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Enhanced Biodegradation of Dissolved Organic Carbon in the Western Boundary Kuroshio Current When Intruded to the Marginal South China Sea

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Key Points:

- Biodegradation of oceanic dissolved organic carbon (DOC) was enhanced during the Kuroshio Current intrusion to South China Sea (SCS)
- Changes of environmental contexts, such as nutrients supply and microbial species, stimulated the biodegradation
- The remineralization of Kuroshio-intruded DOC may partially support the export production in SCS

Supporting Information:

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

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Abstract

The advective supply of allochthonous dissolved organic carbon (DOC) from open ocean to marginal seas through western boundary current intrusion influences the regional carbon inventory and microbial activities. However, there is limited observation about this process and its biogeochemical impacts on marginal seas. In this study, we investigated the biodegradation of allochthonous DOC carried by the intrusion of the Kuroshio Current into South China Sea (SCS). Using an isopycnal mixing model, the exchange and biodegradation processes of Kuroshio-intruded DOC were quantified. We estimated that approximately 10% of the surface DOC was remineralized due to the enhanced biodegradation in the SCS. This result was supported by the on-deck bioassay experiments that were conducted under different environmental contexts. The results of modeling and on-deck incubations indicate that DOC biodegradation was enhanced by the sharp gradient of environment factors, including nutrients supply, microbial species, and bio-lability of DOC in the frontal zone during the surface water mass mixing. The amount of carbon released from the enhanced DOC degradation by Kuroshio intrusion was estimated to be approximately equal to 8.6 Tg C yr^{-1}. Concomitantly, the amount of nitrogen released could contribute 0.19–0.70 mmol N m^{-2} d^{-1} to the surface of SCS which is comparable to the total supply from deeper water and nitrogen fixation in surface waters. This study suggests that the enhanced biodegradation of DOC during the western boundary currents intrusion could serve as an important sink of oceanic DOC, and thus provide an additional nutrient source to marginal seas.

Plain Language Summary

The movement and breakdown of dissolved organic carbon (DOC) in the ocean are two vital processes that regulate atmospheric carbon dioxide concentrations. DOC that accumulates in surface ocean can be transported into deep ocean where the majority of it is degraded by microbes to inorganic components. The horizontal transport of DOC through wind-driven currents in surface is also an important process that regulates carbon and nutrient cycling. In this study, the transport of DOC by the Kuroshio Current (a western boundary current in the Pacific Ocean) and its subsequent breakdown via microbes were investigated in the South China Sea (SCS). The degradable amount of DOC was determined using two independent approaches: a physical mixing model and on-deck incubation experiments that simulated the bacterial breakdown of DOC during the mixing of Kuroshio and SCS waters. Our results demonstrate that the Kuroshio intrusion enhances DOC biodegradation due to the changing environmental conditions such as nutrients and microbial communities, releasing a significant amount of nutrients as a result. This influx of nutrients may help support primary production in the SCS. Thus, this study highlights that the intrusion of western boundary currents into marginal seas could be an important process in carbon and nutrient cycles.

1. Introduction

Oceanic dissolved organic carbon (DOC) is one of the largest carbon reservoirs on the Earth, with 660 ± 32 Pg (10^{15} g) carbon (Hansell & Carlson, 1998). DOC is mainly sourced from primary producers in the euphotic zone, and most of this DOC is consumed by microheterotrophs with turnover time from hours to days (Carlson et al., 2007). The semi-labile fraction of DOC escaping immediate utilization can be further transported to deeper ocean by physical mixing, and meanwhile experience slow degradation (Carlson et al., 2004). The transport and microbial degradation, or biodegradation, of DOC play a critical role in marine biogeochemical cycles. However, factors that control the biodegradation of DOC remain poorly understood (Arrieta et al., 2015; Jiao et al., 2014; Lu et al., 2021; Shen & Benner, 2020). The biodegradation of DOC is regulated by, not only its intrinsic properties, e.g., molecular structure (Hertkorn et al., 2006), size (Benner & Amon, 2015), and concentration (Barber, 1968; Arrieta et al., 2015), but also the ambient environmental context, such as microbial community (Carlson et al., 2004, 2009), nutrients supply (Church et al., 2000; Mills et al., 2008), and solar radiation (Shen & Benner, 2018). The hypothesis of DOC persistence states that most DOC compounds are recalcitrant only in a specific environmental context (Jiao et al., 2014). Therefore, physical mixing of different water mass often creates a gradient of environment factors that can potentially facilitate biodegradation, yet there have been few studies focusing on this process and the biogeochemical impacts.

DOC is produced and accumulates in the surface ocean, especially in subtropical gyres, due to water column stratification and limited heterotrophic consumption (Carlson et al., 2004; Hansell et al., 2009). The accumulated DOC is eventually exported to the interior ocean through overturning circulation, and biodegradation along with the exporting path accounts for the remineralization of DOC (Carlson et al., 2002, 2004, Hansell & Carlson, 2001). Conversely, the deeper refractory DOC in the deep ocean could be transported to the surface ocean and biodegradation could be enhanced by exposure to surface microbial community and solar radiation (Medeiros et al., 2015; Shen & Benner, 2017). The lateral transport of DOC from marginal regions to subtropical gyres by advection and turbulent diffusion has been recently reported as a major source of nutrients that support biological production and enhance vertical export in the open ocean (Letscher et al., 2015, 2016; Reynolds et al., 2014). Likewise, the accumulated DOC in gyres could be transported to adjacent marginal seas through intrusion of western boundary currents, such as the Kuroshio Current (KC) to the South China Sea (SCS), potentially affecting local DOC distribution and microbial activities (Huang et al., 2019; Wu et al., 2015). The Kuroshio intrusions transport a significant volume of water, approximately 6 Sv (1 Sv = 10^6 m^3 s^{-1}) (Xu and Oey, 2014), thus the exchange of DOC and the subsequent biogeochemical impacts should not be overlooked from a quantitative perspective.

The intrusion of the KC to SCS creates a frontal zone with a sharp environmental gradient. SCS is the largest marginal sea of the Pacific and is characterized by a deep basin and oligotrophic surface waters due to the year-round stratification (Du et al., 2013). The Kuroshio, originating from the North Equator Current (NEC), is characterized by relatively high temperature, low nutrients, and high DOC levels compared with the upper layer (<100 m) of the SCS due to the fast replenishment of deep water (Du et al., 2013; Wu et al., 2015; Yang et al., 2013). The Kuroshio intrudes northwestward into the SCS after passing by the Luzon Strait (Figure 1), contributing to the SCS circulation, and thus to the nutrients and DOC dynamics (Du et al., 2013; Li et al., 1998; Nan et al., 2015; Wu et al., 2015). Biogeochemical processes, such as bacterial production, respiration, and ammonium oxidation, are highly active in the frontal zone during the mixing of the two surface water masses; the allochthonous DOC intruded by the KC is thought to fuel these processes (Huang et al., 2019; Xu et al., 2018).

The aim of this study is to better understand the exchange and biodegradation of the Kuroshio-intruded DOC in the SCS. DOC and related biogeochemical parameters were measured during summer and winter in two cruises in the SCS and the western Philippine Sea (WPS). In addition, on-deck incubation experiments were conducted to evaluate the dynamics and mechanisms of DOC biodegradation. Through a combination of field observations and incubation experiments, the results of this work provide insights into factors that control DOC biodegradation, along with the potential impacts of western current intrusion on the biogeochemical cycling of marginal seas.

