LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–17

doi: 10.1002/lno.12803

RESEARCH ARTICLE

Limited degradability of dissolved organic carbon, nitrogen, and phosphorus during contrasting seasons in a tropical coastal environment

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Abstract

The biogeochemistry of dissolved organic matter (DOM) is poorly understood in tropical coastal waters. Here, we quantified the biological and photochemical lability of dissolved organic carbon, nitrogen, and phosphorus, in the tropical coastal waters of Singapore. We conducted experiments during the inter-monsoon, the mid-southwest monsoon, and the late southwest monsoon seasons, which span the greatest range of biogeochemical conditions found in the area. The DOM lability was quantified as concentration changes during 90-d biodegradation and 7-d photoreactor incubations. Overall, DOM showed low lability, even though dissolved organic nitrogen and dissolved organic phosphorus accounted for most of the dissolved nitrogen and phosphorus. In the biodegradation experiments, only 5–15% of dissolved organic carbon, 0–7% of dissolved organic nitrogen, and 8–21% of dissolved organic phosphorus were degraded. The addition of labile dissolved organic carbon, intended to test priming effects and to ensure the microbes were not carbon-limited, had no measurable impact on the results. During our photochemical experiments only 2–10% of the dissolved organic carbon were degraded, while neither dissolved organic nitrogen nor dissolved organic phosphorus showed consistent photochemical losses. The DOM optical properties (absorbance and fluorescence spectra) showed limited or no changes during the biodegradation experiments but larger declines in the photochemical experiments. Overall, the biodegradation of DOM was highest during the inter-monsoon, when autochthonous DOM was most dominant, while photolability was greater during the terrestrial DOM-rich southwest monsoon. Our results illustrate that in some tropical coastal environments, DOM can be fairly resistant to biological and photochemical degradation, and thus does not represent a large stock of potentially available nutrients.

Dissolved organic matter (DOM) constitutes around 90% of the total organic carbon (~ 662 Pg C) in the ocean and it plays a major role in global carbon and nutrient cycling (Hansell et al. 2009; Dittmar and Stubbins 2014). While DOM in the open ocean is mainly produced by photosynthetic plankton, in coastal waters multiple sources exist, including planktonic and benthic microalgae, macroalgae, and seagrasses, as well as terrestrial DOM inputs from rivers, direct marginal inputs, and groundwater discharge (Lønborg et al. 2020; Martin and Bianchi 2024). Generally, microbial and photochemical degradation represents the main removal pathways of DOM in the ocean (Dittmar and Stubbins 2014; Amado et al. 2015). Microbes can take up labile fractions of DOM, such as carbohydrates and amino acids, and convert them into new biomass, respire them to CO_2, or convert them into new DOM compounds (Amado et al. 2015; Omori et al. 2020; Song et al. 2022). Commonly, autochthonous DOM produced in coastal waters (planktonic and benthic microalgae, macroalgae, and seagrasses) is thought to be more available to microbial degradation, while allochthonous DOM, such as from

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Associate editor: Elizabeth Kujawinski

Data Availability Statement: Data are available from https://doi.org/10.21979/N9/0LCM6V.

river input, is less bioavailable (Bushaw et al. 1996; Obernosterer and Benner 2004; Hansen et al. 2016). Similarly, photochemical processes can directly degrade DOM into CO_2 and inorganic nutrients but can also transform DOM into new compounds that are either more bioavailable or less bioavailable for microbial degradation (Bushaw et al. 1996; Cory et al. 2018).

Tropical waters generally are considered nutrient-poor compared to higher-latitude environments. However, tropical coastal waters also receive more than half of the global river input of freshwater and DOM, and high temperatures and sunlight levels allow the fast biogeochemical transformation of DOM (Dai et al. 2012; Jennerjahn 2012; Lønborg et al. 2021). In oligotrophic coastal waters, organic nutrients can play a larger role than inorganic nutrients in fueling productivity, with especially the dissolved organic nitrogen (DON) and phosphorus (DOP) pools being important (Lønborg et al. 2018a). Generally, the cycling of DOM in coastal waters depends both on environmental conditions (e.g., temperature, sunlight) as well as the quantity and composition of the inputs. A compilation of studies conducted in coastal waters globally reported that on average 35 ± 13% and 59 ± 29% of the DON and DOP pools are bioavailable to microbes (Lønborg and Álvarez-Salgado 2012). However, most of these studies were conducted at temperate latitudes. So far, only a few studies have examined DOM dynamics in tropical coastal waters, and most of these works have focused on dissolved organic carbon (DOC) (Lønborg et al. 2024). Research on DON and DOP cycling in the tropics has focused especially on coral reefs, where benthic organisms produce more N- and P-rich DOM compounds than in ambient seawater (Tanaka and Nakajima 2018; Kelly et al. 2022) and where DON and DOP can represent an important source of bioavailable N and P (Lønborg et al. 2018a; Nelson, Wegley Kelly, and Haas 2023). Consistently measurable rates of alkaline phosphatase activity reported in tropical Southeast Asian coastal waters have also been interpreted as potential evidence of rapid turnover of DOP (Lim et al. 2018; Nichols, Moynihan, and Martin 2023). Nevertheless, direct estimates of the DON and DOP bioavailability are scarce in tropical coastal waters, with estimates of the photochemical lability of DON and DOP virtually nonexistent (Lønborg et al. 2021). However, it can be speculated that photochemical processes might play a large role in N and P cycling in tropical waters due to generally high ultraviolet light levels, while permanently high temperatures promote fast rates of microbial metabolism. Therefore, determining the importance of both biological and photochemical processes in the degradation of DON and DOP in tropical coastal waters is important.

DOM lability is partly controlled by its inherent chemical composition, and partly also by environmental conditions (Berggren et al. 2022). In particular, the role of priming effects remains unresolved, that is, whether DOM biodegradation is influenced by the addition of labile carbon. A recent meta-analysis showed that priming effects can be observed for DOM, but this outcome is far from being universal (Sanches et al. 2021). Based on two previous studies, it appears that the DOC pool in Southeast Asian coastal waters may be fairly resistant to biological degradation (Nichols and Martin 2021; Zhou et al. 2021), and it might therefore be speculated that the degradation of DON and DOP could be limited by availability of carbon.

In this study, we investigated the effect of biological and photochemical processes on DOM degradation in the Singapore Strait in Southeast Asia, focusing on DON and DOP. Our experiments aimed to (1) quantify the lability of DOM to microbial and photochemical degradation; (2) test whether the addition of labile DOC affects DOM biodegradation; and (3) test whether DOM lability varies seasonally due to changes in terrigenous and marine DOM sources at our study site.

Materials and methods

Study area

The Singapore Strait is situated in the central Sunda Shelf (Supporting Information Fig. S1). During the southwest (SW) monsoon (mid-May to mid-September), the ocean circulation flows northward from the Java Sea toward the South China Sea, while water in the Malacca Strait flows southward and eastward through the Singapore Strait (Tay et al. 2016). This oceanographic setting delivers large terrestrial DOM and nutrient inputs from peatland-draining rivers on the east coast of Sumatra to the Singapore Strait (Zhou et al. 2021; Martin et al. 2022; Wahyudi et al. 2024). During the northeast monsoon (mid-November to late March), the circulation reverses and carries water from the open South China Sea, which has lower terrestrial influence, westward through the Singapore Strait (Tay et al. 2016). During the inter-monsoon seasons, residual currents are weak, and concentrations of DOM (including chromophoric DOM [CDOM] absorption) and dissolved nutrients reach their annual minimum (Martin et al. 2022). The water column in the Singapore Strait is generally well mixed due to tidal currents and the limited seasonal range in seawater temperature (27–31°C year-round; Martin et al. 2022). Salinity ranges from around 29 during the SW monsoon to 32–33 during the late northeast and inter-monsoon periods (Martin et al. 2022).

Although primary productivity rates have not been measured in or around the Singapore Strait, day–night variability in dissolved oxygen is highest during the late northeast to inter-monsoon seasons in March and April (Martin et al. 2022), suggesting that plankton metabolic rates are highest in this period. This is likely due to higher water-column-integrated light availability during this season (Martin et al. 2021). This means that gross production rates of autochthonous DOC, DON, and DOP are likely higher during the inter-monsoon, such that there is likely a larger fraction of freshly produced DOM than during other seasons.

