

The Flow Regime of Function: Influence of Flow Changes
on Biogeochemical Processes in Streams

Brynn O'Donnell

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Erin R. Hotchkiss, Committee Chair
John E. Barrett
Daniel L. McLaughlin

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ABSTRACT

Streams are ecosystems organized by disturbance. One of the most frequent disturbances within a stream is elevated flow. Elevated flow can both stimulate ecosystem processes and impede them. Consequently, flow plays a critical role in shifting the dominant stream function between biological transformation and physical transportation of materials. To garner further insight into the complex interactions of stream function and flow, I assessed the influence of elevated flow and flow disturbances on stream metabolism. To do so, I analyzed five years of dissolved oxygen data from an urban- and agriculturally-influenced stream to estimate metabolism. Stream metabolism is estimated from the production (gross primary production; GPP) and consumption (ecosystem respiration; ER) of dissolved oxygen. With these data, I evaluated how low and elevated flows differentially impact water quality (e.g., turbidity, conductivity) and metabolism using segmented metabolism- and concentration- discharge analyses. I found that GPP declined at varying rates across discharge, and ER decreased at lower flows but became constant at higher flows. Net ecosystem production (NEP; = GPP - ER) reflected the divergence of GPP and ER and was unchanging at lower flows, but declined at higher discharge. These C-Q patterns can consequently influence or be influenced by changes in metabolism. I coupled metabolism-Q and C-Q trends to examine linked flow-induced changes to physicochemical parameters and metabolism. Parameters related to metabolism (e.g., turbidity and GPP, pH and NEP) frequently followed coupled trends. To investigate metabolic recovery dynamics (i.e., resistance and resilience) following flow disturbances, I analyzed metabolic responses to 15 isolated flow events and identified the antecedent conditions or disturbance characteristics that most contributed to recovery dynamics. ER was both more resistant and resilient than GPP. GPP took longer to recover (1 to >9 days, mean = 2.5) than ER (1 to 2 days, mean = 1.1). ER resistance was strongly correlated with the intensity of the flow event, whereas GPP was not, suggesting that GPP responds similarly to flow disturbances, regardless of the magnitude of flow event. Flow may be the most frequent disturbance experienced by streams. However, streams are exposed to a multitude of other disturbances; here I also highlight how anthropogenic alterations to streams – namely, burying a stream underground – can change biogeochemical function. This thesis proposes novel frameworks to explore the nexus of flow, anthropogenic disturbances, and stream function, and thereby to further our understanding of the complex relationship between streams and disturbances.

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GENERAL AUDIENCE ABSTRACT

A stream is defined by its flowing water. Flow brings the nutrients, organic matter, and other materials necessary to the algae and bacteria within the stream as well as the invertebrates and fishes they sustain, and is consequently integral to in-stream biology and ecology. However, elevated flow is also one of the most frequent disturbances experienced by streams. Elevated flow dilutes or enriches concentrations of water quality parameters, moves the water faster, reduces the amount of time essential nutrients are available to organisms within streams, and scours the algae and bacteria on stream bottoms. Here, I analyzed five years of data from an urban- and agriculturally-influenced stream and estimated stream metabolism to explore the influence of flow on stream biology, chemistry, and ecology. Stream metabolism is a process that reflects the respiration and photosynthesis of bacteria and algae, estimated from the production and consumption of dissolved oxygen. The primary research objective of my thesis was to investigate how changing flow impacts metabolism, by: (1) examining how low and high flows impact metabolism differently, and (2) studying the response and recovery of metabolism following multiple flow disturbances. Flow not only influences in-stream biology and processes, such as stream metabolism, but also changes the water quality of the stream (e.g., conductivity, pH, turbidity). To examine the interconnection between flow-induced changes to water quality parameters and metabolism, I measured how low and high flows impacted water quality and then compared water quality-flow relationships with metabolism at low and high flows. I found that metabolic processes and related water quality parameters were frequently coupled. Next, to test how water quality might also influence the response and recovery of metabolism after a flow disturbance, I examined whether prior environmental conditions (e.g., temperature, light) or the magnitude of the flow disturbance influenced metabolic response and recovery. I found that the size of the flow disturbance did change a critical piece of stream metabolism. Flow is not the only prevalent disturbance streams face: increasingly, streams are being altered by ongoing urban and suburbanization. Therefore, to highlight the full suite of disturbances to streams caused by human modification, I wrote a public science communication piece documenting the biological, chemical, and ecological ramifications of burying streams underground. Ultimately, this thesis proposes new frameworks to more adequately explore the complex relationships between water quality, stream ecology, and disturbances.

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Chapter One: General Introduction

Stream ecosystem scientists were lured by the elusive notion of ecosystem stability for decades (Webster et al. 1975) and yet, empirical evidence of a stable natural ecosystem evaded them. Consequently, in the mid-1980s, they began to embrace the innate pulsing nature of ecosystems, adopting the idea of a pulsing steady state or a pulsing equilibrium in running waters (Odum et al. 1995, Stanley et al. 2010). As more stochastic, nonequilibrium views of ecosystem dynamics became more common, the importance of disturbance as a driver of patterns and conditions of stream processes became quite clear (Resh et al. 1988, Stanley et al. 2010). Here, I adopt the biological definition of disturbance from White and Pickett (1985): “any relatively discrete event in time that disrupts the ecosystem... and changes resources, substrate availability, or the physical environment”. Much of the early work on stream disturbance centered on floods, but has since expanded to include such aspects as increased nutrient loading, geomorphic alterations, physical disturbances, or shifts in upstream land use (Stanley et al. 2010). Two predominant and interrelated disturbances to stream ecosystems are anthropogenic alterations and flow.

Flow is integral to the life within a stream, yet also has the potential to impede biotic function. In fact, Odum et al (1979) proposed a framework to explain how disturbances, such as elevated flow, act upon ecosystems across a “subsidy-stress” gradient. Flow drives stream processes by replenishing resources for microbial activity via distribution of inputs from the terrestrial environment and upstream, such as nutrients, organic matter, and other chemical constituents (e.g., Lamberti & Steinman 1997). However, elevated flow is arguably one of the most predominant disturbances within a stream. Elevated flow can have a replenishing, subsidizing influence on stream microbial processes (e.g., Beaulieu et al. 2013; Roley et al.

2014) or an inhibiting, scouring impact (e.g., Uehlinger 2000, 2006). The disturbance effects of elevated flow (e.g., scour, altered water quality parameters) can alter internal microbial activity, and consequently ecosystem function (e.g., Blaszczyk et al. 2018). However, flow is frequently oscillating, and so the balance between its subsidizing or stressing role is constantly shifting back and forth (Figure 1). The subsidy-stress idea proposed by Odum et al. (1979) was not necessarily created to describe the relationship between elevated flow and stream ecosystem processes, yet no other concept describes their interaction so aptly.

Elevated flow can not only subsidize or stress an ecosystem, but can also shift dominant stream function from the transformation of solutes, including nutrients and organic matter, to transportation of these solutes (Cole et al. 2007). As a dominant transformer, when stream processes are ‘normal’ or subsidized by flow (Fig. 1), stream biota have more ‘biophysical opportunities’ to transform nitrogen, carbon, and other chemical constituents (Battin et al. 2008). When flow becomes more stressing, dominant stream function can shift to transportation (Fig 1.), sending more solutes to downstream ecosystems as the transformative capabilities of stream biota are stunted (Raymond et al. 2016). Ultimately, the subsidy-stress and transformer-transporter frameworks are intricately connected, but are not frequently linked in ecosystem research.

