LIMNOLOGY AND OCEANOGRAPHY
Letters

LETTER

A stream-to-sea experiment reveals inhibitory effects of freshwater residency on organic-matter decomposition in the sea

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Scientific Significance Statement

We present results from an experiment wherein we assessed decomposition rates of organic matter near the mouth of a low-order freshwater stream and in an adjacent fjord. We also transplanted organic matter from the stream to the fjord to mimic the natural flux of organic matter from land to stream to sea. The sea promoted more-rapid decomposition than the stream, and, interestingly, residency in freshwater slowed subsequent decomposition in the fjord. This transplant study is a useful starting point for better understanding coupled freshwater–marine ecosystems, both of which are crucial components of global carbon cycles.

Abstract

One billion tons of carbon are annually transported to the global ocean, and the fate of this carbon hinges not only on marine processing rates, but also on freshwater processing during downstream transport. Using a cotton-strip assay, we assessed the decomposition of organic matter in marine and freshwater sites and simulated its downstream transport from freshwater to the sea by translocating cotton strips approximately half-way through the freshwater incubation period. We observed faster decomposition in the sea relative to the stream and interestingly, an inhibitory effect of stream incubation on subsequent decomposition in the sea. Total nitrogen content and $\partial^{15}N$ in the cotton strips were both greater in the strips incubated entirely in the sea, suggesting greater microbial activity in the marine habitat. Our results lend needed insights into global carbon cycling, the factors that govern organic-carbon processing, and highlight the importance of connections that exist among some of Earth's major ecosystems.

One billion tons of carbon (C) are annually transported to the global ocean by rivers (Schlünz and Schneider 2000; Li et al. 2017), and the fate of this carbon— such as whether it enters long-term storage in marine sediments or is mineralized by microbes into CO_2 or CH_4— hinges not only on marine processing rates, but also on

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freshwater processing during downstream transport. Once treated as simple transport conduits (Leopold 1994), rivers are now viewed as hotspots in the landscape for biogeochemical activity (*sensu* McClain et al. 2003), including organic-matter retention and transformation (Webster et al. 1999; Tank et al. 2010; Costello et al. 2022). Microbial activity in rivers is typically maintained by well-oxygenated water, constant nutrient delivery via stream flow, and a supply of organic matter from overland transport and direct infall. As a result, both the quantity and quality of organic matter that enters the sea and other aquatic ecosystems is strongly modulated by riverine processes.

About 20% (0.2 Pg C yr^{-1}) of all terrestrial C that enters the oceans is in the form of particulate organic carbon (POC) (Meybeck 1993), 50% of which are colonized and remineralized by microbes (Hedges and Keil 1995) and further processed by marine organisms (Fairbanks et al. 2018). A similar amount of the exported terrestrial POC is buried in marine sediments (Dean and Gorham 1998). To date, assessments of *in situ* organic-C turnover rates have relied mostly on assessments of dissolved organic C (DOC, often defined as < 0.2 μm in size) (Catalán et al. 2016), which greatly differs in particle size and degradation pathways from the larger POC (ranging from 0.2 μm to > 1 mm in size) (Jiao et al. 2014). DOC is typically processed more slowly in marine waters than in freshwaters, even though salinity has been suggested as an important catalyst for organic-C decomposition in coastal wetlands (Stagg et al. 2018). Differences in the quality of DOC pools, such as a higher prevalence of refractory C in marine than in freshwater ecosystems, may explain some of the differences in turnover times in recent meta-analyses (Catalán et al. 2016). It remains unclear, however, whether terrestrially derived coarse POC (CPOC, > 1 mm in size), such as leaf litter or similar substrates, has a similar fate to that of DOC (Hedges et al. 1997), since results from such experiments are few and do not show consistent patterns. More important still, particularly to the understanding of global C cycles, freshwater residency of CPOC could have an effect on subsequent marine decomposition (Guenet et al. 2010), but the significance of this and whether it positively or negatively impacts marine-C turnover, remains unknown.