Sample collection and experimental design

Samples for this study were collected in 2022 off St. John's Island (1.216°N, 103.848°E; Supporting Information Fig. S1) during the inter-monsoon (April), peak SW monsoon (July), and late SW monsoon (September), respectively (Table 1). As discussed in the previous section, this spans the two most extreme seasons in terms of DOM concentration and contribution of marine-produced and terrestrial DOM. During other seasons, the DOM composition is likely to be intermediate between these two extremes, with less freshly produced autochthonous DOM than during the inter-monsoon. We therefore expect that DOM lability in the other seasons will be similar to or intermediate between what we report here.

Water samples were collected from the upper 1 m into a 20-L acid-washed carboy using a clean bucket. Salinity and temperature profiles were measured with a Valeport FastCTD. Samples were returned to the laboratory within hours and processed for the experiments. First, an aliquot of unfiltered water was removed as a microbial inoculum for the biological degradation experiment. The remaining water was then filtered through 0.22 μm PolyCap polyethersulfone filters (pre-rinsed with several liters of ultrapure water).

The biological degradation experiment consisted of two treatments: one with only the microbial inoculum (− C), and one with inoculum and added glucose to 30 μmol C L^{-1} (+ C), to test whether added labile carbon would stimulate DON and DOP degradation. For each treatment, three sacrificial replicates were prepared for each of the five time points (days 0, 2, 4, 7, 30, and 75 [September] or 90 [April and July]). Each sacrificial replicate consisted of 475 mL of filtered water + 25 mL of inoculum contained in an acid-washed 500-mL glass Duran bottle (leaving ~ 100 mL of headspace). The + C bottles additionally received 2.5 mL of 1 mmol L^{-1} glucose in ultrapure water (Sigma-Aldrich, BioReagent, G7021-100G). All replicates were incubated in a covered, shaded outdoor location inside a dark box filled with water to stabilize the temperature. Temperature inside the box averaged 27.5 ± 1.0°C (April), 26.7 ± 0.9°C (July), and 26.4 ± 0.8°C (September) (Supporting Information Fig. S2). Triplicates were removed at each time point, filtered through a pre-rinsed 0.22 μm polyethersulfone syringe filter, and stored until analysis. Although dissolved oxygen was not measured, the ambient dissolved oxygen concentrations at our site are generally around 180 μmol L^{-1} (Martin et al. 2022) and thus in stoichiometric excess of DOM; the air headspace additionally provided ~ 900 μmol O_2 per bottle. Given the small changes in DOM and nutrient concentrations in our incubations, we can rule out significant redox fluctuations.

To determine DOM photolability, 0.22-μm filtered sample water was irradiated in quartz cuvettes (~ 35 mL, 50 mm pathlength) in an Atlas Suntest XLS solar test chamber with a daylight filter, providing an irradiance spectrum similar to natural cloud-free ground-level irradiance at solar noon.

Table 1. Initial physical and chemical properties of the seawater at the time of collection. The salinity, temperature, chlorophyll, and concentrations of nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP) are shown together with the colored dissolved organic matter (CDOM) absorption at 350 nm (a_{350}), the spectral slope between 275 and 295 nm ($S_{275-295}$) and the $\delta^{13}C$ of DOC ($\delta^{13}C_{DOC}$).

Sampling date	Salinity	Temperature (°C)	Chlorophyll a (μg L^{-1})	NO_3^- (μmol L^{-1})	NO_2^- (μmol L^{-1})	NH_4^+ (μmol L^{-1})	PO_4^{3-} (μmol L^{-1})	DOC (μmol L^{-1})	DON (μmol L^{-1})	DOP (μmol L^{-1})	CDOM a_{350} (m^{-1})	$S_{275-295}$ (nm^{-1})	$\delta^{13}C_{DOC}$ (‰)
Apr 26, 2022	31.63	30.09	1.25	1.35	0.24	0.33	0.17	78	6.2	0.52	0.41	0.0229	−21.9
Jul 27, 2022	29.68	29.97	0.59	3.95	0.53	0.02	0.29	109	7.0	0.52	1.96	0.0167	−24.1
Sep 1, 2022	30.17	29.63	0.97*	2.19	0.47	0.22	0.22	88	5.8	0.47	1.22	0.0182	−21.6

*Measured using fluorometer on the Valeport FastCTD conductivity temperature depth probe.

Triplicates were collected after 0, 24, 72, 120, and 168 h, filtered through a pre-rinsed 0.22 μm polyethersulfone syringe filter, and stored until analysis. Foil-wrapped dark controls were incubated in the chamber together with the light-exposed samples. The chamber was air-cooled with a set temperature of 40°C (the lowest possible), which is higher than ambient temperatures at our site. Higher temperatures may increase DOM photodegradation rates (Porcal, Dillon, and Molot 2015), although the temperature sensitivity may decrease with longer irradiation (Zhu, Miller, and Fichot 2020). Since we are not quantifying photochemical reaction rates, and the photochemical lability of DOM was low (*see* Results section), we do not consider temperature effects to have biased our conclusions.

In both the biological and photochemical experiments, at each time point, we measured concentrations of dissolved inorganic nutrients (ammonium: NH_4^+; nitrate: NO_3^-; nitrite: NO_2^-; phosphate: PO_4^{3-}), total dissolved nitrogen, total dissolved phosphorus, DOC, and the spectra of CDOM and of fluorescent DOM (FDOM). These parameters were also measured during field sampling as part of an ongoing biogeochemical time series in the Singapore Strait, where we additionally measured chlorophyll *a* and $\delta^{13}C$ of DOC ($\delta^{13}C_{DOC}$) (Chen, Zhou, and Martin 2024). Sampling, storage, and analysis for all parameters followed well-established protocols as described fully in the Supporting Information.

Sample analysis

Dissolved inorganic nutrients (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}), total dissolved nitrogen, and total dissolved phosphorus were analyzed using a segmented-flow autoanalyzer, with DON and DOP concentrations calculated as the differences between total dissolved nitrogen and dissolved inorganic nitrogen (DIN: sum of NO_3^-, NO_2^-, NH_4^+), and total dissolved phosphorus and dissolved inorganic phosphorus (DIP: PO_4^{3-}), respectively. DOC concentrations were determined as nonpurgeable organic carbon using a Shimadzu TOC-L analyzer. CDOM absorbance was measured using a spectrophotometer and is reported as the absorption at 350 nm (a_{350}). We report $SUVA_{254}$ as an aromaticity indicator, and $S_{275–295}$ and S_R as measures of molecular weight and aromaticity. Fluorescence spectra were analyzed using a Fluoromax-4 spectrofluorometer, converted to Raman units (RU) following Lawaetz and Stedmon (2009) and decomposed into four components via parallel factor analysis (PARAFAC), validated using split-half analysis and congruence coefficients. Fluorescence indices (fluorescence index [FI], biological index [BIX], humification index [HIX]) were calculated to assess DOM sources, freshness, and humification. Detailed descriptions are provided in the Supporting Information. The PARAFAC model revealed four fluorescence components (Supporting Information Table S1). The C1 and C2 components are typically referred to as terrestrial humic-like and fulvic-like components (Du et al. 2016; Derrien, Shin, and Hur 2019; Derrien et al. 2020), respectively, while the C3 component is considered to be a humic-like component associated with microbial degradation processes (Graeber et al. 2012; Nimptsch et al. 2015), and lastly, C4 is a protein-like component commonly associated with more labile DOM (Harjung, Sabater, and Butturini 2018; Retelletti Brogi et al. 2019).

Statistical analyses

In this study *t*-tests were used to determine significant differences between final vs. initial values for the bio- and photodegradation experiments, and also to test whether the change over time (i.e., change from initial to final values) was different between + C and − C treatments in the biodegradation experiment. Paired *t*-tests were employed to evaluate the differences in bio- (+ C and − C) and photodegradation. Since the paired *t*-test analyzes the differences between paired measurements, testing for homoscedasticity is not required. We assessed the normality of the difference data using the Shapiro–Wilk test. If the difference data deviated from normality, a log transformation was applied to reach normality.