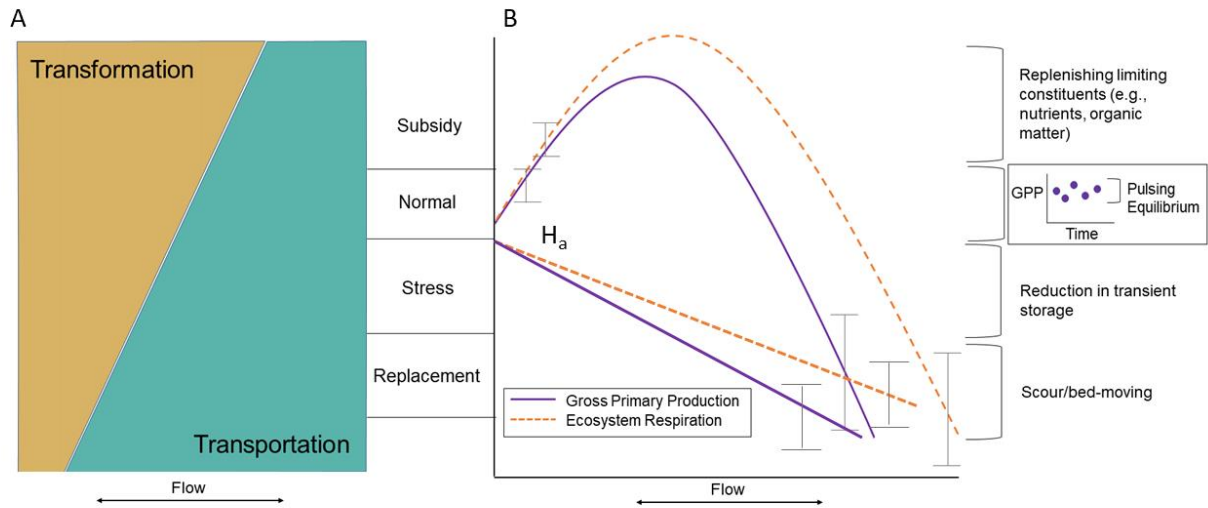


Figure 1. Predicted metabolic response along flow's subsidy-stress gradient (adopted from Odum et al. 1979). The change in flow is on both x-axes. **(A)** The polygons represent the shift from dominant transformation to dominant transportation as flow increases. The y-axis denotes the relative influence of the primary biogeochemical functions of a stream: transformation and transportation. **(B)** The y-axis represents ecosystem metabolism (i.e., gross primary production (GPP) and ecosystem respiration (ER)), and is broken into four categories defined by Odum et al. 1979: subsidy (when subsidization dominates and GPP, ER increase), normal (periods of pulsing equilibrium for GPP and ER under ambient flow), stress (when an ecosystem begins to react negatively to the disturbance) and replacement (when there is a severe reduction in metabolism and communities are scoured or replaced). The inset graph next to the 'normal' bracket depicts GPP over time, delineating how normality is best represented by a pulsing equilibrium rather than a fixed point of stability (*sensu* Odum et al. 1995).

An ecosystem's response and recovery to a flow disturbance can be quantified by characterizing its *resistance* and *resilience*. The ability of stream processes to withstand a disturbance and not shift outside of an established "normal" pulsing equilibrium constitutes its

resistance (Figure 1). *Resilience* is the speed at which an ecosystem returns to this pulsing equilibrium following a disturbance (Carpenter et al. 1992). Streams are especially vulnerable to disturbances because they are restricted in their ability to retain material: water is constantly flowing, carrying contents downstream. However, flow is also a driver of the high resilience of stream processes. The positive, subsidizing effects of lower flows contribute to the high resilience of stream processes in the face of disturbances because the unidirectional flow of water replenishes internal processes (Acuña et al. 2007, Stanley et al. 2010).

Stream metabolism is one of the ecosystem processes that appears to exhibit low resistance and high resilience to flow disturbances (Uehlinger and Naegeli 1998, Reisinger et al. 2017). Stream metabolism is the biologic production and consumption of dissolved oxygen (e.g., gross primary production (GPP) and ecosystem respiration (ER), respectively), through coupled CO₂ fixation (GPP) and organic matter respiration (ER). Net ecosystem production (NEP) is the balance between GPP and ER. The use of metabolism (GPP, ER, NEP) as an indicator of stream health (Fellows et al. 2006; Young et al. 2008) and response to disturbances (Arroita et al. 2019) has increased. Additionally, metabolism is intimately connected to other ecosystem processes, such as nitrogen uptake (Hall & Tank 2003; Hoellein et al. 2007) and food web dynamics (Marcarelli et al. 2011). Seasonality drives annual trends of metabolism, but the frequency of flow disturbances generates smaller time-scale variation (e.g., Uehlinger 2006, Beaulieu et al. 2013; Bernhardt et al. 2018). To recognize trends in metabolism and interpret the flow-induced variation, we must develop a deeper understanding of metabolic responses to flow disturbances (Larsen and Harvey 2017, Bernhardt et al. 2018). To explore the connection between metabolism and flow, I used five years of high-frequency sensor data from a flashy stream (steep rising and falling limb of a hydrograph shortly after a rain event) draining mixed urban-agricultural land

use. I estimated GPP, ER, and NEP to evaluate metabolic response to changing flow, and related these responses to water quality parameters and antecedent conditions across five years as well as within isolated flow events.

Low and high flows can impact metabolism and water quality differently. Interactions between elevated flows and water chemistry (e.g., pH, conductivity, turbidity) are often analyzed via concentration-discharge (C-Q) relationships (e.g., Meybeck & Moatar 2012; Moatar et al. 2017; Walling 1977), where variation in stream solutes is analyzed as a response variable of changing discharge. Segmenting C-Q models quantifies two distinct relationships: one between a solute and flow at low discharges, and one at higher discharges. In Chapter Two, I take the C-Q framework and apply it to stream metabolism, scaling up from water chemistry to ecosystem processes to capture functional responses to high magnitude but less frequent flow events as well as to elevated flow events that occur multiple times a year. I apply the C-Q analytical method to stream metabolism, introducing an innovative, novel conceptual framework – segmented P-Q (process-discharge) curves – to ask: **(1) How does ecosystem metabolism differ at low and high levels of flow?** I also quantified C-Q relationships of water quality parameters (i.e., turbidity, conductivity, pH, temperature, dissolved oxygen) to explore the potential for coupling P-Q and C-Q relationships to answer: **(2) What are the interactions between flow, flow-induced changes to water quality parameters, and metabolic responses to changing flow?**

In Chapter Three, I then assessed metabolism-flow relationships at the scale of individual storms to better understand event-based responses and recovery. Here, I sought to answer: **(3) What are the metabolic recovery dynamics (e.g., resistance and resilience) of GPP & ER across 15 different storms?** To tackle recovery dynamics of the pulsing baselines of ecosystem metabolism (Figure 1), I implemented a new, more conservative method for calculating recovery

dynamics by characterizing disturbances as a deviation from the pulsing equilibrium, rather than from a fixed point of stability. I also analyzed antecedent conditions (e.g., time since last flow event, season, prior light and temperature) and characterized each disturbance event (e.g., magnitude of flow disturbance, time of day of peak discharge) to evaluate: **(4) What antecedent conditions or disturbance characteristics drive recovery dynamics of GPP and ER?**

Ultimately, understanding how streams respond to smaller, more recurrent storms may yield new insight into the overall impact of frequent flow disturbances on ecosystem processes.

Heavily altered, urban streams are infamously impacted by myriad stressors (Walsh et al. 2005). Namely, as urban areas spread, streams are often paved over and placed in pipes. When streams are buried in an attempt to domesticate natural flowing waters to prioritize development, these streams are hydrologically modified – disconnected from their floodplains and increasingly channelized (Paul and Meyer 2001, Groffman et al. 2003). Although stream burial has been a longstanding activity, how ecosystem functions and biogeochemical processes are altered when we engineer streams within pipes is still not fully understood. Moreover, urban streams are flashy and highly vulnerable to storm pulse events (Kaushal et al. 2012; Walsh et al. 2016; Walsh et al. 2005), exacerbating the extreme effect that flow has on stream ecosystems. In my fourth chapter, I wrote an accessible, engaging science communication piece to answer: **(5) What are the potential biogeochemical dangers of burying urban streams, and how are cities and stakeholders addressing this?** As flow disturbances are projected to increase in the face of anthropogenically-induced climate change (Davis et al., 2013), it is important to understand how additional anthropogenic alterations, such as expanding urbanization, can drastically disturb stream function.

It is essential that we deepen our understanding of metabolic response to flow disturbances, given the projected increase in storms, the flashy nature of altered streams, and the substantial influence of storms on critical ecosystem functions. By exploring how metabolism responds to flow disturbances across multiple flow events, studying metabolic recovery dynamics at the event scale, and communicating biogeochemical consequences of stream burial, this thesis advances our understanding of ecosystem responses to disturbances and will hopefully inspire others to adopt and expand the novel conceptual frameworks illustrated in the following chapters.

