



Seasonal patterns in riverine carbon form and export from a temperate forested watershed in Southeast Alaska

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Received: 21 February 2024 / Accepted: 14 August 2024 / Published online: 23 August 2024
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Abstract Riverine export of carbon (C) is an important part of the global C cycle; however, most riverine C budgets focus on individual forms of C and fail to comprehensively measure both organic and inorganic C species in concert. To address this knowledge gap, we conducted high frequency sampling of multiple C forms, including dissolved organic C (DOC), inorganic carbon (as alkalinity), particulate organic C (POC), coarse particulate organic C (CPOC), and

invertebrate biomass C across the main run-off season in a predominantly rain-fed watershed in Southeast Alaska. Streamwater concentrations were used to model daily watershed C export from May through October. Concentration and modeled yield data indicated that DOC was the primary form of riverine C export (8708 kg C/km²), except during low flow periods when alkalinity (3125 kg C/km²) was the dominant form of C export. Relative to DOC and alkalinity, export of particulate organic C (POC: 992 kg C/km²; CPOC: 313 kg C/km²) and invertebrates (40 kg C/km²) was small, but these forms of organic matter could disproportionately impact downstream food webs because of their higher quality, assessed via C to nitrogen ratios. These seasonal and flow driven changes to C form and export likely provide subsidies to downstream and nearshore ecosystems such that predicted shifts in regional hydroclimate could substantially impact C transfer and incorporation into aquatic food webs.

Responsible Editor : Steven J. Hall

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10533-024-01175-7>.

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Keywords Riverine carbon export · Biogeochemistry · Hydrology · Organic matter stoichiometry

Introduction

The conveyance of carbon (C) from watersheds to the ocean is an essential component of global C cycling (Cole et al. 2007) and is currently estimated at 0.9 Pg

C/yr (Drake et al. 2018). The dominant forms of C exported laterally from watersheds are typically dissolved organic C (DOC) and inorganic C (Drake et al. 2018; Chaplot and Mutema 2021). However, the form of riverine C export (e.g., dissolved vs. particulate, organic vs. inorganic) can vary substantially by region and can determine the role and fate of C in recipient aquatic ecosystems (e.g., pH and buffering, energy source, sedimentation; Kandasamy and Nath 2016; Tank et al. 2018). Despite the importance of riverine C to the terrestrial ecosystem C balance, many watershed-scale export studies have only focused on one or two forms of C, typically dissolved and particulate organic C (DOC or POC), leaving other forms of C unquantified (e.g., de Wit et al. 2015) and thus, underestimate total watershed C export. Given this gap, better accounting of a full suite of C forms would provide a more complete picture of the riverine C budget of forested watersheds (e.g., Butman et al. 2016).

In many coastal regions, watersheds contribute substantial amounts of carbon to marine ecosystems (Ward et al. 2017; Qui et al. 2023). The form and magnitude of these carbon fluxes can determine their fate in marine ecosystems. Fluxes of inorganic C, for instance, can react with water and bicarbonate to alter the buffering capacity of coastal waters (Hauri et al. 2020). Watershed export of dissolved organic matter is a reduced source of C, providing energy for heterotrophic microbial communities (le Fouest et al. 2013; Woodland et al. 2015). Particulate forms of organic C and drifting stream invertebrates may enter the food web at a higher trophic level, providing energy for benthic consumers (Attrill et al. 2009), filter feeders (Antonio et al. 2010), zooplankton (Harfmann et al. 2019) and would likely be consumed by higher consumers, such as nearshore fishes (Whitney et al. 2018). Different forms of organic C could also undergo processes like photochemical breakdown (Maavara et al. 2021), flocculation (Khoo et al. 2022), or add to the pool of stable oceanic C (Medeiros et al. 2016) based on their structure. Thus, effects of terrestrial subsidies on stream and nearshore ecosystems are likely influenced by the quality, magnitude, and timing of C fluxes (Bauer et al. 2013). However, few studies have simultaneously examined all these factors in the same watershed limiting our understanding of watershed-scale C budgets and the interactive effects that differing forms of C may have on the

ecological and biogeochemical processes of recipient aquatic ecosystems (Fig. 1).

Utilization of organic C in recipient ecosystems will also depend on the “quality” or lability of exported organic matter (OM) (Marcarelli et al. 2011). Different forms of OM (e.g., dissolved organic matter, particulate organic matter, and coarse particulate organic matter; DOM, POM, and CPOM) may have different fates based on their quality (Hessen et al. 2013) and the physicochemical properties of the recipient environment (Ward et al. 2016). Quality is often described in terms of bulk carbon to nitrogen ratio (C:N), with a lower C:N indicating higher quality and vice versa. For instance, watershed DOC has been shown to have relatively high C:N relative to particulate organic matter and aquatic organisms (Islam et al. 2019; Dunkle 2022). In turn, watershed fluxes of higher quality OM could have impacts on recipient ecosystems disproportionate to their availability.

Here, we quantify the magnitude, composition, quality, and timing of riverine C export from a temperate forested watershed in coastal Southeast Alaska to determine how the relative contribution of different forms of C changes seasonally. The prevalence of small, steep undeveloped coastal watersheds paired with abundant precipitation and C dense forests makes Southeast Alaska an ideal location to study biogeochemical linkages between the land and ocean (Edwards et al. 2021). High frequency sample collection from May through October allowed us to model daily and seasonal yields of four different forms of organic C (DOC, POC, coarse particulate organic C, and drifting aquatic invertebrates) and inorganic carbon (alkalinity). Furthermore, we compared C:N of the different forms of OM exported from the study watershed. To our knowledge, watershed export of these five different forms of C have not been simultaneously compared in a single study.

Based on previous work in the region (Stackpoole et al. 2017; Hood et al. 2020; Fellman et al. 2021), we expected that DOC would be the primary C export during our study period, except during high flow events when abundant POC and invertebrates can be transported to surface water via saturation-excess overland flow and floodplain inundation (Dhillon and Inamdar 2014; Power and Rainey 2000). Little work has been done to quantify

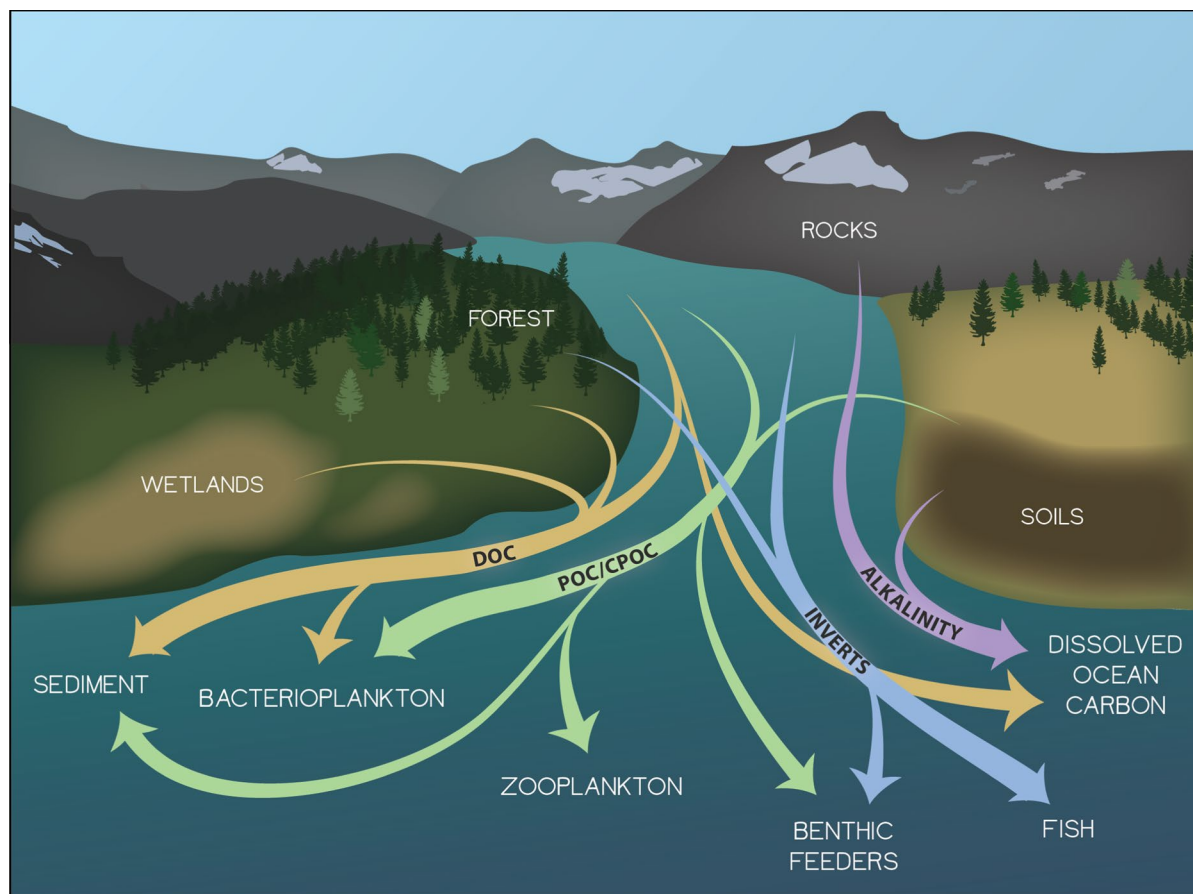


Fig. 1 Conceptual figure outlining potential terrestrial and freshwater sources and nearshore fates for the different forms of C exported from watersheds in Southeast Alaska. Sources

and fates of carbon are drawn from multiple studies as cited and the size of arrow does not indicate any relative value

exports of alkalinity, although we expected dissolved inorganic C (DIC) to contribute relatively more to total C concentrations during baseflow because of increased groundwater contributions to stream discharge (Cole et al. 2007; Dinsmore and Billett 2008). Further, we expected that the quality or bulk C:N for each pool of OM will decrease as a function of increasing concentration where ratios of DOC to dissolved organic N (DON) would be the highest (lowest quality) followed by POC:PON and CPOC:CPON (highest quality). If so, this pattern would create a temporal gradient of OM bioreactivity where periods of high OC export would be associated with lower quality OM (DOC) and periods of low OC export with higher quality OM (CPOM and invertebrates).