Principal component analysis is a commonly used multivariate statistical analysis method that aims to extract the main features of data by reducing dimensionality, while retaining the main information in the data, to better understand and interpret the results. In this study, principal component analysis was used to analyze differences and commonalities in the parameters related to the bio- and photodegradation experiments from the different sampling periods.

Results

Initial environmental conditions

The initial environmental conditions for our three water samples followed expected seasonality (Table 1). Temperature, and DON and DOP concentrations varied little, ranging between 29.6°C and 30.1°C, and 5.8 and 7.0 μmol L^{-1} (DON) and 0.47 and 0.52 μmol L^{-1} (DOP). In the inter-monsoon (April), salinity was highest (31.6), and the lowest concentrations were detected for dissolved inorganic nutrients (DIN: 1.94 μmol L^{-1}; DIP: 0.17 μmol L^{-1}) and for DOC (78 μmol L^{-1}). The CDOM absorption was low in this period and dominated by marine-like CDOM, based on the high CDOM spectral slope (a_{350}: 0.41 m^{-1}, $S_{275–295}$: 0.0229 nm^{-1}). The FDOM data during the inter-monsoon showed the highest FI, BIX, and protein-like component values, and the lowest HIX and contribution of humic-like components (FI: 1.66, BIX: 0.87, HIX: 3.1, and fluorescence components C1–C4: 0.029, 0.047, 0.021, and 0.019 RU). The $\delta^{13}C$-DOC was − 21.9‰ in the inter-monsoon, consistent with predominantly marine-produced DOM (Lamb, Wilson, and Leng 2006).

The mid-SW monsoon season (July) had lowest salinity (29.7), higher concentrations of dissolved inorganic nutrients (DIN: 4.50 μmol L^{-1}; DIP: 0.29 μmol L^{-1}) and DOC

(109 μmol L^{-1}), higher CDOM absorption (a_{350}: 1.96 m^{-1}, $S_{275–295}$: 0.0167 nm^{-1}), and lower $\delta^{13}C_{DOC}$ (− 24.1‰). The July sample also had the lowest values of FI, BIX, and protein-like component C4, but the highest values of HIX and the humic-like components (FI: 1.40, BIX: 0.68, HIX: 8.8, and fluorescence components C1–C4: 0.108, 0.147, 0.057, and 0.011 RU), indicating a larger terrestrial influence.

The late SW monsoon (September) had intermediate concentrations of dissolved inorganic nutrients (DIN: 2.88 μmol L^{-1}; DIP: 0.22 μmol L^{-1}) and DOC (88 μmol L^{-1}), CDOM absorption (a_{350}: 1.22 m^{-1}, $S_{275–295}$: 0.0182 nm^{-1}), and FDOM values (FI: 1.44, BIX: 0.75, HIX: 5.8, PARAFAC components C1–C4: 0.067, 0.095, 0.042, and 0.017 RU) compared with the other sampling dates, but also the highest $\delta^{13}C_{DOC}$ (− 21.6‰).

The chlorophyll *a* concentration was highest during the inter-monsoon (1.25 μg L^{-1}), lowest during the mid-SW monsoon (0.59 μg L^{-1}), and intermediate during the late SW monsoon (0.97 μg L^{-1}; Table 1). The phytoplankton phenology in the study area is still poorly resolved, but this result is consistent with previous findings that diel changes in dissolved oxygen concentration are greatest during the first inter-monsoon season (*see* Discussion section), suggesting higher rates of planktonic metabolism during this season (Martin et al. 2022).

Inorganic nutrient dynamics

In the − C biodegradation experiments, we observed only small changes in the DIN and DIP concentrations, with final values slightly higher than at the start of the experiment

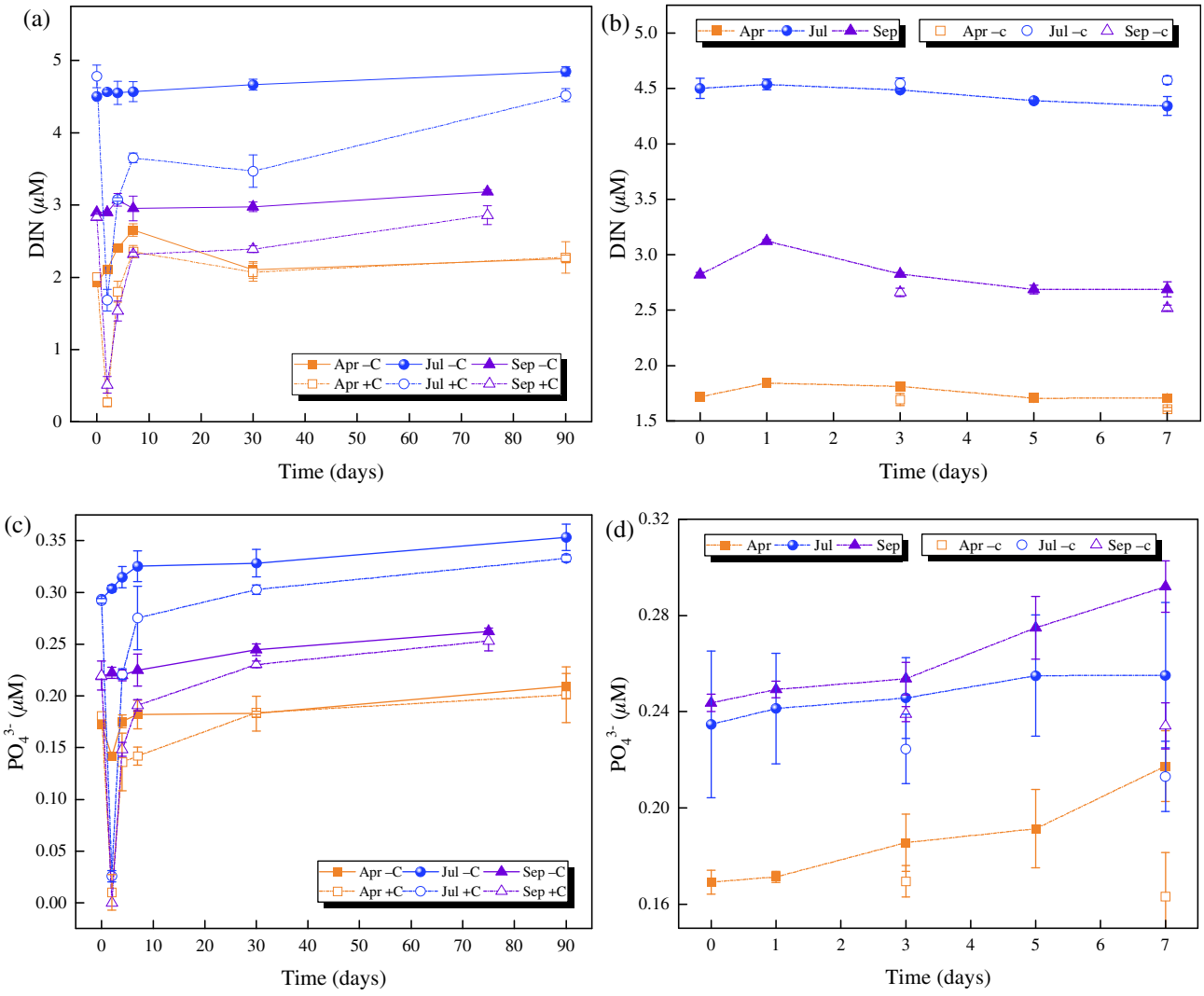

Fig. 1. Changes in dissolved inorganic nitrogen (DIN) and phosphorus (PO_4^{3-}) concentrations during the biological and photochemical degradation experiments. (**a**, **c**) Biodegradation experiments contained filtered (0.22 μm) seawater plus 5% unfiltered seawater with some treatments receiving an additional 30 μmol C L^{-1} (+ C) while others did not receive any additional carbon (− C). (**b**, **d**) Photodegradation experiment only contained 0.22 μm filtered seawater. Here Apr-c, Jul-c, and Sep-c represent the dark control group in the photodegradation experiments.