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Chapter Two: Biogeochemical Consequences of Stream Flow Variation: Coupling Concentration- and Metabolism-Discharge Relationships

B. O'Donnell^{1*}, E. R. Hotchkiss¹

¹Department of Biological Sciences, Virginia Tech

*Corresponding author: Brynn O'Donnell (brynnmodonnell@gmail.com)

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Abstract

Ecosystem processes within a stream, such as metabolism, are dynamically impacted by flow intensity. Yet, few studies have quantified metabolic response to flow changes. Moreover, concentration-discharge (C-Q) analyses often overlook the influence of biotic processes by not quantifying biogeochemical transformation and removal. To understand how flow variation alters ecosystem processes, we analyzed 5 years of water quality and stream metabolism data to create and compare segmented (C-Q) and process-discharge (P-Q) relationships. We compared C-Q and P-Q relationships to examine the dynamic effects of discharge on both processes and physicochemical parameters. The behavior of ecosystem respiration (ER), gross primary production (GPP), and net ecosystem production (NEP) was different at high and low flows with varying degrees of statistical significance, demonstrating the potential for divergent metabolic responses across changing flows. GPP declined across discharge at varying rates. ER declined across discharge below the breakpoint, but became unchanging at higher flows. NEP, the balance between ER and GPP, reflected the divergent trends between ER and GPP, as it was constant at lower discharge but declined at higher flows. Interrelated physicochemical parameters and ecosystem processes, such as pH and NEP, had coupled responses to discharge. Ultimately, we can better understand ecosystem response to flow by coupling analyses of flow, water quality, and metabolism.

Plain Language Summary

Currently, we lack information about how biology and water quality change during high flow. To examine water quality at different flows, concentration-discharge (C-Q) relationships are often quantified. However, by only looking at how water quality changes across flow, we miss key information: life within the stream. Life within a stream influences, and is influenced by, water quality and flow. To understand how and why water quality changes across flow, we must (1) identify how the metabolism of stream organisms changes across flow via metabolism-discharge analyses, and (2) compare C-Q and metabolism-discharge trends to discover how they may influence one another. Here, we analyzed 5 years of water quality data and calculated stream metabolism, which comprises the balance of photosynthesis and respiration conducted by the algae and bacteria within a stream. We found that stream metabolism exhibited different responses at low versus high flows. Moreover, multiple C-Q relationships had mirrored responses to related metabolism-Q relationships. Ultimately, this study demonstrates that by not accounting for different metabolic responses across flow, we are likely missing key ecosystem responses. By coupling C-Q and P-Q relationships, we can better understand the effects of changing flow on streams.

1 Introduction

Streams function along gradients of ‘transformers’ to ‘transporters’ of solutes (Cole et al. 2007). As a transformer, a stream carries out the processes that make up many of the ecosystem services we value: nitrogen is assimilated and reduced, carbon is fixed and respired. However, different environmental factors can shift the dominant stream function between transformer or transporter, elongating or shortening biogeochemical processing length: shifting stoichiometric limitations, hydrologic disturbance, or changing allochthonous inputs (Fisher et al. 1998, Dodds

et al. 2004, Seybold and McGlynn 2018). Arguably the most influential factor in shaping whether a stream functions as a predominant transporter or transformer is flow (Poff et al. 1997). Flow has the ability to impact stream function by loading solutes from the surrounding catchment, changing concentrations of physicochemical constituents (e.g., turbidity, conductivity) within the stream, reducing water residence time, and inducing scour (Raymond et al. 2016; Wollheim et al. 2018). At low flows, a stream is more of an active transformer of nutrients and organic matter, as longer hydrologic residence times are conducive to biogeochemical processing and transformations such as uptake, mineralization, and denitrification (Drummond et al. 2016; Hall et al. 2009). At high flows, upper stream reaches may be more of a ‘transporter’ of materials, as higher flows can reduce biotic activity by scouring the benthos and decreasing transient storage (Fisher 1982), ultimately shuttling more solutes to downstream ecosystems (Raymond et al. 2016). The extent to which stream function is altered by the combination of flow-induced changes to physicochemical parameters as well as water residence time has not yet been extensively quantified (Wollheim et al. 2018).

Precipitation events activate different catchment sources and flow paths (McGlynn and McDonnell 2003), with large influences on stream solute concentrations and physicochemical parameters (Boyer et al. 1997). The relationship between solute concentrations and discharge are often depicted using concentration-discharge (C-Q) curves (Williams 1989). When specific flow paths become connected to running waters (e.g., deep groundwater, riparian zones, floodplains, disconnected wetlands), solute concentrations change. Changes to concentrations with increasing flow induce either an enriching, positive C-Q relationship if the solute is transport-limited, or a diluted, negative relationship if the element is source-limited and not abundant within the catchment (Inamdar et al. 2004, Basu et al. 2011). If concentration does not have a significant

relationship with discharge, and the slope of the C-Q relationship is zero, the C-Q is considered chemostatic. The relationships between discharge and solute concentrations often follow power law distributions; however, slope changes frequently occur at certain thresholds of discharge (Diamond and Cohen 2018). The prevalence of these power-function slope changes in C-Q relationships has led to the use of segmented, piecewise regressions to explain the consequences of changing discharge on concentrations (Meybeck and Moatar 2012, Moatar et al. 2017). Physicochemical (e.g., turbidity, conductivity, pH) relationships with discharge can be impacted by and segmented due to multiple factors, including: availability within the catchment, source activation, or antecedent conditions (Diamond and Cohen 2018, McMillan et al. 2018).

Flow intensity can also impact in-stream ecosystem processes, such as stream metabolism. Stream metabolism is a measure of the fixation of carbon by autotrophs as gross primary production (GPP) and the breakdown of organic carbon by both autotrophs and heterotrophs as ecosystem respiration (ER). The balance between GPP and ER is net ecosystem production (NEP). Increased flow - at low amplitudes - can have enriching effects on stream ecosystems, subsidizing biotic transformations of reactive solutes. For instance, low- to mid-intensity flows can load fresh supplies of organic carbon into streams (McLaughlin and Kaplan 2013), which can stimulate ER (Demars 2018). In contrast, higher flows can stress and disturb the ecosystem, inducing drastic changes in temperature and prolonged increases in turbidity (Roberts and Mulholland 2007, Blaszcak et al. 2018). Elevated flow also has the potential to impede biotic processing by reducing transient storage, diminishing light, and scouring benthos (Uehlinger and Naegeli 1998, Blaszcak et al. 2018). As a result, the signal from in-stream biotic processes may diminish at higher discharges when abiotic factors have more control (Gasith &

Resh 1999; Mulholland & Hill 1997). Indeed, the divergent effects of different levels of flow influence stream processes along a “subsidy-stress gradient” (sensu Odum et al. 1979).

Because discharge affects stream processes along a subsidy-stress gradient, process-discharge relationships may exhibit contrasted, segmented trends. Although the adoption of piecewise regressions to quantify C-Q relationships has become more prevalent, most previous work has used linear or power law relationships to assess associations between metabolism and discharge (e.g., Demars 2018; Lamberti & Steinman 1997). We do not yet understand the relationship between discharge and metabolism that spans a range of flow magnitudes. To address this knowledge gap, we explored the dynamic and potentially segmented patterns of stream metabolism across discharges via a P-Q (process-discharge) relationship. A segmented P-Q relationship between metabolism and discharge may yield a more comprehensive understanding of flow controls on transformations vs. transport and thus stream function.

Processes captured in P-Q analyses have the potential to influence and be influenced by C-Q trends. Although hydrology and catchment connectivity are critical to understanding solute-discharge relationships, they only capture part of the picture; the feedbacks between in-stream biotic processes and C-Q relationships are missing. C-Q trends are frequently interpreted as changes caused by varying catchment sources and flow paths (Herndon et al. 2015, Musolff et al. 2017). However, in-stream biotic processes can subsequently alter solute concentrations and physicochemical parameters (Mulholland 1992; Mulholland & Hill 1997; Roberts & Mulholland 2007). Thus, quantifying the impact stream biology has on C-Q dynamics is essential to furthering our understanding of solute transformation and export. For instance, stream metabolism includes the net production or consumption of dissolved organic carbon (Hall & Hotchkiss 2017). ER also alters stream chemistry by lowering dissolved oxygen (DO)

concentrations and elevating CO₂ (Hall & Hotchkiss 2017), with associated pH changes (Maberly 1996). Similarly, physicochemical parameters affect stream metabolism. Both temperature and DO can affect respiration (Sinsabaugh et al. 1997), and turbidity can decrease GPP by inhibiting access to light (Hall et al. 2015; Young & Huryn 1996). The interactions among solutes, biota, and flow may be represented by coupling analyses of segmented C-Q and P-Q relationships (Figure 1, Moatar et al. 2017).

