). Compound-specific carbon isotope compositions of individual long-chain n-alkanes in severe Asian dust episodes in the North China coast in 2002. *Chinese Science Bulletin*, *51*(17), 2133–2140. https://doi.org/10.1007/s11434-006-2071-7

Hage, S., Galy, V. V., Cartigny, M. J. B., Acikalin, S., Clare, M. A., Gröcke, D. R., et al. (2020). Efficient preservation of young terrestrial organic carbon in sandy turbidity-current deposits. *Geology*, *48*(9), 882–887. https://doi.org/10.1130/g47320.1

21699291, 2025, 4, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2024JC021994 by Ziyang Yang - Ocean University Of China , Wiley Online Library on [04/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Halász, J., Kotroczó, Z., Szabó, P., & Kocsis, T. (2022). Biomonitoring and assessment of dumpsites soil using phospholipid fatty acid analysis (PLFA) method—Evaluation of possibilities and limitations. *Chemosensors*, *10*, 409. https://doi.org/10.3390/chemosensors10100409

Hayes, J. M. (1993). Factors controlling ^{13}C contents of sedimentary organic compounds: Principles and evidence. *Marine Geology*, *113*(1–2), 111–125. https://doi.org/10.1016/0025-3227(93)90153-m

Hayes, J. M. (2001). Fractionation of carbon and hydrogen isotopes in biosynthetic processes. *Reviews in Mineralogy and Geochemistry*, *43*(1), 225–277. https://doi.org/10.2138/gsrmg.43.1.225

Hedges, J. I., & Keil, R. G. (1995). Sedimentary organic matter preservation: An assessment and speculative synthesis. *Marine Chemistry*, *49*(2–3), 81–115. https://doi.org/10.1016/0304-4203(95)00013-h

Hemingway, J. D., Hilton, R. G., Hovius, N., Eglinton, T. I., Haghipour, N., Wacker, L., et al. (2018). Microbial oxidation of lithospheric organic carbon in rapidly eroding tropical mountain soils. *Science*, *360*(6385), 209–212. https://doi.org/10.1126/science.aao6463

Hill, G. T., Mitkowski, N. A., Aldrich-Wolfe, L., Emele, L. R., Jurkonie, D. D., Ficke, A., et al. (2000). Methods for assessing the composition and diversity of soil microbial communities. *Applied Soil Ecology*, *15*(1), 25–36. https://doi.org/10.1016/s0929-1393(00)00069-x

Hilton, R. G., & West, A. J. (2020). Mountains, erosion and the carbon cycle. *Nature Reviews Earth & Environment*, *1*(6), 284–299. https://doi.org/10.1038/s43017-020-0058-6

Horan, K., Hilton, R. G., Dellinger, M., Tipper, E., Galy, V., Calmels, D., et al. (2019). Carbon dioxide emissions by rock organic carbon oxidation and the net geochemical carbon budget of the Mackenzie River Basin. *American Journal of Science*, *319*(6), 473–499. https://doi.org/10.2475/06.2019.02

Huang, W., Yang, H., He, S., Zhao, B., & Cui, X. (2023). Thermochemical decomposition reveals distinct variability of sedimentary organic carbon reactivity along the Yangtze River estuary-shelf continuum. *Marine Chemistry*, *257*, 104326. https://doi.org/10.1016/j.marchem.2023.104326

Huettel, M., Berg, P., & Kostka, J. E. (2014). Benthic exchange and biogeochemical cycling in permeable sediments. *Annual Review of Marine Science*, *6*(1), 23–51. https://doi.org/10.1146/annurev-marine-051413-012706

Inthorn, M., Wagner, T., Scheeder, G., & Zabel, M. (2006). Lateral transport controls distribution, quality, and burial of organic matter along continental slopes in high-productivity areas. *Geology*, *34*(3), 205–208. https://doi.org/10.1130/g22153.1

Jonasdottir, S. H. (2019). Fatty acid profiles and production in marine phytoplankton. *Marine Drugs*, *17*(3), 151. https://doi.org/10.3390/md17030151

