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The influence of lithology on stream metabolism in headwater systems

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Abstract

Physical disturbances in streams have important effects on rates of gross primary production (GPP) and ecosystem respiration (ER). Underlying lithology can control sediment size, amount, and evolution in the stream, influencing substrate stability and in turn benthic organisms. We assessed patterns of disturbance and recovery for metabolic processes of GPP and ER associated with periods of increased flow and suspended sediment flux between December and April in two streams in the Oregon Coast Range with differing lithologies (basalt and sandstone). The results of whole-stream metabolism modelling indicate that the two study streams have varying patterns of response and recovery rates after storm events. Both streams were heterotrophic during the entirety of the study period with changes in heterotrophy driven by changes in ER. Poststorm GPP decreased in both streams, but the basalt basin had greater proportional decreases and recovered slower than the sandstone basin. This result was unexpected and appeared to be associated with lower light availability in the basalt basin driven by increased turbidity during storm events; the coarser basalt substrate weathers into smaller size fractions than the finer sandstone substrate, remaining in suspension over longer periods and limiting light availability to benthic primary producers. The rates of ER in the sandstone basin did not change from prestorm to poststorm, whereas rates of ER in the basalt basin had varying responses. Overall, our results indicated that the underlying lithology of small mountain streams can drive variability in GPP by controlling sediment size and light availability during storms events.

KEYWORDS

disturbance, floods, Oregon, primary production, quantile regression, stream ecology, suspended load

1 | INTRODUCTION

Key stream ecosystem functions, such as the cycling of carbon and nutrients, are influenced by the metabolic processes of gross primary production (GPP) and ecosystem respiration (ER). Factors that control stream metabolism can therefore influence resources and energy cycles in lotic systems (Bernhardt et al., 2018). Benthic algae are the dominant autotrophs in some headwater streams (McCutchan & Lewis, 2002), and a great deal of research has been conducted to explore factors that limit or control the rates of autotrophy by benthic algae. Temperature (Hill et al., 2000; Larned, 2010), nutrient status (Bernot et al., 2010), and light availability (Acuña et al., 2004; Roberts et al., 2007) are recognized as important factors affecting stream metabolism through their influence on the rates of biological processes (Hill et al., 2011; Larned, 2010). An additional factor that has the potential to affect stream metabolism is the direct removal of benthic material by the flow and the mobilization of stream substrates during high flow events (Cronin et al., 2007). In contrast to temperature, nutrients, and light, the influence of high flows and bed mobility on stream metabolism is derived primarily from mortality of benthic autotrophs associated with the mobilization of stream sediments or detachment of benthic biofilm cells, which resets the benthic algal community rather than through mediation of metabolic rates (Barry et al., 1999; Fisher et al., 1982; O'Connor et al., 2012). Where bed disturbances occur frequently (Uehlinger et al., 2002) or where recovery rates following disturbance are slow (Segura et al., 2011), these events can have a strong influence on the overall standing stocks and productivity of benthic biofilms in streams.

Three main processes physically disturb the benthic biofilms during high flow events: removal of material by the flow of water (Biggs & Thomsen, 1995), abrasion of material by small particles (sand) (Luce et al., 2013), and overturning of the substrate itself. This last mechanism can both abrade material and shade any remaining biofilm, thereby reducing the capacity for primary production even if the benthic materials remain in place (Barry et al., 1999; Biggs & Close, 1989). Substrate size and especially the abundance of smaller grains can be important factors influencing biofilm scour. In gravel bed streams, sand size particles are mobilized over a wider range of flows than coarser material, and the movement of this size fraction can abrade biofilms attached to infrequently mobilized gravel–cobble size particles. The effect of abrasion in decreasing biofilm biomass can be significant even at moderate flows without movement of larger grains (Luce et al., 2010). Further, the abundance of small particles can enhance the movement of all size fractions (Curran & Wilcock, 2005; Wilcock et al., 2001). Therefore, in systems dominated by fine sediment fractions (i.e., fractions that are easily mobilized), GPP may be more susceptible to ecosystem-level impacts from moderate and higher flow events than in systems characterized by coarser channel beds.

Increased sensitivity of GPP to flow disturbance events with increasing abundance of fine material in the streambed has been observed in urbanized systems (Blaszczak et al., 2019; Qasem et al., 2019); however, this has not been explored in forested systems. Yet there is a wide range of natural landscapes with fine sediment in their channel bed substrates, primarily controlled by the underlying lithology (Mueller & Pitlick, 2013). Given the importance of the abundance of fine particles on scour frequency, underlying lithology of forested stream systems may be an important factor controlling metabolism with streams in friable rock (with more fine sediment) experiencing more frequent disturbances than streams draining more competent rock (with less fine sediment).

Several earlier studies have explored the effects of physical disturbance on benthic biofilm communities and standing stocks. O'Connor et al. (2012) found that although larger flood pulses destroyed bed habitat and resulted in increased recovery times of benthic organisms, small pulses that did not disturb the bed but increased turbidity resulted in faster recovery times for GPP after flood events. Biggs and Thomsen (1995) found that spates without movement of bed load could have varying magnitudes of disturbance to the benthic biofilms due to different resistances of periphyton communities. Several studies identify losses in biomass due to increased flow (Biggs, 1995; Biggs & Close, 1989; Clausen & Biggs, 1997; Katz et al., 2018; Segura et al., 2011; Tett et al., 1978); others concluded that adding sediment to high flows in experiments further disturbed benthic organisms (Francoeur & Biggs, 2006). Several studies found that the periphyton taxonomic makeup can also play a role in the resilience and resistance of the communities due to disturbance (Biggs & Thomsen, 1995; Francoeur & Biggs, 2006; Grimm & Fisher, 1989; Peterson & Stevenson, 1992).

Through high-resolution measurements of changes in dissolved oxygen concentrations and modelled or measured estimates of oxygen–air exchange rates (Appling et al., 2018b; Holtgrieve et al., 2010; O'Donnell & Hotchkiss, 2019), several studies have found that stream GPP declined during and soon after flooding (Cronin et al., 2007; O'Donnell & Hotchkiss, 2019), as expected based on earlier studies of benthic standing stocks (e.g. Biggs & Close, 1989; Fisher et al., 1982; Matthaei et al., 2003; Power & Stewart, 1987; Uehlinger, 2006; Uehlinger et al., 2003). In assessing metabolic responses to flood changes, GPP and ER were not always linked (Qasem et al., 2019; Uehlinger, 2000, 2006). In some cases, ER rates may be more resistant to flow disturbance because in addition to metabolism of surface biofilms, there is significant exchange with the hyporheic zone where respiration rates are high (Corson-Rikert et al., 2016; Fellows et al., 2001; Naegeli & Uehlinger, 1997). Further, although aerobic processes dominate estimates of ER from whole-system studies of oxygen, metabolism may not reflect the total amount of carbon that is mineralized through all metabolic processes because ER can be fuelled by other electron acceptors (Marcarelli et al., 2011).

Time of year is also an important factor that affects patterns in stream metabolism in temperate regions due to larger shifts in seasonal light availability and shading associated with deciduous riparian plants (Roberts et al., 2007; Uehlinger, 2000, 2006; Uehlinger et al., 2003). In forested mid-order streams, the effects of canopy cover as it relates to light availability has been a key consideration in the context of riparian shading, but light attenuation through the water column by turbid water is also an important process that can limit light availability to the stream benthos (Davies-Colley et al., 1992; Izagirre et al., 2008; Kirk et al., 2020). With increased turbidity, a reduction in light may also reduce stream GPP during or soon after storm events, even if no abrasion occurs. Indeed, a recent study in urban systems found that as stream flashiness increased, the ability for surface measurements of light availability to account for variability in stream metabolic rates declined, which could in part be attributed to a decrease in water clarity (Blaszczak et al., 2019). This suggests that stream turbidity and suspended sediments may warrant consideration as additional factors affecting metabolic rates during storm events that alter fine sediment loads but which are too small to create scouring flows that move the majority of the streambed.

The goal of this study was to understand how underlying lithology and its influence on stream bed sediment size and mobility affect stream metabolism in two Oregon (USA) streams with contrasting lithologies (sandstone- and basalt-dominated). We focused on both flow magnitude and the amount of suspended sediment through the rainy season in streams with a Mediterranean climate. We expected that in the more friable sandstone basin, where the smaller particles could be disturbed and reset even under moderate flows, the metabolic rates (GPP and ER) would be more sensitive to storm events and have a slower recovery of stream GPP than in the basalt basin with larger and competent channel bed material.

2 | STUDY SITES

This study was conducted in two streams underlain by contrasting lithology in the Oregon Coast Range in United States (Figure 1). In order to isolate the effects of lithology and its associated influence on stream sediment grain sizes, we selected study reaches that were similar in size, land cover, slope, channel form (pool-riffle morphology), and climate (Table 1). The Oregon Coast Range has a Mediterranean climate, with wet winters and mild summers. The overall climate regime is the same between the two sites that are ~37 km apart. Given their proximity, the two streams generally experience the same large storm events; however, due to a rainfall gradient across the coast range, total annual precipitation is slightly higher in South Fork Mill Creek, the stream reach closer to the coast (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu/, created 12 October 2019) (Table 1). Both watersheds are forested, with upland forests dominated by stands of mid-succession Douglas fir (*Pseudotsuga menziesii*).