(Fig. 1). However, the individual DIN species were dynamic: NO_2^- was nearly fully depleted in all treatments, with an accompanying increase in NO_3^-, between days 7 and 30 (Supporting Information Fig. S5). From days 0 to 7, all experiments showed an initial increase in NH_4^+ concentrations (between 0.1 and 2.1 μmol L^{-1}), followed by a decline to ≤ 0.2 μmol L^{-1} by day 30 (Supporting Information Fig. S5). In the + C (but not the − C) treatments we observed a decrease by > 60% in DIN and DIP between days 0 and 2 followed by a return to around initial and subsequently stable or slightly increasing concentrations (Fig. 1). The + C treatments also showed a large decrease in NO_3^- concentration by 1.4 to 2.9 μmol L^{-1} between days 0 and 7, and a larger increase in NH_4^+ concentrations by day 7 than in the − C treatments (Supporting Information Fig. S5).

In the photodegradation experiments, NO_2^- concentrations decreased exponentially by 0.17 to 0.36 μmol L^{-1}, while NO_3^- and of NH_4^+ increased by a corresponding amount (Supporting Information Fig. S5). Overall, however, the concentrations of DIN and DIP varied by ≤ 0.15 μmol L^{-1} in the photodegradation experiments (Fig. 1), indicating no observable photoproduction of inorganic nutrients.

Dissolved organic C, N, and P dynamics

In the − C treatments of all biodegradation experiments, DOC concentrations decreased slightly over time (Fig. 2a). The DOC bioavailability was higher (12 ± 2 μmol L^{-1}, 15% of DOC) during the inter-monsoon, compared with the mid- (6 ± 4 μmol L^{-1}, 5% of DOC) and late SW monsoon seasons (7 ± 2 μmol L^{-1}, 8% of DOC). DON showed a small decrease in the inter-monsoon (0.5 ± 0.2 μmol L^{-1}, 7% of DON), while in the SW monsoon season, no consistent change was found, indicating a very small bioavailable DON pool during July and September (Fig. 2c). Concentrations of DOP decreased by < 0.1 μmol L^{-1} in all − C experiments (Fig. 2e). However, this accounted for 21% of the DOP pool in the inter-monsoon sample, while for the mid- and late SW monsoon, the decrease was less consistent over time, accounting for only 10% and 8% of the DOP pool. This suggests an overall higher bioavailability of the DOP pool compared to DOC and DON, especially in the inter-monsoon (Fig. 2). In the + C treatments, the added labile C was comsumed rapidly (by day 2; Fig. 2), but had no measurable impact on DOC degradation. However, the + C treatments all had higher final DOP concentrations than on day 0, and final DON concentrations in + C treatments were higher than on day 0 in the two SW monsoon samples (Fig. 2). This suggests a small net production of DON and DOP due to the added labile carbon (between 0.2 and 0.5 μmol L^{-1} for DON and 0.10 and 0.25 μmol L^{-1} for DOP, in July and September).

The photolability of DOC was highest during the mid-SW monsoon (July), with a 10% decrease after irradiation (11 ± 2 μmol L^{-1}). In contrast, during the inter-monsoon and late SW monsoon periods, there were only minor decreases (1 ± 2 μmol L^{-1} in April, and 2 ± 2 μmol L^{-1} in September, amounting to less than 2 ± 2% of the total DOC pool; Fig. 3b). Thus, DOC biolability was highest in the inter-monsoon, but DOC photolability was highest in the SW monsoon (Fig. 3). Photodegradation had no consistent impact on DON and DOP concentrations, with changes being within 0.5 and 0.05 μmol L^{-1}, respectively, of the initial values (Figs. 1 and 2). This is consistent with the lack of clear photochemical production of inorganic nutrients.

Changes in CDOM and FDOM

The CDOM properties showed minor changes during the biodegradation experiments (Fig. 3), with small decreases in a_{350} (inter-monsoon: 5%; mid-SW monsoon: 2%; late-SW monsoon: < 1%), increases in $S_{275–295}$ (inter-monsoon: 7%; mid-SW monsoon: 4%; late SW monsoon: 6%), and essentially no change in $SUVA_{254}$ (inter-monsoon: < 0.1%, mid-SW monsoon: < 0.1%, late-SW monsoon: < 0.2%). In the + C treatment, the addition of glucose lowered $SUVA_{254}$ initially, but this difference disappeared once the additional carbon was consumed. Glucose addition had no other influence on the CDOM dynamics (Supporting Information Table S2).

In contrast, photodegradation strongly decreased a_{350} (inter-monsoon: 61%; mid-SW monsoon: 74%; late SW monsoon: 71%) and $SUVA_{254}$ (inter-monsoon: 25%; mid-SW monsoon: 31%; late SW monsoon: 34%), and increased $S_{275–295}$ (inter-monsoon: 43%; mid-SW monsoon: 73%; late SW monsoon: 64%; Fig. 3).

For FDOM, the FI and BIX showed no or very minor changes during biodegradation, although HIX consistently decreased from day 0 to 4 followed by a subsequent increase, especially during the two SW monsoon experiments (Fig. 4). In contrast, photodegradation caused large decreases in HIX and FI, but inconsistent changes for BIX: During the inter-monsoon, BIX first increased and then decreased, during the mid-SW monsoon BIX increased, and during the late SW monsoon BIX did not change (Fig. 4).

During biodegradation, small or no changes were observed for C1, C2, and C3 (Supporting Information Table S3; Fig. 5a). In the inter-monsoon experiment, C1 and C2 showed an initial decrease (days 0–7), while C3 initially increased and then decreased during the first 7 days, but subsequently all three components remained constant (Fig. 5a). In both SW monsoon experiments, C1 and C2 increased slightly over the experimental period, especially in July, while C3 remained stable (Fig. 5a). In comparison, C4 was more dynamic and decreased in all experiments, although in both the inter-monsoon and mid-SW monsoon there was an initial increase from days 0 to 4 (Fig. 5). Carbon addition had no significant effects on FDOM components except for an increase in C1 in the late SW monsoon experiment (Supporting Information Table S2). Conversely, in the photodegradation experiments, large and roughly exponential decreases were seen for C1, C2, and C3, while C4 increased (Fig. 5), with these changes being