To close these knowledge gaps, we used an identical field assay in marine and freshwater sites to evaluate the capacity of these two ecosystems to decompose CPOC. In addition, we simulated the downstream transport and processing of CPOC from freshwaters to the sea by deploying the assay at stream sites for approximately half of the incubation period before transplanting some of the experimental materials to marine sites. We also used stable isotopes of C and nitrogen (N) to help track the incorporation of marine and terrestrial nutrients by microbes into our standardized substrate. With this research, we wish to highlight the biogeochemical connections that exist among Earth's major ecosystems and the role of streams in global C cycles.

Methods

Field sites

We conducted the study in Kaldfjord, a fjord near Tromsø, Northern Norway (69°44′N 18°37′E) at the mouth of Urdaelva, a second-order sub-Arctic mountain stream. The stream and the fjord have sustained minimal human impacts, and the catchment is characterized by the presence of small birch trees (< 3 m tall *Betula pubescens*) and shrubs in the riparian zone. Kaldfjord is an ice-free fjord about 2 km wide and 15 km long, with steep carved sides that quickly descend to 150 m depth in front of the river mouth. Its water is characterized as a modified variety of Norwegian coastal water, with salinity in autumn at around 32–33 ppt in its surface waters (0–5 m) and a near depletion of macronutrients in late summer and autumn (Jones et al. 2020).

Deployment of the organic-matter assay

In both the stream and sea, we deployed a cotton-strip assay using cotton strips (8 × 2.5 cm) made from a single bolt of "Artist's fabric" (Fredrix-brand heavy-weight unprimed 12-oz. cotton, Style #548, Fredrix, Lawrenceville, Georgia, USA; Slocum et al. 2009; Tiegs et al. 2013). Cotton strips consist of ~ 94% cellulose, which is a polymer of $C_6H_{10}O_5$ that contains 410 mg C per 1 g of cellulose and may also contain small amounts of N in the form of proteins. Prior to incubation, the strips had ~ 41% C, a similar level to that expected from the cellulose molecules alone and small amount of N, corresponding to ~ 2 mg N g^{-1} cotton strip (0.2% of the strip mass).

Before incubating the strips in the field, we inserted a cable binder through a small opening created between threads near the end of each strip, and the binder was then fastened to a nylon cord. In both stream and sea, replicate cotton strips were distributed across four groups. In the stream, each group was deployed in an individual pool, where the two ends of the cord were attached to individual iron bars that were hammered into the substrate. Each pool contained six cotton strips placed 10 cm apart. Pools were located ~ 20 m upstream from the confluence of the stream with the sea at 2 m above sea level at the highest tide. In the sea, we deployed strips on the fjord slope, 30 m from the stream mouth, at 2 m depth during the lowest tide. We attached these strips to a nylon cord tied to weights on both ends and at the middle of the cord and placed them in groups of four, with 10 cm between strips. We repeated this procedure four times at every 1 m along the cord. Anchoring and heavy weights assured that both stream and sea strips were kept near the benthos. The fjord slope quickly reaches > 50 m in depth, and the choice of 2 m was both due to logistic reasons and based on field observations that indicate accumulation of terrestrial organic matter at those depths.

We deployed cotton strips at stream and marine sites at the beginning of autumn (08 October 2017). We retrieved eight replicates (two from each stream pool/marine group) after 15 and 41 d, rinsed them under tap water, and oven-dried

them at 60°C for 24 h. In addition, we retrieved two strips from each stream pool at 15 d and immediately transferred them to the sea, incubating them among the remaining strips on the sea bottom until final retrieval at 41 d. We recorded temperature hourly in both the stream and sea using HOBO Pendant Temperature loggers (Onset Computer Corporation, USA).