The first study site is a 160-m reach in Oak Creek, a stream underlain by basaltic lithology (Milhous, 1973; O'Connor et al., 2014). Upper canopy riparian vegetation includes big leaf maple (*Acer macrophyllus*), alder (*Alnus sp*), and black cottonwood (*Populus trichocarpa*). The study reach has a bankfull discharge of 3.4 $m^3\ s^{-1}$, a bankfull width of 6 m, and a slope of 0.014 $m\ m^{-1}$ with a contributing drainage area of about 6.7 km^2 (Katz et al., 2018). The median grain size (D_{50}) of the channel bed surface is 47.6 mm, the D_{16} is 21.2 mm, and the D_{84} is 84.6 mm (Katz et al., 2018) (Figure 2). For the winter months of 2019, the mean nitrate nitrogen concentration in streamwater was 180 $\mu g\ L^{-1}$ ($N = 5$), and the mean concentration of phosphate phosphorus was 18 $\mu g\ L^{-1}$ ($N = 5$) (Table 1).

The second study site is a 160-m reach in the South Fork Mill Creek, a tributary of the Siletz River located in the central Coast Range of Oregon. This stream is underlain by the Tyee formation, a sequence of sandstone and siltstone lithologies (Snavely et al., 1964). The riparian vegetation is primary deciduous, including vine maple (*Acer circinatum*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*). The study reach has a bankfull discharge of 2.5 $m^3\ s^{-1}$, a bankfull width of 7 m, and a slope of 0.008 $m\ m^{-1}$, with a contributing drainage area of about 4.3 km^2 (Bair et al., 2019). The D_{50} of the surface is 28.6 mm, the D_{16} is 12.4 mm, and the D_{84} is

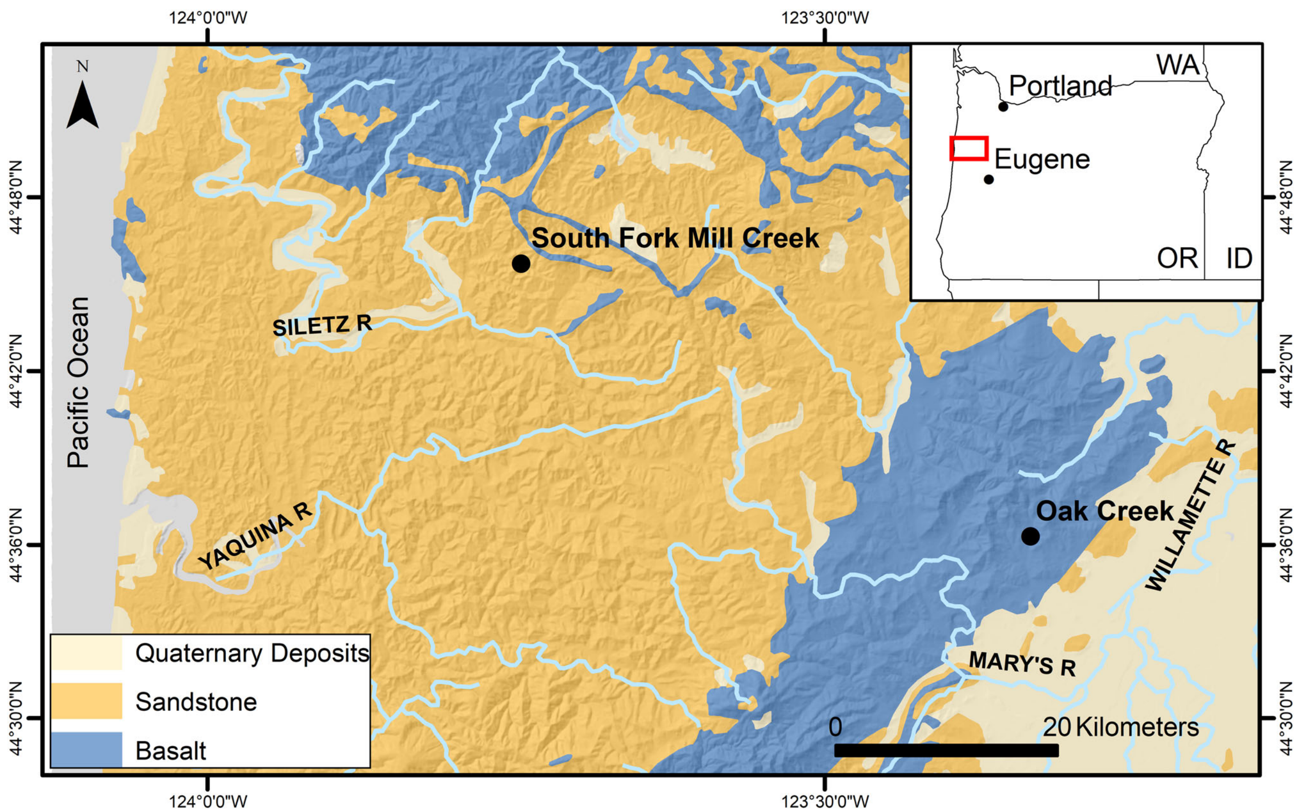

FIGURE 1 Location of the two study streams, Oak Creek and South Fork Mill Creek. Both streams are in the Oregon Coast Range. Oak Creek is underlain by basalt, whereas South Fork Mill Creek is underlain by sandstone (Walker & MacLeod, 1991)

TABLE 1 Reach characteristics of study sites in the two focal streams in western Oregon, Oak Creek and South Fork Mill Creek

Characteristic	Oak Creek	South Fork Mill Creek
Coordinates (latitude, longitude)	44°36′17.9532″, −123°19′59.5632″	44°45′43.0302″, −123°44′44.7678″
Drainage area (km^2)[a]	6.7	4.3
Bankfull width (m)	5.6 ± 0.2	7.4 ± 1.6
D_{50} (mm)	47.6 ± 1.8	28.6 ± 1.5
Bankfull discharge ($m^3\ s^{-1}$)	3.4	2.5
Mean daily PAR (mol m^{-2})	4.1 (3.8)	3.1 (2.7)
Mean temperature (°C)	7.6 (1.6)	8.0 (1.4)
Slope (m/m)	0.014	0.009
[NO_3^-–N] (μg L^{-1})	177 (61)	939 (107)
[PO_4^{-3}–P] (μg L^{-1})	18.5 (4.4)	6.8 (0.7)
Mean annual precipitation, 1997–2018 (mm)	1623.83	1978.98

Note: Values in parentheses are standard deviations and the ± are standar errors.
Abbreviation: PAR, photosynthetically active radiation.
[a]Derived from LiDAR (Oregon Spatial Data Library, https://gis.dogami.oregon.gov/arcgis/rest/services/Public/BareEarth/ImageServer, 8 September3 2018).

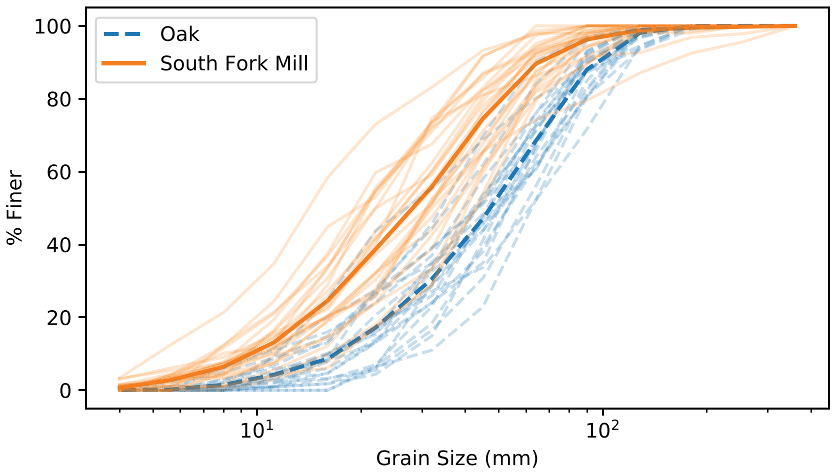

FIGURE 2 Surface grain size distributions (with mean distributions shown as bolded lines) of South Fork Mill Creek (sandstone, orange, 29 cross sections) and Oak Creek (basalt, blue, 23 cross sections)

56.9 mm (Figure 2). The mean winter nitrate nitrogen concentration (N = 4) in the 2019 water year was 940 μg L^{-1}, and the mean winter phosphate–phosphorus concentration was 6.8 μg L^{-1} (N = 4) (Table 1). We measured stream water concentrations of phosphate phosphorus and nitrate nitrogen for both streams at the Oregon State University Institute for Water and Watersheds (IWW) Collaboratory using a Dionex Ion Chromatograph (Dionex ICS-1500). As currently configured, the detection limit for these ions is 2 μg L^{-1} for nitrate and 3 μg L^{-1} for phosphate on this analyser.