Jørgensen, B. B., Wenzhöfer, F., Egger, M., & Glud, R. N. (2022). Sediment oxygen consumption: Role in the global marine carbon cycle. *Earth-Science Reviews*, *228*, 103987. https://doi.org/10.1016/j.earscirev.2022.103987

Kleber, M., Bourg, I. C., Coward, E. K., Hansel, C. M., Myneni, S. C. B., & Nunan, N. (2021). Dynamic interactions at the mineral–organic matter interface. *Nature Reviews Earth & Environment*, *2*(6), 402–421. https://doi.org/10.1038/s43017-021-00162-y

Kleeberg, A., Hupfer, M., Gust, G., Salka, I., Pohlmann, K., & Grossart, H.-P. (2013). Intermittent riverine resuspension: Effects on phosphorus transformations and heterotrophic bacteria. *Limnology & Oceanography*, *58*(2), 635–652. https://doi.org/10.4319/lo.2013.58.2.0635

Lammers, J. M., Reichart, G. J., & Middelburg, J. J. (2017). Seasonal variability in phytoplankton stable carbon isotope ratios and bacterial carbon sources in a shallow Dutch lake. *Limnology & Oceanography*, *62*(6), 2773–2787. https://doi.org/10.1002/lno.10605

Leifeld, J., & von Lützow, M. (2014). Chemical and microbial activation energies of soil organic matter decomposition. *Biology and Fertility of Soils*, *50*(1), 147–153. https://doi.org/10.1007/s00374-013-0822-6

Lin, B., Liu, Z., Zhao, M., Sompongchaiyakul, P., Zhang, H., Blattmann, T. M., et al. (2023). Compositions and sources of sedimentary organic carbon on the tropical epicontinental sea. *Geochimica et Cosmochimica Acta*, *351*, 32–44. https://doi.org/10.1016/j.gca.2023.04.030

Liu, D., Li, X., Emeis, K. C., Wang, Y., & Richard, P. (2015). Distribution and sources of organic matter in surface sediments of Bohai Sea near the Yellow River Estuary, China. *Estuarine, Coastal and Shelf Science*, *165*, 128–136. https://doi.org/10.1016/j.ecss.2015.09.007

Liu, X., Qiao, L., Zhong, Y., Wan, X., Xue, W., & Liu, P. (2020). Pathways of suspended sediments transported from the Yellow River mouth to the Bohai Sea and yellow sea. *Estuarine, Coastal and Shelf Science*, *236*, 106639. https://doi.org/10.1016/j.ecss.2020.106639

Luo, W., Lu, J., Zhu, S., Yue, Y., & Xiao, L. (2022). Investigation of the impact of hydrodynamic conditions on sediment resuspension in shallow lakes. *International Journal of Digital Earth*, *15*(1), 1676–1691. https://doi.org/10.1080/17538947.2022.2131007

Lyons, M. M., Ward, J. E., Gaff, H., Hicks, R. E., Drake, J. M., & Dobbs, F. C. (2010). Theory of island biogeography on a microscopic scale: Organic aggregates as islands for aquatic pathogens. *Aquatic Microbial Ecology*, *60*, 1–13. https://doi.org/10.3354/ame01417

Martin, J. M., Zhang, J., Shi, M. C., & Zhou, Q. (1993). Actual flux of the Huanghe (Yellow River) sediment to the Western Pacific ocean. *Netherlands Journal of Sea Research*, *31*(3), 243–254. https://doi.org/10.1016/0077-7579(93)90025-n

Nielsen, P., & Petersen, S. O. (2000). Ester-linked polar lipid fatty acid profiles of soil microbial communities: A comparison of extraction methods and evaluation of interference from humic acids. *Soil Biology and Biochemistry*, *32*(8–9), 1241–1249. https://doi.org/10.1016/s0038-0717(00)00041-9