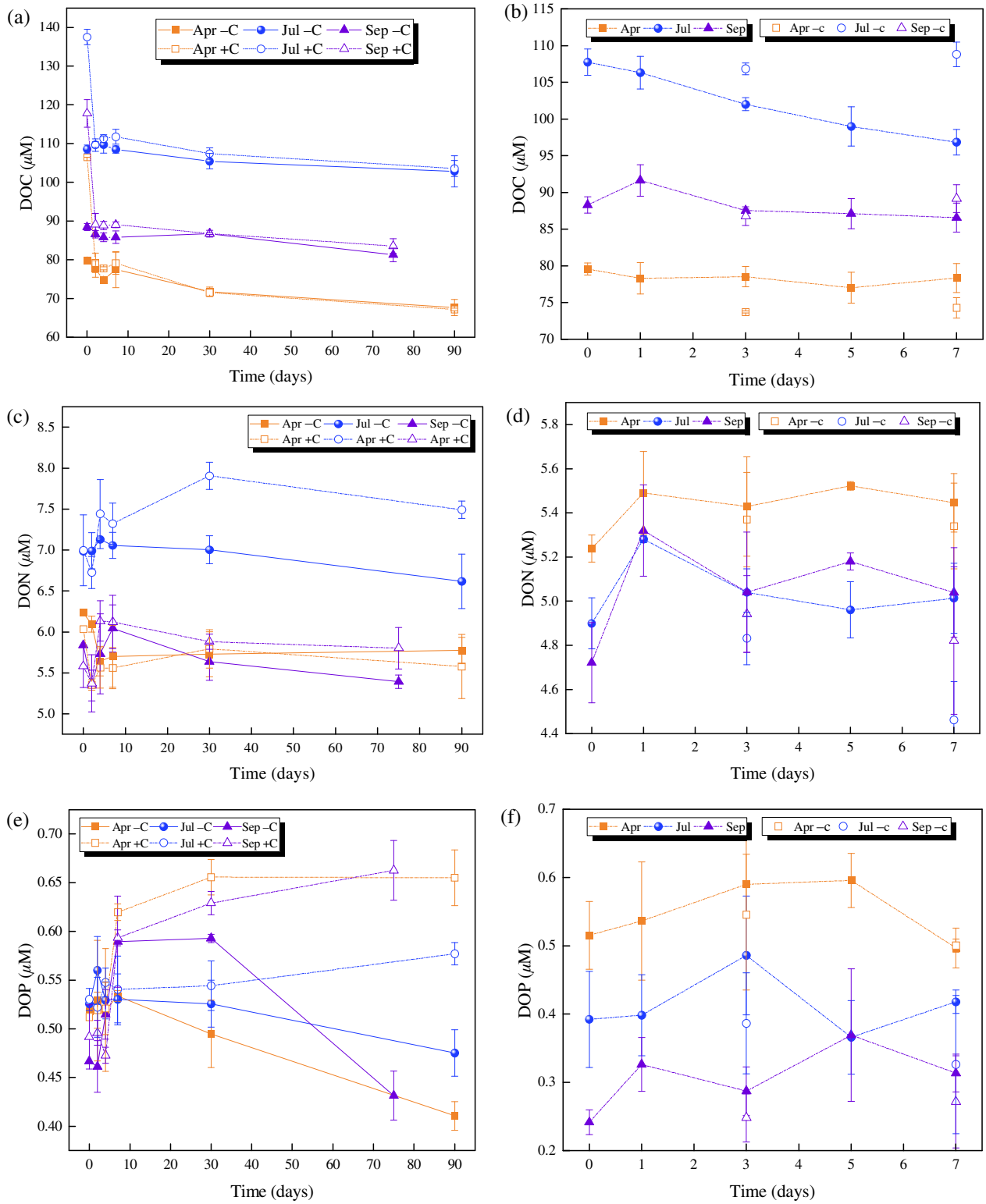

Fig. 2. Changes in dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP) concentrations during the biological and photochemical degradation experiments (Apr, Jul, and Sep). (**a**, **c**, **e**) Biodegradation experiments which contained filtered (0.22 μm) seawater plus 5% unfiltered seawater, with some receiving additional 30 μmol C L^{-1} (+ C) while others did not (− C). (**b**, **d**, **f**) Photodegradation experiment only contained 0.22 μm filtered seawater. Here Apr-c, Jul-c, and Sep-c represent the dark control group in the photodegradation experiments.

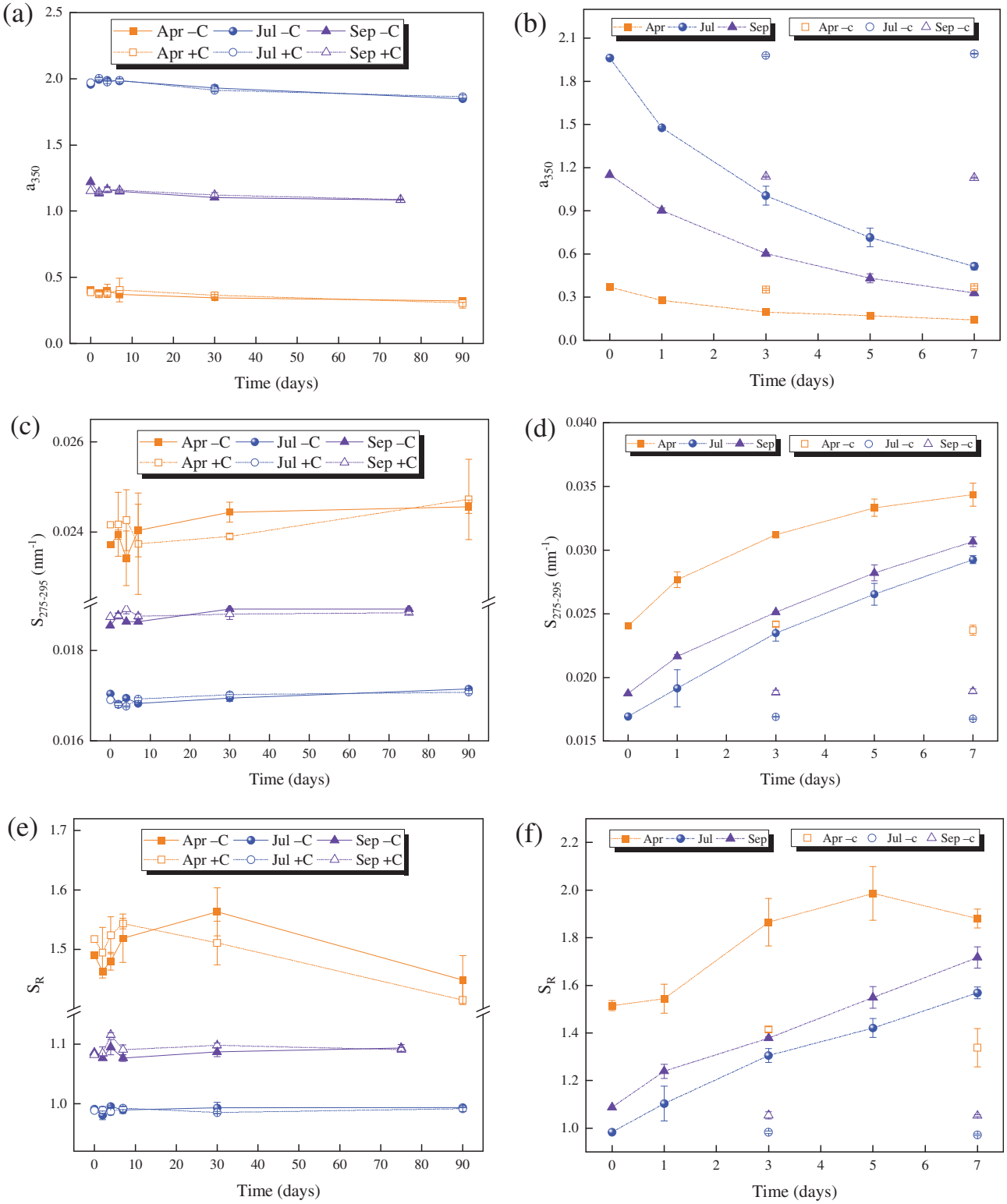

Fig. 3. Changes in colored dissolved organic matter (CDOM) absorption at 350 nm (a_{350}), CDOM spectral slope ratio (S_R), and the carbon specific absorbance at 254 nm ($SUVA_{254}$) during the biological and photochemical degradation experiments. (**a**, **c**, **e**, **g**) Biodegradation, contained filtered (0.22 μm) seawater plus 5% unfiltered seawater, some treatments received an additional 30 μmol C L^{-1} (+ C) while others did not (− C). (**b**, **d**, **f**, **h**) Photodegradation experiment only contained 0.22 μm filtered red seawater. Here Apr-c, Jul-c, and Sep-c represent the dark control group in the photodegradation experiments.