2. Materials and Methods

2.1. Sample Collection and Analysis

Two cruises were conducted in the SCS and the WPS, including the Luzon strait, in November 2014 and July 2017, respectively (Figure 1 and Table S1 in Supporting Information S1). Samples for DOC analysis were collected from Niskin bottles, transferred directly into pre-combusted 60 mL glass bottles and immediately placed in a freezer at −20°C. Samples for DOC incubation were sequentially filtered through

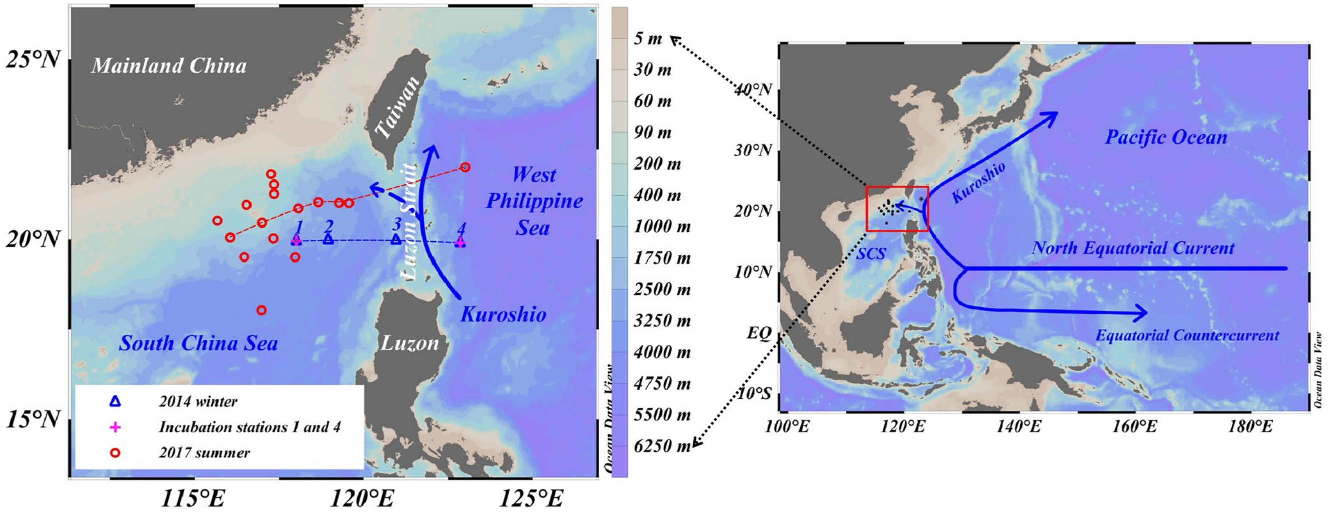

Figure 1. Map of the sampling stations in the South China Sea (SCS) during the cruises in winter 2014 (blue triangles) and summer 2017 (red circles). The dashed red (summer) and blue (winter) lines in both panels denote the sections across the Luzon Strait. Pink crosses denote stations where the incubation samples were collected during the 2014 cruise.

pre-combusted GF/F filters (Whatman, pore size 0.7 μm) to remove large particles and then polycarbonate filters (Millipore, 0.2 μm) to remove microorganisms. Unfiltered water with ambient microbial consortia was used as inoculum for the incubation experiments. Samples for bacterial community analyses (1 L) were filtered onboard through 0.2-μm polycarbonate filters (Millipore) at a pressure of <0.03 MPa, at the beginning and at the end of the incubation. Samples for bacterial abundance were fixed with glutaraldehyde at a final concentration of 1% (Vaulot et al., 1989) and frozen in liquid nitrogen prior to storage at −80°C. Bacterial abundance was measured using a flow cytometer (Becton Dickinson) after staining with SYBR Green I (Marie et al., 1997). Bacterial diversity and communities were monitored by the PCR amplified 16S rRNA genes (Zhang et al., 2014). Details about PCR sequencing and sequence analysis are included in Supporting Information S1 (Text S1 and Figure S1 in Supporting Information S1). To determine the functional potential of bacterial community, taxonomically annotated operational taxonomic units (OTUs) were related to metabolic function groups using Functional Annotation of Prokaryotic Taxa (FAPROTAX v.1.1). An output functional table was created with 34 functional groups (Figure S2 in Supporting Information S1).

DOC was analyzed using a Shimadzu TOC-V_{CPH} (Li et al., 2018). Standardization of DOC was achieved using potassium hydrogen phthalate. Deep seawater and low carbon reference waters (Hansell lab, University of Miami), were measured every five samples to assess the daily variability. The precision for DOC analyses was 1 μM. Samples for nutrient analysis were collected from the Niskin bottles directly and analyzed onboard using a Four-channel Continuous Flow Technicon AA3 Auto-Analyzer (Bran-Lube GmbH) (Du et al., 2013). The detection limits for dissolved inorganic nitrogen (nitrate + nitrite, DIN) and soluble reactive phosphorus (SRP) were 0.03 μM. The precisions for DIN and SRP analysis were better than ±1% and ±2%, respectively. Depth profiles of temperature and salinity were determined with a SBE911 CTD recorder.

2.2. Evaluation of DOC Biodegradation

An isopycnal mixing model was used to evaluate DOC biodegradation during the Kuroshio intrusion to the SCS basin (Wu et al., 2015). In this model, the relative contributions of SCS and Kuroshio waters along the isopycnal surface for any in situ observed water parcels shown in the T-S diagram (Figure 2), can be calculated based on the conservation of salinity and potential temperature (Equations 1–3).

$$R_{SCS}\theta_{SCS} + R_{Kuroshio}\theta_{Kuroshio} = \theta \text{ or } R_{SCS}S_{SCS} + R_{Kuroshio}S_{Kuroshio} = S \quad (1)$$

$$R_{SCS} + R_{Kuroshio} = 1 \quad (2)$$

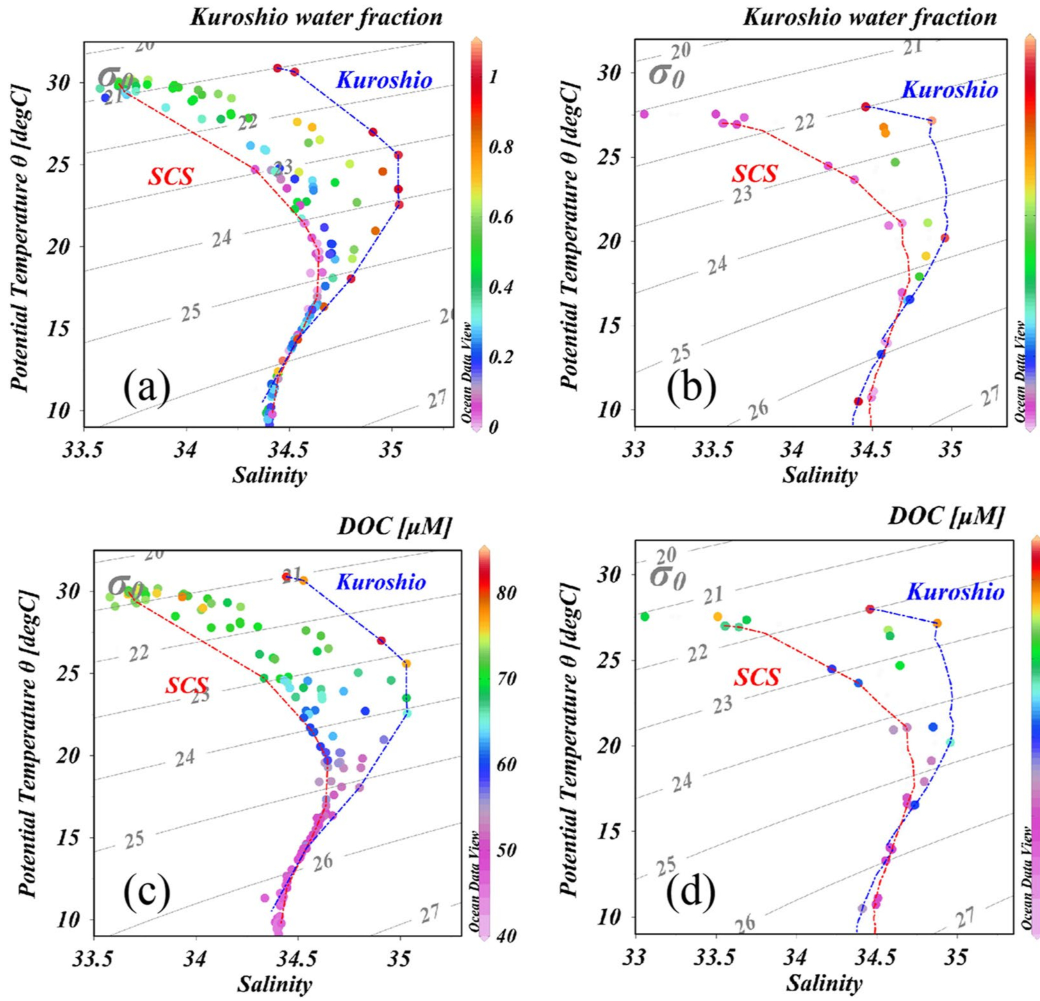

Figure 2. Potential temperature versus salinity plots in the upper 500 m for the sampling stations in the South China Sea (SCS) and Kuroshio Current, superimposed by Kuroshio water fractions (a) and (b) and the field observed dissolved organic carbon (DOC) concentrations (c) and (d). The red dot-dash line in the panels denote the endmember of typical SCS water (Stations A11 and 1 collected in the summer and winter curises, respectively), while the blue dot-dash lines denote the endmember of typical Kuroshio water (Stations F2 and 4 collected in the summer and winter cruises, respectively).