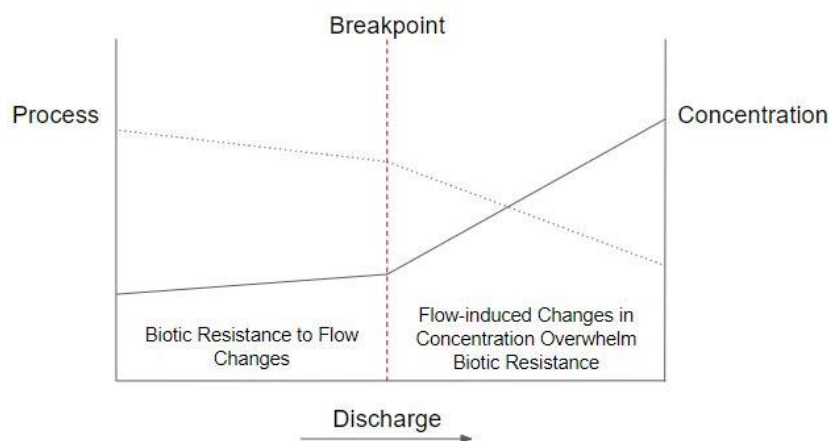


Figure 1. One of many possible outcomes of coupled concentration- and process-discharge analyses (adopted from Moatar et al. 2017). The dashed vertical line represents a statistically-derived breakpoint. Below the breakpoint, in this example, the stream acts as a predominant ‘transformer’ of solutes as flow has not yet created conditions that drastically inhibit biology. Above the breakpoint, in this example, flow creates conditions unfavorable to biological processes and elevates transport-limited solutes, making the stream a dominant “transporter”.

To quantify metabolism-discharge relationships and examine the interconnection of C-Q and P-Q behavior, we analyzed over 5 years of stream water quality and metabolism data in a mixed urban and agricultural catchment in southwest Virginia. Our objectives were to (1) assess

metabolism-Q dynamics to improve our understanding of stream function at different flows and (2) compare C-Q and metabolism-Q model results to examine the relationship between biogeochemical processes and physicochemical parameters as they are both acted upon by changes in flow. We predicted that physicochemical parameters will have opposite, mirrored trends compared to the processes they affect (e.g., turbidity and GPP) or are affected by (e.g., pH and ER).

2 Materials and Methods

2.1 Study Site

Stroubles Creek (37°12'36" N, 80°26'42" W) is a 9.2-mile, third order stream draining a 15 km² sub-watershed of the New River in Montgomery County of southwest Virginia (Figure 2). Land use in the contributing catchment is approximately 87% developed, 10.9% agriculture, and 2.9% forest (Homer et al. 2015; Figure 2A), resulting in excess sediment and pathogen loads. Our study site is a part of the Stream Research, Education, and Management Lab (StREAM Lab, <https://vtstreamlab.weebly.com/>). Virginia Tech's Biological Systems Engineering Department (BSE) has monitored StREAM Lab since 2008 (Thompson et al. 2012). In 2010, BSE completed a restoration project that involved removing cattle and sloping back and stabilizing vertical banks in efforts to remove Stroubles Creek from the EPA's 303(d) impaired list for benthic impairment caused by excessive sediment (Wynn et al. 2010). While we do not have solute data at the same resolution as long-term sensor data, summer sampling in 2018 suggested nitrogen saturation with a low ratio of dissolved organic carbon: nitrate (DOC: NO₃), at ~ 3:1 (O'Donnell, unpublished data). During summer 2018, NO₃ ranged from 0.97 to 1.7 mg/L, DOC from 3.0 to 5.6 mg/L, phosphate was consistently below 0.02 mg/L, and ammonium

ranged from 0.01 to 0.03 mg/L. Our study reach along the stream was selected for its data availability, accessibility, and land use type.

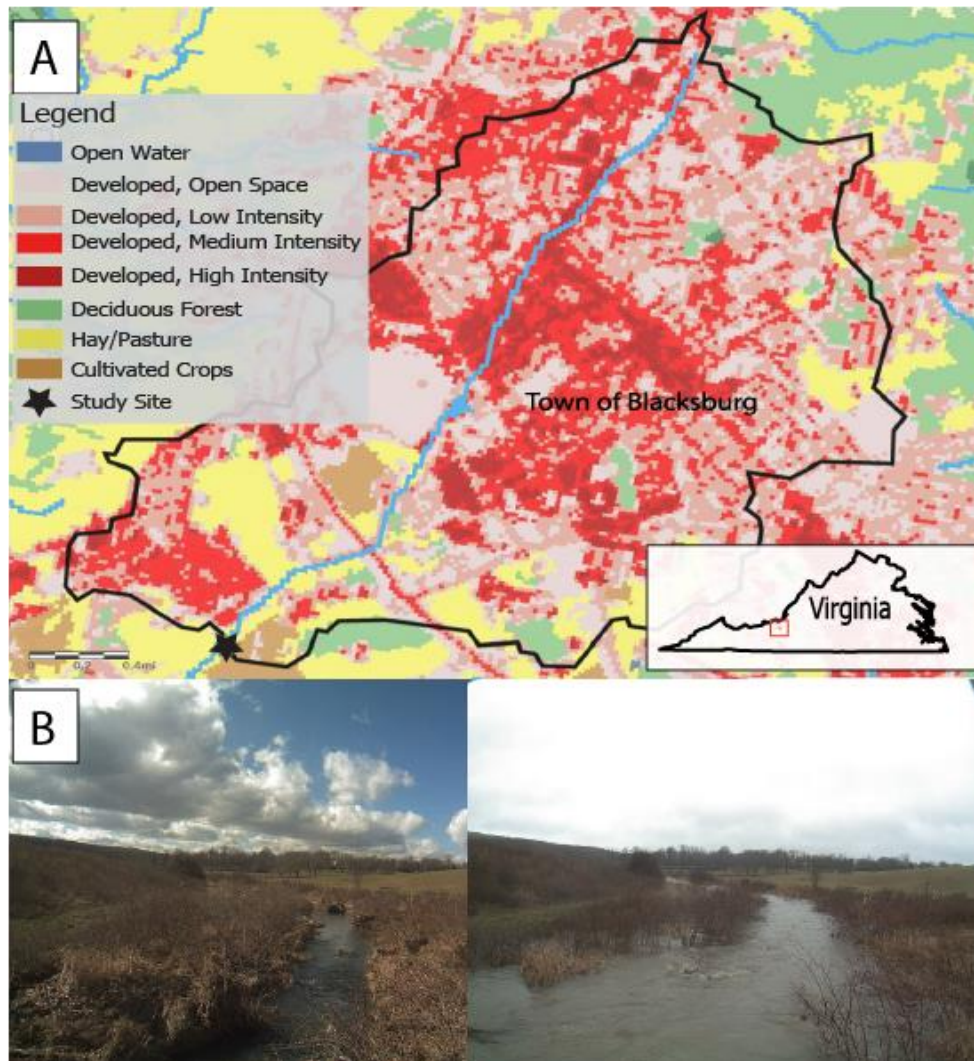


Figure 2: **A)** Map of Stroubles Creek watershed and land use. Black line encompasses the drainage area for our study site. **B)** Photos immediately downstream of our study reach at low (left) and high (right) flows.

2.2 Data Collection

High temporal resolution measurements of physicochemical parameters were collected from 12/10/2012 – 5/1/2018. An *in-situ* YSI 6920V2 sonde measured conductivity, pH, dissolved oxygen, turbidity, and temperature at 15-minute intervals. We also recorded dissolved oxygen data with a PME MiniDOT at 15-minute intervals from 8/31/2017 to 5/1/2018, and these were used for metabolism measurements from 9/1/2017 – 4/14/18 after a freeze event impaired dissolved oxygen measurements from the YSI (Figure S1). Sensors were calibrated every 2-4 weeks, and all data were quality-checked to exclude outliers due to sensor error (Text S1, Figure S2 – S4). A Campbell Scientific CS451 pressure transducer recorded stage at 10-minute intervals. A stage-discharge relationship developed in 2013 and confirmed using salt dilution gaging in 2018 was used to calculate discharge using 10-minute stage data. Velocity and width measurements were taken across multiple years to create relationships with stage. Average stream channel depth (z) was calculated as $\frac{Q}{v \cdot w}$, where Q = discharge, v = velocity, and w = wetted width, to create a stage-depth rating curve. Oxygen at saturation was calculated using sonde water temperature and barometric pressure (Garcia and Gordon 1992). We obtained light measurements from a local weather station that uses a Campbell Scientific CS300. We applied the *interp* function in R to merge discharge, light, and water quality datasets at matching 30-minute intervals (R Core Team 2017).

Because daily aggregated medians of physicochemical parameters were needed for the C-Q analysis, we calculated the daily median of each parameter for days in which sensors collected measurements for at least 80% of the complete 24-hour period, a percentage we confirmed had minimal impacts on estimating central tendencies. Daily medians were then natural log-transformed. pH was not logged because it is log-transformed $[H^+]$. We binned seasons as

following: June - August as summer (n=205 total days of data), September - November as fall (n=180), December - February as winter (n=237), and March - May as spring (n=311).