Tensile-strength measurement

We analyzed cotton strips for the loss of tensile strength (the resistance of the material to tearing under strain), a process that reflects the microbial catabolism of cellulose (Imberger et al. 2010; Tiegs et al. 2019). In the lab, we determined tensile strength by placing the ends of each cotton strip in the jaws of a Mark-10 MG100 tensiometer mounted to a motorized test stand and pulling them at a rate of 20 mm min^{-1} (Tiegs et al. 2013). Decomposition of organic material is expected to follow a negative exponential pattern (Petersen and Cummins 1974) and can be described using the equation: $-k = \ln(S_t/S_0)/t$, where k is the tensile decomposition rate, S_t is the tensile strength at t, S_0 is the initial

tensile strength, and t is either time in days for time-corrected values or the sum of daily average temperatures for temperature-corrected values. This latter approach accounts for the effects of temperature differences among sites on decomposition rates. We estimated initial tensile strength (S_0) by determining the mean tensile strength of 10 randomly chosen cotton strips that were identical to the others except that they were not incubated in the field. We also calculated the specific decomposition rates for the period between $t = 15$ and $t = 41$ for the cotton strips transferred from the stream to the sea (i.e., the marine phase of decomposition of those strips), and the equivalent period for the strips only incubated in the sea. For this component of the experiment, initial tensile strength (S_0) was calculated as the average tensile strength at $t = 15$ in the stream for the stream-to-sea strips and $t = 15$ in the sea for the sea-only strips.

Nutrient concentration and stable isotope analysis

To determine the C and N content of the cotton strips and ∂^{13}C and ∂^{15}N isotope content, we cut small discs from multiple locations across the surface of each cotton strip after
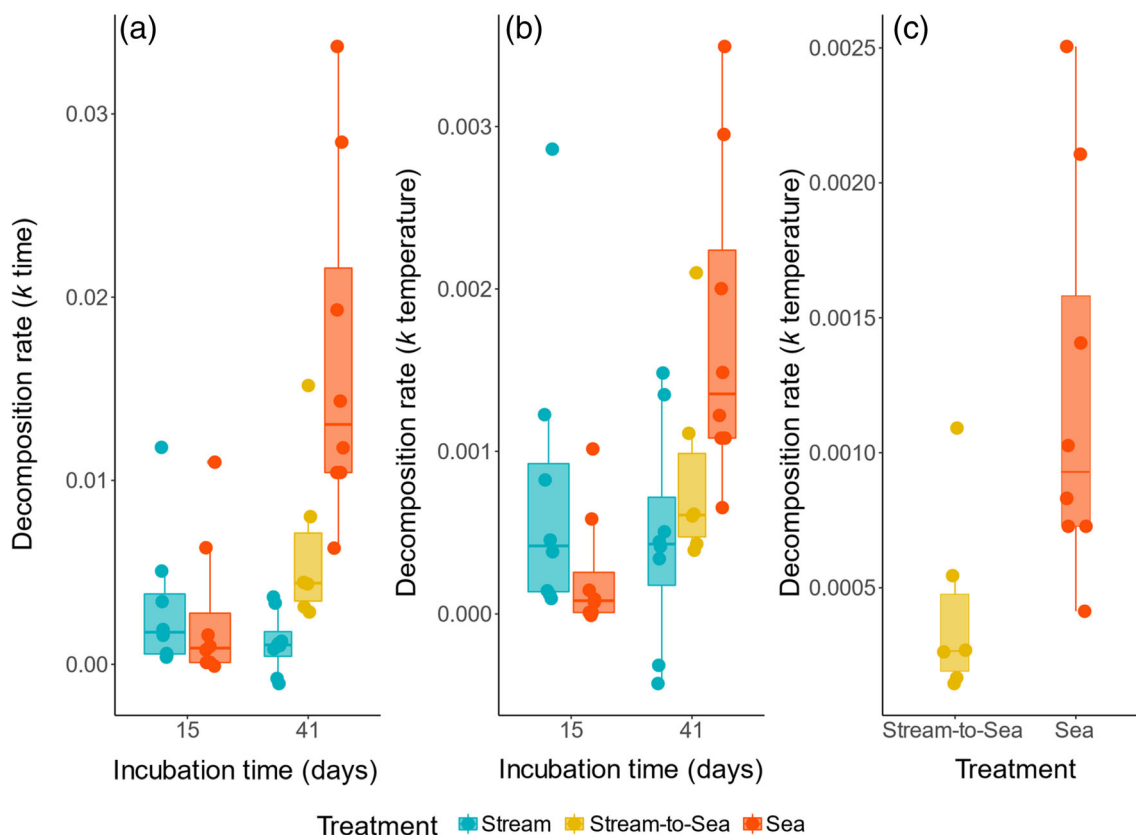