$$R_{Kuroshio} = \frac{\theta - \theta_{SCS}}{\theta_{Kuroshio} - \theta_{SCS}} \text{ or } R_{Kuroshio} = \frac{S - S_{SCS}}{S_{Kuroshio} - S_{SCS}} \tag{3}$$

where R_{scs} and $R_{Kuroshio}$ represent the fractions of SCS and Kuroshio waters in the mixed layer, respectively; θ_{SCS} and $\theta_{Kuroshio}$ are the endmember potential temperatures for SCS and Kuroshio waters, respectively; and S_{scs} and $S_{Kuroshio}$ are the endmember salinity for SCS and Kuroshio waters, respectively.

With the derived SCS and Kuroshio fractions, DOC concentration (DOC_{Model}) in the *in situ* water parcel can be calculated using Equation 4, assuming conservative mixing along the isopycnal surface between the end members of SCS (DOC_{SCS}) and Kuroshio ($DOC_{Kuroshio}$).

$$DOC_{Model} = DOC_{SCS}R_{SCS} + DOC_{Kuroshio}R_{Kuroshio} \tag{4}$$

where DOC_{Model} is the DOC concentration due to the conservative mixing between SCS water and Kuroshio water along the isopycnal surface. DOC_{SCS} and $DOC_{Kuroshio}$ are the endmember values of DOC for SCS water and Kuroshio water, respectively. Based on Fick's law of diffusion, we calculated the isopycnal and diapycnal fluxes according to the concentration gradient and the constant of diffusivity from Du et al. (2013). During

Table 1
Concentrations of Initial Dissolved Organic Carbon (DOC), Residual DOC (RDOC) and Biodegradable DOC (BDOC), as Well as the Derived Bacterial Growth Rate (BGR) and Degradation Rate Constant (k_M) in Different Incubation Treatments

Experimental Treatments	Initial DOC (μM)	RDOC (μM)	BDOC (μM)	BGR[a]	k_M (d^{-1})	Modeled decay equations
$K_{DOM} + K_{Micro}$	79.5 ± 0.6	76.9 ± 0.4	2.6 ± 0.7	0.17	0.35 ± 0.09	$DOC_{(t)} = 2.6\ e^{-0.35t} + 76.9$, $R^2 = 0.92$
$S_{DOM} + S_{Micro}$	70.2 ± 0.8	66.9 ± 0.9	3.3 ± 1.2	0.045	0.24 ± 0.10	$DOC_{(t)} = 3.3\ e^{-0.24t} + 66.9$, $R^2 = 0.84$
$S_{DOM} + K_{Micro}$	73.2 ± 0.4	68.9 ± 1.5	4.3 ± 1.6	0.26	0.011 ± 0.01	$DOC_{(t)} = 4.3\ e^{-0.011t} + 68.9$, $R^2 = 0.42$
$K_{DOM} + S_{Micro}$	80.0 ± 0.5	74.9 ± 0.3	5.1 ± 0.6	0.38	0.10 ± 0.03	$DOC_{(t)} = 5.1\ e^{-0.10t} + 74.9$, $R^2 = 0.96$
$K_{DOM} + S_{Micro} + N$	80.5 ± 0.5	71.0 ± 0.3	9.5 ± 0.6	0.57	0.32 ± 0.04	$DOC_{(t)} = 9.5\ e^{-0.32t} + 71.0$, $R^2 = 0.98$

Note. $K_{DOM} + K_{Micro}$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole Kuroshio surface water. $S_{DOM} + S_{Micro}$: 8 L of South China Sea (SCS) surface filtered water inoculated with 2 L whole SCS surface water. $S_{DOM} + K_{Micro}$: 8 L of SCS surface filtered water inoculated with 2 L whole Kuroshio surface water. $K_{DOM} + S_{Micro}$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole SCS surface water. $K_{DOM} + S_{Micro} + N$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole Kuroshio surface water and amended with the inorganic nutrient.

[a]BGR was calculated from the difference of the bacterial abundance in the first 3 days of the experiments during which bacterial abundances did not decline.

the cruise in summer 2017, the horizontal gradient of DOC at 100 m was estimated to be ~2.0×10^{-5} mmol m^{-4} based on the distance of 750 km and a concentration difference of ~20 μM in DOC between WPS and SCS. The vertical gradient of DOC at 100 m in the SCS was ~1.0×10^{-1} mmol m^{-4}. Thus, the isopycnal flux was estimated to be 1.0×10^{-2} mmol $m^{-2}\ s^{-1}$, which was about 4 orders of magnitude larger than the diapycnal flux of 1.0×10^{-6} mmol $m^{-2}\ s^{-1}$. This result indicated that the isopycnal mixing dominated the diffusive transport of DOC in the upper SCS.

During the mixing of the SCS and the Kuroshio water parcels along the isopycnal surface, the biologically mediated degradation and/or production of DOC is equals to the difference (ΔDOC) between the field measurements (DOC_{Field}) and the model predicted DOC_{Model}, as calculated using Equation 5:

$$\Delta DOC = DOC_{Field} - DOC_{Model} \tag{5}$$

A negative ΔDOC value indicates net removal of DOC, while a positive value is net DOC production. The uncertainty associated with the calculation of ΔDOC was estimated within the range of 1.5–1.6 μM (Wu et al., 2015).

2.3. Incubation Experiments

On-deck incubation experiments were carried out during the winter cruise in 2014 using surface seawater (5 m) collected by Niskin bottles from stations 1 and 4 located in the SCS and the WPS, respectively (Figure 1). We chose winter for the incubation because Kuroshio intrusion is relative stronger in winter than other seasons (Nan et al., 2015 and references therein). The T-S diagram confirmed that these two stations are representative of SCS and Kuroshio water masses, respectively (Figure 2).

The incubation setup was modified from a previous report (Carlson et al., 2002). Briefly, the incubation bottles contained 8 L of seawater (0.2 μm filtered) and 2 L of inocula (unfiltered). The control (without microbes) treatment contained 8 and 2 L of filtered Kuroshio and SCS seawater, respectively. Five different incubation treatments were conducted to quantify the biodegradation potential of the surface Kuroshio and SCS dissolved organic matter (DOM) pools when exposed to their native and switched microbes. As shown in Table 1, the incubation experiments (Table 1) included the native treatments of DOC biodegradation ($K_{DOM} + K_{Micro}$ and $S_{DOM} + S_{Micro}$), treatments with switched microbes ($S_{DOM} + K_{Micro}$ and $K_{DOM} + S_{Micro}$), and the nutrients-amended treatment ($K_{DOM} + S_{Micro} + N$). The nutrients-amended treatment was designed to test the effects of inorganic nutrients on the Kuroshio DOC consumption by SCS bacterioplankton; potassium nitrate and monopotassium phosphate were spiked into the incubation to final concentrations of 1.5-μM NO_3^- and 0.1-μM PO_4^{3-}, respectively. These values correspond to the concentrations at ~75 m depth, which is representative of the mixing layer in the SCS in winter (50–90 m; Du et al., 2013). The incubation bottles were well mixed and stored in the dark and under controlled *in situ* temperature (25°C). At each time point during the 45 days of incubation (0, 1, 2, 3, 4, 5, 7, 9, 12, 14, 45 days), single whole bottles were scarified and aliquots were collected for DOC and microbial abundance analyses as described above.