2.3 Metabolism Estimates

We used Bayesian inverse modeling to estimate daily GPP and ER using the *streamMetabolizer* R package (Appling et al. 2018b). This modeling approach iteratively seeks to find the combination of GPP, ER, and air-water gas exchange of oxygen (K_O) that gives the best match between modeled (mO) and measured (O) dissolved oxygen (Hall & Hotchkiss 2017; Equation 1). All parameters are defined, with units, in Table 1.

$$mO_i = mO_{i-\Delta t} + \frac{GPP * PAR_t}{z * \sum PAR} + \frac{ER}{z} \Delta t + K_O (O_{sat(i-\Delta t)} - mO_{i-\Delta t}) \Delta t \quad [\text{Equation 1}]$$

Table 1: *Terms Used in Equation 1*

Parameter symbol	Parameter description (units)
mO	Modeled O_2 ($g\ O_2\ m^{-3}$)
Δt	Measurement interval (d)
GPP	Gross primary production ($g\ O_2\ m^{-2}\ d^{-1}$)
ER	Ecosystem respiration ($g\ O_2\ m^{-2}\ d^{-1}$)
z	Depth (m)
K_O	Air-water gas exchange of O_2 (d^{-1})
O_{sat}	Oxygen at saturation ($g\ O_2\ m^{-3}$)
PAR	Photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$)

To decrease the likelihood of equifinality of parameter estimates by simultaneously solving for GPP, ER, and K (Appling et al. 2018a), we took the difference between maximum and minimum discharge and divided into six bins per year. The hierarchical modeling framework used by *streamMetabolizer* then established K~Q relationships by using the bins to constrain air-water gas exchange (K_0 ; d^{-1}) as a function of discharge (Appling et al. 2018a). We confirmed modeled K using nighttime linear regression of dissolved oxygen (Hall & Hotchkiss 2017, Figure S5). We removed 30 days with K values below the 1% ($< 3.38 \text{ d}^{-1}$) and above the 99% ($> 27.21 \text{ d}^{-1}$) quantiles to further decrease the chances of using biased metabolism estimates due to uncertainty in K (Figure S6).

Within *streamMetabolizer*, we configured specifications for our metabolism estimates (Supplemental Code S1). We specified a Bayesian model with observation error and process error. We visualized model convergence of four chains via a *traceplot* in the *rstan* package (Stan Development Team 2018). Based off this traceplot, we used a conservative number of burn-in steps: 500. Saved steps were set to 2000, and the Markov chain Monte Carlo (mcmc) model objects were kept on model run to inspect the traceplot. Default package specifications were otherwise used.

Metabolism estimates passed our model output quality checks for 87% of days with complete 24-hour datasets (1405/1621 days). However, 216 days of these days were removed from analysis either due to biologically impossible values (negative GPP or positive ER), poor model convergence, or poor fit of the modeled O_2 data to observed O_2 . We used diagnostics from *fit()* in *rstan* to quantify model fit, including *Rhat* and *N_eff* (Stan Development Team 2018). Convergence of mcmc occurs when *Rhat* is equal to 1, so we removed days with *Rhat* exceeding 1.1 (Gelman and Rubin 1992). *N_eff* is the number of effective samples, and should be less than

the product of the number of mcmc chains run (4) and the number of saved steps (2000) (Howell 2017). Therefore, if the N_{eff} value ended on or exceeded 8000, we assumed no convergence and we removed those days. We removed an additional 472 days due to unreasonable K values or missing physicochemical data. Only days that had solute, discharge, and metabolism estimates were included in our assessment of site-specific C-Q and metabolism-Q relationships, totaling 933 dates from 2013 - 2018.

2.4 Concentration-Discharge and Process-Discharge Analysis

Varying methods exist to characterize segmented C-Q relationships beyond single power functions, such as segmenting regressions around statistically-derived breakpoints in the discharge data (Diamond & Cohen 2018) or median discharge (Meybeck and Moatar 2012; Moatar et al. 2017). We used the Davies test from the *segmented* package in R to iteratively search across 10 quantiles for a significant change of slope in the model of the $\ln[C]$ - and $\ln[P]$ - $\ln[Q]$ relationships and subsequently identified breakpoints (Muggeo 2008). The *segmented* package tests for the point of segmentation on the explanatory variable (Muggeo 2008) and requires the user to input a starting value to estimate the breakpoint. We did not find any influence of choosing different starting values (Table S1). We compared using the Davies test to inform segmentation with segmenting at median daily Q (as in Meybeck and Moatar 2012, Moatar et al. 2017; see Supplemental Figures S7 & S8 and Supplemental Table S2); the trends below and above median Q breakpoints did not differ from the Davies segmentation so we chose to focus on parameter-specific, statistically-derived C-Q and P-Q breakpoints for our study.

After segmenting the hydrograph according to where the *segmented* package found a breakpoint, we retrieved the slopes (β) of the $\ln$ - $\ln$ relationship between each concentration or

metabolism parameter and discharge above and below the breakpoint (Supplemental Code S2). The slopes can be used to characterize the trends of physicochemical parameters (e.g., Godsey et al. 2009; Moatar et al. 2017) and metabolism. To test for chemostasis (when $\beta = 0$), we used an analysis of variance test of independence (Ott and Longnecker 2015). We calculated significant slope differences using a two-tailed z-test (Paternoster et al. 1998). All analyses were conducted in R (R Core Team 2017).

3 Results

3.1 Hydrology and Chemistry

The Stroubles Creek hydrograph was characterized by frequent flow increase events (Figure 3). Median daily discharge ranged from 0.03 to 0.47 m³ s⁻¹, with an average of 0.11 m³ s⁻¹. Spring flow typically exceeded annual medians, with an average median spring discharge of 0.14 m³ s⁻¹. Ranges in median discharge were similar across 2013, 2014 and 2015 (0.05 - 0.41, 0.06 - 0.0.39, and 0.04 - 0.47 m³ s⁻¹ respectively); however, there was a notable decline in flow in 2016 and 2017, lessening to a maximum of 0.31 and 0.26 m³ s⁻¹ respectively. Yearly trends of physicochemical parameters can be found in Figures S2 – S4.

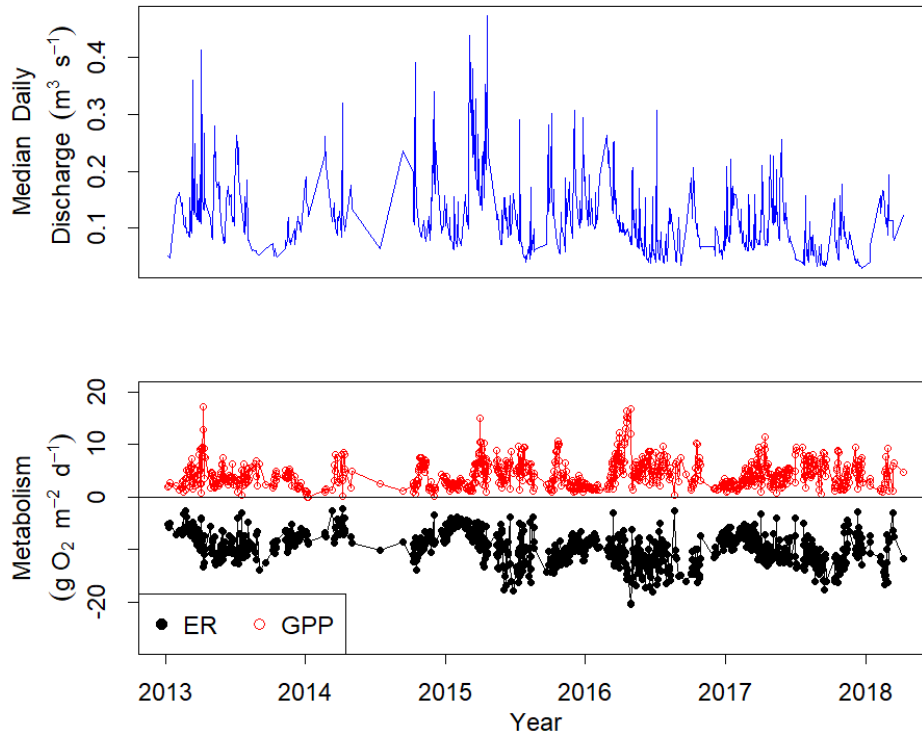


Figure 3: Estimates of Stroubles Creek daily discharge (top), gross primary production (GPP), and ecosystem respiration (ER) (bottom) from 2013 – 2018.