Methods

Site description

The study watershed was upper Kaxdigoowu Héén (also known as Montana Creek), located near Juneau, Alaska, USA (Fig. 2). Juneau has a mean annual temperature and precipitation of 5.6 °C and 170 cm, respectively at the Juneau International Airport (NOAA Climate Normals 1991–2020). Kaxdigoowu Héén is typical of the region in that it is small and steep, with an area of 9.5 km² with an average relief of 18° (Edwards et al. 2021). Our study site was approximately 8 km (straight line distance) from point to point and approximately 9.3 km in stream length from its tidally influenced outlet in the Mendenhall River. Kaxdigoowu Héén has no glacial coverage,



Fig. 2 Map of Kaxdigoowu Héen watershed with the sampling location indicated by the yellow star and the National Weather Service stream gauge indicated by the green star

but seasonally accumulates snowpack in the upper reaches of the watershed. Landcover is dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forest (85% landcover) and by organic carbon-rich peatlands (7% landcover). However, the watershed also contains alpine tundra, with exposed bedrock, poorly developed soils, and sparse vegetation dominated by alders (*Alnus* spp.). The watershed supports anadromous runs of Pacific salmon (*Oncorhynchus* spp.) that spawn throughout the summer and early autumn.

Field methods

We collected streamwater ($n = 65$) and drift samples (consisting of CPOC and drifting macroinvertebrates)

($n = 73$) at least once per week during periods of baseflow and up to twice per day for 1–3 days during high flow events from late April through October 2021. High flows were defined as a doubling or more in discharge from baseflow to peak flow. This sampling period was selected because >70% of the total annual runoff from the watershed occurs during this period (Fellman et al. 2014b). Streamwater grab samples were analyzed for DOC and total dissolved nitrogen (TDN), nitrate (NO_3^- -N), and ammonium (NH_4^+ -N). Samples were field-filtered through a pre-combusted (450 °C for 4 h) 0.7 μm Whatman glass fiber filter (GF/F) into pre-combusted glass vials for DOC/TDN and into acid-washed high density polyethylene bottles for inorganic N. Unfiltered streamwater samples for alkalinity (collected with

no headspace), total suspended solids (TSS), and stable water isotopes ($\delta^{18}\text{O}$) were also collected and processed within 24 h of collection. One snow and two rainfall samples were collected for $\delta^{18}\text{O}$ analysis to capture the range in endmember values for water sources contributing to streamflow (Riitti-Shati et al. 2000; Fellman et al. 2014a). These reference samples were collected opportunistically, with rain collected using a funnel with a table tennis ball in the funnel to reduce evaporation, while snow was melted in a plastic bag.

Stream drift samples were collected in a square drift net (adapted from Fellman et al. 2023; 30 × 30 cm, 250- μm mesh) fixed just above (<5 cm) the stream bed with rebar that was pounded into the stream bed. The drift net was set in approximately the same well-mixed location (stream riffle during all sample events) within the stream during each sample event. Set time varied from 5 to 120 min depending on flow, with shorter set times under high flow conditions to avoid net clogging and backflow (Muehlbauer et al. 2016). Stream velocity was measured at the beginning and end of the set with a handheld stream flowmeter (Geopacks ZMFP51) and was used to calculate the volume of water sampled. Drift net material was rinsed into a 250- μm sieve and stored in a plastic bag with 95% ethanol until processing in the laboratory.

Stage height was measured using a pressure transducer (In-Situ Level TROLL 500, Fort Collins, Colorado, USA) recording measurements at 15-minute intervals across the study period. Discharge was measured 20 times throughout the season under variable flow conditions with a SonTek Flowtracker (San Diego, California, USA) current meter. A stream-discharge rating curve was used to calculate discharge at 15 min intervals for the sampling period following Rantz et al. (1982) (Fig. S1). Interruptions in stage height measurements occurred during 5–6 May and 13–14 August. We estimated missing values during these periods based on a regression equation developed between discharge at our site and at a National Weather Service gauge (NWS MCAA2), approximately 6 km downstream of the study reach.

Laboratory and analytical methods

The TSS samples were vacuum filtered through a pre-combusted 0.7 μm GF/F filter of known mass and

filtered water volume was recorded. Filters for TSS were visually inspected for larger pieces (> 250 μm) that would be defined as CPOC, and none were found. Filters were dried at 50 °C for 24 h and re-weighed, then frozen, acid fumigated with concentrated hydrochloric acid (Harris et al. 2001), and sent to the University of Hawaii (UH) Hilo Analytical lab to be processed for POC and PON. Alkalinity was measured as CaCO_3 via hydrochloric acid (0.02 N) titration to pH end points 4.4 and 4.7 (Method 2320, Standard Methods for the Examination of Water and Wastewater 1999). Alkalinity was converted to mg C/L and was assumed that the majority of dissolved inorganic C (DIC) exported was bicarbonate (Cole et al. 2021). Samples for DOC/TDN were immediately acidified with hydrochloric acid, stored in the refrigerator, and analyzed within one month of collection. Concentrations of DOC (as non-purgeable organic carbon) and TDN were analyzed by high temperature combustion on a Shimadzu TOC/TN-L-CSH analyzer. Samples for NO_3^- -N and NH_4^+ -N were frozen at -20 °C until sent to the UH Hilo Analytical Lab. Dissolved organic nitrogen (DON) was calculated by difference between TDN and the sum of NO_3^- -N and NH_4^+ -N. Streamwater $\delta^{18}\text{O}$ samples were stored with zero headspace at 4 °C and processed within six months on a Picarro L2120-i Cavity Ring Down Spectrometer. Streamwater $\delta^{18}\text{O}$ values are reported in per mil (‰) after normalization to Vienna standard mean ocean water (VSMOW).

Drift samples were stored in 95% ethanol at room temperature in the dark until processing. Invertebrates were separated from CPOM using a dissecting scope, identified to family level (Merritt and Cummins 1984), and length was measured to the nearest mm. Published length–weight regressions were used to estimate invertebrate biomass, measured as dry mass, using an R-based (R ver. 4.3.1 and RStudio ver. 2022.02.1) freshwater macroinvertebrate analysis program and taxa traits for benthic, drift, and fish diet samples developed by Aquatic Biology Associates (Weissman and Weissman 2022). This program also categorized invertebrates as either freshwater or terrestrial. Invertebrate dry mass was converted to mass (mg C/L) based on locally derived %C relationships (Dunkle 2022), and when not locally available, %C data at the lowest taxonomic level found from literature review (Evans-White et al. 2005; Sullivan et al. 2014).

The CPOM from the drift samples was dried at 50 °C until a constant weight, ashed at 450 °C for a minimum of 4.5 h, re-wet, dried, and weighed. A subset of samples was ashed multiple times to ensure that temperature and durations of ashing were adequate. The remaining ash weight was subtracted from the initial dry mass to calculate ash-free dry mass (AFDM) in grams. This weight was then divided by the volume of water passed through the drift net for each sample, resulting in CPOC concentrations (mg/L). The OM from six drift samples (one per month of sampling) were sorted into categories of moss, woody debris, deciduous leaves, conifer needles, and amorphous debris and were reported as CPOC concentrations as described above.

Biogeochemical load modeling

We calculated the mean, range, and coefficient of variation (CV; mean divided by the standard deviation) for each form of C. Streamwater C exports were calculated using concentration and flow data collected across the approximately six-month study period. Daily loads were modeled for five main forms of C: DOC, alkalinity, POC (>0.7 and <250 μm), CPOC (>250 μm), and C from drifting invertebrates (>250 μm). The package LoadEstimator (LoadEst; Runkel et al. 2004) in R was used to estimate daily loads (kg/day). LoadEst selects the best-fit top model from nine models of the daily flow and concentration data based on Akaike's Information Criterion (AIC). Estimates of daily, monthly, and seasonal loads based on observed discharge data and associated standard errors (SE) for these measurements are derived from the LoadEst top model. Area-weighted watershed yields were calculated by normalizing C load by watershed area.

Carbon to nitrogen ratios

Molar ratios of C to N were calculated as the measured DOC:DON and POC:PON. The C:N of CPOM as calculated using literature derived values (McGroddy et al. 2004; Peterson and Matthews 2009; Romashkin et al. 2018; Dunkel 2022). Values of CPOC:C:N were based on the six CPOC samples that were separated into categories by percent AFDM of the total sample. The C:N were found for each of those categories to yield a bulk

C:N of the whole sample. We calculated the mean, range, and CV for C:N for DOC:DON, POC:PON, and CPOC:CPON. In R, the Tukey HSD test was applied to determine statistical differences in mean values between C:N ratios of dissolved (DOC:DON), particulate (POC:PON), and coarse particulate (CPOC:CPON) species.