Pancost, R. D., & Sinninghe Damsté, J. S. (2003). Carbon isotopic compositions of prokaryotic lipids as tracers of carbon cycling in diverse settings. *Chemical Geology*, *195*(1–4), 29–58. https://doi.org/10.1016/s0009-2541(02)00387-x

Papadopoulou, E. S., Karpouzas, D. G., & Menkissoglu-Spiroudi, U. (2011). Extraction parameters significantly influence the quantity and the profile of PLFAs extracted from soils. *Microbial Ecology*, *62*(3), 704–714. https://doi.org/10.1007/s00248-011-9863-2

Pedler, B. E., Aluwihare, L. I., & Azam, F. (2014). Single bacterial strain capable of significant contribution to carbon cycling in the surface ocean. *Proceedings of the National Academy of Sciences*, *111*(20), 7202–7207. https://doi.org/10.1073/pnas.1401887111

Polimene, L., Sailley, S., Clark, D., Mitra, A., & Allen, J. I. (2016). Biological or microbial carbon pump? The role of phytoplankton stoichiometry in ocean carbon sequestration. *Journal of Plankton Research*, *39*, 180–186. https://doi.org/10.1093/plankt/fbw091

Pond, D. W., Kunihiro, T., Veuger, B., Vasquez-Cardenas, D., Pozzato, L., Le Guitton, M., et al. (2014). Phospholipid-derived fatty acids and quinones as markers for bacterial biomass and community structure in marine sediments. *PLoS One*, *9*(4), e96219. https://doi.org/10.1371/journal.pone.0096219

Qiao, S., Shi, X., Wang, G., Zhou, L., Hu, B., Hu, L., et al. (2017). Sediment accumulation and budget in the Bohai Sea, yellow Sea and east China sea. *Marine Geology*, *390*, 270–281. https://doi.org/10.1016/j.margeo.2017.06.004

Risse-Buhl, U., Anlanger, C., Kalla, K., Neu, T. R., Noss, C., Lorke, A., & Weitere, M. (2017). The role of hydrodynamics in shaping the composition and architecture of epilithic biofilms in fluvial ecosystems. *Water Research*, *127*, 211–222. https://doi.org/10.1016/j.watres.2017.09.054

Ruben, M., Hefter, J., Schubotz, F., Geibert, W., Butzin, M., Gentz, T., et al. (2023). Fossil organic carbon utilization in marine Arctic fjord sediments by subsurface micro-organisms. *Nature Geoscience*, *16*(7), 625–630. https://doi.org/10.1038/s41561-023-01198-z

Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., et al. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*, 49–56. https://doi.org/10.1038/nature10386

21699291, 2025, 4, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2024JC021994 by Ziyang Yang - Ocean University Of China , Wiley Online Library on [04/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Shultz, D. J., & Calder, J. A. (1976). Organic carbon variations in estuarine sediments. *Geochimica et Cosmochimica Acta*, *40*(4), 381–385. https://doi.org/10.1016/0016-7037(76)90002-8

Simon, M., Grossart, H. P., Schweitzer, B., & Ploug, H. (2002). Microbial ecology of organic aggregates in aquatic ecosystems. *Aquatic Microbial Ecology*, *28*, 175–211. https://doi.org/10.3354/ame028175

Tao, F., Huang, Y., Hungate, B. A., Manzoni, S., Frey, S. D., Schmidt, M. W. I., et al. (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, *618*(7967), 981–985. https://doi.org/10.1038/s41586-023-06042-3

Tao, S., Eglinton, T. I., Montluçon, D. B., McIntyre, C., & Zhao, M. (2015). Pre-aged soil organic carbon as a major component of the Yellow River suspended load: Regional significance and global relevance. *Earth and Planetary Science Letters*, *414*, 77–86. https://doi.org/10.1016/j.epsl.2015.01.004

Temperoni, B., Massa, A., & Viñas, M. D. (2018). Fatty acids composition as an indicator of food intake inMerluccius hubbsilarvae. *Journal of the Marine Biological Association of the United Kingdom*, *99*(4), 983–990. https://doi.org/10.1017/s002531541800070x