3.2 Ecosystem Metabolism

ER mirrored GPP seasonally, but rates of ER exceeded GPP in all seasons except for occasionally in the spring (Figure 3, 4). GPP ranged from 0 to 17.3 g O₂ m⁻² d⁻¹, with an average of 4.23 and a median of 3.69 g O₂ m⁻² d⁻¹ (Figure 3, 4). ER, reported as a negative flux of O₂ (i.e., consumption), ranged from -2.19 to -20.46 g O₂ m⁻² d⁻¹, with an average of -9.60 and a median of -9.56 g O₂ m⁻² d⁻¹. NEP ranged from -15.36 to 4.86 g O₂ m⁻² d⁻¹. There were 29 measured days (3% total) when GPP was greater than ER (positive NEP), all of which occurred in the spring (Figure 4). K estimates ranged from 3.9 to 27.1 d⁻¹, with an average of 18.0 d⁻¹. Our

K-ER correlation was negative and weak ($R^2 = 0.19$; Supplemental Figure 9), suggesting low equifinality issues related to simultaneously estimating GPP, ER, and K with *streamMetabolizer*.

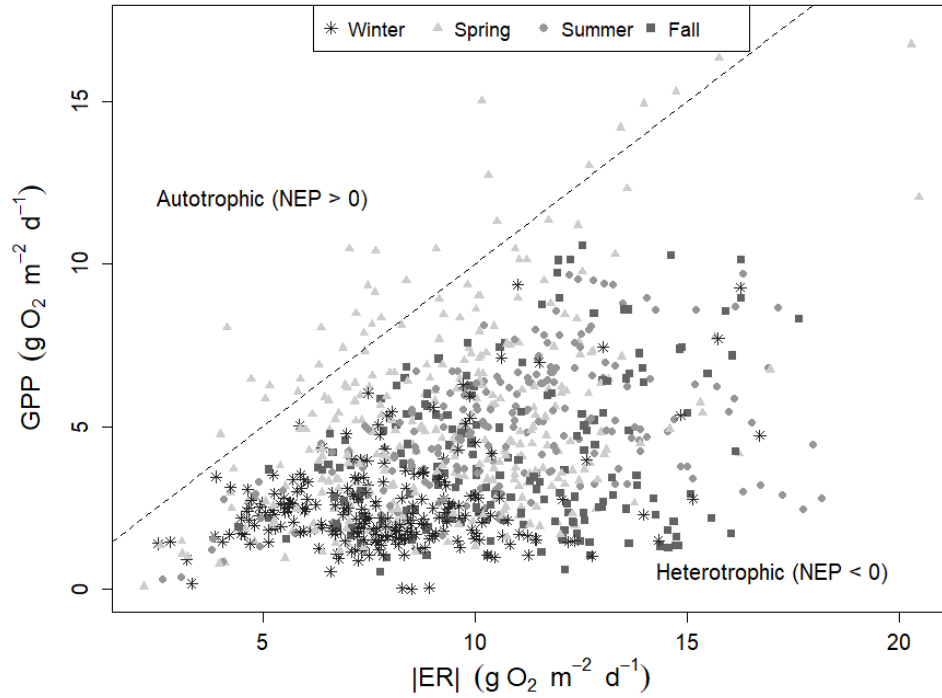


Figure 4: Relationship between GPP and ER and seasonality of metabolism estimates. Points above the 1:1 line depict when the stream was autotrophic ($GPP > ER$); Stroubles Creek was almost always heterotrophic ($ER > GPP$).

3.3 Concentration-Discharge

Discharge had a significant effect on most parameters above and below their breakpoint, most of which were close to median discharge (Table 2). However, dissolved oxygen and conductivity were both chemostatic above their breakpoints (Table S3), but increased below ($\beta = 0.16, 0.80$ respectively; Fig 5). Turbidity was chemostatic below the breakpoint (Table S3), but followed common upward trends above the breakpoint ($\beta = 1.15$; Moatar et al., 2017; Fig 5). pH

declined above the breakpoint ($\beta = -0.23$) but increased below ($\beta = 0.17$). DO and temperature varied seasonally, where DO decreased at lower flows below the breakpoint in summer, but increased during fall and winter (Table S4). Above breakpoints at higher flows, DO declined in fall and winter but increased in summer. Changes to DO slopes at low and high flows during spring were not significant. At lower discharges below season-specific breakpoints, temperature declined in the fall and increased in the winter (Table S4). Above the breakpoint at higher flows, temperature declined in the winter and increased in fall. Spring and summer temperatures did not have significant slope breaks above and below breakpoints. When analyzed with all seasons combined, all physicochemical parameters had significantly different slopes above and below the breakpoint (Table 2).

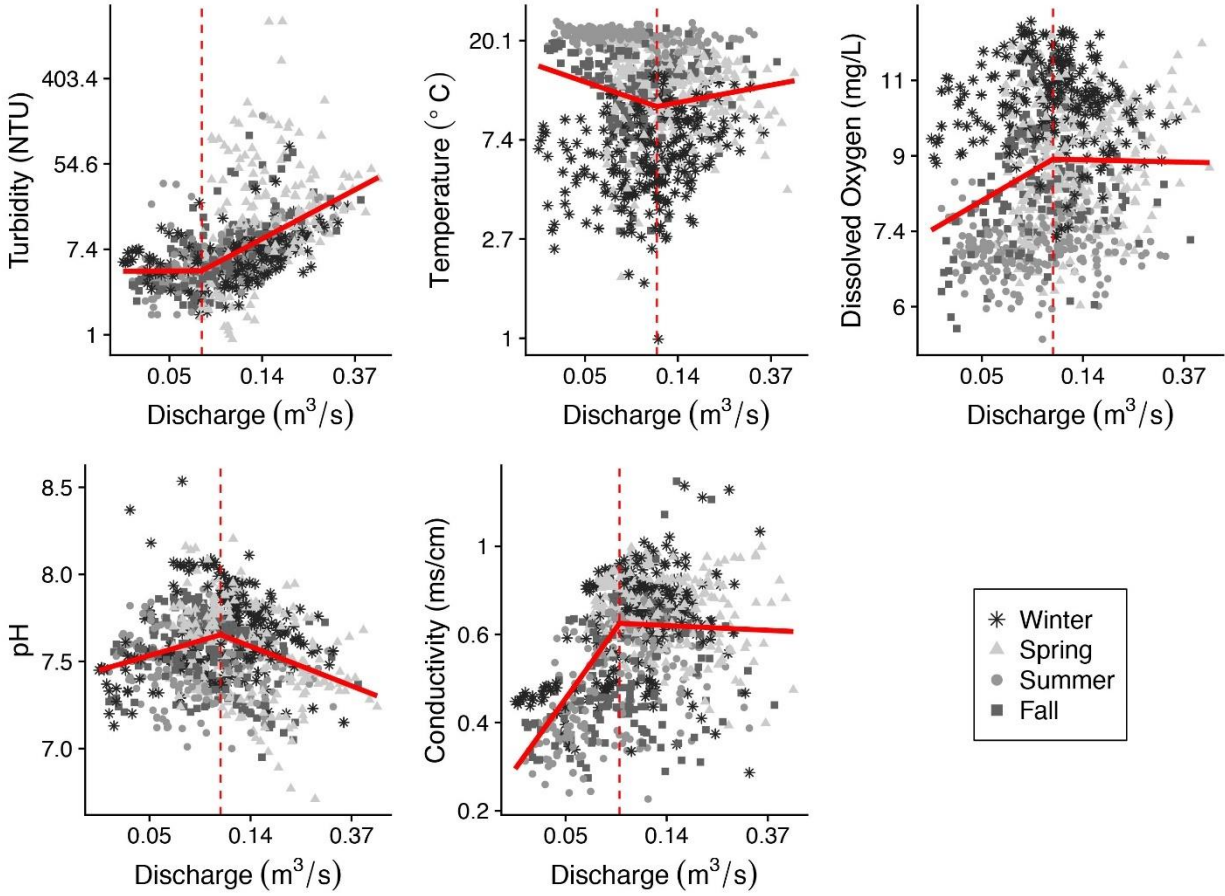


Figure 5: Concentration-discharge (C-Q) graphs of segmented physicochemical parameters (turbidity, temperature, dissolved oxygen, pH, and conductivity) in Stroubles Creek. Graphs are natural log-scaled, but numbers on axes are not log-transformed for more intuitive interpretation of values. The dashed vertical line represents the statistically-derived breakpoint; the solid regression lines below and above the breakpoint were all significantly different (Table 2).