Fig. 1. Cotton-strip decomposition rates by (**a**) time in days and (**b**) by accumulated degree days for all the retrieval times, and (**c**) by accumulated degree days calculated only for the 26 d of the sea-phase of the stream-to-sea strips and the same 26 d of the sea-only strips. By 41 d, we observed the most rapid decomposition in the sea-only cotton strips, followed by the stream-to-sea strips, and with the slowest decomposition being observed in the stream-only strips. The boxes show the lower and upper quartiles, the whiskers represent 1.5 × the interquartile range; the thick lines are the median.

tensile-strength measurement and packed them into tins before shipping the samples to the University of California, Davis Stable Isotope Facility. We weighed samples to the nearest 0.001 mg, with target weights being approximately 1.25 mg for C and 15 mg for N. We analyzed C and N stable isotopes with an elemental analyzer front-loaded to a mass spectrophotometer.

Data analyses

Because data for stream-to-sea strips are only available at 41 d, we analyzed decomposition rates with two separate ANOVAs, one for the strips retrieved at 15 d of incubation (two levels: stream-only and sea-only) and a second for the strips retrieved at 41 d of incubation (three levels: stream-only, stream-to-sea, and sea-only) using the *aov* function in the R *stats* package version 4.0.5 (R Core Team 2021). We used a similar approach to investigate the sea-phase of the decomposition of the stream-to-sea strips and compared it with the equivalent time for the sea-only strips. We corrected decomposition rates for time (k_{time}) and for temperature ($k_{temperature}$) and analyzed them separately. For determination of $k_{temperature}$, we substituted degree days (i.e., the sum of mean daily temperatures during the incubation period) for time in the exponential

decay model presented above. This procedure normalizes the effects of temperature between sites, allowing for assessment of drivers other than temperature on decomposition. Further, we used post-hoc Tukey's honestly significant difference (HSD) test to confirm potential differences between the three treatment groups at 41 d of incubation. We analyzed C and N concentrations and stable isotope delta values in the cotton strips similarly using ANOVA.