3 | METHODS

3.1 | Data collection

3.1.1 | Metabolism data

Changes in dissolved oxygen over a diel cycle are used to model production and consumption of organic carbon through the photosynthesis and respiration processes within a stream community (stream metabolism). Along with dissolved oxygen concentrations, stream metabolism estimates also require data on (1) water temperature, (2) available photosynthetically active radiation (PAR), (3) barometric pressure, and (4) oxygen exchange rates with the atmosphere. In Oak Creek, data loggers were deployed to quantify and record dissolved oxygen, temperature, and PAR from December 2017 to April 2018 and from December 2018 to April 2019. In South Fork Mill Creek similar loggers were deployed from December 2018 to April 2019 (Figures S1–S3). Dissolved oxygen (O_2, mg L^{-1}) and water temperature (°C) were recorded every 10 min using MiniDOT optical dissolved oxygen and temperature loggers (Precision Measurement Engineering; Vista, California, USA).

Light for each reach was characterized based on the average PAR from three Odyssey loggers (Dataflow Systems Ltd; Christchurch, New Zealand) that collected integrated measurements over 10-min intervals in μmol $m^{-2}\ s^{-1}$ along the edge of each stream. Given the small size of the stream and their uniform second-growth forested conditions, we assumed that the irradiance in the edge of the stream is representative to the irradiance of the stream channel (Warren et al., 2013). The loggers were calibrated with a LI-COR quantum sensor (Campbell Scientific; Logan, Utah, USA). During a sensor malfunction period of 34 days between February and March 2019 in Oak Creek, PAR was estimated using a relationship between the sensor at the stream and solar radiation values recorded at a nearby weather station (located 0.8 km away) (r^2 = 0.85) (Cargill, 2019). There was a sensor malfunction in South Fork Mill Creek as well from March to April 2019 (total of 43 days). For this period, a similar method was used to estimate PAR, using a relationship between data at the stream and a solar radiation sensor from a weather station located 21 km away (r^2 = 0.70) (Cargill, 2019).

The downstream end of each reach was instrumented with a Levelogger Edge water level datalogger (Solinst; Georgetown, Ontario, Canada) to measure water stage every 10 min. Barometric pressure (kPa) was measured at the same time interval with a Barologger Edge absolute pressure sensor (Solinst; Georgetown, Ontario, Canada) placed in each watershed: in Oak Creek, at the downstream of the reach, and in Mill Creek, at a site in a sub-watershed about 1.5 km away and with less than 20 m difference in elevation from our study reach. The 10-min interval water height data were compensated with the barometric pressure data and then converted to discharge based on depth-discharge rating curves (Figure S4). The level loggers were located at the downstream end of each reach in representative cross sections. Discharge was calculated using the velocity area method (Dingman, 2008) by measuring velocity with a Hach FH950 Portable Velocity Meter (Hach; Loveland, Colorado, USA). In both streams, stage in metres (H) and discharge in $m^3\ s^{-1}$ (Q) were related by a power–law relationship where $Q = aH^b$. During a sensor malfunction period of 23 days between February and March 2019 in Oak Creek, depth and discharge were estimated based on a relationship between mean daily depth at Oak Creek and stage measured 5 km downstream (Cargill, 2019).

3.1.2 | Suspended sediment data

To measure suspended sediment concentration (SSC), we deployed Teledyne ISCO 3700 automated samplers (Teledyne ISCO; Lincoln, Nebraska, USA) at the downstream end of each reach. The samplers collected a 900-ml water sample at midnight every 24 h for most of the rainy season (November–April). In Oak Creek, sampling frequency was increased to every 3–6 h during some storm events. Samples for suspended sediment concentrations analysis were filtered with 1.5-μm glass fibre filters, and dried at 105°C for 24 h before weighing the inorganic sediment load following standard protocols (Lewis & Eads, 2009). A total of 333 samples were collected in Oak Creek—145 in the 2018 water year and 188 in the 2019 water year—and a total of 133 samples were collected in South Fork Mill Creek in the 2019 water year (Figure 3). Daily sediment flux was calculated for both streams based on a power–law relationship between discharge (Q) and SSC (Figures S5 and S6 and Table S1).

3.2 | Modelling stream metabolism

3.2.1 | Model parameters

We modelled stream metabolism from measurements of dissolved oxygen using a single-station open-channel method (Holtgrieve

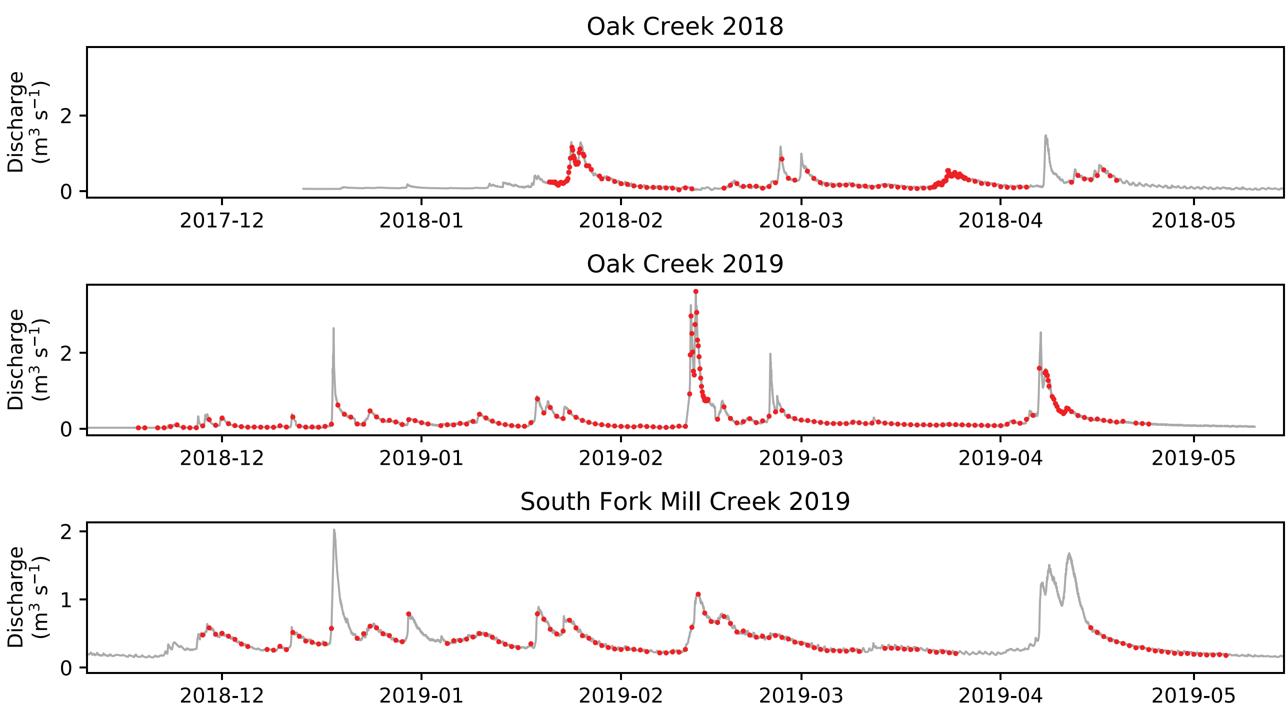

FIGURE 3 Discharge and times of suspended sediment sampling in Oak Creek and South Fork Mill Creek in 2018 and 2019. Grey lines represent discharge (from 10-min intervals), and each red dot represents a collected sample

et al., 2010; Odum, 1956). We utilized the streamMetabolizer R package (Appling et al., 2018a; Appling et al., 2018b) under R version 3.6.2, which uses inverse-modelling methods to estimate rates of GPP (g O_2 m^{-2} day^{-1}), ER (g O_2 m^{-2} day^{-1}) and K_{600} (a gas exchange rate standardized for a Schmidt number of 600, day^{-1}) from diel O_2 curves. As the sites are oligotrophic freshwater streams, we assumed salinity was 0 for both sites.

For South Fork Mill Creek, we used the binned pooling method with model defaults for estimating K_{600}. This method relates K_{600} and the discharge with piecewise linear functions, while still allowing some variation in K_{600} to be independent of discharge. This method yielded estimates that were consistent with K_{600} estimated from an SF_6 release (at a discharge of 0.29 m^3 s^{-1}) (Cargill, 2019). This modelling method was not successful in Oak Creek. Gas tracer releases experiments indicated that the gas exchange rates were much greater than model estimates in Oak Creek over a range of flows. Given these high gas exchange rates, we ran the Oak Creek model without pooling K_{600} values and instead defined a prior distribution for K_{600} that would force a higher K_{600} value. The model required the mean and standard deviation of the lognormal distribution of K_{600} values, for which we used 5.298 (the natural logarithm of 200 day, our chosen value of K_{600}) and 0.1, respectively.

Models were run with 3000 Markov Chain Monte Carlo iterations (1500 burn-in iterations). Doubling the number of iterations did not result in an improved modelling outcome. Model performance success was assessed through the following criteria: R-hat values less than 1.1 for daily GPP, ER and K_{600}, and RMSE of modelled DO versus observed DO < 0.05 mg L^{-1} (~10% of daily change in observed DO) (Grace et al., 2015). All subsequent analyses relating discharge and suspended sediment to stream metabolism metrics (GPP and ER) include only days on which these threshold criteria for a viable model fit were met.