2.4. Biodegradation Rate Constants and Bacterial Growth Rates

The biodegradation of DOC during the course of bioassay experiments is assumed to follow pseudo-first order reaction, with the degradable DOC plus the residual DOC at the end of the incubation (Equation 6) (Lønborg & Álvarez-Salgado, 2012).

$$DOC_{(t)} = BDOC \cdot \exp\left(-k_M \cdot t\right) + RDOC \tag{6}$$

where $DOC_{(t)}$ is the DOC concentration at time t; k_M is the degradation rate constant; BDOC is the degradable DOC; and RDOC is the concentration of residual DOC at the end of the bioassay experiment. Therefore, BDOC is the concentration difference between the initial DOC and RDOC that modeled from Equation 6.

Bacterial growth rate (BGR) was estimated from Equation 7 (Xu et al., 2013):

$$\mu = \ln\left(B_t / B_i\right) / \Delta t \tag{7}$$

where B_i and B_t represent the bacterial abundance at day 0 and day 3 of the bioassay experiment, respectively. The time interval (Δt) and the bacterial abundance for the calculation of BGR was chosen in the first three days of the incubations to represent the fast bacterial growth before it began to decrease. The modeled BDOC and k_M in the different treatments, and the estimated μ from the bacterial abundance are listed in Table 1. It is worth noting that the BDOC estimated here and ΔDOC estimated from the field data (Section 2.2) both represent biodegradable DOC, but derived from two independent approaches. BDOC refers to the fraction of the initial DOC that was degraded under the incubation conditions, and ΔDOC refers to the estimated fraction that has been degraded during the mixing of the KC and SCS water masses.

3. Results

3.1. Exchange and Removal of the Kuroshio-Intruded DOC in the SCS

Hydrological and biogeochemical measurements indicated water mixing between the SCS and KC in the top 500-m water (Figures 2–4). Samples from the KC had higher potential temperature and salinity in both seasons (Figure 2). DOC concentrations in the Kuroshio surface water were higher (80.4–84.6 μM) than those in the surface (5 m) northern SCS (67.2–75.6 μM) (Figures 3g and 4g). The nitrocline in the KC (~200 m) was deeper than that in the SCS (~50 m) (Figures 3d and 3e and 4d and 4e). The depth of maximum chlorophyll concentrations (50–70 m) was close to the nitrocline, except at Station 3 in the Luzon Strait during the winter cruise where the maximum depth was shallower (Figure 4f). According to the T-S diagram, most samples collected in the top 500 m in the two seasons fell between the endmembers of SCS and Kuroshio water masses (Figure 2), suggesting the contribution of the Kuroshio intrusion.

From the isopycnal mixing model the Kuroshio water fractions ($R_{Kuroshio}$) were estimated to be 0–0.85 and 0–0.77 in the top 500-m water of SCS in 2014 and 2017, respectively. Generally, the $R_{Kuroshio}$ fractions in the upper 500 m decreased from east to west across the Luzon Strait (~120° E) (Figures 3c and 4c). Based on the isopycnal mixing model ΔDOC values in the SCS were estimated to be −5.3–0.9 and −7.9–2.9 μM during the winter and summer cruises, respectively (Figures 3h and 4h). The negative ΔDOC values exceeded the uncertainty of ΔDOC (±1.6 μM), indicating a significant net removal of DOC in the SCS. The transactional distribution of ΔDOC in the two seasons showed a similar pattern. The net removal of DOC mainly occurred in the top 150 m waters close to the Luzon Strait, where there was strong mixing between the Kuroshio and SCS waters (Figures 3h and 4h).

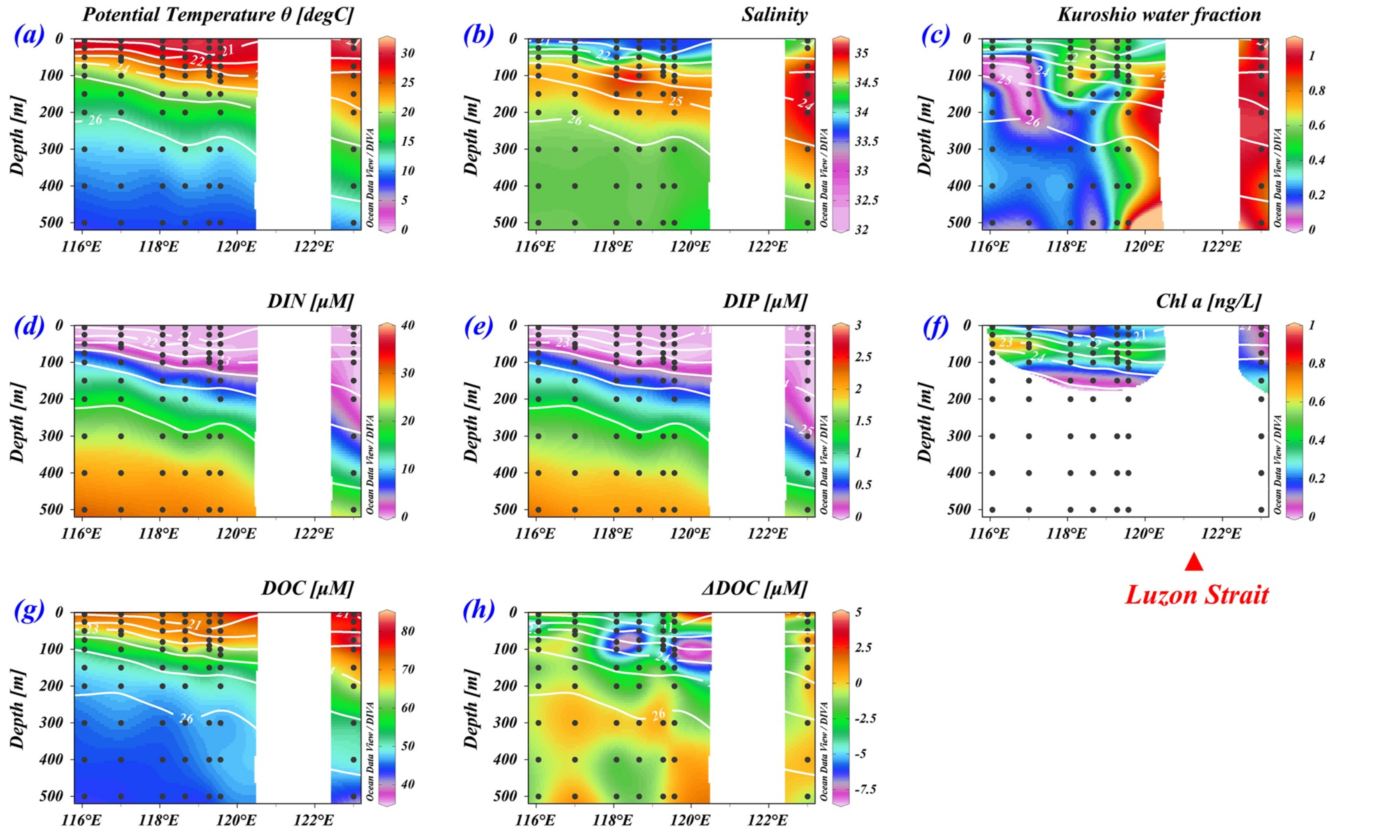

Figure 3. Cross-section distribution of (a) temperature; (b) salinity; (c) estimated Kuroshio water fraction; (d) dissolved inorganic nitrogen (DIN); (e) dissolved inorganic phosphorus (DIP); (f) chlorophyll a (Chl a); (g) dissolved organic carbon (DOC); and (h) estimated ΔDOC for the summer cruise in July 2017. Location of the Luzon Strait is labeled in panel (f).