Tesi, T., Semiletov, I., Dudarev, O., Andersson, A., & Gustafsson, Ö. (2016). Matrix association effects on hydrodynamic sorting and degradation of terrestrial organic matter during cross-shelf transport in the Laptev and East Siberian shelf seas. *Journal of Geophysical Research: Biogeosciences*, *121*(3), 731–752. https://doi.org/10.1002/2015jg003067

Vestal, J. R., & White, D. C. (1989). Lipid analysis in microbial ecology. *BioScience*, *39*(8), 535–541. https://doi.org/10.2307/1310976

Vishnupriya, S., Jabir, T., Krishnan, K. P., & Mohamed Hatha, A. A. (2021). Bacterial community structure and functional profiling of high Arctic fjord sediments. *World Journal of Microbiology and Biotechnology*, *37*(8), 133. https://doi.org/10.1007/s11274-021-03098-z

Wang, A., Wang, H., Bi, N., & Wu, X. (2016). Sediment transport and dispersal pattern from the Bohai Sea to the yellow sea. *Journal of Coastal Research*, *74*, 104–116. https://doi.org/10.2112/si74-010.1

Wang, N., Liu, J., Zhang, Y., Xia, C., Lin, D., Che, Y., et al. (2021). Influences of oxidation ability on precision in nitrogen isotope measurements of organic reference materials using elemental analysis-isotope ratio mass spectrometry. *Rapid Communications in Mass Spectrometry*, *35*(14), e9122. https://doi.org/10.1002/rcm.9122

Wang, X. H., Qiao, F., Lu, J., & Gong, F. (2011). The turbidity maxima of the northern Jiangsu shoal-water in the Yellow Sea, China. *Estuarine, Coastal and Shelf Science*, *93*(3), 202–211. https://doi.org/10.1016/j.ecss.2010.10.020

Wetz, M. S., Hales, B., & Wheeler, P. A. (2008). Degradation of phytoplankton-derived organic matter: Implications for carbon and nitrogen biogeochemistry in coastal ecosystems. *Estuarine, Coastal and Shelf Science*, *77*(3), 422–432. https://doi.org/10.1016/j.ecss.2007.10.002

Whaley-Martin, K. J., Mailloux, B. J., van Geen, A., Bostick, B. C., Silvern, R. F., Kim, C., et al. (2016). Stimulation of microbially mediated arsenic release in Bangladesh Aquifers by young carbon indicated by radiocarbon analysis of sedimentary bacterial lipids. *Environmental Science & Technology*, *50*(14), 7353–7363. https://doi.org/10.1021/acs.est.6b00868

White, D. C., Davis, W. M., Nickels, J. S., King, J. D., & Bobbie, R. J. (1979). Determination of the sedimentary microbial biomass by extractible lipid phosphate. *Oecologia*, *40*(1), 51–62. https://doi.org/10.1007/bf00388810

Willers, C., Jansen van Rensburg, P. J., & Claassens, S. (2015). Phospholipid fatty acid profiling of microbial communities-a review of interpretations and recent applications. *Journal of Applied Microbiology*, *119*(5), 1207–1218. https://doi.org/10.1111/jam.12902

Wotton, R. S. (2007). Do benthic biologists pay enough attention to aggregates formed in the water column of streams and rivers? *Journal of the North American Benthological Society*, *26*, 1–11. https://doi.org/10.1899/0887-3593(2007)26[1:dbbpea]2.0.co;2

Wu, W., Li, H., Wang, N., Huo, X., Zhong, G., Zhu, L., et al. (2023). An approach for carbon content measurement in marine sediment: Application of organic and elemental carbon analyzer. *Marine Environmental Research*, *188*, 106000. https://doi.org/10.1016/j.marenvres.2023.106000

Wu, Y., Ding, N., Wang, G., Xu, J., Wu, J., & Brookes, P. C. (2009). Effects of different soil weights, storage times and extraction methods on soil phospholipid fatty acid analyses. *Geoderma*, *150*(1–2), 171–178. https://doi.org/10.1016/j.geoderma.2009.02.003