3.2.2 | Measuring gas exchange rates

When the metabolism signal is weak due to low GPP and high gas exchange, there can be unrealistic model outputs due to equifinality, where many possible combinations of GPP, ER, and K_{600} yield undistinguishable diel curves of dissolved oxygen (Appling et al., 2018b). We found this to be an issue in Oak Creek, where high turbulence causes high gas exchange rates. Therefore, to further explore the relationship between K_{600} and discharge, we conducted three separate gas tracer releases in Oak Creek (Cargill, 2019). Linear regressions between ER and K_{600} show relatively low coefficients of determination (r^2 = 0.17 for Oak Creek and r^2 = 0.44 for South Fork Mill Creek), suggesting a reduced influence of equifinality in our estimates, but the uncertainty is higher at the South Fork Mill Creek site (Figure S7).

To calculate K_{600} using gas tracer releases, we dripped into the stream a solution that included dissolved sulfur hexafluoride (SF_6) gas and a dissolved conservative (nonbioreactive) tracer—in this case salt (NaCl) dissolved in stream water (Tobias et al., 2009). We then measured the decline in SF_6 concentrations relative to concentrations of the conservative tracer downstream from the addition site at the top of the reach. Samples were collected at 0, 30, 60, 90, 120 and 150 m downstream from the top of the reach. Starting at the downstream end of the reach, we collected water samples in triplicate at each sampling location. Water samples were collected and sealed underwater to ensure no gas loss. In the lab, gas was extracted from each water sample and immediately analysed on an Agilent 7890A Gas Chromatograph to determine the relative decline in SF_6 concentrations downstream. The absolute value of the slope of the best-fit line relating the natural log of SF_6 concentration to distance downstream was multiplied by the average velocity of the stream at that time of the release to determine the gas exchange coefficient for SF_6 in units of day. This K_{SF6} value was then converted to K_{600} using the water temperature *T* in degrees Celsius, with the following equation (Raymond et al., 2012):

$$K_{600} = \left(\frac{600}{3255 - 217.13T + 6.837T^2 - 0.0861T^3}\right)^{-0.5} \times K_{SF6}$$

These K_{600} values were matched with the average discharge over the period of the gas tracer release (Cargill, 2019) (Table S2). The resulting K_{600} values did not show a strong relationship with discharge but were much higher than—about double—those estimated by the metabolism model. We used these gas tracer release results to inform the definition of a high-magnitude prior distribution for the Oak Creek model discussed above. Modelled K_{600} in Oak Creek had a median value of 178.7 day^{-1}, with a range from 73.6 to 330.5 day^{-1} which aligned well with the empirical estimate of K_{600} from the SF6 releases (Figure S8) and were correlated to discharge (Figure S9) over a modest range of flows (~0.1–0.6 m^3 s^{-1}). In South Fork Mill Creek, modelled K_{600} had a median of 29.9 day^{-1}, and a range from 18.0 to 38.9 day^{-1} (Figure S8).

The rates of GPP and ER estimated here represent processes occurring throughout the larger stream segments than the 160-m study reaches over which we characterize channel morphology and grain size. On the basis of the flow and K_{600} rates, we estimated that GPP and ER rates encompass processes from 290 to 680 m upstream of the logger in Oak Creek and 500 to 3500 m upstream of the logger in South Fork Mill Creek (Table S3). The 160-m study reaches are assumed to be representative of processes in these larger stream segments, which are relatively homogeneous over these lengths given constant channel slope, similar bankfull widths, and the absence of major tributaries.

3.3 | Analysis

3.3.1 | Quantile regressions

Quantile regressions are a useful statistical tool for estimating the effects of ecological limiting factors (Cade & Noon, 2003). This method estimates relationships between variables for different portions of the distribution, as opposed to a least squares regression, which only estimates a relationship for the mean of the distribution. Due to the complexity of interactions between factors that affect organisms, it can be more meaningful to focus on the quantiles near the maximum response, where the limiting factor is driving the response (Cade & Noon, 2003). Because stream metabolism metrics can be limited by multiple factors and we were focused on exploring flow and sediment load as potential limiting factors for GPP and ER, quantile regression was an optimal analysis for this study.

We conducted four initial quantile regression analyses. We first calculated the slope of the regression along the 75th quantile of the relationship between GPP and two physical attributes that we expected to relate most directly to potential disruption of aquatic biofilms: maximum daily discharge and daily suspended sediment flux. We also calculated the 75th quantile regression slopes between daily P/R ratio and these two physical attributes. The 75th quantile was chosen because it was the upper-most quantile before sampling variation began to rapidly increase in our data set (Cade et al., 1999) (Figures S10 and S11, Tables S4 and S5).

These four initial quantile regressions represent the relationship between the physical attributes (maximum daily discharge and daily suspended sediment flux) on a given day and the 75th quantile of the estimated GPP or P/R ratio on that same day. However, focusing on the physical conditions on a single day does not capture potential legacy effects of earlier scouring events that may cause a more persistent decline in biofilm activity, ultimately reducing GPP or P/R ratios after the event. In order to quantify a lagged effect of bed load movement events on stream metabolism in addition to effects during the event itself, we began by calculating the 75th quantile regression slopes between GPP or P/R on a given day and the maximum discharge that occurred one day prior (1-day lag). This lagged regression was repeated for an additional 2–18 days between the occurrence of the physical attribute (discharge or sediment flux) and the metabolic rates on a given day. The series of slopes for each combination were plotted over time to explore the legacy effects of elevated discharge and suspended sediment flux on GPP and the P/R ratio. We use the word legacy here to refer to the influence of antecedent conditions on pattens of GPP and ER.

3.3.2 | Storm before–after analysis

The quantile regression analyses evaluated relationships between flow or suspended sediment flux and stream metabolism over the rainy season, but as a regression, it lacks the capacity to directly relate responses to a specific event. We therefore also explored differences in GPP and ER prestorm and poststorm for the three largest flows in the 2019 study period that occurred during the same general time periods in Oak Creek and South Fork Mill Creek. For each of the three storms in each stream, we established the peak discharge and an end date for the flood (chosen as the date when flows returned to prestorm levels). We binned values of GPP and ER from between 1 and 12 days before the peak of the storm for a 'before' category and then binned values between 1–3, 4–6, 7–9, 10–12, and 13–15 days after the end of the storm. In each 'after' category, the box plots had between 1 and 3 data points depending on availability of modelled data during that period. From these binned data, we compared patterns in disturbance and recovery associated to each storm. We considered including in the analysis the likelihood of bed load movement as indicating of bed disturbance. However, the mean shear stress values associated to the flow levels during the study periods at the study reaches were only high enough to mobilized the median grain size 1 day in Oak Creek (Katz et al., 2018; Monsalve et al., 2020) and 0 days in South Fork Mill Creek.

4 | RESULTS

4.1 | Calculation and modelling results

4.1.1 | Metabolism modelling

Our analysis yielded successful models of GPP, ER and K_{600} for 95 days in South Fork Mill Creek between December 2018 and April 2019, and for 101 days in Oak Creek between December 2017 and April 2018 and between December 2018 and April 2019. Most days without successfully modelled metabolic rates were due to the model failing to converge. Modelled GPP and ER had larger ranges in Oak Creek than South Fork Mill Creek; GPP at Oak Creek ranged from 0.0 to 0.8 g O_2 m^{-2} day^{-1}, whereas the modelled ER ranged from −12.6 to −5.5 g O_2 m^{-2} day^{-1} (Figures S12 and S13). Modelled GPP in South Fork Mill Creek ranged from 0.0 to 0.7 g O_2 m^{-2} day^{-1}, whereas ER ranged from −8.9 to −2.9 g O_2 m^{-2} day^{-1} (Figure S14). The 2019 winter–spring period had higher magnitude flow events than 2018. In Oak Creek, the highest flow during the 2018 study period was 0.43 Q_{bf}, although the highest flow was 1.06 Q_{bf} in the 2019 study period. In South Fork Mill Creek, the highest flow was 0.81 Q_{bf}. Analysis of the relationship between GPP and ER revealed some degree of decoupling in both systems. The GPP-ER relations were weak for both streams (r^2 = 0.01–0.02, p = 0.19–0.24, Figure S15).

4.1.2 | Suspended sediment analysis

The SSC of samples collected from Oak Creek ranged from 0.65 to 876 mg L^{-1}, whereas the range of SSC of samples collected from South Fork Mill Creek was substantially lower (from 0.35 to 70.21 mg L^{-1}) (Figure S5) but included a lower range of flows. Both streams showed an increase in suspended sediment with discharge, but for similar levels of discharge, South Fork Mill Creek generally had a lower suspended sediment flux (Figure 4).