3.2. Biodegradation of DOM

3.2.1. DOC Biodegradation Dynamics

DOC concentration and bacterial abundance were monitored throughout the incubation period (Figure 5 and Table 1). Initial DOC concentrations of the treatments were consistent with the mass balance calculations of mixing 0.2-μm filtered surface Kuroshio and SCS waters (83.1 and 69.4 μM, respectively) and surface unfiltered Kuroshio and SCS water (83.6 and 67.6 μM, respectively), indicating that there was no contamination during the experimental preparation. DOC concentrations remained relatively constant in the controls throughout the incubation (Figure 5a). The DOC in all treatments degraded rapidly in the first five days, and then remained relatively stable during the rest of the incubation (Figures 5a and 5b). As described previously in Section 2.4, DOC biodegradation seems to follow pseudo-first order reaction (Equation 6), where BDOC and RDOC can be derived. Table 1 shows the BDOC, RDOC, degradation rate constant (k_M), bacterial growth rate (BGR), and the modeled decay equations in the five different treatments. The R^2 of the fitting curves were in the range of 0.42–0.98. Degradation rate constants in the different treatments ranged from 0.011 to 0.35. BDOC levels were in the range of 2.6 ± 0.7 to 9.5 ± 0.6 μM, with the highest level observed in the nutrient-amended treatment (9.5 ± 0.6 μM, $K_{DOM} + S_{Micro} + N$). And the BDOC in Kuroshio seems to be particularly impacted by the SCS microbes. For example, the BDOC observed in the $K_{DOM} + S_{Micro}$ treatment (5.1 ± 0.6 μM) was higher than the of the $S_{DOM} + K_{Micro}$ treatment (4.3 ± 1.6 μM), and the native biodegradation treatments (2.6 ± 0.7 and 3.3 ± 1.2 μM for $K_{DOM} + K_{Micro}$ and $S_{DOM} + S_{Micro,}$ respectively).

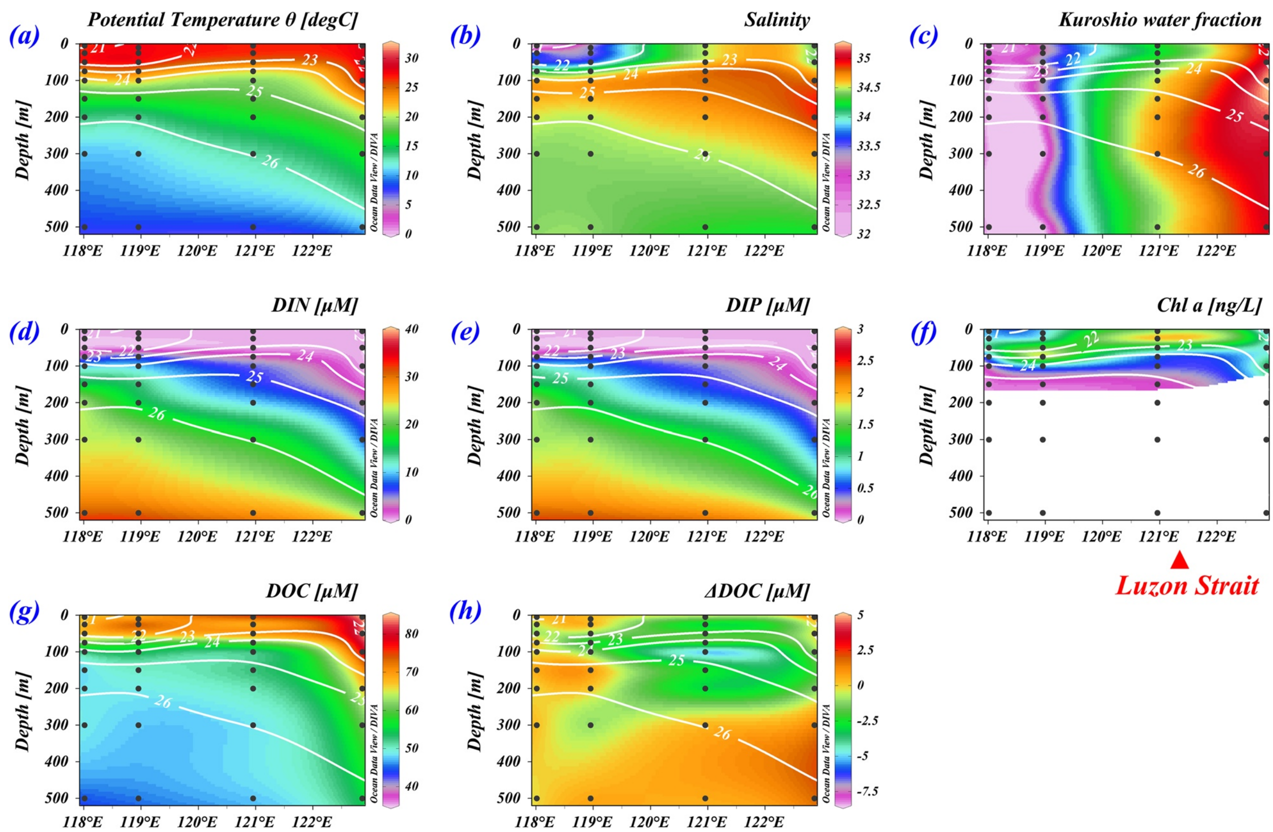

Figure 4. Cross-section distribution of (a) temperature; (b) salinity; (c) estimated Kuroshio water fraction; (d) dissolved inorganic nitrogen (DIN); (e) dissolved inorganic phosphorus (DIP); (f) chlorophyll a (Chl a); (g) dissolved organic carbon (DOC); and (h) estimated ΔDOC for the winter cruise in November 2014. Location of the Luzon Strait is labeled in panel (f).

3.3. Bacterial Growth and Community Structure Shift

Concomitant with the DOC degradation, bacterial abundances in all treatments peaked at day 3, except the $K_{DOM} + K_{Micro}$, and stabilized within the following two days, and then gradually decreased until the end of the incubation (Figures 5c and 5d). As shown in Table 1, the estimated BGR in the different treatments generally followed a similar trend as the BDOC, with the highest value observed in the nutrients-amended treatment (0.57 d^{-1} for $K_{DOM} + S_{Micro} + N$), followed by the switched treatments (0.26 and 0.38 d^{-1} for $S_{DOM} + K_{Micro}$ and $K_{DOM} + S_{Micro}$, respectively), and the native treatments (0.17 d^{-1} and 0.045 d^{-1} for $K_{DOM} + K_{Micro}$ and $S_{DOM} + S_{Micro}$, respectively).

For the functional bacterial community potential, 180,000 reads were obtained after quality control. These were then clustered to 1890 OTUs at a 97% similarity level. Good's coverage values varied between 98.8% and 99.0% across samples (Table S2 in Supporting Information S1). Both the species diversity indicated by the Shannon index (Shannon, 1948) and species richness indicated by the Chao 1 and ACE (Chao, 1984; Gotelli & Colwell, 2011) were higher at the start of the SCS treatment ($K_{DOM} + S_{micro}$, Table S2 in Supporting Information S1), while the Shannon index increased in the $S_{DOM} + K_{micro}$ + 14 d treatment after 14 days of incubation. The rarefaction curve approached saturation, indicating that the diversity of bacteria was well represented in the library (Figure S1 in Supporting Information S1). For different treatments the bacterial diversity of samples were collected at days 0 and 14 when both DOC and bacterial abundance reached constant (Figure 6). Bacterial community structures differed between the SCS and Kuroshio surface samples at both phylum and class levels. The microbial communities differed as the KC had relatively more *Proteobacteria* and less *Bacteroidetes* and *Cyanobacteria* ($S_{DOM} + K_{Micro}$ + 0d and $K_{DOM} + S_{Micro}$ + 0d, in Figure 6). *Alphaproteobacteria*, *Acidimicribiia*, *Gammaproteobacteria*, *Bacteroidia* and *Oxyphotobacteria* were the dominant classes initially, and the abundances of *Bacteroidia* and *Oxyphotobacteria* decreased