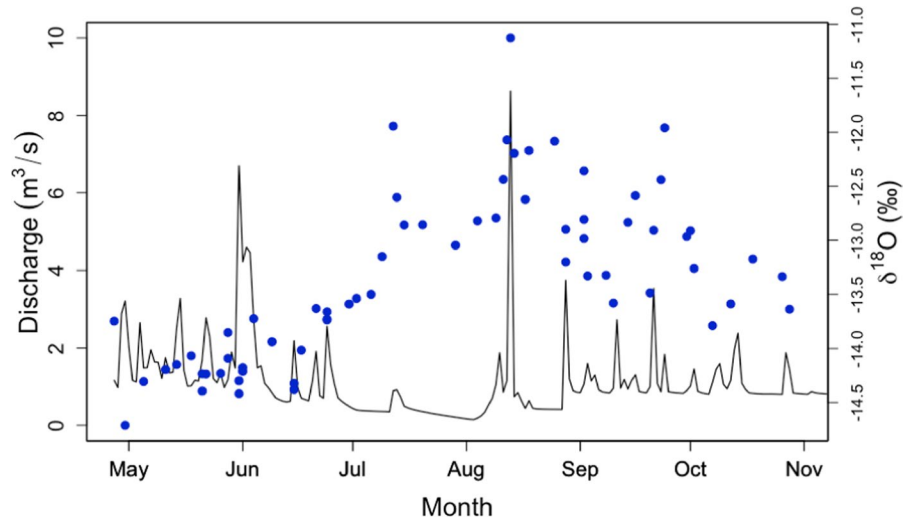
Results

Watershed hydrology

Precipitation at the Juneau International Airport (NOAA USW00025309), approximately 10 km from our study watershed, was 108.84 cm during our sampling period, which accounted for 56% of total annual precipitation for 2021. The driest month was July (6.48 cm) and wettest month was September (25.27 cm). Variations in precipitation combined with the seasonal accumulation of snow and subsequent melt resulted in high variability in streamflow over the study period. Daily average streamflow ranged from 0.15 m^3/s on August 3rd to 8.63 m^3/s on August 13th (Fig. 3). The lowest flows of the study period occurred between June and August and were interspersed with rain-fed discharge peaks. Higher flows from mid-August onward were driven by large rain events. By the end of October, streamflow became less responsive to precipitation, due to cooler temperatures and snow accumulation at high elevation.

Streamwater $\delta^{18}\text{O}$ values averaged -13.34‰ over the study period but were variable (range = -14.71‰ to -11.12‰ , CV = 0.06; Fig. 3). Our snowmelt and mean rainfall $\delta^{18}\text{O}$ samples were -15.37‰ and -9.61‰ , respectively, which bracketed the observed streamwater values. These precipitation values were consistent with previous samples collected in the Juneau area (Fellman et al. 2014a). Streamwater $\delta^{18}\text{O}$ values were the most depleted in April/June reflecting the influence of snowmelt on discharge. However, values became more variable and similar to rainfall sample during the July dry period. In August and September, $\delta^{18}\text{O}$ values became more depleted and similar to the seasonal rainfall signature (Fellman et al. 2014a) in the area (Fig. 3).

Fig. 3 Time series of mean daily discharge (m^3/s ; solid line) and stream water $\delta^{18}\text{O}$ (‰) values (blue dots) from Kaxdigoowu Héén during the sampling season



Constituent C concentrations

Dissolved organic C was typically the dominant form of streamwater C, except during summer low flow periods (particularly July) when

alkalinity concentrations were elevated relative to DOC (Fig. 4a–b). Based on the coefficient of variation (CV) across the sampling period, concentrations of alkalinity were the least variable, while POC was the most variable of all the C forms, particularly in

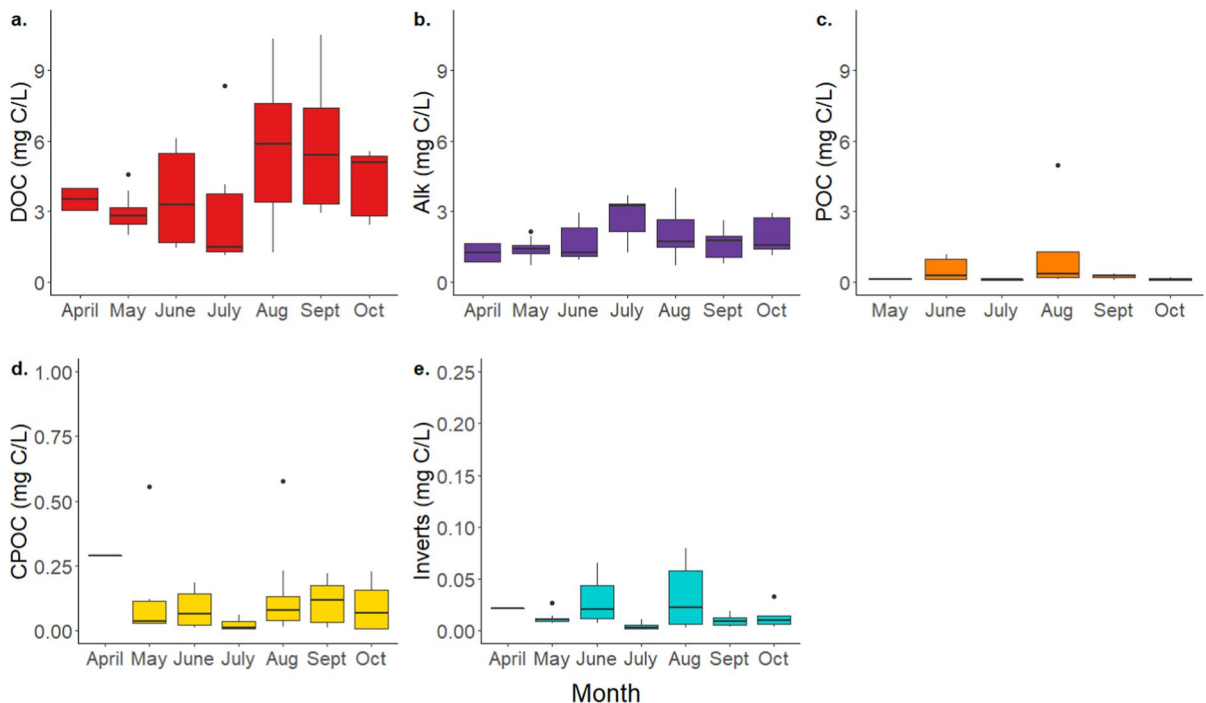


Fig. 4 Concentrations (mg C/L) of **a** DOC, **b** alkalinity (Alk), **c** POC, **d** CPOC, and **e** drifting invertebrate biomass C (Inverts) by month in Kaxdigoowu Héén. Note that the y-axis scale is the same for the top three panels but different for the

bottom two. Boxes represent the inter-quartile range (IQR) with the median in bold, whiskers extend to a maximum of 1.5 times the IQR. Outliers are marked by points

August (Fig. 4c). Concentrations of CPOC were lowest and least variable in July (Fig. 4d). Invertebrate drift C concentrations were the lowest of all five C forms in every month (Fig. 4e).

Constituent C yields

Constituent yields were generally largest during higher flows, which occurred primarily in the spring snowmelt months of May and June, or in the wet season months (mid-August through October; Fig. 5). In contrast, daily yields for all constituents were generally lowest in July and early August when streamflow was at its lowest (Fig. 5). Given this relationship, yields for all constituents usually had a U-shaped seasonal pattern, with mid-summer minima in July and higher yields associated with spring snowmelt and the fall rainy season (Fig. S2).

Compared to yields in July through September, yields of DOC were less responsive to streamflow during the spring snowmelt runoff in April and May, and the largest yields of DOC occurred during high flows in mid-August and September (Fig. 5b). The

highest alkalinity yields occurred during spring high flows and during the large storm in early August; however, during the low flows in July yields of alkalinity exceeded those of DOC (Fig. 5). Daily yields of POC, CPOC, and drifting invertebrates had the lowest yields during periods of low flow (generally summer) and highest yields associated with high flow events during spring and fall (Fig. 5d–f). Total watershed C export for the study period was 13,180 kg/km² for all forms of C (Table S1). Total C yields were highest in August (3085 kg/km²) and lowest in July (608 kg/km²).