Results

Water temperature

Temperatures were warmer and less variable in the marine habitat. Sea-water temperature at deployment and retrieval of the cotton strips was 10.7°C and 7.7°C, respectively (mean ± SD = 9.4°C ± 0.7), whereas stream water temperature at deployment and retrieval was 5.7 and 0.12°C, respectively (mean ± SD = 2.4°C ± 1.5). At 15 d of incubation, the sum of daily mean temperatures was 162°C and 62 °C in the sea and stream, respectively. At 41 d of incubation (the end of the experiment), the sum of daily mean temperatures was 395°C and 101°C in the sea and stream, respectively. Strips transplanted to the sea after 15 d of incubation in the stream experienced
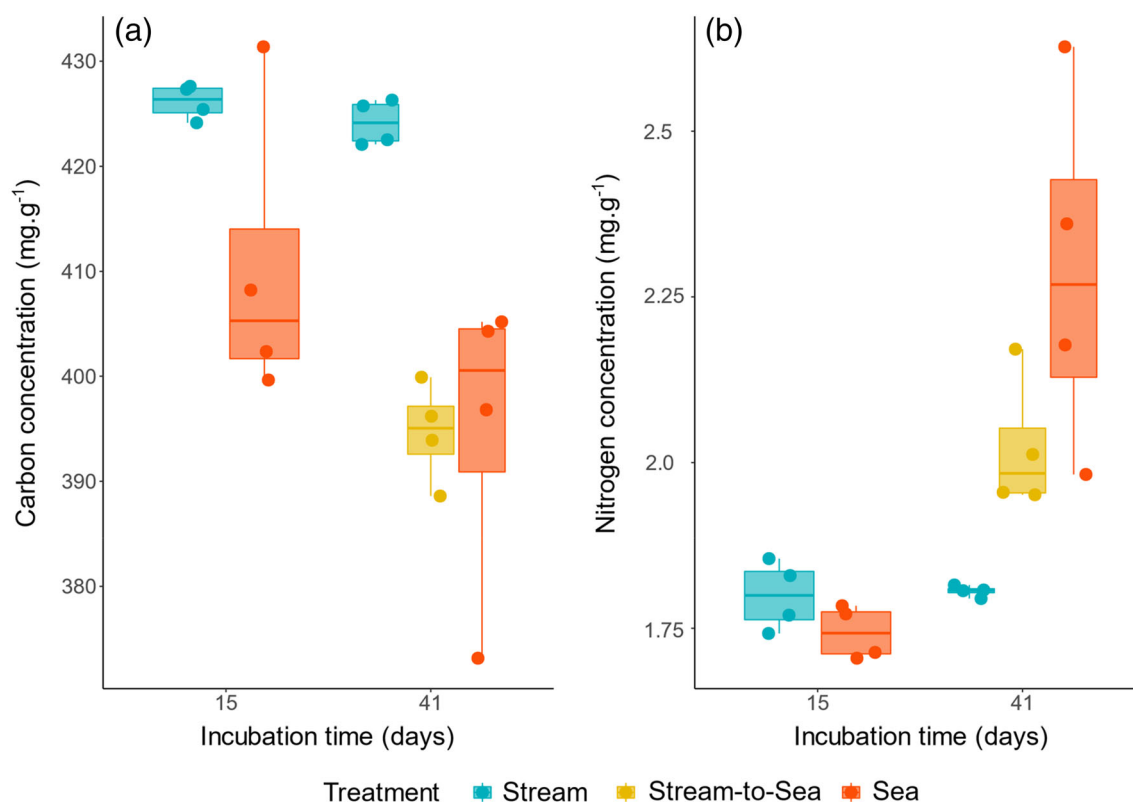

Fig. 2. Carbon (**a**) and nitrogen (**b**) concentration (in mg/g) in cotton strips incubated in the stream and sea for 15 and 41 d and transplanted to the sea (stream-to-sea) after 15 d in the stream. At 41 d, there was greater N content in the sea-only cotton strips, followed by the stream-to-sea strips, with the least N content in the steam-only strips. The boxes show the lower and upper quartiles, the whiskers represent 1.5× the interquartile range, and the thick lines are the median.
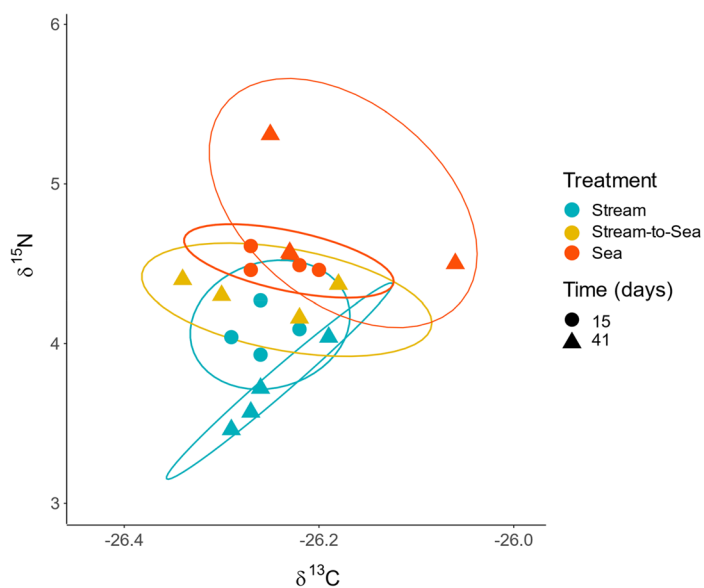
Fig. 3. Carbon and nitrogen stable isotope biplots showing concentrations of heavy isotopes relative to light isotopes, expressed as delta values. Cotton strips were exposed for 15 and 41 d in the stream and sea or transplanted to the sea after 15 d in the stream (stream-to-sea). Ellipses are based on assumptions of *t*-distribution of the data using the *stat_ellipse* function in the R package ggplot2 (Wickham 2016) and are plotted to aid with visualization only.