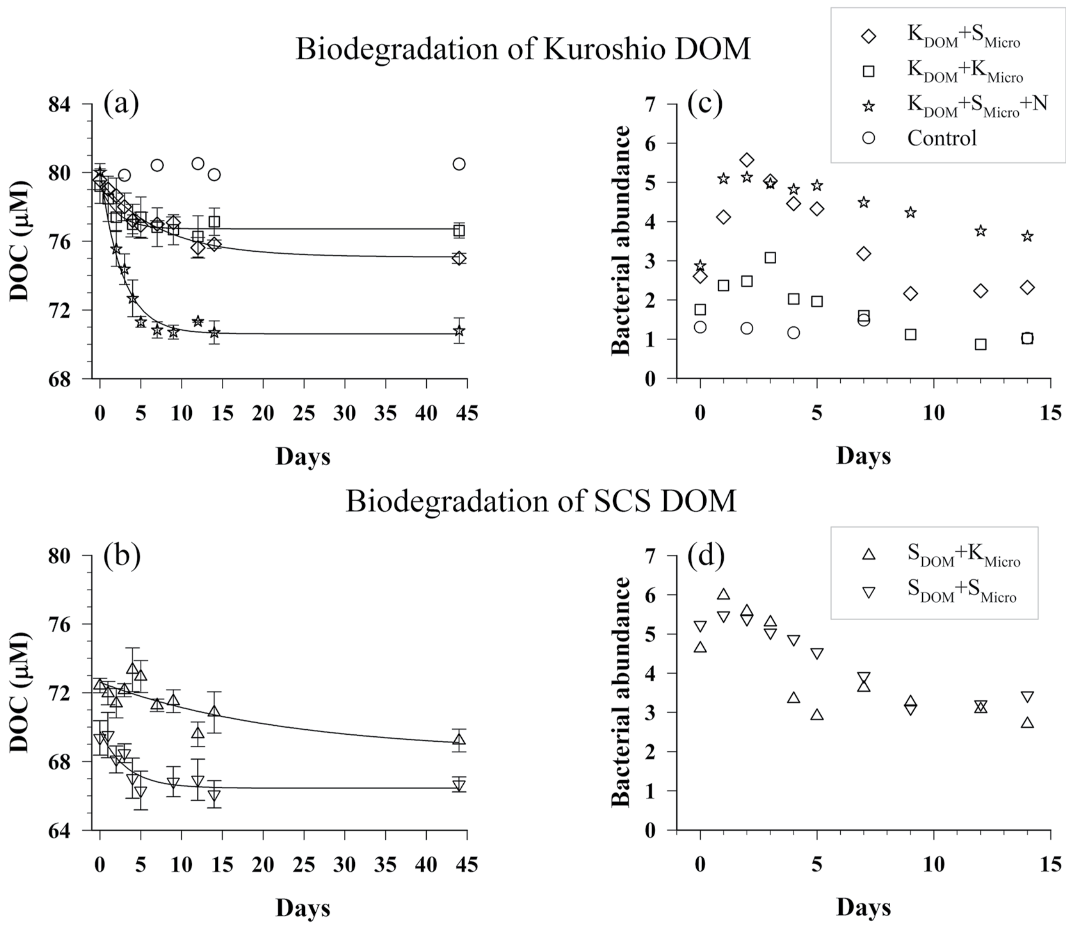

Figure 5. Changes in (a) and (b) dissolved organic carbon (DOC) and (c) & (d) bacterial abundance ($\times 10^8$) during incubation with different treatments. $K_{DOM} + K_{Micro}$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole Kuroshio surface water; $S_{DOM} + S_{Micro}$: 8 L of South China Sea (SCS) surface filtered water inoculated with 2 L whole SCS surface water; $S_{DOM} + K_{Micro}$: 8 L of SCS surface filtered water inoculated with 2 L whole Kuroshio surface water; $K_{DOM} + S_{Micro}$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole SCS surface water; $K_{DOM} + S_{Micro} + N$: 8 L of Kuroshio surface filtered water inoculated with 2 L whole Kuroshio surface water and amended with inorganic nutrients. The solid lines represent the regressions of pseudo first order reaction for biodegradation of DOC in different treatments.

significantly after two weeks of incubation ($S_{DOM} + K_{Micro}$ + 14d and $K_{DOM} + S_{Micro}$ + 14d, in Figure 6). Comparing with the Kuroshio, the SCS bacterial community had a relatively higher abundance of OTUs related to the functional groups of photoautotrophy, aromatics, aromatic hydrocarbons, aliphatic non-methane hydrocarbons degradations, fermentation and nitrate reduction (Figure S2 in Supporting Information S1). And the highest abundance of OTUs related to the organic matter degradation was observed in the nutrient-amended treatment after 14 days (Figure S2 in Supporting Information S1).

4. Discussion

4.1. Watermass Mixing Enhanced the Biodegradation of DOC in the SCS

Through the isopycnal mixing model, we estimated that the biodegradable the DOC (ΔDOC) along the mixing of water masses reached −7.9 μM (Figures 3 and 4), consistent with incubation experiments, where up to 9.5 μM DOC was degraded when SCS microbes and nitrate were added to the Kuroshio water. Therefore, 9.8%–14% of the surface DOC is degradable by the enhanced biodegradation in the mixing zone of SCS and KC. The ΔDOC of each sample was plotted against the estimated Kuroshio water fractions ($R_{Kuroshio}$) and water depths, and most of the low ΔDOC values occurred in samples with $R_{Kuroshio}$ of 0.4–0.8 (Figures 7a