4.2 | Relationships between discharge, suspended sediment flux, and ecosystem metrics

The upper range (75th quantile) of estimated GPP declined as both stream discharge and stream suspended sediment flux increased at

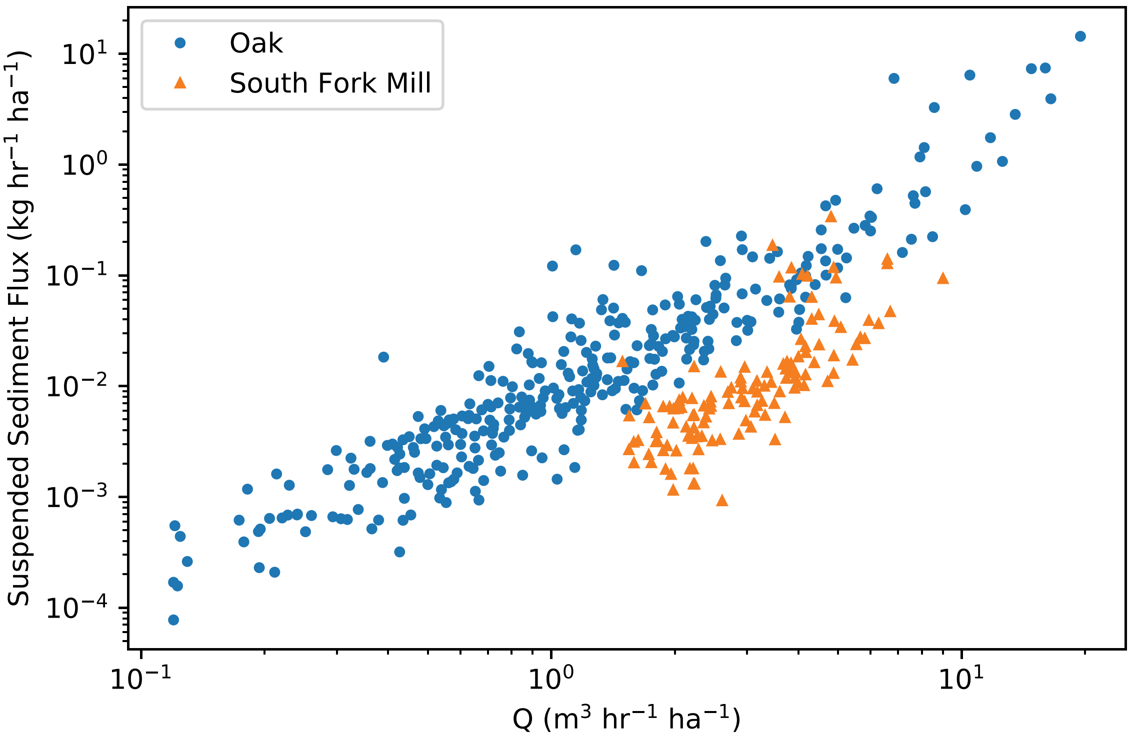

FIGURE 4 Suspended sediment flux and discharge from samples collected in Oak Creek and South Fork Mill Creek. Oak Creek generally showed more suspended sediment flux than South Fork Mill Creek at similar levels of discharge. The suspended sediment rating curves are included in Figure S5 and Table S1

both study sites (Figure 5a,b). This is illustrated by negative slopes of the 75th quantile regressions between daily GPP and maximum discharge on the same day and between daily GPP and the total estimated sediment flux through each reach during the same day. Slopes of these relationships were similar in Oak Creek and South Fork Mill Creek (−0.24 in Oak Creek and −0.29 in South Fork Mill Creek). Similarly, the relationship between the upper range of estimated GPP and sediment flux over the same time period had a slope of −0.11 in Oak Creek and −0.13 in South Fork Mill Creek.

We also investigated the legacy of elevated discharge and sediment flux through a quantile regression analysis between the upper range of estimated GPP on a given day and the maximum discharge or suspended sediment flux one to eighteen days before that day (Figure 5c,d). Based on the point at which the slope of the quantile regression approached 0 (indicating no relationship between a given day's GPP and maximum discharge or suspended sediment flux a given number of days before), maximum discharge had less of a legacy effect on GPP in South Fork Mill Creek than in Oak Creek despite higher phosphate–phosphorus concentrations in Oak Creek than in South Fork Mill Creek (Table 1). The 75th quantile regression slope was at or near 0 after about 7 days in South Fork Mill Creek (Figure 5c), whereas in Oak Creek, it took 17 days before the slope of the 75th quantile regression between maximum discharge and GPP reached 0 (Figure 5c). The relation between the upper range of GPP and suspended sediment flux showed a similar pattern to the relation between the upper range of GPP and maximum discharge, with the slope of the regression in South Fork Mill Creek approaching 0 around 10 days before Oak Creek (Figure 5d).

The upper range of the estimated P/R ratio in both streams declined with increasing discharge and suspended sediment flux (Figure 6a,b). The slope of the 75th quantile regression with maximum daily discharge was −0.04 in Oak Creek and −0.07 in South Fork Mill Creek. The slope of the 75th quantile for the same-day suspended sediment flux relationship was −0.02 in Oak Creek and −0.03 in South Fork Mill Creek. In contrast to the site differences in legacies of both sediment flux and maximum discharge on GPP (Figure 5c,d), the relationship between P/R and discharge and sediment flux were similar. That is, although the same-day relationships in South Fork Mill Creek had steeper slopes than in Oak Creek, the legacy of maximum discharge and suspended sediment flux on the P/R ratio showed similar patterns for both streams with slopes nearing zero 10 days after a discharge event (Figure 6c,d). Quantile regression analysis was calculated for ER, but the results were not interpretable (Figure S16).

4.3 | Evaluating individual storm effects on GPP and ER

For the three largest storms in 2019 (Table 2), we observed a decrease in GPP after the event (Figure 7). Across the three storms, the decrease in mean GPP from before the storm to 1–3 days after the storm ranged from 49.6% to 87.5% in Oak Creek and from 30.6%

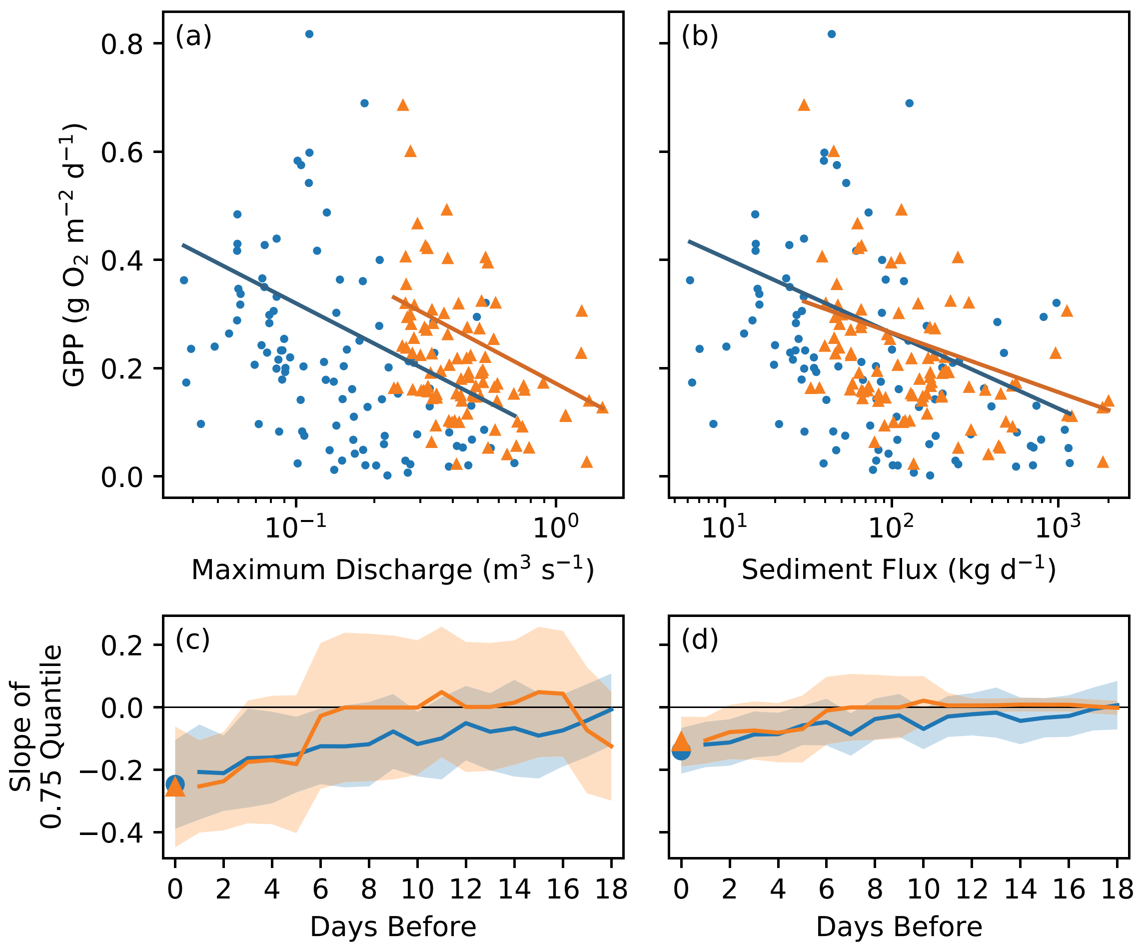

FIGURE 5 Results of 75th quantile regressions between (a) gross primary productivity (GPP) and same-day maximum discharge and (b) between GPP and same-day sediment flux. The bottom panels show the slopes of the 75th quantile regressions between GPP and the physical variable ([c] maximum discharge or [d] daily sediment flux) *x* days before the day GPP was modelled with 95% confidence bounds. The points in (c) and (d) at Day 0 represent the slopes of the 75th quantile regressions shown in (a) and (b). A slope of 0 indicates no relationship with the physical attribute

to 61.1% in South Fork Mill Creek (Table 2). In other words, primary producers in South Fork Mill Creek were relatively more resistant (Uehlinger, 2000) to the effects of these storm events than the primary producers in Oak Creek. Over the course of the season, the prestorm GPP increased in both streams, with the December storm having the lowest preceding GPP and the April storm having the highest preceding GPP. The GPP in Oak Creek declined by over 80% following the April storm, which had a peak flow of 75% of bankfull (Table 2). In South Fork Mill Creek, the April and December storms had comparable impacts on GPP with about a 60% decline in GPP following storms that were 81% and 67% of bankfull for the December and April storms, respectively. In regard to legacy effects, this storm-specific analysis yielded results that were largely comparable with the quantile regression results (Figure 5c,d), with GPP recovering more quickly in South Fork Mill Creek than in Oak Creek for all three storms (Figure 7).