296.5°C in total (64°C while in the stream and 232.5°C while in the sea).

Tensile strength and decomposition rate

Patterns of decomposition rates between the stream and the sea were similar, regardless of whether time- or temperature-corrected rates were analyzed (k_{time} and $k_{temperature}$, respectively). Sea-only and stream-only cotton strips had similar decomposition rates at 15 d (both k_{time} and $k_{temperature}$: $F_{2,19} < 1.1$, $p > 0.34$) (Fig. 1a,b). Decomposition rates differed, however, between those treatments at 41 d of incubation (both k_{time} and $k_{temperature}$: $F_{2,19} > 5.3$, $p < 0.015$) (Fig. 1a,b). At 41 d, the sea-only k_{time} was 20 times greater and the $k_{temperature}$ was five times greater than the stream-only strips. Cotton strips first incubated in the stream and then transplanted to the sea (the stream-to-sea strips) had slightly faster decomposition rates than the steam-only strips at 41 d but slower decomposition rates than the sea-only strips during the same 41 d (Tukey HSD between sea-only and the other two treatments: $p < 0.02$) (Fig. 1a,b). Decomposition rates during the marine phase of the stream-to-sea strips and the equivalent time for the sea-only strips confirmed a faster decomposition for the strips that had only been incubated in the sea vs. the strips that were transplanted from the stream (both k_{time} and $k_{temperature}$: $F_{1,12} > 6$, $p < 0.03$) (Fig. 1c).

C and N cycling in the cotton strips

Analyses of C content of the cotton strips indicated differences between treatments, with the stream-only treatment having greater C concentration than the other treatments both at 15 d of incubation ($F_{2,9} = 4.63$, $p = 0.041$) and at 41 d of incubation ($F_{2,9} = 12.61$, $p = 0.002$) (Fig. 2a). We did not find a clear difference in N concentration between stream-only and sea-only treatments at 15 d of incubation ($F_{2,9} = 1.76$, $p = 0.227$), but at 41 d, stream-only strips had much lower N concentration than the other treatments ($F_{2,9} = 8.08$, $p = 0.01$) (Fig. 2b).

Carbon and nitrogen isotopes

Analyses of C and N isotopes indicate that the sea-only strips had higher $\partial^{15}N$ than stream-only strips at 15 d of incubation, and higher than both sea-only and stream-to-sea strips at 41 d of incubation (both $F_{2,9} > 14.5$, $p = 0.001$). We did not see any clear difference in $\partial^{15}N$ between sea-only and stream-to-sea strips at 41 d (Tukey's HSD: $p > 0.12$). In addition, we did not see clear differences in $\partial^{13}C$ across the treatments in both 15 and 41 d of incubation (both $F_{2,9} < 1.09$, $p > 0.38$) (Fig. 3).

Discussion

We deployed an identical organic-matter decomposition assay in freshwater and marine habitats and found considerably faster decomposition rates in the sea and an inhibitory effect on decomposition rates for cotton strips that were first incubated in freshwater and then transplanted to the sea. This experiment helps to fill a critical gap in the literature given the lack of direct comparisons between the functioning of freshwater and marine systems (Hedges et al. 1997; Weyhenmeyer et al. 2012; Kothawala et al. 2021).

Streams are often understood as being biogeochemical hotspots in the landscape, with stream flow providing greater rates of nutrient delivery to stream microbial communities relative to other aquatic habitats. Streamflow should, therefore, be particularly effective at stimulating the decomposition of nutrient-poor CPOC, such as that used in our cotton-strip assay. Even so, our comparative field experiment found that CPOC can have a faster decomposition rate in coastal marine waters than in streams, especially after accounting for differences in temperature. Similar comparisons in the literature were, in aggregate, not conclusive. Bierschenk et al. (2012) found higher rates of cotton strip decomposition in streams than in marine sites, whereas Feio et al. (2021) found highest decomposition rates of natural leaf litter in estuarine zones than in headwater streams, and Franzitta et al. (2015) showed contrasting patterns of decomposition rates among three plant species along a salinity gradient from freshwater to saline water.