Dissolved organic C was the largest component of total C flux (66%) in every month except July (Fig. 6). In July, alkalinity was the largest portion (53%) of total C export followed by POC and CPOC, both of which accounted for their highest proportion of the monthly C flux (~20% together) in August. Drifting invertebrates consistently made up the smallest portion of total C export and typically comprised less than 1% of monthly C export. Invertebrate biomass C consisted primarily of aquatic taxa (Ephemeroptera, Diptera, Aquatic non-insects,

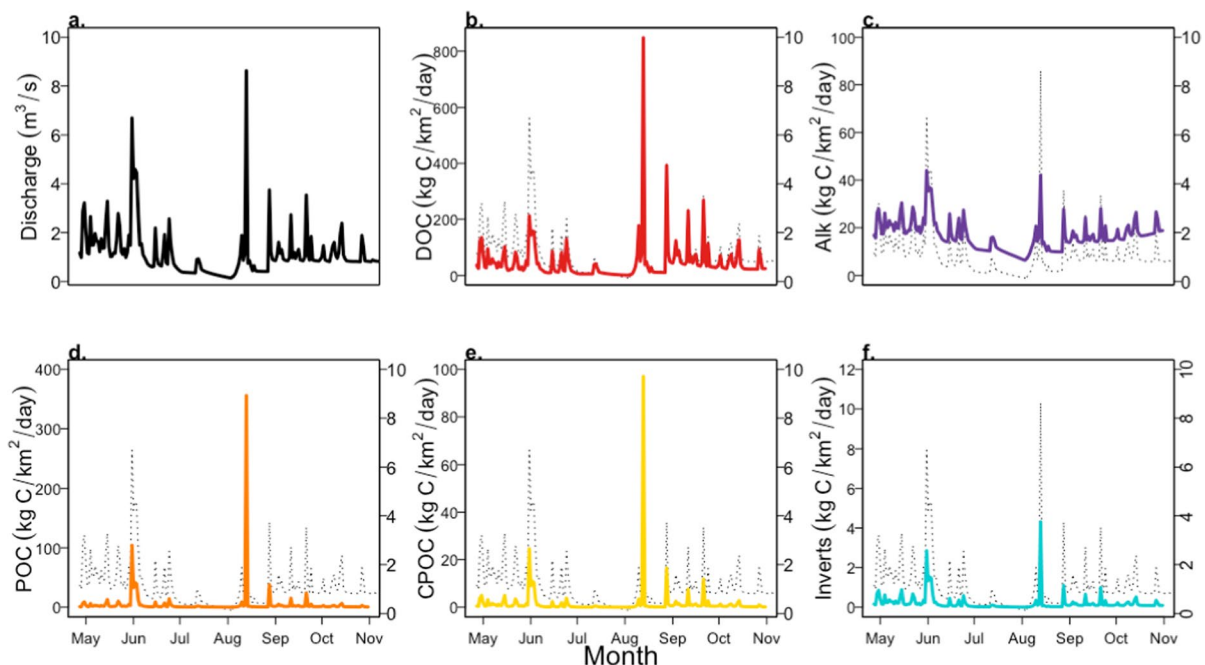


Fig. 5 a Discharge in Kaxdigoowu Héen and modeled daily yields for b DOC, c alkalinity (Alk), d POC, e CPOC, and f invertebrate biomass C (Inverts). For model outputs the dotted line represents mean daily discharge in m³/s for all plots other

than (a) and the solid-colored line represents daily modeled yields for (b–f). Note the y-axis scale on the left-hand side is different among each panel

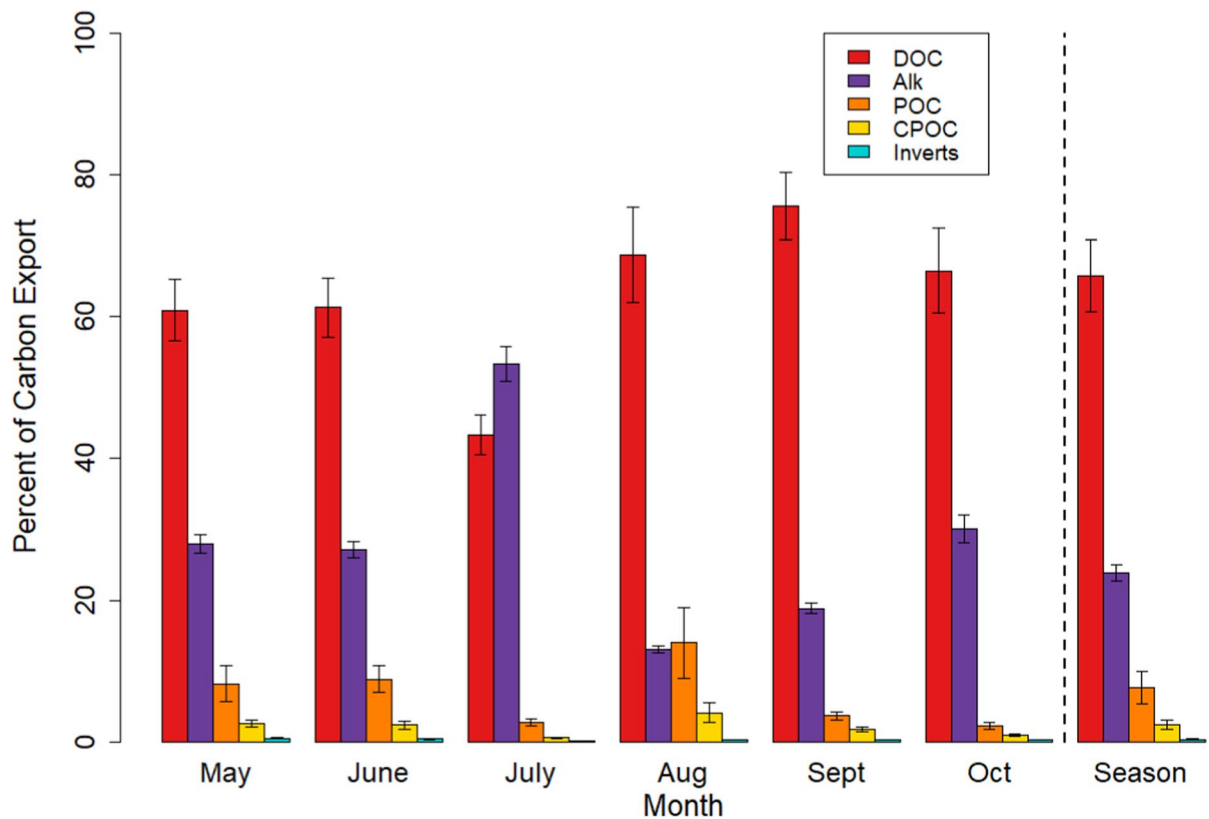


Fig. 6 Percent contribution of each form of C to total export from Kaxdigoowu Héen for each month and for the sampling season. Error bars represent \pm standard error for each estimate.

Alk corresponds to alkalinity and Inverts corresponds to drifting invertebrate biomass

Trichoptera, and Plecoptera), with lower concentrations of terrestrial taxa (primarily Coleoptera, Hymenoptera, Nematocera, Gastropoda and Collembolla; Table S2). Aquatic invertebrates were the largest portion of invertebrate drift C throughout study period, although the percent contribution decreased over the study period. In contrast, the contribution of terrestrial invertebrates to drift C increased across the study period, from 2% in May to 24% in October. This trend is due to an overall decrease in aquatic invertebrate C into autumn and an increase in terrestrial invertebrate biomass contributing to drifting biomass C (Fig. S3).

Molar ratio of C to N in dissolved and particulate OM

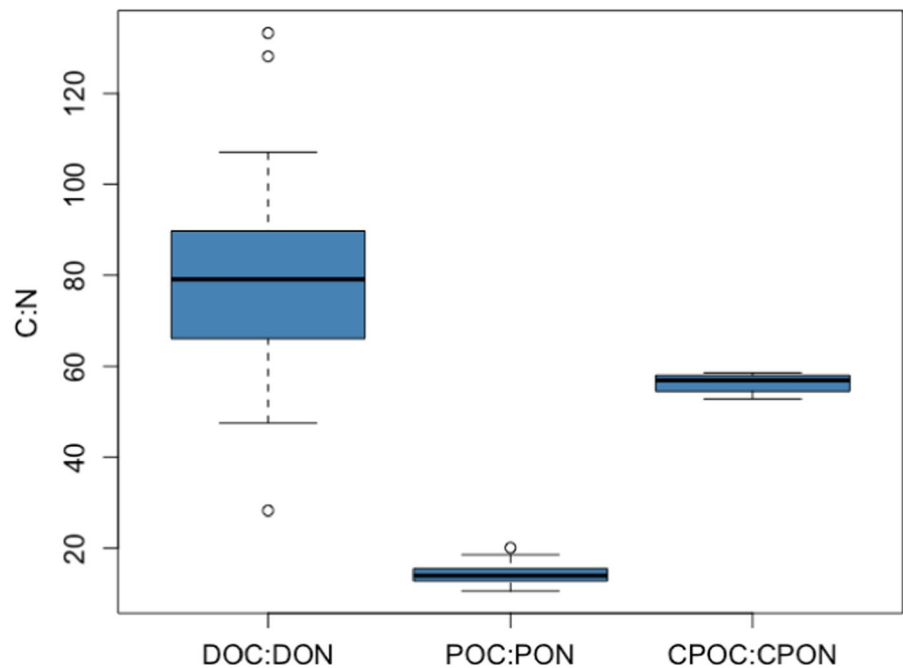
Molar ratios of DOC to DON were, on average, the highest of any OM form and varied widely (CV = 0.31) across the study period, ranging from 20

to 133 (mean = 78; Fig. 7). Molar ratios of POC to PON were the lowest of any OM form, ranging from 10 to 15 (mean = 14, CV = 0.16) while CPOC:CPON ranged from 52 to 58 (mean=56; CV=0.04). Ratios of these three pools differed significantly from one another in aggregate (DOC:DON~POC:PON, $p < 0.001$; DOC:DON~CPOC:CPON, $p = 0.001$; CPOC:CPON~POC:PON, $p < 0.001$).