The ER responses to the storm events in December, February, and April of 2019 differed markedly from the GPP responses in Oak Creek and South Fork Mill Creek. The December storm had minimal effects on mean ER in Oak Creek (Table 2), and following the storms in both February and April, poststorm mean ER increased (became more negative), which contrasts with the declines observed in mean GPP at this site after these storms. In South Fork Mill Creek, ER remained relatively consistent before and after the storms (both short term and long term) with no more than 16% change after any of the storms (Table 2, Figure 8).

4.4 | Light and temperature

Differences in water temperature and light availability also warrant consideration in this analysis as they could also lead to differences in both GPP and ER in streams that would confound conclusions about the influence of physical processes in this study. Overall, light and temperature were largely comparable along the two study reaches. Daily water temperature during the study period ranged from 3.89°C to 11.7°C in Oak Creek, and from 4.88°C to 10.55°C in South Fork Mill Creek (Table 1). Daily PAR ranged from 0.64 to 14.93 mol m^{-2} in Oak Creek and from 0.40 to 16.48 mol m^{-2} in South Fork Mill Creek.

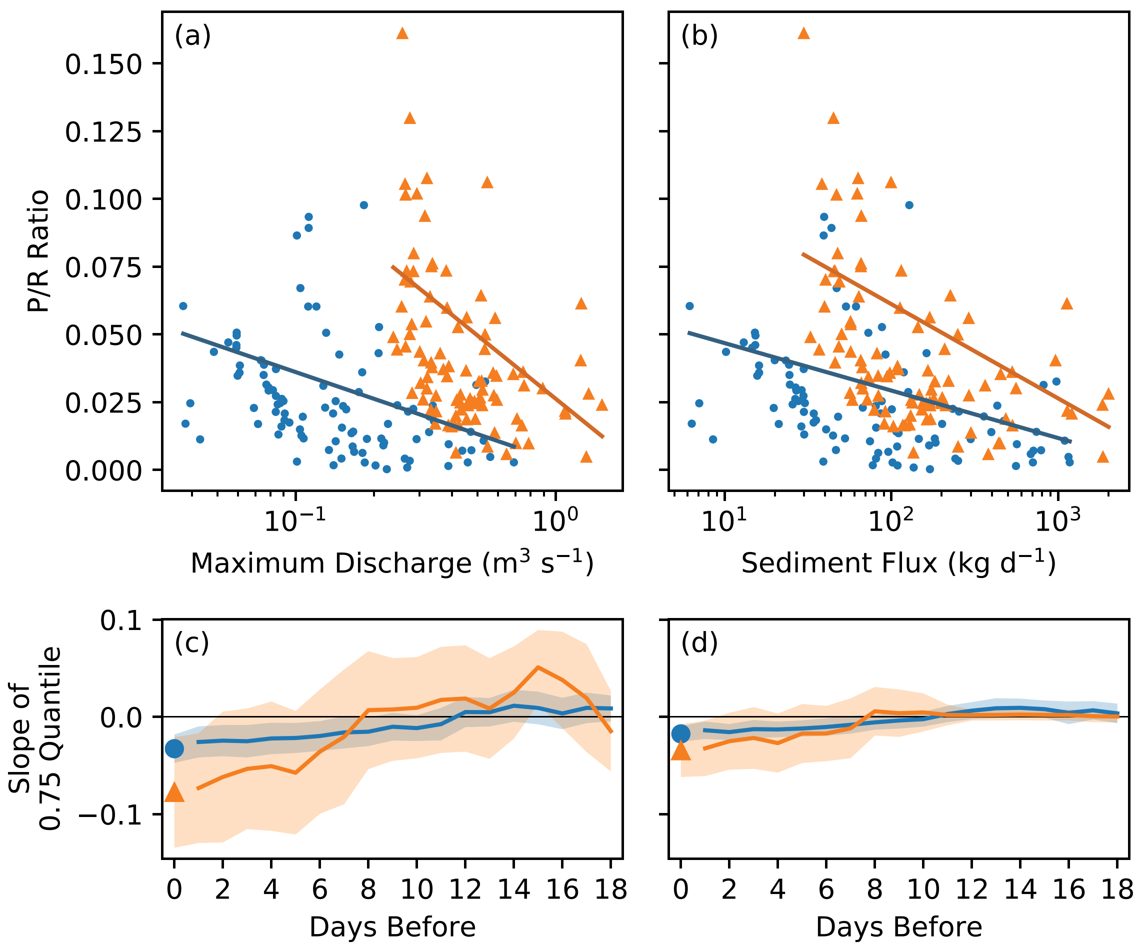

FIGURE 6 Results of 75th quantile regressions between (a) the P/R ratio and same-day maximum discharge and between (b) the P/R ratio and same-day sediment flux. The bottom panels show the slopes of the 75th quantile regressions between the P/R ratio and the physical variable ([c] maximum discharge or [d] daily sediment flux) *x* days before the day the P/R ratio was calculated with 95% confidence bounds. The points in (c) and (d) at day 0 represent the slopes of the 75th quantile regressions shown in (a) and (b). A slope of 0 indicates no controlling effect by the physical attribute

TABLE 2 Storm characteristics for the three largest storms in the 2019 water year

Reach	% Drop in GPP (1–3 days after)	% Drop in ER (1–3 days after)	Peak date	End date	Peak discharge (Q_i/Q_{bf})
Oak	57.8%	18.1%	12/18/18	1/4/19	0.78
	49.6%	−84.5%	2/12/19	3/1/19	1.06
	87.5%	−27.8%	4/7/19	4/11/19	0.75
South Fork Mill	61.1%	−4.5%	12/18/18	1/2/19	0.81
	30.6%	−5.6%	2/12/19	3/1/19	0.44
	60.0%	−16.0%	4/11/19	4/17/19	0.67

Note: The storm with the highest peak in Oak Creek (1.06 Q_{bf}) was in February, whereas the storm with the highest peak in South Fork Mill Creek (0.81 Q_{bf}) was in December. For the % drop values, negative percentages represent an increase in rates of GPP and ER.

Neither stream had a strong or significant relationship between light or temperature and GPP during our study period ($r^2 < 0.003$, $p > 0.5$) (Figure S17, Table S6). In Oak Creek, temperature was not significantly related with ER ($r^2 = 0.05$, $p > 0.05$). Similarly, there was no significant relationship between ER and temperature in South Fork Mill Creek ($r^2 < 0.03$, $p > 0.1$) (Figure S17, Table S6).