More importantly, however, our cotton-strip transplant experiment indicates that CPOC residence in freshwater can have an inhibitory effect on subsequent marine processing rates. The mechanisms behind this inhibitory effect are not known but may include osmotic stress associated with the movement of a freshwater community to a saline environment (for a review on the

effects of salinization in freshwaters, see Canhoto et al. 2021), thus delaying the decomposition process, or growth of autotrophs, which can have a negative effect on CPOC decomposition in both coastal marine sediments (Gontikaki et al. 2013) and streams (Elosegi et al. 2018; Halvorson et al. 2019). The greater N immobilization in our marine strips is indicative of greater microbial activity relative to strips incubated in the stream, and evidence that marine resources were being incorporated into the substrate. Furthermore, the stream strips are characterized by lighter isotope values as the incubation period progresses, whereas the marine strips become characterized by heavier isotope values at the same time, providing further evidence of more-rapid microbial processing in the sea relative to the stream or simply a lower N immobilization in the freshwater strips. This difference could be indicative of greater biomass of autotrophic organisms in the stream (Feio et al. 2021), but microbial analyses are needed to better illuminate the biological mechanisms and characteristics behind these colonization dynamics and the mechanisms for the inhibitory effect of the stream residency.

Cotton consists of nearly 95% cellulose, the most abundant organic polymer on the planet and the primary constituent of plant litter. Although the proportion of cellulose export to the oceans is unknown, cellulose is a form of organic C that is highly relevant for global C cycling and riverine food webs and is a component of organic-C transport to the global ocean. Cotton strips have also been used in hundreds of streams and other habitats across the planet (Tiegs et al. 2019), providing a substantial set of reference values to which decomposition rates can be directly compared. Tiegs et al. (2019) found a mean decomposition rate per day (k_{time}) value in boreal streams of 0.0062, with a range of 0.0018–0.031. At 41 d, the mean k_{time} of our stream-only strips was 0.0012, while the marine-only strips k_{time} was 0.017, indicating that the stream used in this study lies below the lower range of values for boreal systems. Although we expect plant-litter decomposition rates to differ from those found here using cotton strips, they have been shown to track the relative decomposition rates of leaf litter across habitats (Tiegs et al. 2007). The data presented here are a step toward understanding the relative organic-matter decomposition rates across ecosystems, helping with the needed integration of methods across disciplines currently advocated for in the literature (Kothawala et al. 2021).

Our study was conducted in a small mountain stream flowing to a fjord in northern Norway. This is in contrast to the majority of global studies analyzing and estimating the flow and fate of organic C from rivers to the sea, which normally investigate only the largest rivers on Earth (Meybeck 1993; McClelland et al. 2008). Many regions, however, lack large rivers, and a key source of terrestrial organic matter is from considerably smaller streams. Small streams are also more likely to export more-labile C to the oceans because of the limited time for completing full degradation of POC during the freshwater residency compared to large rivers, where POC resides much longer.

Our results indicate that organic-matter residency in small streams can slow subsequent decomposition in the sea. A key implication of this inhibitory effect is that it increases the likelihood that the CPOC enters long-term marine-storage pools. Understanding the coupling between terrestrial, freshwater, and marine ecosystems and how decomposition and mineralization of terrestrially derived organic substrates is affected during their residency in these ecosystems is needed to improve current global C budget models (Aufdenkampe et al. 2011). Future work is still needed to determine the degree to which these results apply to other systems, including small streams draining into estuaries, reservoirs, and lakes given the importance of these systems to global carbon cycles and as sources of greenhouse gas emissions. Lastly, given the profound impacts that human activities have on freshwaters, such as nutrient loading and warming, anthropogenic changes to organic matter during its residency in freshwaters will likely have implications for the fate of C once it enters marine habitats and other ecosystems downstream.

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