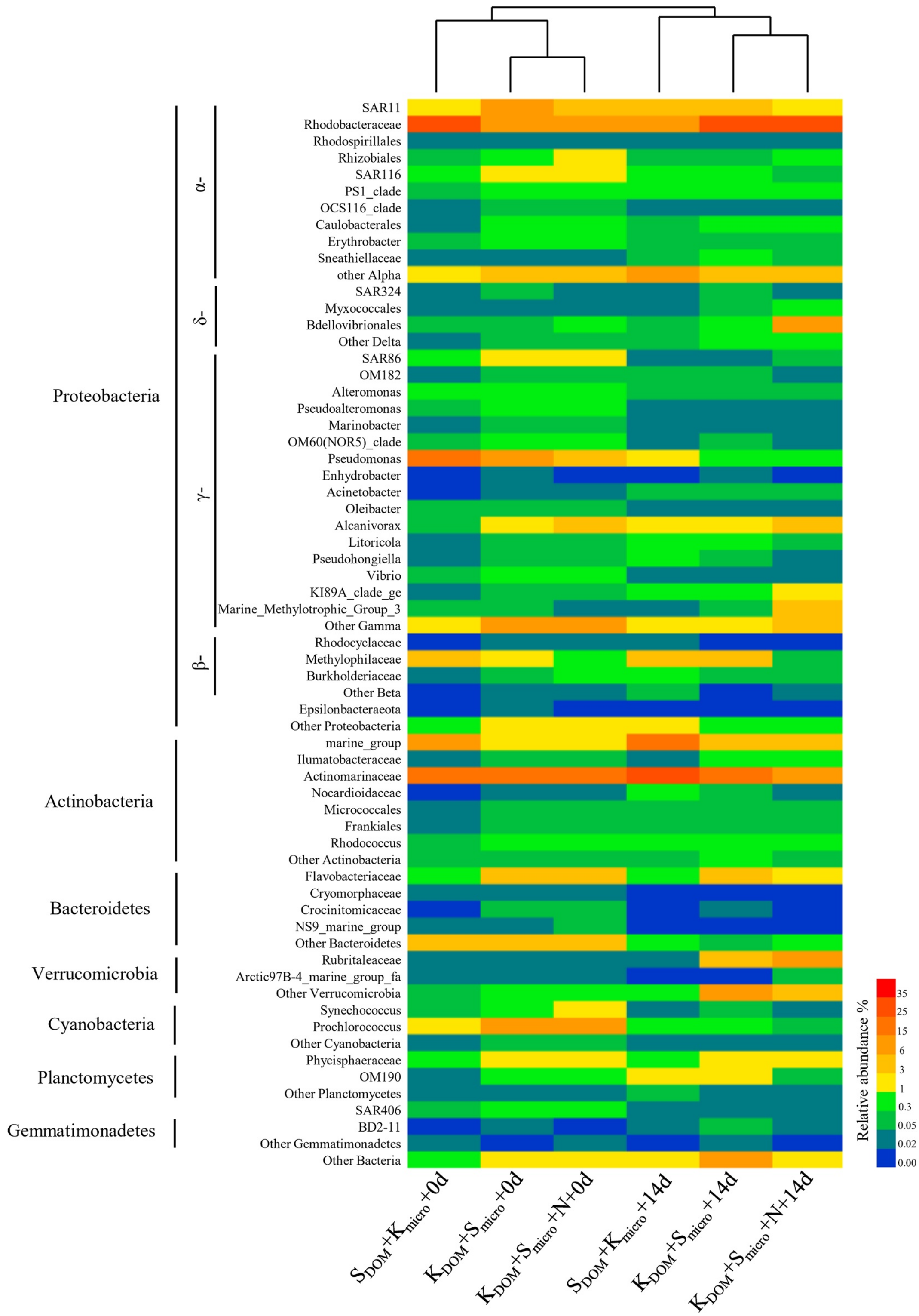

Figure 6. Heat map showing the phylogenetic distribution of the incubation samples collected at days 0 and 14. Color bars represent the relative percentages of different bacterial classifications. Samples clustering is based on the Bray-Curtis similarity (%).

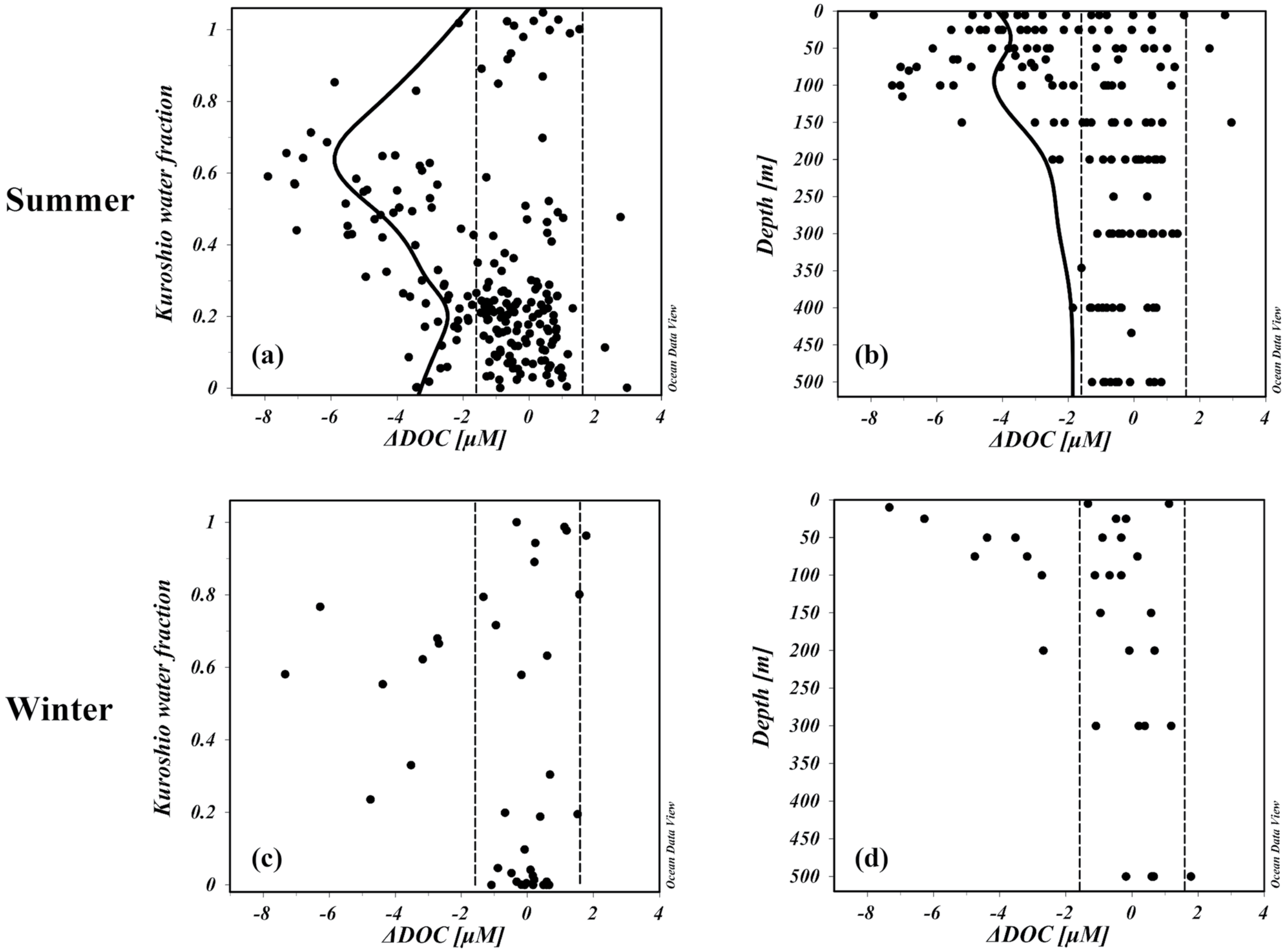

Figure 7. Distribution of modeled ΔDOC with (a) and (c) different Kuroshio water fractions and (b) and (d) sampling depths in surface samples collected during 2017 summer and 2014 winter cruises respectively. The solid lines in (a) and (b) show the average values of ΔDOC outside the estimated uncertainties (dashed lines).

and 7c) in the upper 100-m samples (Figures 7b and 7d), suggesting that DOC was removed more efficiently in the mixing zone of the Kuroshio intrusion. The co-occurrences of negative ΔDOC and the sharp spatial gradient of R_{Kuroshio} were also observed in cross-sectional contour maps in the surface SCS, near the Luzon Strait (Figures 3c and 3h and 4c and 4h). Resutls from the incubation experiments further support the enhanced degradation of Kuroshio derived DOC in the SCS due to the water mixing (Table S1 and Figure S3 in Supporting Information S1). Relative higher BDOC and BGR were observed in the $K_{\text{DOM}} + S_{\text{Micro}}$ treatment (5.1 μM and 0.38, respectively) than in native treatments ($K_{\text{DOM}} + K_{\text{Micro}}$, 2.6 μM and 0.17; $K_{\text{DOM}} + K_{\text{Micro}}$, 3.3 μM and 0.045, respectively), suggesting that biodegradation of Kuroshio DOC was enhanced when inoculated with microbes from the SCS. As what was described in the experimental section, ΔDOC and BDOC are two independent ways of quantifying the biodegradation potential of DOC in the SCS influencing by the Kuroshio intrusion. The incubation experiments showed the enhanced BDOC from the KC when using the microbes in the SCS (Table 1), while the ΔDOC referred to the estimated fraction that has been degradated during the mixing of the KC and SCS watermasses. Therefore, considering that the time interval for surface water current across the Luzon Strait to the western SCS (about 40–60 days assuming the geostrophic flows are 0.2–0.3 m s^{-1}, Nan et al., 2015) is similar to the time length of the incubation experiment, these two parameters are rationally consistent in terms of the time scale. The distinct environmental context between the two water masses of SCS and KC (e.g., temperature, salinity, DOC concentrations, nutrients supply and microbial community structures) may enhance the biodegradation in the mixing zone.