5 | DISCUSSION

The goal of this study was to compare patterns in stream metabolism between streams with contrasting underlying lithologies. We expected the site with finer substrates (South Fork Mill Creek) to be more sensitive to storm events, with a steeper slope in the

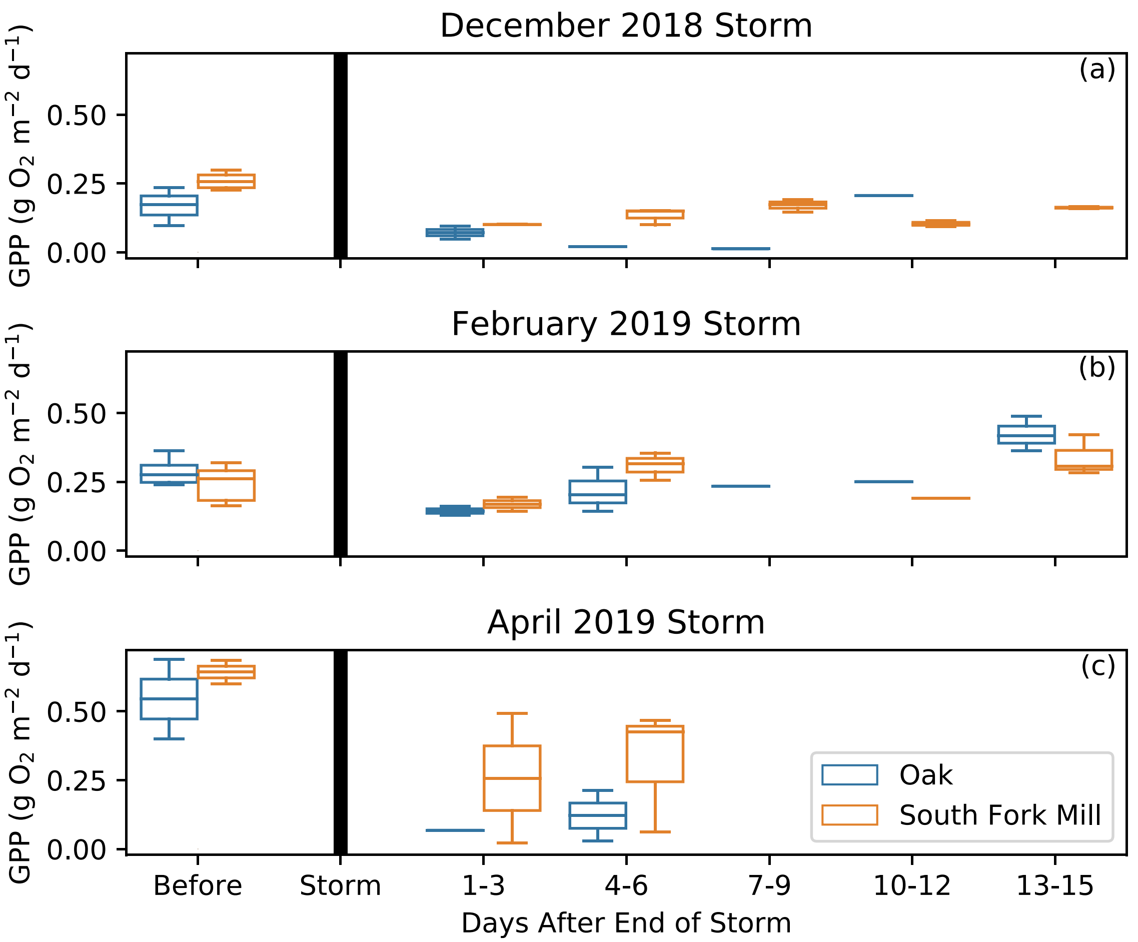

FIGURE 7 Gross primary productivity (GPP) before and after the three largest storm events in the 2019 water year. The 'before' category included data from 1 to 12 days before the peak of the storm. The 'after' category included data from after the end of the storm—when flows returned to pre-storm levels. Over the course of the study period, the pre-storm GPP rose, resulting in a larger drop due to the storm. In all three cases, South Fork Mill Creek appeared to recover more rapidly after the storms

relationship between discharge or sediment flux and the upper range of GPP, larger declines in GPP and ER following specific storm events, and slower recovery of stream GPP than the site with larger and competent channel bed material. As expected, South Fork Mill Creek, the sandstone basin, did generally show a stronger initial response to high flow events in the quantile regression analysis relative to Oak Creek. However, in contrast to our expectations, South Fork Mill Creek showed a more muted response to larger disturbances and faster recovery from high flow events relative to Oak Creek, the basalt basin (Figure 7). The rates of ER in South Fork Mill Creek did not change from prepost to poststorm, whereas rates of ER in Oak Creek had varying responses (increases and decreases) (Figure 8). This led to much stronger responses of P/R ratios to high flow events in South Fork Mill Creek (Figure 6a,b), and given the responses of GPP, the two streams had largely comparable recovery time of the P/R ratio (Figure 6c,d). Overall, differences in underlying lithology between these two basins likely did influence their response to high flow, but the differences were smaller and slightly different than expected.

We explored legacy effects of storm events in these two systems through a comparison of prestorm and poststorm means and a quantile regression analysis. Understanding legacy effects is important. Although ecosystem function can be briefly disrupted by physical disturbances, overall effects of disturbance on stream ecosystem function can be small if recovery is rapid (e.g. Roberts et al., 2007). In contrast, if recovery is prolonged, the disturbance can be key in structuring the ecosystem (e.g. Segura et al., 2011). The quantile regression analysis provides information on the storm event as one of many potential limiting factors for GPP, ER, or P/R ratios. A more negative slope for the upper quantile in this study represents a larger decline in the maximum (upper 25% of the distribution in this study) value of a metric (GPP, ER or P/R) in response to a storm event. We consistently saw the steepest 75th quantile slope during or shortly after a storm (Figures 5c,d and 6c,d), indicating maximum effect during and shortly after the event. Over time, the effect of the storm event on GPP and P/R declined, reflecting recovery of these processes from the storm disturbance, with the time (in days) that it takes to return to a slope of 0 in the 75th quantile reflecting the overall recovery time. From this analysis, we inferred that although the initial influence of flow on GPP is larger (steeper slope) in South Fork Mill Creek, the system recovered more quickly with the transition to a slope of 0 in the 75th

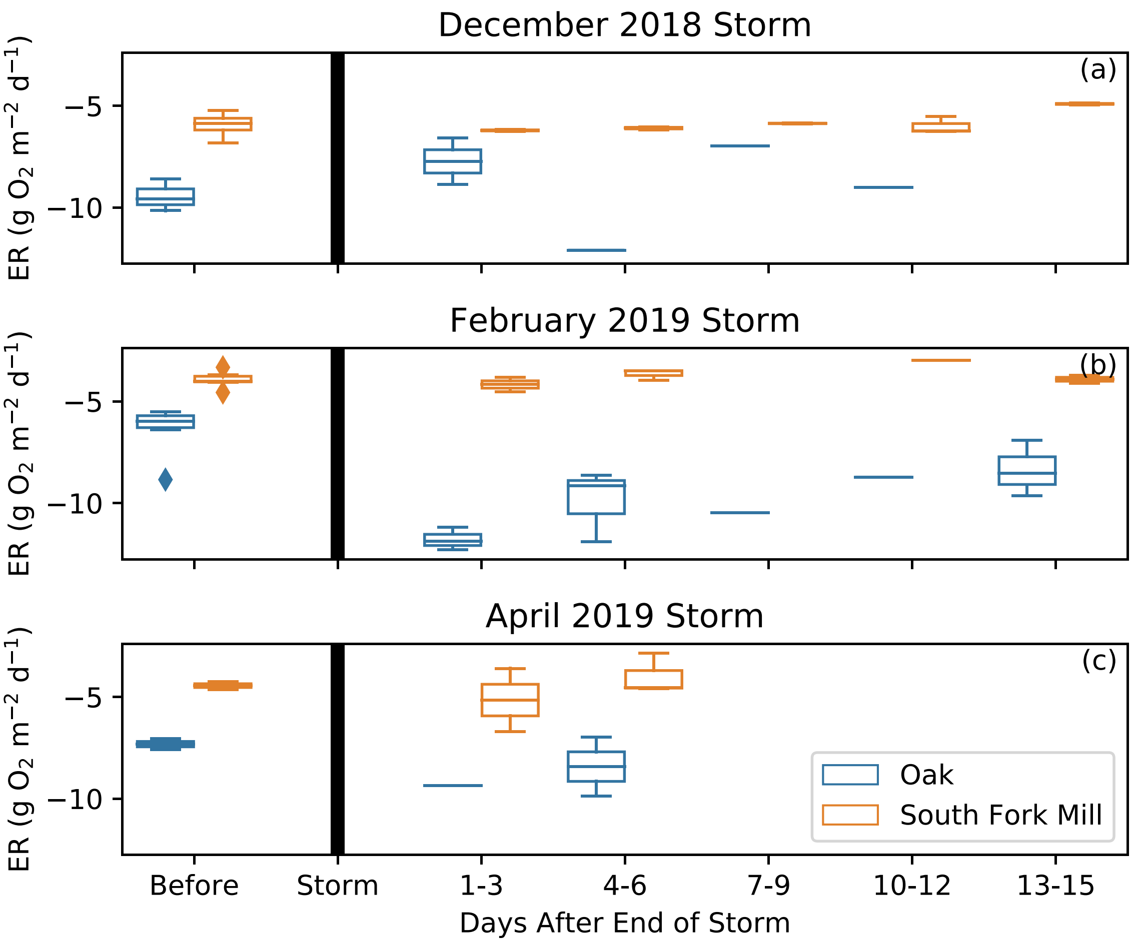

FIGURE 8 Ecosystem respiration (ER) before and after the three largest storm events in the 2019 water year. The 'before' category included data from 1 to 12 days before the peak of the storm. The 'after' category included data from after the end of the storm—when flows returned to prestorm levels. Over the course of the study period, ER had varying responses to storms in Oak Creek, whereas in South Fork Mill Creek, ER remained relatively consistent

quantile within 6 days. In contrast, the influence of flow on GPP at Oak Creek was smaller (milder slope), but it took the system over 2 weeks to recover. Another possibility to account for the differences in legacy effects is that difference in the algal community and disturbance history between the two streams drive different patterns of recovery after disturbance. Indeed, a previous study in Oak Creek reported that benthic algae recovery between 5 and 31 days was faster in areas that are more frequently disturbed and attributes this to possible differences in the algal community composition (Katz et al., 2018).