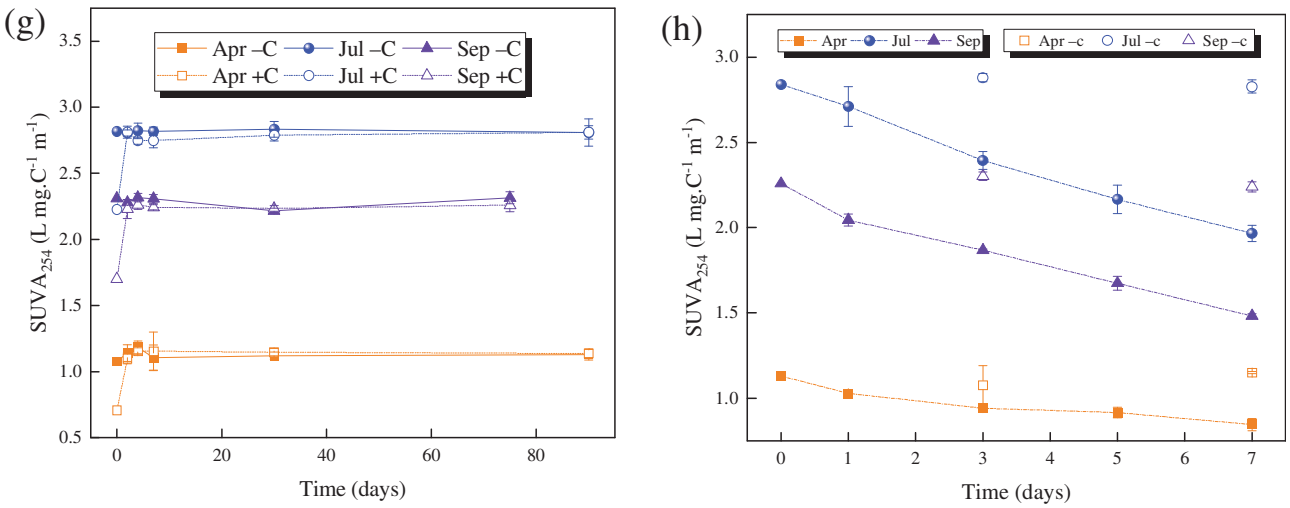

Fig. 3 (Continued)

significant (Supporting Information Table S4). The photoproduction of C4 was largest in the mid-SW monsoon (Fig. 5h).

In our principal component analysis, we found that biodegradation principal component 1 explained 61.1% of the variance, representing the HIX of DOM, and this separated the samples from the three periods (Supporting Information Fig. S7). For the photodegradation experiment, principal component 1 explained 68.1% of all variances and was closely related to the aromaticity of DOM, indicating that the aromaticity gradually decreased with photodegradation (from day 0 to 7), which is consistent with the results for $SUVA_{254}$. In addition, the aromaticity of DOM was positively correlated with the humification degree, and the humification degree also decrease during the photodegradation process, while the mid-SW monsoon sample contained a large amount of terrestrial humic matter components and had higher aromaticity.

Discussion

Biologically driven dynamics of nutrients and DOM

The DOM pool at our site is clearly more bioavailable during the inter-monsoon (around 15% of DOC, 7% of DON, and 21% of DOP), and more refractory during the SW monsoon (5–8% for DOC, not detectable for DON, and 8–10% for DOP). This probably results from the greater contribution of autochthonous marine DOM during the inter-monsoon. The fact that the chlorophyll *a* concentration, fluorescence of protein-like C4, and BIX were all higher in the inter-monsoon than the SW monsoon is consistent with higher rates of planktonic production during this season (Martin et al. 2022). This indicates a potentially higher contribution of freshly produced marine DOM during the inter-monsoon, which can be effectively degraded by microbes (Grunert et al. 2021). In contrast, the higher contribution of humic-rich, terrigenous DOM during the SW monsoon, as indicated by the higher DOC concentrations and values of a_{350}, C1 and C2, and HIX, and lower values of FI, $S_{275–295}$, and $\delta^{13}C_{DOC}$ appears to result in a more refractory DOM pool during this season.

However, even the inter-monsoon DOM pool is less bioavailable compared to the average coastal bioavailability reported in a compilation of mostly temperate and subtropical studies, which is 22% (DOC), 35% (DON), and (70%) DOP (Lønborg and Álvarez-Salgado 2012). The low DOM bioavailability in our samples is particularly notable given our high incubation temperatures (averaging 26.5–27.5°C), which should stimulate microbial degradation rates. However, our bioavailable fractions were also mostly lower than those reported in coastal waters of the Great Barrier Reef, which averaged 16 ± 5% for DOC, 32 ± 4% for DON, and 68 ± 8% for DOP (Lønborg et al. 2018a). This is even though our initial concentrations were comparable to or higher than those reported in the Great Barrier Reef, which ranged between 57 and 84 μmol L^{-1} for DOC, 4.7 and 6.2 μmol L^{-1} for DON, and only 0.16 and 0.28 μmol L^{-1} for DOP (Lønborg et al. 2018a). The higher bioavailable fraction in the Great Barrier Reef might originate from benthic sources, especially corals, which release relatively bioavailable N- and P-rich DOM (Tanaka and Nakajima 2018; Nelson, Wegley Kelly, and Haas 2023). Coral reefs are less densely distributed across the Sunda Shelf than the Great Barrier Reef, and benthic habitats are too limited in extent within Singapore to contribute substantially to the overall ecosystem primary production (Tan, Acerbi, and Lauro 2016). However, the fact that the DOP pool consistently had a higher bioavailability than DOC and DON agrees both with previous studies in coastal waters (Lønborg and Álvarez-Salgado 2012; Lønborg et al. 2018a) and in the open ocean (Letscher and Moore 2015).

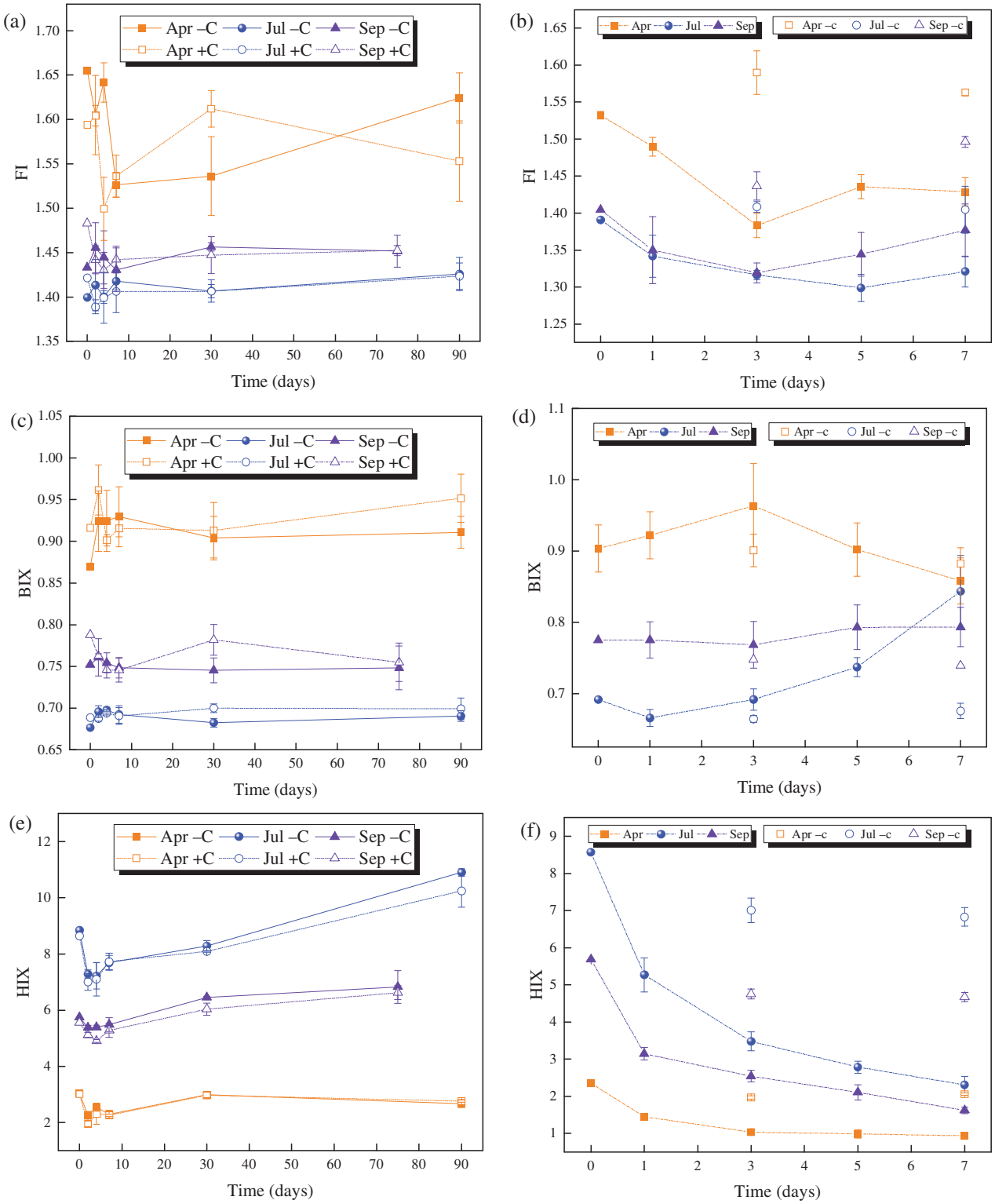

Fig. 4. Changes in fluorescent dissolved organic matter (FDOM) fluorescence indexes (BIX, biological index; FI, fluorescence index; HIX, humification index) in the biological and photochemical degradation experiments. (**a**, **c**, **e**) Biodegradation, contained filtered seawater (0.22 μm) plus 5% unfiltered seawater, with some treatments receiving an additional 30 μmol C L^{-1} (+ C) and others did not (− C). (**b**, **d**, **f**) Photodegradation experiment only contained 0.22 μm filtered seawater. Here Apr-c, Jul-c, and Sep-c represent the dark control group in the photodegradation experiments.