Similar to the Sargasso Sea, surface waters in both SCS and WPS are stratified, oligotrophic, and with accumulated DOC, likely due to the limitations of nutrients supply and initial energy for bacterial consumption (Carlson et al., 2002). Letscher et al. (2013) reported that dissolved organic nitrogen (DON) produced at the surface of a marginal sea (Florida Strait, USA) resisted microbial remineralization, but was rapidly utilized by upper mesopelagic bacterioplankton. The potential nutrient supply from deep to surface water varies between the two regions due to stronger diapycnal mixing in the SCS over the North Pacific, caused by mesoscale eddies and internal tides (Tian et al., 2009). Nutrient concentrations in the surface SCS and WPS are both below detection limits, however, the nutricline in the SCS is much shallower (50–70 m, Figures 3 and 4), leading to an increased supply of nutrients through the turbulent diffusion and winter mixing compared to the WPS (Du et al., 2017). The BDOC and BGR increased even further in the nutrients-amended treatments ($K_{DOM} + S_{Micro} + N$; 9.5 μM and 0.57, respectively), again suggesting the limitation of nutrients on biodegradation. In addition to the nutrients supply, the shift of microbial community structure may also contribute to the enhanced biodegradation. The microbial communities differed as the KC had relatively more *Proteobacteria* and less *Bacteroidetes* and *Cyanobacteria* ($S_{DOM} + K_{Micro}$ + 0d and $K_{DOM}S_{Micro}$ + 0d, in Figure 6). The SCS bacterial community had a relatively higher abundance of OTUs related to the functional groups of organic carbon degradation, as well as in the nutrient-amended treatment after 14 days, e.g., aromatics, aromatic hydrocarbons, aliphatic non-methane hydrocarbons, and hydrocarbons (Figure S2 in Supporting Information S1). This pattern is consistent with the observed positive effects of nutrient addition on biodegradation of aliphatic and aromatic hydrocarbons (Chaîneau et al., 2005; Liu et al., 2017).

Another potential limiting factor for biodegradation under oligotrophic conditions is the initial energy supported by labile organic molecules. Carlson et al. (2002) found that adding inorganic nutrients did not enhance oceanic DOC biodegradation in the surface water of Sargasso Sea, unless spiked with a labile organic compound, such as glucose. However, Liu et al. (2014) showed that glucose could not be used efficiently by bacteria when nutrients were limited. Considering similar oligotrophic conditions in the KC and SCS, higher DOC levels observed in the KC (Figures 3g and 4g) indicate that more labile compounds are contained in the KC DOM than those of the surface SCS DOM. Thus the KC intrusion may alleviate the initial energy limitation of biodegradation. This enhanced degradation is analogous to the priming effect often observed when terrestrial organic matter is exported to estuaries and coastal ocean (Bianchi, 2011). The Kuroshio intrusion in the SCS, therefore, changes many environmental factors, including microbial community, nutrients, and extrogenous labile organic materials that may jointly facilitate DOC biodegradation. Results from the orthogonal incubation experiments and field observations provide direct evidence for this process. However, further work is required to better understand how each single factor regulates the biodegradation process, as well as their coupling effects. It is also unclear how much of the biodegraded DOC was sourced from the SCS versus Kuroshio DOC, which is a rather challenging question to address.

4.2. Impacts of DOC Remineralization Along the Western Boundary Current Intrusion

The surface advective transport and the subsequent remineralization of semi-labile DOC are potentially important in controlling carbon and nitrogen export at both global and regional scales (Letscher et al., 2016; Kelly et al., 2021). To evaluate the total flux of BDOC derived from Kuroshio intrusion to the SCS, we assumed that what was observed in the nutrients addition treatment ($K_{DOM} + S_{Micro} + N$) represents the upper limit of the biodegradable DOC derived from the KC intrusion within the time scale of the water mass mixing. According to the degradation model (Table 1), the RDOC estimated from $K_{DOM} + S_{Micro} + N$ is 71 μM. Next, we took vertical sectional averages of the DOC concentrations in the WPS (station 4), and estimated the BDOC of each depth section by minusing the RDOC value (Table S3 in Supporting Information S1). Then we determined sectional annual water flows across the Luzon Strait from the HYCOM model and calculated the annual water flux across the strait at each depth section by multiplying the cross-sectional area (Table S3 in Supporting Information S1). The annual flux of BDOC at each section was estimated by multiplying the annual water flux to the BDOC concentration (Flux of BDOC in Table S3 in Supporting Information S1). Therefore, in the top 150 meters across the Luzon Strait, approximately 8.6 Tg carbon per year can be transferred and potentially remineralized in the SCS. This equals to ∼6% of the net global DOC production in the western boundary currents regions (140 Tg C yr^{-1}) (Hansell & Carlson, 1998). The major sink of surface accumulated DOC is believed to be through microbial mineralization in the upper mesopelagic zone (~200 m) through the overturning circulation of the ocean (Carlson et al., 2002, 2004, 2004; Hansell et al., 2009). However, this estimation is based on a regional scale, thus this result can only be viewed as preliminary but does emphasize the significance of marginal seas exchanging with western boundary currents as an important sink of oceanic DOC.

The advective transport of semi-labile DOC from coastal oceans to subtropical gyres is an important source of nutrients, released from remineralization of DOM, which can support the productivity and exports in open ocean (Letscher et al., 2016). However, our results demonstrate that the opposite process can be quite important as well. The Kuroshio intrusion brings subtropical gyre water to the SCS through the Luzon Strait (Figure 1), and the mixing significantly enhanced the energy and mass exchange between SCS and Pacific Ocean (Li et al., 1998; Nan et al., 2015), thus affecting the biogeochemical cycles in the SCS (Dai et al., 2013; Du et al., 2013). From the degradable DOC flux estimated above, the degradable N derived from the Kuroshio intrusion is approximately 1.2 Tg nitrogen per year assuming a global average C/N ratio (~8.1, Letscher & Moore, 2015) for the biodegradable Kuroshio DOM. Considering the area of northern SCS and the whole SCS basin (3.48×10^{11} m^2 and 1.28×10^{12} m^2, respectively, Zhai et al., 2013), the contribution of DIN released from the degradation of Kuroshio-intruded DON are 0.19 mmol m^{-2} d^{-1} and 0.70 mmol m^{-2} d^{-1} to the whole SCS basin and the northern SCS, respectively. This nitrogen source derived from the Kuroshio intrusion is comparable to the upper diapycnal diffusive NO_3^- flux across nutricline (0.11 mmol m^2 d^{-1}) (Du et al., 2017), and the average flux of N_2 fixation in the upper layer of the SCS basin (0.057 mmol m^2 d^{-1}) (Kao et al., 2012). Taken together, the input of bioavailable Kuroshio DOC to the SCS may be a key source of nitrogen that potentially influences biogeochemical cycling and the export production in the SCS.

5. Concluding Remarks

The horizontal transport and biodegradation of DOC from ocean gyres to marginal seas and vice versa, have important implications on the carbon cycling, export production and thus climate changes (Kelly et al., 2021; Letscher et al., 2016), yet this topic has not been well studied. This work provides a case study on the transport and biodegradation of Kuroshio-intruded DOC in the SCS, where Kuroshio intrusion dominates the DOC exchange between SCS and western Pacific Ocean, and significantly influences DOC distribution in the upper layer of the SCS. The availability of Kuroshio DOC to the SCS microbes was investigated through two independent approaches, an isopycnal mixing model and on-deck incubation. The isopycnal mixing model indicated a significant removal of Kuroshio DOC (2–7.9 μM) between the Kuroshio and SCS water masses. Furthermore, the incubation experiments indicated that SCS microbes could consumed more Kuroshio DOC than the Kuroshio microbes, and inorganic nutrients could enhance biodegradation. The amount of nitrogen released from the biodegradation of Kuroshio-derived DOC is comparable to the fluxes from diapycnal mixing of deep water and nitrogen fixation, respectively. These results suggest that the changing environmental context along the western boundary current intrusion facilitates biodegradation of DOC, and the nutrients released from biodegradation can potentially support the carbon production and export in marginal seas.

Data Availability Statement

The other data used in this study can be downloaded at https://doi.org/10.6084/m9.figshare.15177594.v2.

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