Discussion

Quantifying high resolution yields for multiple forms of C is critical for evaluating the role of watershed C export in the C budget of terrestrial ecosystems (Butman et al. 2016) and important for our understanding of C delivery to nearshore environments (Gao et al. 2023). Consistent with our hypothesis, we found that DOC was the dominant form of watershed C export,

Fig. 7 Molar carbon to nitrogen ratio (C:N) for three pools of organic matter in Kaxdigoowu Héén: DOC:DON, POC:PON, and CPOC:CPON. Boxes represent the inter-quartile range (IQR) with the median in bold, whiskers extend to a maximum of 1.5 times the IQR



except during extended summer dry periods (July) when alkalinity yields exceeded DOC. In contrast to our expectations, we did not find that the concentrations of particulate forms of carbon (POC, CPOC, or invertebrates) ever exceeded DOC, even during months that experienced higher flows. Even though these particulate forms of C comprised a proportionally small amount of total C export, as we hypothesized, they had lower C:N that could render them more bioavailable to stream or estuarine communities (Hopkinson et al. 1998). These findings portend the potential importance of seasonally dynamic and diverse C exports both from the perspective of accurate watershed carbon budgets (Ward et al. 2017; Qiu et al. 2023) as well as understanding C subsidies to downstream and nearshore ecosystems (sensu Atwood et al. 2012; McMahon et al. 2021).

Concentrations of carbon forms

Our finding of a strong seasonal pattern in streamwater DOC concentrations was likely linked to evolving watershed controls on DOC production and transport across the terrestrial-aquatic interface. In April and May, the depleted $\delta^{18}\text{O}$ values (relative to the rest of the study period) and low streamwater DOC concentrations (Figs. 3, 4) were likely attributed to

the spring snowmelt period where cool temperatures limit soil C mineralization and prolonged soil saturation and subsequent dilution of soil pools of DOC leads to minimal transport to surface waters. Studies show seasonal fluctuations in water table levels (and increased aeration) and warm soil temperatures can stimulate DOC production (Hribljan et al. 2014; D'Amore et al. 2015) via enhanced soil organic C mineralization (Clark et al. 2009). Our finding that the greatest DOC yields occurred during high flow events (supported by streamwater $\delta^{18}\text{O}$ values becoming more similar to rainfall, Fig. 3) following the July and August low flow periods supports the notion the transport of DOC from soils into surface waters is reliant on watershed hydrologic connectivity (e.g. Kiewiet et al. 2020), as rain events may mobilize different pools of DOC that might not be hydrologically connected to the stream network during drier periods (Wen et al. 2020). That said, other studies show that water table draw-down and associated elevated aeration in the soil profile enhances consumption of DOC by soil microbial communities and ultimately can exhaust labile pools of OM that are available for transport to surface waters (Pastor et al. 2003; Clark et al. 2009). Overall, these findings highlight both the sensitivity of DOC production and transport to changing hydroclimatic conditions and the need to

elucidate interacting controls on DOC dynamics to fully understand the impacts of a changing climate on watershed C export.

Alkalinity responded differently to changing season and flow conditions relative to DOC, with higher concentrations observed during lower mid-summer flows when $\delta^{18}\text{O}$ values indicated a predominance of groundwater flow paths contributing to streamflow (Figs. 3, 4). Other studies in the subarctic have found similar patterns where DIC dominated streamwater C export in summer low flow conditions (Jantze et al. 2015; Koch et al. 2021). This suggests that DIC, likely from geogenic sources (Duvert et al. 2018), originates mainly from groundwater and/or deep soil horizons which primarily sustain streamflow during drier periods (Dinsmore and Billett 2008).

Particulate forms of organic C are often mobilized during high flow events that disturb stream beds, cause overland flow and bank erosion (Dhillon and Inamdar 2014; Johnson et al. 2018), and flush terrestrial invertebrates into the stream (Wipfli and Musselwhite 2004). These more episodic process may contribute to the high variability in streamwater POC, CPOC, and invertebrate concentrations compared to dissolved constituents (Fig. 4). Flow paths for dissolved and particulate organic C typically differ from one another, with DOC and alkalinity entering the stream through soil and groundwater paths that can originate from numerous locations within the watershed, whereas particulate fluxes are generally sourced closer to the stream from soil surface water runoff, riparian vegetation, and the stream channel itself (Lloret et al. 2013; Ward et al. 2017). This difference in sourcing and flow path likely contributes to the seasonal and/or flow driven variability in the observed streamwater C concentrations. Although we collected hourly concentration data for DOC and alkalinity for the study site where we analyze seasonal patterns in concentration-discharge relationships (Delbecq et al. in prep), addressing the specific mechanisms of C source and transport through the watershed is out of the scope of this study.

Total carbon yields

The seasonal variability in C concentration and flux was mirrored over shorter time scales by the presence and absence of rainfall events that enhance terrestrial-aquatic connectivity. These types of connections

define the Pacific Coastal Temperate Rainforest of Southeast Alaska, particularly during the summer months when dry stretches are often interspersed with rain events. The largest form of C export from the study stream was DOC, which corroborates other studies in high-latitude watersheds (Fig. 6; Table S1; Koch et al. 2021) and other temperate forested watersheds (Hood et al. 2020; Pérez-Rodríguez and Biester 2022). The coastal temperate rainforest in Southeast Alaska is known to have organic C-rich watersheds with the majority of C export originating from small ($<20 \text{ km}^2$), forested watersheds similar to Kaxdigoo-wu Héen (Edwards et al. 2021). This contrasts to global riverine C export trends, where DIC often dominates lateral C export (Stackpoole et al. 2017; Chaplot and Mutema 2021). Although both DOC and alkalinity export decrease during low flows, alkalinity has higher concentrations at low flows, thus increasing its export relative to DOC (Figs. 4–5). This interplay between two major forms of C export may be impacted by interannual variability in flow conditions, such that alkalinity could represent the largest pool of C export from the watershed during multiple months during dry years. In total, particulate forms of C (POC, CPOC, and invertebrates) averaged 10% of total C export and about 14% of total organic C export (Table S1). The proportion of DOC to POC flux has been shown to be approximately equal on the global scale (Li et al. 2017) but can vary significantly by region (Kandasamy and Nath 2016). Thus, excluding particulate and drifting biomass C forms from the riverine C budget could result in a systematic underestimation of total watershed C export.

Drifting invertebrates can contribute substantially to fish diets. Thus, the seasonal shift in invertebrate drift concentration and composition may impact food availability to fish (Kawaguchi et al. 2003; Eberle and Stanford 2010). Aquatic invertebrates dominated drifting biomass throughout the study period, but terrestrial invertebrates played an increasingly important role in the late summer and fall (Fig. S3; similar to Fellman et al. 2023). This is consistent with fish foraging studies conducted in the basin, which similarly report increased consumption of terrestrial relative to aquatic invertebrates by juvenile salmonids during late summer and fall compared to spring (Fitzgerald et al. 2023). Within different taxa, a combination of discharge, species life history, and behavior can all play a role in observed drift dynamics (Naman et al.

2016). Based on these results, terrestrial invertebrate drift appears to be an important food resource for stream fishes in the late summer and autumn in the study stream. Notably, this could be beneficial to fish growth and condition prior to winter, when foraging and growth opportunities have been shown to be limited (Bellmore et al. 2022).

Organic matter quality

Terrestrial-derived OM is a strong driver of aquatic microbial production (Berggren and del Giorgio 2015), and large quantities of bioreactive OM are delivered from watersheds to coastal ecosystems like those in Southeast Alaska (St. Pierre et al. 2020; Edwards et al. 2021). While the timing and quantity of resource yields may influence the fate of C, so does the quality of those yields. The C:N of OM yields is likely to shift as watershed sources of streamwater OM vary through time (e.g., wetlands, soils, and throughfall; Behnke et al. 2022). Variable watershed hydrologic connectivity and water flow paths change how connected or disconnected different terrestrial sources of OM are to streamwater (Tank et al. 2018). Thus, the interaction between watershed hydrologic connectivity and variability in DOM quality associated with shifting precursor material could create ecosystem controls points (Bernhardt et al. 2017) or patches of differential processing rates of DOM along soil-stream continuum, resulting in highly variable C:N of streamwater OM. Further, our findings suggest that the highest processing rates of OM along the soil-stream network would be associated with forms of OM that exist in the lowest concentrations (e.g. drifting invertebrates), since biogeochemical processing rates are not always associated with the highest elemental concentrations (e.g. Fellman et al. 2009). These results support previous research in European rivers showing that OM bioreactivity is lower during years with high total OC export (Berggren and Al-Kharusi 2020).