Table 2: *Statistical results for slope segmentation of concentration-discharge and metabolism-discharge relationships*

Parameter (units)	p-value from Davies ^a	Estimated breakpoint (m ³ /s)	Estimated breakpoint standard error	β below breakpoint	β below breakpoint standard error	β above breakpoint	β above breakpoint standard error	p-value Z-test ^b
Temp (°C)	0.001*	0.11	0.12	-0.32	0.08	0.18	0.09	<0.001*
pH	<0.001*	0.10	0.06	0.17	0.03	-0.23	0.03	<0.001*
DO (mg/L)	0.001*	0.10	0.12	0.16	0.03	-0.006	0.03	<0.001*
Conductivity (ms/cm)	<0.001*	0.08	0.04	0.80	0.06	-0.03	0.03	<0.001*
Turbidity (NTU)	<0.001*	0.07	0.09	0.01	0.23	1.15	0.08	<0.001*
ER (g O ₂ m ⁻²)	0.03*	0.07	0.14	-0.29	0.11	0.03	0.03	0.005*
GPP (g O ₂ m ⁻²)	0.14	0.23	0.16	-0.51	0.05	-1.48	0.53	0.07
NEP (g O ₂ m ⁻²)	0.07	0.08	0.16	-0.03	0.07	-0.26	0.04	0.004*

^asegmented output for the Davies p-value

^bDifference in slopes according to two-sided Z test

*Significant p-values (p < 0.05)

3.4 Process-Discharge

GPP had the highest breakpoint across all parameters ($Q = 0.23 \text{ m}^3/\text{s}$), but with an insignificant slope change ($p = 0.07$, $\alpha = 0.05$). GPP's rate of change with Q did steepen from $\beta = -0.51$ below breakpoint to $\beta = -1.48$ above (Figure 6). ER and NEP had significantly different slopes below and above their P-Q breakpoints ($Q = 0.07$ and $0.08 \text{ m}^3/\text{s}$, respectively). ER was chemostatic above the breakpoint, and declined below ($\beta = -0.29$), whereas NEP declined above the breakpoint ($\beta = -0.26$) and was chemostatic below (Figure 6; Table S3).

We observed coupled responses between GPP and turbidity as well as pH and NEP (Figure 6). GPP and turbidity followed predicted, opposite trends; as turbidity β increased (from chemostasis to a slope of 1.15), the β for GPP- Q became more negative above the breakpoint (Figure 6; Table 2). GPP's breakpoint occurred much later than turbidity (0.23 versus $0.07 \text{ m}^3/\text{s}$). ER had the same breakpoint as turbidity ($0.07 \text{ m}^3/\text{s}$), near to conductivity's breakpoint ($0.08 \text{ m}^3/\text{s}$); however, it did not follow appear to coupled trends with any of the physicochemical parameters. pH and NEP had breakpoints at approximately the same discharge (0.10 and $0.08 \text{ m}^3/\text{s}$ respectively). As NEP declined, so did pH (Table 2).

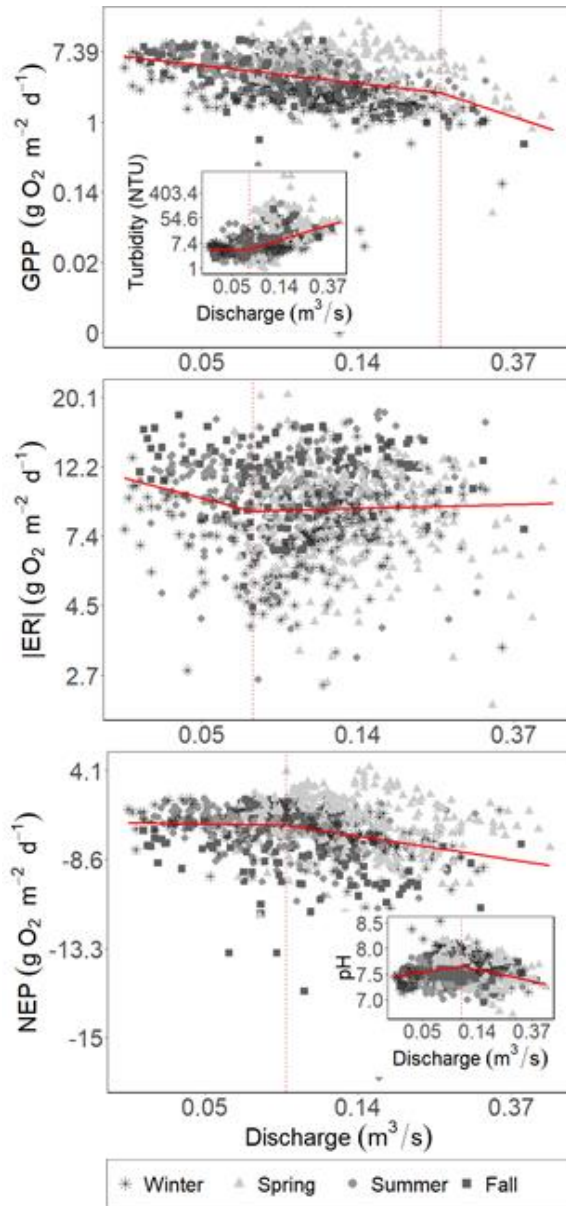


Figure 6: Metabolism-discharge graphs for gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP). Insets are concentration-discharge plots that correlate with metabolism. Graphs are natural log-scaled, but numbers on axes are not log-transformed for more intuitive interpretation of values. The vertical dashed line is the statistically-derived breakpoint; regression lines below and above the breakpoint illustrate changing metabolism trends across discharge. ER and NEP had a significant slope break, and the

slopes were significantly different. GPP did not have a significant slope break and the slopes above and below the statistically-derived breakpoint were not significantly different.

4 Discussion

Constant power functions may oversimplify the complex relationship between processes and discharge. Increasing flow does more than just scour the bed or introduce solutes; it influences metabolism by changing the physicochemical conditions that underlie microbial energy production and respiration. We found statistical support for using segmented power law regressions to quantify distinct changes in ER and NEP with varying discharge above and below breakpoints. Additionally, C-Q and metabolism-Q relationships of parameters predicted to directly affect one another - such as turbidity and GPP or pH and NEP – followed coupled breakpoint behaviors, with varying degrees of statistical significance. These couplings illustrate the potential utility for using P-Q and C-Q relationships together to explain both functional responses and biogeochemical consequences of flow changes.

4.1 Concentration-Discharge

Precipitation events are ‘hot moments’ of solute export, shuttling disproportionately large fluxes of solutes downstream (McClain et al. 2003, Raymond et al. 2016). C-Q relationships are often used to quantify regimes of solutes at these ‘hot moments’ to better understand downstream export (Horowitz 2003; Musolff et al. 2015). Transport or source limitations are frequently used to explain enrichment or dilution trends at higher flows, respectively (Basu et al. 2011, Moatar et al. 2017). In Stroubles Creek, C-Q trends were similar to findings of other segmented C-Q studies. Elsewhere, conductivity has predominantly exhibited dilution or chemostasis followed by dilution (Moatar et al. 2017), though a few other catchments have shown enrichment followed

by dilution, similar to our results (Moatar et al. 2017). Although conductivity often exhibits source-limited dilution across discharge (Diamond and Cohen 2018), the initial increase observed below the breakpoint may be a result of the dominantly developed catchment that drains into our study site, as urban streams are inundated with ions that elevate conductivity (Paul and Meyer 2001, Kaushal et al. 2018). However, higher flows may reverse this trend after depleting the sources of ions and diluting the concentrations that remain. The enrichment of turbidity at higher flows at our study site aligned with common dynamics of total suspended solids across discharge, due to erosion and transport limitation (Moatar et al. 2017). At higher flows, Stroubles pH exhibited the decline seen in other C-Q studies, potentially as a result of accessing CO₂-rich groundwater or soils (Jenkins 1989, Diamond and Cohen 2018). Dissolved oxygen and temperature are not typically analyzed in segmented C-Q studies focused on describing solute transport. The C-Q relationships for dissolved oxygen and temperature are heavily influenced by seasonality (Figure 5; Table S4). Overall, the similarity of Stroubles Creek physicochemical trends to those seen in other streams makes the findings of our coupled C-Q and P-Q relationships applicable to other systems. However, classifying C-Q dynamics by transport or source limitations alone may not capture physicochemical behavior across discharge.

4.2 Process-Discharge

Precipitation events generate multiple abiotic changes that can influence stream ecosystem processes: flow increases, physicochemical conditions are altered, and cloud cover reduces photosynthetically active radiation. Yet, we do not account for likely thresholds or breakpoints in processes the same way we do for physicochemical-discharge relationships. Ultimately, statistically-derived segmented P-Q relationships allow us to quantify when a stream

becomes a predominant ‘transporter’ from ‘transformer’ by determining if and when a significant threshold of process resistance to discharge exists.