When considering specific storm events, GPP decreased in both streams following a storm event, as we expected. This is consistent with previous results (Uehlinger, 2000; Uehlinger et al., 2003). However, the magnitude of the disturbance (percent change in metabolic rates) was smaller in South Fork Mill Creek than in Oak Creek. Similarly to the result of Roberts et al. (2007) in a forested headwater stream, we found that the magnitude of the disturbance appeared to be related not only to the size of the storm but also to prestorm conditions and the time of the season in which the storm took place. Storms had a larger effect in April in both of our streams, when prestorm rates of GPP were higher, resulting in a larger proportional change in GPP. In both our comparison of GPP rates before and after storms and in our analysis of legacy responses, South Fork Mill Creek showed a faster recovery of GPP than Oak Creek. Given the much longer recovery time in Oak Creek and the larger proportional impacts across three major storms in this stream relative to South Fork Mill Creek, the effects of flow disturbances on overall winter GPP in Oak Creek may be greater than in South Fork Mill Creek. This contrasts to our expectations of greater disturbance in South Fork Mill Creek given that its channel bed substrate is likely more unstable (being finer) than in Oak Creek (being coarser).

One explanation for the high sensitivity of GPP to elevated flows in Oak Creek is an increase in the concentration of clay particles in Oak Creek during moderate–large flows, which results in the attenuation of light to the stream bed for a longer period after storm events as clay sediments can remain suspended in the water column for much longer than coarser particles (Hall et al., 2015; O'Connor et al., 2012). In South Fork Mill Creek, we measured generally lower suspended sediment concentrations for similar flow conditions, and we did observe lower water clarity at the Oak Creek site during winter and spring. This result is likely due to differences in the breakdown of the rock types that underlie the basins. Sandstone is more friable (O'Connor et al., 2014) but weathers into sand and does not get much smaller than that size fraction (McBride & Picard, 1987). In contrast, although basalt is a harder rock (O'Connor et al., 2014), the products of basalt weathering are clays (Glasmann & Simonson, 1985). Clays are much finer and more readily mobilized than sand, possibly resulting in the higher suspended sediment concentrations in Oak Creek. Sand grains in South Fork Mill Creek are likely still transported, but possibly as bed load rather than suspended sediment load. The clays transported in suspension in Oak Creek stay in suspension longer and can strongly influence light penetration. Thus, in Oak Creek, high flow events appear to disturb GPP not only through the movement of sediment but also through the reduction of light.

In small forested streams, ER can be coupled with GPP during periods of high primary production (Roberts et al., 2007). However, much of the year, ER is largely driven by the decomposition of allochthonous sources of organic matter (McCutchan & Lewis, 2002), leading to decoupled GPP and ER rates. In addition, floods may enhance community respiration through the entrainment of organic matter while reducing GPP (Roberts et al., 2007; Uehlinger et al., 2003). We found evidence for decoupling between GPP and ER in both streams during our study period (winter and early spring; Figure S15). This GPP-ER decoupling suggests that stored organic matter supports significant biological activity when primary productivity is low (Webster & Meyer, 1997). In our steams, it is likely that allochthonous inputs may exceed in situ GPP, particularly during winter when temperatures are low and days are short (Bernhardt et al., 2018). In general, ER was more resilient to high flow disturbance events. We initially expected that like GPP, ER would also be disturbed in our study streams during and after high flow events. However, as GPP and ER appear largely decoupled in these streams (during winter and early spring), the response of ER and the ER legacy effects did not meet these expectations and showed notable differences between the two streams. Storms had no effect on the magnitude of ER in South Fork Mill Creek. In Oak Creek, the magnitude of ER increased after storms in some cases and decreased in other cases (Figure 8). Elevated flows can change ER through a combination of processes including declines associated with bed movement that scours biofilms and increases associated with spikes in the external inputs of dissolved organic carbon (DOC) and greater infiltration of carbon-rich surface water into deeper sections of the hyporheic zone. Bed movement can displace not only primary producers on the surface of the stream bed but also other microscopic and macroscopic organisms that reside deeper within the sediment of the channel bed (Naegeli & Uehlinger, 1997). Decreases in ER have been documented as result of increased flow velocities and bed movement disrupting benthic organisms (Uehlinger, 2000, 2006). Studies have also documented that storms result in an influx of DOC from the area surrounding the stream, which can temporarily increase ER by providing a labile food source to consumers in the system (Beaulieu et al., 2013; Webster & Meyer, 1997). Both systems in our study are forested with organic material that can be easily leached into the stream during winter, and so they likely did receive high inputs of DOC even during small flow events (Raymond & Saiers, 2010), which would lead to increases in ER by heterotrophic microbes during and in periods soon after the storm.

Light, temperature, and nutrients are all resources that can affect GPP and ER, but their relative importance is influenced by their availability in relation to other limiting factors (Bernhardt et al., 2018). We found that during our study period, neither light (above the water) nor temperature had a significant relationship with GPP or ER; this result is likely due to low winter light, low-temperature conditions and a higher relevance of other factors such as increased flow and abrasion (Blaszczak et al., 2019). Although temperature can affect daily GPP and ER estimates, the range of water temperatures for these streams was relatively small during the study period (i.e. $\sim 8^{\circ}$C for Oak Creek and $\sim 6^{\circ}$C for South Fork Mill Creek). Given this low degree of variability and considering all the uncertainties with metabolism modelling, we decided to make as few assumptions as possible and preserve as much as possible the empirical values for the analysis. We therefore did not correct daily GPP for temperature. This correction may be needed in future research exploring these relationships across more streams and encompassing sites with a wider range of temperatures. Light, nutrients and temperature affect biological processes in benthic biofilms, which in turn affect metabolic rates in streams, but physical disturbances represent a different kind of control—an abiotic resetting mechanism rather than a driver of biotic processes. Lithology appears to be affecting stream metabolism in the investigated streams, but not in the way we initially expected. Differing P/R ratios between sites was driven largely by differences in ER response rather than response in GPP. While we acknowledge the narrow scope of inference in comparing two streams in the Oregon Coast Range, this study provides an initial assessment of how differences in streambed sediment characteristic among natural systems affect stream metabolism and how the control of underlying lithology on metabolic processes can be unexpectedly driven by the effect of fine suspended sediment on light availability in this system rather than by the abrasion of benthic biofilms by the movement of sediment. Further improving our understanding of the effects of storms on metabolic processes in natural gravel-bed streams will require more in-depth comparisons with other lithologies and a three-dimensional view of the stream bed, as storms affect organisms both on the surface of the bed and organisms deeper within the substrate, as well as requiring further exploration into the possible carbon sources fuelling the system via allochthonous carbon inputs from the riparian area or from the groundwater.

We also acknowledge that many challenges remain when attempting to obtain metabolic estimates in small mountainous streams with low productivity and high gas exchange. In our case, we were not able to obtain metabolic rates for the entire period of analysis due to lack of convergence in our modelling approach. This prevented us from having daily metabolic rates for the study period that would have allowed us to make stronger statements about the differences between the two sites and on the legacy effects of storm events at each site.

6 | CONCLUSION

Lithology in forested mountain streams can be an important driver of the metabolic response to flow disturbance by affecting stream primary productivity. The effect of discharge and sediment flux on stream GPP includes both instantaneous and legacy components. For two sites with contrasting lithology in the Oregon Coast Range, a quantile regression analysis between daily GPP and maximum daily discharge and sediment flux indicated negative slopes at both sites (GPP decreases with increasing discharge or sediment flux) but stronger (more negative) slopes for the site with finer and more variable sediment distribution (South Fork Mill Creek), although this site showed less disturbance and higher recovery rates for larger storm events. The ER response to large flows was not as consistent as GPP and differed between the sites, with variable ER rates at the site with coarser bed sediment and less variable sediment distribution (Oak Creek). ER rates did not change from prestorm to poststorm conditions at South Fork Mill Creek. These differences are likely due to interactions between several factors. We suggest that storm-associated inputs of DOC increased ER in Oak Creek, whereas in South Fork Mill Creek, DOC input could have been more muted and/or disturbances in the substrate could have reached deeper into the stream bed, disturbing hyporheic heterotrophs as well as surface biofilms dominated by autotrophs. Variations of the P/R ratio were driven primarily by difference in the responses of ER, which was largely decoupled from GPP in these systems following storm events. Both streams became more heterotrophic post-storm, with South Fork Mill Creek showing a larger effect from higher flows than Oak Creek. However, the limiting impact of flow and sediment disappeared in both streams over the same timescale, implying a similar recovery period for P/R ratio. The quantile regression analysis helped to explore the interactions between possible drivers of metabolic responses to disturbance as well as to evaluate the legacy of these disturbances. Through this analysis, our study contributes to an understanding of the effects of sediment mobility and disturbance on metabolic processes in small mountain streams.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sets of suspended sediment concentration and environmental variables used to model stream metabolism and the modelled stream metabolism results for two streams are available at the ScholarsArchive@OSU (https://doi.org/10.7267/1v53k431f).

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