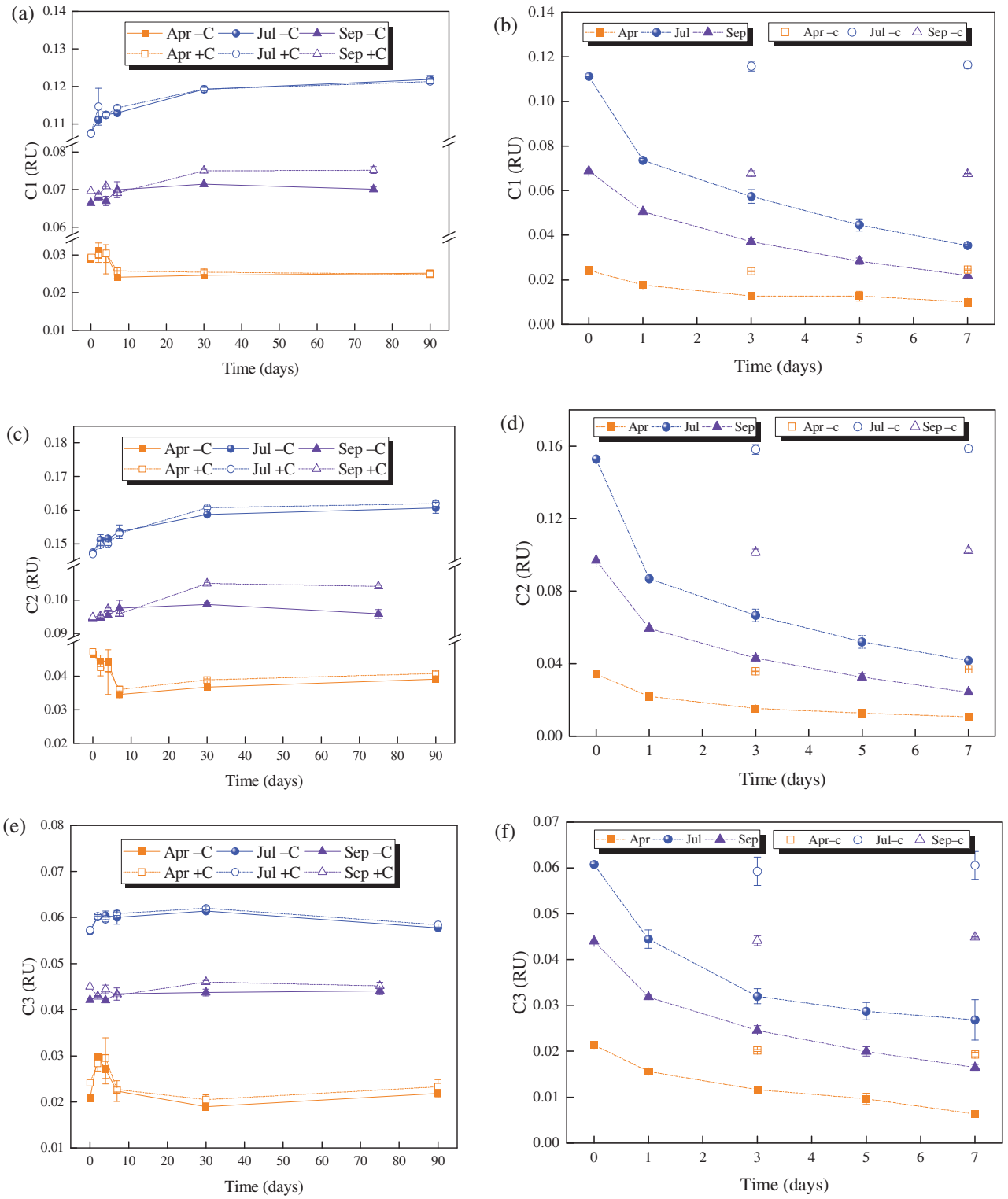

Fig. 5. Changes in the identified four PARAFAC components for the colored dissolved organic matter fluorescence (FDOM) pool in the biological and photochemical degradation experiments. (**a**, **c**, **e**, **g**) Biodegradation, contained filtered (0.22 μm) seawater plus 5% unfiltered seawater, with some treatments receiving an additional 30 μmol C L^{-1} (+ C) and others did not (− C). (**b**, **d**, **f**, **h**) Photodegradation experiment only contained 0.22 μm filtered seawater. Here Apr-c, Jul-c, and Sep-c represent the dark control group in the photodegradation experiments.

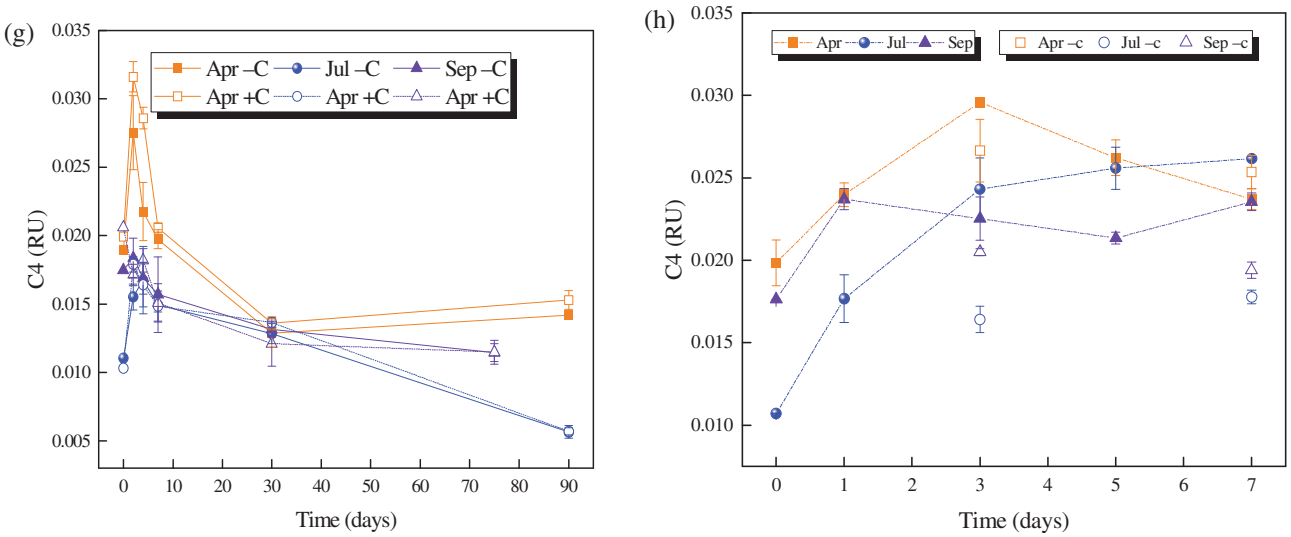

Fig. 5 (Continued)

The high temperatures and sunlight intensities should promote faster bio- and photodegradation of DOM in the tropics than at high latitudes (Fichot and Miller 2010; Lønborg et al. 2018b). This likely leads to the rapid removal of any newly produced labile compounds and promotes refractory DOM accumulation, as seen in the subtropical ocean gyres (Yamashita et al. 2017). Thus, even though the inter-monsoon DOM pool at our study site most likely had a higher contribution of freshly produced material than the other seasons, bioavailable compounds are unlikely to accumulate and thus the DOM bioavailability is not much higher than during the SW monsoon.