Based on our C:N in the OM pools, streamwater exports of POM and drifting invertebrates may have a disproportionate impact on downstream food webs in small, forested watersheds. While we did not measure invertebrate C:N ratios, data from other studies in Southeast Alaska suggests that invertebrate C:N typically ranges between 5 and 7 (Dunkle 2022). The yields of POC, CPOC, and invertebrates were lower

than DOC yields, but their corresponding OM pools had lower and less variable C to N ratios, potentially making them a higher quality subsidy to aquatic communities (Figs. 5, 6). This corroborates research in the Sacramento-San Joaquin River Delta that found POC has a higher percentage of C that is bioavailable compared to DOC (Sobczak et al. 2002). The lower variability in CPOM and POM-C:N could stem from the lack of source variability, as well as proximate sourcing from the riparian zone or within the stream (Qiao et al. 2020) relative to DOC, which may enter the stream after traveling through a variety of physicochemical environments and undergoing varying levels of processing along the soil-stream continuum. Lower POM exports could also reflect elevated in-stream processing rates of this higher quality material (i.e., measured exports reflect material that communities preferentially are less able to process). Future studies should examine the combined downstream ecosystem effects of relatively small and high-quality OM fluxes (CPOM, POM) combined with larger and lower-quality OM (DOM) fluxes (e.g., Marcarelli et al. 2011) to determine whether the absolute amount of bioreactive OM or the percentage of OM is a more important driver of stream C cycling.

Conclusions

The links between watershed hydrology and C biogeochemistry are important to understand in the context of a changing climate. Predicted changes in climate in the region such as increasing precipitation, shifts in the length and severity of dry periods, and intensity and frequency of rain events (Lader et al. 2020) will impact streamflow (Sergeant et al. 2020) and the delivery of C to the ocean. Differing forms of C, might be more impacted by these changes depending on how they are mobilized under different flow conditions and cycled or retained along the flow network. For instance, POC and CPOC concentrations varied widely over the study period while alkalinity had the lowest CV (Table S1), suggesting particulate rather than dissolved forms of C might be more responsive to changes in hydroclimate. Additionally, conditions that precede dry periods or storm events might impact the flux of these different constituents (Kiewiet et al. 2020; Tiwari et al. 2022), all

of which will be altered under new climate conditions. Changes in hydroclimate might also impact the watershed level controls that influence these yields, like changes to terrestrial productivity (Schwalm et al. 2011; Ma et al. 2015), the timing of spring snowmelt (Sergeant et al. 2020), or returns of spawning Pacific salmon (Warkentin et al. 2022). Given the projected change in regional hydroclimatic patterns, it is crucial to better understand the dynamics of C export and the fate of these exports in both fluvial and nearshore ecosystems. Overall, particulate forms of organic C and drifting invertebrates accounted for a proportionally small amount of total streamwater C export, although these forms of OM had a lower C:N that could render them more likely to be incorporated into aquatic food webs. From an ecological context, our findings highlight the importance of quantifying multiple forms of lateral C export and reactivity. However, quantifying particulate forms of C maybe less important within the context of the annual watershed total C budget. Together, our study underscores the need for a more nuanced understanding of watershed-scale C cycling by considering the reactivity, form, and magnitude of lateral C export in concert.

Acknowledgements This work was funded by the U.S. Geological Survey Alaska Climate Adaptation Science Center and the U.S. Forest Service (USFS) Pacific Northwest Research station. Support for University of Alaska Southeast (UAS) undergraduate researchers was provided by Alaska EPSCOR (#OIA-1753748) and NSF (#1557186). We thank Molly Tankersley for Figure 1 and Josh Paul and Brennen McCulloch for Figure 2 and Mark Lukey (USFS), Di Johnson (USFS), Ezra Grey (UAS), John Seymour (UAS), Lucy Franklin (UAS), Randy Brannan (UAS), and Naomi Boyles-Muehleck (UAS) for field and lab assistance, Jeff Muehlbauer (University of Alaska Fairbanks) and members of the Freshwater Fish Ecology Lab and Alaska Coastal Rainforest Center for their helpful reviews and support, and our two anonymous reviewers for their feedback and suggestions. This work took place on the lands of the Aak'w Kwáan Tlingit, we are grateful for their past, present, and future stewardship of these lands and resources. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions JBF, JRB, and JAF conceptualized the study. CD, EW, and KF conducted the field work. CD and EW conducted the lab work. CD, EW, and JBF analyzed the data. CD, JBF, JRB, JAF and EH wrote the manuscript.

Funding Alaska Climate Adaptation Science Center, University of Alaska Fairbanks, USFS Pacific Northwest Research

Station, Alaska EPSCoR (OIA-1753748), National Science Foundation (1557186; EAR 2227821).

Data availability All data in this study are available online (<https://doi.org/10.5066/P14IKGTB>) through ScienceBase.

Declarations

Competing interests The authors have not disclosed any competing interests.

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References

- Antonio ES, Kasai A, Ueno M, Kurikawa Y, Tsuchiya K, Toyohara H, Ishihi Y, Yokoyama H, Yamashita Y (2010) Consumption of terrestrial organic matter by estuarine molluscs determined by analysis of their stable isotopes and cellulase activity. *Estuar Coast Shelf Sci* 86:401–407. <https://doi.org/10.1016/j.ecss.2009.05.010>
- Attrill MJ, Rundle SD, Fraser A, Power M (2009) Oligochaetes as a possible entry route for terrigenous organic carbon into estuarine benthic food webs. *Mar Ecol Prog Ser* 384:147–157. <https://doi.org/10.3354/meps08019>
- Atwood TB, Wiegner TN, MacKenzie RA (2012) Effects of hydrological forcing on the structure of a tropical estuarine food web. *Oikos* 121:277–289. <https://doi.org/10.1111/j.1600-0706.2011.19132.x>
- Bauer JE, Cai WJ, Raymond PA, Bianchi TS, Hopkinson CS, Regnier PAG (2013) The changing carbon cycle of the coastal ocean. *Nature* 504:61–70. <https://doi.org/10.1038/nature12857>
- Behnke MI, Fellman JB, D'Amore DV, Gomez SM, Spencer RGM (2022) From canopy to consumer: what makes and modifies terrestrial DOM in a temperate forest. *Biogeochemistry* 164:185–205. <https://doi.org/10.1007/s10533-022-00906-y>
- Bellmore JR, Fellman JB, Hood E, Dunkle MR, Edwards RT (2022) A melting cryosphere constrains fish growth by synchronizing the seasonal phenology of river food webs.