Xu, X., Shi, R., Lv, C., Liu, H., Yang, W., Qian, S., et al. (2021). Hydrodynamic-driven changes in the source and composition of sedimentary organic matter via grain size distribution in shallow lakes. *Journal of Geophysical Research: Biogeosciences*, *126*(11), e2021JG006502. https://doi.org/10.1029/2021jg006502

Yang, Z., Ji, Y., Bi, N., Lei, K., & Wang, H. (2011). Sediment transport off the Huanghe (Yellow River) delta and in the adjacent Bohai Sea in winter and seasonal comparison. *Estuarine, Coastal and Shelf Science*, *93*(3), 173–181. https://doi.org/10.1016/j.ecss.2010.06.005

Yang, Z. S., & Liu, J. P. (2007). A unique Yellow River-derived distal subaqueous delta in the Yellow Sea. *Marine Geology*, *240*(1–4), 169–176. https://doi.org/10.1016/j.margeo.2007.02.008

Yu, M., Eglinton, T. I., Haghipour, N., Montluçon, D. B., Wacker, L., Hou, P., et al. (2021). Contrasting fates of terrestrial organic carbon pools in marginal sea sediments. *Geochimica et Cosmochimica Acta*, *309*, 16–30. https://doi.org/10.1016/j.gca.2021.06.018

Zhang, C. L., Fouke, B. W., Bonheyo, G. T., Peacock, A. D., White, D. C., Huang, Y., & Romanek, C. S. (2004). Lipid biomarkers and carbon-isotopes of modern travertine deposits (Yellowstone National Park, USA): Implications for biogeochemical dynamics in hot-spring systems. *Geochimica et Cosmochimica Acta*, *68*(15), 3157–3169. https://doi.org/10.1016/j.gca.2004.03.005

Zhang, L. J., Wang, L., Cai, W. J., Liu, D. M., & Yu, Z. G. (2013). Impact of human activities on organic carbon transport in the Yellow River. *Biogeosciences*, *10*(4), 2513–2524. https://doi.org/10.5194/bg-10-2513-2013

Zhang, X., Chen, Q., Wang, C., Zhang, H., Zhao, Y., Zhang, L., et al. (2021). Characteristic analysis of phospholipid fatty acids (PLFAs) in typical nutrient polluted lake sediment in Wuhan. *International Journal of Sediment Research*, *36*(2), 221–228. https://doi.org/10.1016/j.ijsrc.2020.09.002

Zhang, Y., Galy, V., Yu, M., Zhang, H., & Zhao, M. (2022). Terrestrial organic carbon age and reactivity in the Yellow River fueling efficient preservation in marine sediments. *Earth and Planetary Science Letters*, *585*, 117515. https://doi.org/10.1016/j.epsl.2022.117515

Zhang, Y., Naafs, B. D. A., Huang, X., Song, Q., Xue, J., Wang, R., et al. (2022). Variations in wetland hydrology drive rapid changes in the microbial community, carbon metabolic activity, and greenhouse gas fluxes. *Geochimica et Cosmochimica Acta*, *317*, 269–285. https://doi.org/10.1016/j.gca.2021.11.014

Zhang, Y., Zheng, N., Wang, J., Yao, H., Qiu, Q., & Chapman, S. J. (2019). High turnover rate of free phospholipids in soil confirms the classic hypothesis of PLFA methodology. *Soil Biology and Biochemistry*, *135*, 323–330. https://doi.org/10.1016/j.soilbio.2019.05.023

Zheng, X., Zhang, H., Li, Y., Zou, T., Liu, X., & Xing, Q. (2021). The features and mechanisms of the north Shandong coastal current: A case study in 2014. *Journal of Oceanography*, *77*(4), 631–646. https://doi.org/10.1007/s10872-021-00597-3

21699291, 2025, 4, Downloaded from https://agupubs.onlinelibrary.wiley.com/doi/10.1029/2024JC021994 by Ziyang Yang - Ocean University Of China , Wiley Online Library on [04/04/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License