We also only found limited or no changes in the CDOM and FDOM properties during the biodegradation experiments. The very minor changes in a_{350}, $S_{275–295}$, and S_R, suggest that the CDOM pool was among the more refractory components of DOM. Interestingly, the three humic-like components (C1–C3) and HIX showed a slight increase throughout the biodegradation experiment in the SW monsoon samples. Possibly, the microbial community produced refractory humic-like DOM during the incubation, as has been suggested in other studies (Chen et al. 2022; Shelton et al. 2022). Moreover, biodegradation removed the more labile protein-like component (C4), likely resulting in a higher relative content of humic substances and an increased humification degree.

The addition of labile carbon can stimulate the degradation of otherwise nondegradable organic matter (Hernes and Benner 2003; Obernosterer and Benner 2004; Logozzo et al. 2021). Relatively few studies have tested the effects of labile carbon addition on marine DOM degradation, with some showing stimulation and others not (Carlson et al. 2004; Lønborg et al. 2018a). We observed no evidence for enhanced DOM removal because of labile carbon addition, and therefore no indication of any priming effect. Our results for the SW monsoon incubations are consistent with Textor et al. (2018), who reported low biodegradability and no priming effect for DOC loss in blackwater rivers from subtropical North America. However, our data also indicate that the dynamics of autochthonous DOM during the inter-monsoon are not influenced by priming effects. Nevertheless, microbial activity clearly was enhanced by the carbon additions, with higher turnover of inorganic nutrients, and production of DON (in SW monsoon) and DOP (in all seasons) relative to the treatments without labile carbon addition. This likely reflects microbial production of refractory DON and DOP during the experiments, although little differences were seen in the CDOM and FDOM properties between the + C and − C treatments, suggesting that any newly produced DOM was not optically active. Previous short-term (24-h) incubations in the Singapore Strait demonstrated that glucose stimulated alkaline phosphatase enzyme activity, which was attributed to heterotrophic microbes (Nichols, Moynihan, and Martin 2023). Our results suggest, however, that this does not result in the degradation of a large fraction of the DOP pool.

Photochemically driven dynamics of nutrients and DOM

Few studies have investigated the photodegradation of DOM in tropical coastal water (Timko et al. 2015; Zhou et al. 2023). Exposure to simulated sunlight led to rapid production of NH_4^+ (Supporting Information Fig. S5). However, the concentrations of DON and DOP remained relatively stable throughout the irradiation period (Figs. 1 and 2). Photodegradation did significantly alter the DOM optical properties, and reduced DOC concentration by up to 10%. This indicates that part of the DOM pool clearly is photolabile. Specifically, the fact that only photochemical processes significantly removed a_{350} (Supporting Information Table S2–S4; Fig. 4), especially during the SW monsoon, while

also increasing the $S_{275–295}$ and S_R, and decreasing the $SUVA_{254}$, indicates the effective sunlight degradation of terrigenous aromatic DOM fractions resulting in decreased apparent molecular weight and aromaticity (Weishaar et al. 2003; Fichot and Benner 2012). This is consistent with our FDOM results, where there was a significant decrease in the content of the three humic-like components (C1–C3) and of HIX during the photodegradation experiments (Supporting Information Table S4; Fig. 5). These changes were most pronounced during the mid-SW monsoon experiment when the contribution of terrigenous DOM was highest. Our data are consistent with previous research showing that sunlight has a more pronounced impact on humic-rich DOM and removes FDOM with longer-wavelength emission (Amaral et al. 2016). However, it appears that DON and DOP are not part of this photolabile humic-rich terrigenous fraction, since we observed only minor variations in their concentrations. This is consistent with the fact that the terrigenous DOM at our study site originates mainly from tropical peatlands, which are nutrient-poor systems (Troxler 2007; Mishra et al. 2021) and would therefore not be expected to supply large inputs of DON or DOP.

Effects of sunlight on DON and especially DOP reactivity have been examined in only a limited number of studies compared to the effects of sunlight on the DOC pool. Photochemical mineralization of DON to DIN has been reported by several studies for natural DOM samples (Bushaw et al. 1996; Wiegner and Seitzinger 2001) and also for DON from wastewater treatment plant effluent (Bronk et al. 2010). Conversely, other studies have reported no photochemical mineralization of DON or DOP to DIN and phosphate (Wiegner and Seitzinger 2001; McCallister et al. 2005).

Partial photodegradation often enhances the subsequent microbial degradation of DOC, but this effect is not consistently observed for natural DON and DOP samples (McCallister et al. 2005). Interestingly, we observed that photodegradation led to an increase in the protein-like FDOM component, which could suggest that part of the DOM was being converted to more biolabile substances, such that photodegradation might stimulate subsequent biodegradation of at least some fractions of the DOM pool in our study area. However, this was not specifically tested in these experiments and therefore needs to be addressed in future research.

Conclusions and implications

Our data provide further insights into DOM cycling in tropical coastal waters, by demonstrating that the DON and DOP as well as DOC pool, in our study area are notably resistant to both biological and photochemical degradation processes. This contrasts with higher DOM biolability reported for other coastal tropical systems such as the Great Barrier Reef (Lønborg et al. 2018a; Carreira, Talbot, and Lønborg 2021). Photochemical lability was chiefly observed for CDOM and for humic-like FDOM components, and for a modest fraction of the DOC pool during the SW monsoon season, but we observed no clear evidence for photochemical degradation of DON or DOP. In contrast, we found that DOP was the most bioavailable fraction, with DOC and DON showing limited or no bioavailability depending on the season. CDOM and FDOM were mostly unchanged during our biodegradation experiment, except for the protein-like FDOM component, which was clearly biolabile. The bioavailability of the DOM pool was furthermore not enhanced by the addition of labile carbon, even though this stimulated the uptake of the inorganic nutrients by the microbial community.

Because the Singapore Strait has consistent and seasonally varying residual currents, we consider our results to reflect wider regional patterns, with the inter-monsoon data characteristic of coastal waters in the shelf sea waters of the southern South China Sea, while the SW monsoon data are characteristic of waters in the Malacca Strait. The importance of our data lies in demonstrating that the DON and DOP pools, despite constituting a large fraction of the total dissolved N and P in these waters, do not contribute a large standing stock of bioavailable nutrients that could fuel primary production. Instead, our results most likely reflect that DOM production and degradation are closely balanced in our study area, where temperature shows very little seasonality (Martin et al. 2022) and ultraviolet radiation is fairly high year-round (Zhou et al. 2023). More generally, we suggest that the low DON and DOP lability could be representative of tropical coastal waters in regions with lower impact of local primary producers, for example, in areas less directly affected by especially benthic primary producer communities such as coral reefs. More research is needed to further expand our understanding of DOM lability, especially for DON and DOP, in a broader range of tropical coastal environments.

Author Contributions

Jiangyong Chu: Designed experiments; conducted experiments and data analysis; interpreted the results; drafted the initial version of the manuscript; revised the paper. Christian Lønborg: Designed experiments; interpreted the results; revised the manuscript. Patrick Martin: Designed experiments; interpreted the results; revised the manuscript.

Acknowledgments

We thank Woo Oon Yee, Heng Su Ping, and Yuan Chen for technical support with the field and laboratory work, and the captain and crew of RV *Galaxea* for help with sample collection. The research was funded by the Singapore Ministry of Education through an Academic Research Fund Tier 2 grant (MOE-MOET2EP10121-0007) and by the National Research Foundation, Singapore, Prime Minister's Office, through the Marine Environment Sensing Network grant (NRF-NRI-2020-MESN), both to Patrick Martin, and by the China

Scholarship Council through an award to Jiangyong Chu (award numbers [2020] 101 and [2021] 2047). During the drafting of the manuscript Christian Lønborg received funding from the Independent Research Fund Denmark Grant 1127-00033B. We are grateful to three anonymous reviewers for constructive criticism that improved the original submission.

Conflicts of Interest

None declared.

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Supporting Information

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

Submitted 12 March 2024
Revised 23 August 2024
Accepted 08 January 2025