- Glob Change Biol 28:4807–4818. <https://doi.org/10.1111/gcb.16273>
- Berggren M, Al-Kharusi ES (2020) Decreasing organic carbon bioreactivity in European rivers. *Freshw Biol* 65:1128–1138. <https://doi.org/10.1111/fwb.13498>
- Berggren M, del Giorgio PA (2015) Distinct patterns of microbial metabolism associated to riverine dissolved organic carbon of different source and quality. *J Geophys Res Biogeosci* 120:989–999. <https://doi.org/10.1002/2015JG002963>
- Bernhardt ES, Blaszczak JR, Ficken CD, Fork ML, Kaiser KE, Seybold EC (2017) Control points in ecosystems: Moving beyond the hot spot hot moment concept. *Ecosystems* 20:665–682. <https://doi.org/10.1007/s10021-016-0103-y>
- Butman D, Stackpoole S, Stets E, McDonald CP, Clow DW, Striegl RG (2016) Aquatic carbon cycling in the conterminous United States and implications for terrestrial carbon accounting. *Proc Natl Acad Sci USA* 113:58–63. <https://doi.org/10.1073/pnas.1512651112>
- Chaplot V, Mutema M (2021) Sources and main controls of dissolved organic and inorganic carbon in river basins: a worldwide meta-analysis. *J Hydrol* 603:126941. <https://doi.org/10.1016/j.jhydrol.2021.126941>
- Clark JM, Ashley D, Wagner M, Chapman PJ, Lane SN, Evans CD, Heathwaite AL (2009) Increased temperature sensitivity of net DOC production from ombrotrophic peat due to water table draw-down. *Glob Change Biol* 15:794–807. <https://doi.org/10.1111/j.1365-2486.2008.01683.x>
- Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CN, Kortelainen P, Downing JA, Middelburg JJ, Melack J (2007) Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:171–184. <https://doi.org/10.1007/s10021-006-9013-8>
- Cole JJ, Hararuk O, Solomon CT (2021) The carbon cycle: With a brief introduction to global biogeochemistry. *Fundamentals of Ecosystem Science*. Elsevier, Amsterdam, pp 131–160
- D'Amore DV, Edwards RT, Herendeen PA, Hood E, Fellman JB (2015) Dissolved organic carbon fluxes from hypopedologic units in Alaskan coastal temperate rainforest watersheds. *Soil Sci Soc Am J* 79:378–388. <https://doi.org/10.2136/sssaj2014.09.0380>
- de Wit HA, Austnes K, Hylen G, Dalsgaard L (2015) A carbon balance of Norway: terrestrial and aquatic carbon fluxes. *Biogeochemistry* 123:147–173. <https://doi.org/10.1007/s10533-014-0060-5>
- Delbecq CD, Fellman JB, Bellmore JR, Whitney EJ, Fitzgerald KA, Falke J (in prep) Season and antecedent conditions impact concentration-discharge relationships for dissolved organic carbon and inorganic carbon in a Southeast Alaskan watershed.
- Dhillon GS, Inamdar S (2014) Storm event patterns of particulate organic carbon (POC) for large storms and differences with dissolved organic carbon (DOC). *Biogeochemistry* 118:61–81. <https://doi.org/10.1007/s10533-013-9905-6>
- Dinsmore KJ, Billett MF (2008) Continuous measurement and modeling of CO₂ losses from a peatland stream during stormflow events. *Water Resour Res* 44:W12417. <https://doi.org/10.1029/2008WR007284>
- Drake TW, Raymond PA, Spencer RGM (2018) Terrestrial carbon inputs to inland waters: a current synthesis of estimates and uncertainty. *Limnol Oceanogr Lett* 3:132–142. <https://doi.org/10.1002/lol2.10055>
- Dunkle MR (2022) Building a food web portfolio: Hydrologic heterogeneity creates food web diversity on a glacial meltwater landscape. Ph.D. Dissertation, University of Idaho, Moscow, ID. <https://doi.org/10.1016/j.pcean.2006.09.011>
- Duvert C, Butman CE, Marx A, Ribolzi O, Hutley LB (2018) CO₂ evasion along streams driven by groundwater inputs and geomorphic controls. *Nat Geosci* 11:813–818. <https://doi.org/10.1038/s41561-018-0245-y>
- Eberle LC, Stanford JA (2010) Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian federation). *River Res Appl* 26:682–694. <https://doi.org/10.1002/rra.1270>
- Edwards RT, D'Amore DV, Biles FE, Fellman JB, Hood EW, Trubilowicz JW, Floyd WC (2021) Riverine dissolved organic carbon and freshwater export in the eastern Gulf of Alaska. *J Geophys Res Biogeosci* 126:e2020JG005725. <https://doi.org/10.1029/2020JG005725>
- Evans-White MA, Stelzer RS, Lamberti GA (2005) Taxonomic and regional patterns in benthic macroinvertebrate elemental composition in streams. *Freshw Biol* 50:1786–1799. <https://doi.org/10.1111/j.1365-2427.2005.01455.x>
- Fellman JB, Hood EW, Spencer RGM, Stubbins S, Raymond PA (2014a) Watershed glacier coverage influences dissolved organic matter biogeochemistry in coastal watersheds of Southeast Alaska. *Ecosystems* 17:1014–1025. <https://doi.org/10.1007/s10021-014-9777-1>
- Fellman JB, Nagorski S, Pyare S, Vermilyea AW, Scott D, Hood E (2014b) Stream temperature response to variable glacier coverage in coastal watersheds of Southeast Alaska. *Hydrol Process* 28:2062–2073. <https://doi.org/10.1002/hyp.9742>
- Fellman JB, Hood E, D'Amore DV, Edwards RT, White D (2009) Seasonal changes in the chemical quality and biodegradability of dissolved organic matter exported from soils to streams in coastal temperate rainforest watersheds. *Biogeochemistry* 95(2):277–293. <https://doi.org/10.1007/s10533-009-9336-6>
- Fellman JB, Hood E, D'Amore DV, Edwards RT (2021) Streamflow variability controls N and P export and speciation from Alaskan coastal temperate rainforest watersheds. *Biogeochemistry* 152:253–270. <https://doi.org/10.1007/s10533-020-00752-w>
- Fellman JB, Bellmore JR, Johnson C, Dunkle MR, Hood EW (2023) Glacier runoff influences biogeochemistry and resource availability in coastal temperate rainforest streams: Implications for juvenile salmon growth. *Limnol Oceanogr* 68:70–83. <https://doi.org/10.1002/lno.12251>
- Fitzgerald KA, Bellmore JR, Fellman JB, Cheng MLH, Delbecq CE, Falke JA (2023) Stream hydrology and a pulse subsidy shape patterns of fish foraging. *J Anim Ecol* 92:2386–2398. <https://doi.org/10.1111/1365-2656.14018>
- Gao S, Schwinger J, Tjiputra J, Bethke I, Hartmann J, Mayorga E, Heinze C (2023) Riverine impact on future projections of marine primary production and carbon uptake.

- Biogeosciences 20:93–119. <https://doi.org/10.5194/bg-20-93-2023>
- Harfmann J, Kurobe T, Bergamaschi B, Teh S, Hernes P (2019) Plant detritus is selectively consumed by estuarine copepods and can augment their survival. *Sci Rep* 9:9076. <https://doi.org/10.1038/s41598-019-45503-6>
- Harris D, Horwath WR, van Kessel C (2001) Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. *Soil Sci Soc Am J* 65:1853–1856. <https://doi.org/10.2136/sssaj2001.1853>
- Hauri C, Schultz C, Hedstrom K, Danielson S, Irving B, Doney SC, Dussin R, Curchitser EN, Hill DF, Stock CA (2020) A regional hindcast model simulating ecosystem dynamics, inorganic carbon chemistry, and ocean acidification in the Gulf of Alaska. *Biogeosciences* 17:3837–3857. <https://doi.org/10.5194/bg-17-3837-2020>
- Hessen DO, Elser JJ, Sterner RW, Urabe J (2013) Ecological stoichiometry: an elementary approach using basic principles. *Limnol Oceanogr* 58:2219–2236. <https://doi.org/10.4319/lo.2013.58.6.2219>
- Hood E, Fellman JB, Spencer RGM (2020) Glacier loss impacts riverine organic carbon transport to the ocean. *Geophys Res Lett*. <https://doi.org/10.1029/2020GL089804>
- Hopkinson CS, Buffam I, Hobbie J, Vallino J, Perdue M, Eversmeyer B, Prah F, Covert J, Hodson R, Moran MA, Smith E, Baross J, Crump B, Findlay S, Foreman K (1998) Terrestrial inputs of organic matter to coastal ecosystems: an intercomparison of chemical characteristics and bioavailability. *Biogeochemistry* 43:211–234. <https://doi.org/10.1023/A:1006016030299>
- Hribljan JA, Kane ES, Pypker TG, Chimner RA (2014) The effect of long-term water table manipulations on dissolved organic carbon dynamics in a poor fen peatland. *J Geophys Res Biogeosci* 119:577–595. <https://doi.org/10.1002/2013JG002527>
- Islam MJ, Jang C, Eum J, Jung S, Shin M, Lee Y, Choy Y, Kim B (2019) C:N: P stoichiometry of particulate and dissolved organic matter in river waters and changes during decomposition. *J Ecol Environ*. <https://doi.org/10.1186/s41610-018-0101-4>
- Jantze EJ, Laudon H, Dahlke HE, Lyon SW (2015) Spatial variability of dissolved organic and inorganic carbon in sub-arctic headwater streams. *Arct Antarct Alp Res* 47:529–546. <https://doi.org/10.1657/AAAR0014-044>
- Johnson ER, Inamdar S, Kan J, Vargas R (2018) Particulate organic matter composition in stream runoff following large storms: Role of POM sources, particle size, and event characteristics. *J Geophys Res Biogeosci* 123:660–675. <https://doi.org/10.1002/2017JG004249>
- Kandasamy S, Nath BN (2016) Perspectives on the terrestrial organic matter transport and burial along the land-deep sea continuum: caveats in our understanding of biogeochemical processes and future needs. *Front Mar Sci* 3:259. <https://doi.org/10.3389/fmars.2016.00259>
- Kawaguchi Y, Taniguchi Y, Nakano S (2003) Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology* 84:701–708. [https://doi.org/10.1890/0012-9658\(2003\)084\[0701:TIIDTL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0701:TIIDTL]2.0.CO;2)
- Khoo CLL, Sipler RE, Fudge AR, Beheshti Foroutani M, Boyd SG, Ziegler SE (2022) Salt-induced flocculation of dissolved organic matter and iron is controlled by their concentration and ratio in boreal coastal systems. *J Geophys Res* 127:e2022JG006844. <https://doi.org/10.1029/2022JG006844>
- Kiewiet L, Van Meerveld I, Stähli M, Seibert J (2020) Do stream water solute concentrations reflect when connectivity occurs in a small, pre-Alpine headwater catchment? *Hydrol Earth Syst Sci* 24:3381–3398. <https://doi.org/10.5194/hess-24-3381-2020>
- Koch JC, Dornblaser MM, Striegl RG (2021) Storm-scale and seasonal dynamics of carbon export from a nested sub-arctic watershed underlain by permafrost. *J Geophys Res* 126:e2021JG006268. <https://doi.org/10.1029/2021JG006268>
- Lader R, Bidlack A, Walsh JE, Bhatt UA, Bieniek PA (2020) Dynamical downscaling for Southeast Alaska: historical climate and future projections. *J Appl Meteorol Climatol* 59:1607–1623. <https://doi.org/10.1175/JAMC-D-20-0076.1>
- Le Fouest V, Babin M, Tremblay JE (2013) The fate of riverine nutrients on Arctic shelves. *Biogeosciences* 10:3661–3677. <https://doi.org/10.5194/bg-10-3661-2013>
- Li M, Peng C, Wang M, Xue W, Zhang K, Wang K, Shi G, Zhu Q (2017) The carbon flux of global rivers: a re-evaluation of amount and spatial patterns. *Ecol Ind* 80:40–51. <https://doi.org/10.1016/j.ecolind.2017.04.049>
- Lloret E, Dessert C, Pastor L, Lajeunesse E, Crispi O, Gaillet J, Benedetti MF (2013) Dynamic of particulate and dissolved organic carbon in small volcanic mountainous tropical watersheds. *Chem Geol* 351:229–244. <https://doi.org/10.1016/j.chemgeo.2013.05.023>
- Ma X, Huete A, Moran S, Ponce-Campos G, Eamus D (2015) Abrupt shifts in phenology and vegetation productivity under climate extremes. *J Geophys Res Biogeosci* 120:2036–2052. <https://doi.org/10.1002/2015JG003144>
- Maavara T, Logozzo L, Stubbins A, Aho K, Brinkerhoff C, Hosen J, Raymond P (2021) Does photomineralization of dissolved organics matter in temperate rivers? *J Geophys Res* 126:e2021JG006402. <https://doi.org/10.1029/2021JG006402>
- Marcarelli AM, Baxter CV, Mineau MM, Hall RO (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwater. *Ecology* 92:1215–1225. <https://doi.org/10.1890/10-2240.1>
- McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. *Ecology* 85:2390–2401. <https://doi.org/10.1890/03-0351>
- McMahon KW, Ambrose WG, Reynolds MJ, Johnson BJ, Whiting A, Clough LM (2021) Arctic lagoon and nearshore food webs: Relative contributions of terrestrial organic matter, phytoplankton, and phyto-benthos vary with consumer foraging dynamics. *Estuar Coast Shelf Sci* 257:107388. <https://doi.org/10.1016/j.ecss.2021.107388>
- Medeiros PM, Seidel M, Niggemann J, Spencer RGM, Hernes PJ, Yager PL, Miller WL, Dittmar T, Hansell DA (2016) A novel molecular approach for tracing terrigenous dissolved organic matter into the deep ocean. *Global Biogeochem Cycles* 30:689–699. <https://doi.org/10.1002/2015GB005320>

- Merritt RW, Cummins KW (1984) An Introduction to the aquatic insects of North America. Kendall/Hunt Pub.Co, Dubuque
- Muehlbauer JD, Kennedy TA, Copp AJ, Sabol TA (2016) Deleterious effects of net clogging on the quantification of stream drift. *Can J Fish Aquat Sci* 74:1041–1048. <https://doi.org/10.1139/cjfas-2016-0365>
- Naman SM, Rosenfeld JS, Richardson JS (2016) Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Can J Fish Aquat Sci* 73:1292–1305. <https://doi.org/10.1139/cjfas-2015-0363>
- Pastor J, Solin J, Bridgman SD, Updegraff K, Harth C, Weishampel P, Dewey B (2003) Global warming and the export of dissolved organic carbon from boreal peatlands. *Oikos* 100:380–386. <https://doi.org/10.1034/j.1600-0706.2003.11774.x>
- Pérez-Rodríguez M, Biester H (2022) Sensitivity of river catchments to discharge-controlled dissolved carbon export: a study of eight catchments in southern Patagonia. *Biogeochemistry* 160:177–197. <https://doi.org/10.1007/s10533-022-00947-3>
- Peterson M, Matthews R (2009) Retention of salmon-derived N and P by bryophytes and microbiota in mesocosm streams. *J N Am Benthol Soc* 28:352–359. <https://doi.org/10.1899/08-104.1>
- Power ME, Rainey WE (2000) Food webs and resource sheds: towards spatially delimiting trophic interactions. In: Hutchings MJ, John EA, Stewart AJA (eds) *Ecological Consequences of habitat heterogeneity*. Blackwell Scientific, Oxford, pp 291–314
- Qiao J, Bao H, Huang D, Li DW, Lee TY, Huang JC, Kao SJ (2020) Runoff-driven export of terrigenous particulate organic matter from a small mountainous river: sources, fluxes and comparisons among different rivers. *Biogeochemistry* 147:71–86. <https://doi.org/10.1007/s10533-019-00629-7>
- Qiu H, Zhang X, Yang A, Wickland KP, Stets EG, Chen M (2023) Watershed carbon yield derived from gauge observations and river network connectivity in the United States. *Scientific Data* 10:278. <https://doi.org/10.1038/s41597-023-02162-7>
- Rantz, SE (1982) Measurement and Computation of Stream-flow. Report. Vol. 1 & 2. Water Supply Paper, USGS Publications Warehouse. <https://doi.org/10.3133/wsp2175>
- Rietti-Shati M, Yam R, Karlen W, Shemesh A (2000) Stable isotope composition of tropical high-altitude fresh-waters on Mt. Kenya. *Equatorial East Africa Chemical Geology* 166:341–350. [https://doi.org/10.1016/S0009-2541\(99\)00233-8](https://doi.org/10.1016/S0009-2541(99)00233-8)
- Romashkin I, Shorohova E, Kapitsa E, Galibina N, Nikerova K (2018) Carbon and nitrogen dynamics along the log bark decomposition continuum in a mesic old-growth boreal forest. *Eur J Forest Res* 137:643–657. <https://doi.org/10.1007/s10342-018-1131-2>
- Runkel RL, Crawford CG, Cohn TA (2004) Load Estimator (LOADEST): a FORTRAN program for estimating constituent loads in streams and rivers. U.S. Dept. of the Interior, U.S. Geol Surv. <https://doi.org/10.3133/tm4A5>
- Schwalm CR, Williams CA, Schaefer K (2011) Carbon consequences of global hydrologic change, 1948–2009. *J Geophys Res Biogeosci* 116:G03042. <https://doi.org/10.1029/2011JG001674>
- Sergeant CJ, Falke JA, Bellmore RA, Bellmore JR, Crumley R (2020) A classification of streamflow patterns across the coastal Gulf of Alaska. *Water Resour Res* 56:2019026127. <https://doi.org/10.1029/2019WR026127>
- Sobczak WV, Cloern JE, Jassby AD, Müller-Solger AB (2002) Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources. *Proc Natl Acad Sci USA* 99:8101–8105. <https://doi.org/10.1073/pnas.122614399>
- St. Pierre KA, Oliver AA, Tank SE, Hunt BPV, Giesbrecht I, Kellogg CTE, Jackson JM, Lertzman KP, Floyd WC, Korver MC (2020) Terrestrial exports of dissolved and particulate organic carbon affect nearshore ecosystems of the Pacific coastal temperate rainforest. *Limnol Oceanogr* 65:2657–2675. <https://doi.org/10.1002/lno.11538>
- Stackpole SM, Butman DE, Clow DW, Verdin KL, Gaglioti BV, Genet H, Striegl RG (2017) Inland waters and their role in the carbon cycle of Alaska. *Ecol Appl* 27:1403–1420. <https://doi.org/10.1002/eap.1552>
- Standard methods for the examination of water and wastewater (1999) American Public Health Association.
- Sullivan ML, Zhang Y, Bonner TH (2014) Carbon and nitrogen ratios of aquatic and terrestrial prey for freshwater fishes. *J Freshw Ecol* 29:259–266. <https://doi.org/10.1080/02705060.2014.888524>
- Tank SE, Fellman JB, Hood R, Kritzberg ES (2018) Beyond respiration: controls on lateral carbon fluxes across the terrestrial-aquatic interface. *Limnol Oceanogr Lett* 3:76–88. <https://doi.org/10.1002/lo2.10065>
- Tiwari T, Sponseller RA, Laudon H (2022) The emerging role of drought as a regulator of dissolved organic carbon in boreal landscapes. *Nat Commun* 13:5125. <https://doi.org/10.1038/s41467-022-32839-3>
- Ward ND, Bianchi TS, Sawakuchi HO, Gagne-Maynard W, Cunha AC, Brito DC, Neu V, de Matos VA, da Silva R, Krsche AV, Richey JE, Keil RG (2016) The reactivity of plant-derived organic matter and the potential importance of priming effects along the lower Amazon River. *J Geophys Res Biogeosci* 121:1522–1539. <https://doi.org/10.1002/2016JG003342>
- Ward ND, Bianchi TS, Medeiros PM, Seidel M, Richey JE, Keil RG, Sawakuchi HO (2017) Where carbon goes when water flows: Carbon cycling across the aquatic continuum. *Front Mar Sci* 4:7. <https://doi.org/10.3389/fmars.2017.00007>
- Warkentin L, Parken CK, Bailey R, Moore JW (2022) Low summer river flows associated with low productivity of Chinook salmon in a watershed with shifting hydrology. *Ecol Solut Evidence* 3:e12124. <https://doi.org/10.1002/2688-8319.12124>
- Wen H, Perdrial J, Abbott BW, Bernal S, Dupas R, Godsey SE, Harpold S, Rizzo D, Underwood K, Adler T, Sterle G, Li L (2020) Temperature controls production but hydrology regulates export of dissolved organic carbon at the catchment scale. *Hydrol Earth Syst Sci* 24:945–966. <https://doi.org/10.5194/hess-24-945-2020>
- Whitney EJ, Beaudreau AH, Howe ER (2018) Using stable isotopes to assess the contribution of terrestrial and riverine organic matter to diets of nearshore marine consumers in a

- glacially influenced estuary. *Estuaries Coasts* 41:193–205. <https://doi.org/10.1007/s12237-017-0260-z>
- Wipfli MS, Musslewhite J (2004) Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia* 520:153–163. <https://doi.org/10.1023/B:HYDR.0000027734.95586.24>
- Wisseman RW, Wisseman AR (2022) R-based freshwater macroinvertebrate analysis program and taxa traits for benthic, drift and fish diet samples developed by Aquatic Biology Associates, Inc., Corvallis, OR. 2022 version.
- Woodland RJ, Thomson JR, Mac Nally R, Reich R, Evrard V, Wary FY, Walker JP, Cook PLM (2015) Nitrogen loads explain primary productivity in estuaries at the ecosystem scale. *Limnol Oceanogr* 60:1751–1762. <https://doi.org/10.1002/lno.10136>
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