Within a stream at a precipitation event scale, GPP is negatively impacted by flow (Fisher 1982, Reisinger et al. 2017). GPP also declined at our study site, appearing to have a greater reduction with flow above a breakpoint threshold (Figure 6), potentially as a result of enhanced scouring or cloud cover. GPP trends above and below the breakpoint were not significantly different however (Table 2). Consequently, we did not detect a significantly greater GPP reduction at higher flows as a result of the compounding influence of elevated turbidity, reduced light, or intensified scour. While our data suggest a higher threshold and later breakpoint ($0.23 \text{ m}^3/\text{s}$) for GPP relative to any other metabolism or concentration-discharge relationships (Fig 6), this higher breakpoint means we did not have enough estimates of GPP from enough high-flow events to find a statistically significant change in slope (Table 2). Moreover, seasonality may significantly influence segmented P-Q patterns. To examine the impact of seasonality and yearly data on metabolism-Q relationships, we conducted breakpoint analyses per scenario (each season, each year). Although we did not have enough data to detect significant differences for most metabolism-Q relationships when data were subset, GPP was consistently, significantly negative above the breakpoint for four scenarios (i.e., 2018, 2013, fall, spring), out of ten total scenarios (Figure S10). The presence of a significant slope change for these scenarios, but not for the composite P-Q for all GPP estimates, may indicate that variability from the insignificant scenarios may drive the lack of a significant slope change for all estimates.

ER is also affected by flow-induced changes: reductions in residence time, scour that may remove respiring microbes, and influxes of terrestrial organic matter. Storms frequently increase ER (Roley et al. 2014), potentially as a result of the increased concentrations of

stimulating organic matter (Demars 2018). We found no evidence for flow-induced stimulation of ER in Stroubles Creek, perhaps due to reductions in residence time and mild scouring concomitant with minimal loading of bioreactive organic matter from urbanized riparian zone. ER includes respiration by autotrophs and heterotrophs; the pre-breakpoint ER reduction may have been a result of autotrophic scouring more so than heterotrophic, as GPP declined at a much faster rate than ER below the breakpoint (Table 2). Heterotrophs tucked away in the hyporheic zone may be more resistant to scour than autotrophs exposed on the stream bed (Uehlinger and Naegeli 1998, Uehlinger 2000). However, ER was chemostatic above the breakpoint (Figure 6, Table S3). As catchment connectivity increases, organic matter may be flushed into the stream (Buffam et al. 2001). Consequently, this shift to chemostasis above the breakpoint could be due to balanced stimulation from fresh organic matter when Stroubles Creeks spills overbank and disturbance caused by scour. Additionally, statistically significant breakpoint analyses by season or year (Figure S10) suggest inconsistent slope trends for ER above and below the breakpoint according to year or season of data collection, which may be a result of external organic matter loading varying seasonally. Lower or higher flows can induce contrasting effects on ER.

The relationship between NEP and flow reflects the net balance between changes occurring to GPP and ER. NEP remained relatively constant below the NEP-Q breakpoint (Table S3). Although GPP declined at a faster rate than ER below the breakpoint ($\beta = -0.51, -0.29$ respectively) (Table 2), there was not a great enough change in either process to drive a shift in NEP. Chemostasis below this point signifies that the balance between GPP and ER was not significantly impacted by discharge, suggesting that other factors at lower flows may be more dominantly impacting NEP. Above the breakpoint, the significant decline of NEP was a result of decreases in GPP that exceeded those of ER. The resistance of hyporheic heterotrophs to scour

relative to the vulnerability of surface autotrophs can lead to a greater reduction in GPP than ER (Uehlinger and Naegeli 1998, Uehlinger 2000), a trend observed in multiple storm and metabolism studies (Roley et al. 2014, Reisinger et al. 2017). Further work is needed to understand how other drivers of metabolism change across flows to truly discern what dictates segmented P-Q relationships and metabolic balance in different ecosystems.

In ecosystems with less flashy hydrology or where GPP is lower, NEP may reflect different responses from GPP and ER. High GPP in our study reach exceeded GPP in other studies that have examined the influence of flow on metabolism in urban streams (Smith and Kaushal 2015, Reisinger et al. 2017), but was within the range of metabolism found in other agriculturally-impacted streams (Griffiths et al. 2013a, Roley et al. 2014). High GPP in our study reach and the prevalence of scour as a result of the flashy stream draining a highly modified landscape gave us a unique opportunity to view potentially contrasting responses of ER or GPP at low and high flows (Walsh et al. 2005b). Because the range of GPP is generally narrower in less impacted streams, distinguishing significant statistical changes as a result of precipitation events is much more difficult. Across other human-modified sites with high GPP, however, the opportunity exists to select streams or stream reaches across a gradient of transient storage to evaluate the influence of surface-subsurface connectivity and highly variable flows (e.g., “flashiness” in many urban streams) on NEP. Do longer water residence times lead to increased resistance of ER relative to GPP, resulting in a NEP breakpoint occurring at a higher flow? The segmented response of NEP to discharge can potentially yield insights into how different channel morphology and water flowpaths can alter ecosystem resistance.

4.3 C-Q and P-Q Coupling

The true promise of P-Q relationships lies in coupling them with C-Q dynamics to explore the influence that flow-induced changes of C-Q and P-Q can have on one other. Flow-induced changes to physicochemical parameters have the potential to either stimulate or suppress metabolism. For instance, turbidity hinders the permeability of light throughout the stream. As light is a key driver of GPP (Blaszczak et al. 2018; Larsen & Harvey 2017; Mulholland et al. 2001), increasing turbidity induces a decline of GPP (Hall et al. 2015). Therefore, we predicted that increasing turbidity above the breakpoint would decrease GPP. As the upward slope of turbidity intensified above its breakpoint, so did GPP's rate of decline (Figure 6). If directly influenced by the enrichment of turbidity, GPP had a lagged effect, with a breakpoint much later than turbidity (Table 2). Changes to physicochemical parameter trends across flows can stimulate or constrain stream metabolism.

The relationship between physicochemical parameters and ecosystem processes is not unidirectional; processes can also influence physicochemical parameters and potentially reduce solute export. Respired or fixed CO₂ reduces or increases pH (Maberly 1996). Here, we observed coupled responses of pH and NEP (Figure 6), exhibiting slope changes at approximately the same discharge breakpoint (Table 2). Above the breakpoint, the decline of pH and NEP at similar rates could be a result of more CO₂ production due to increased rates of ER relative to GPP. Ultimately, biotic processes don't happen in isolation; they have the potential to influence the physicochemical parameters in their surrounding environment, and we expect there may be many more instances of common breakpoints and linked trends in water chemistry and ecosystem processes.

Although comparing physicochemical parameters with processes is informative, a missing piece within this long-term sensor dataset is the ability to directly compare metabolism-

Q relationships with carbon and nutrients, such as DOC and NO_3 , that are frequently the limiting elements of stream metabolism. When we quantify export regimes of solutes such as DOC and NO_3 based on transport- or source-limitation, we exclude the biological processes that produce or transform these solutes. For instance, the ratio of DOC: NO_3 declined or remained about the same across flows in most of the catchments studied by Moatar et al. (2017). Depending on the most limited element in a stream, a changing ratio of DOC: NO_3 could stimulate or repress biological processes by enriching the limiting solute or further diluting it. DOC predominantly enriches at higher flows (Moatar et al. 2017; Musolff et al. 2017). Would systems with greater DOC limitation and higher respiration potential be more capable of reducing that higher DOC loads at high flows?

Expanding the coupling of C-Q and P-Q relationships to include solutes such as NO_3 and DOC is an exciting next step to further understand how P-Q patterns both can directly influence, and be acted upon by, reactive solute dynamics. As logging sensor deployments become more prevalent, our capacity to create coupled C-Q and P-Q analyses will drastically expand. The data will likely soon be available to simultaneously assess DOC-Q and metabolism-Q relationships across variable systems and conditions. For example, through using high-frequency USGS sensor data, it is possible to analyze sites across the U.S. that have metabolism and discharge estimates (Appling et al. 2018c) and physicochemical data. By combining our existing knowledge of export regimes with a quantitative understanding of how flow can change biological processes, we can better understand the mechanisms behind ecosystem-level responses to changing flow and export of solutes downstream.

4.4 Conclusion

Stream flow changes have hydrologic and biogeochemical consequences. Hydrologically, higher flows are regarded as agents of catchment connectivity, simultaneously unleashing or diluting solutes into freshwater ecosystems. Biogeochemically, physical disturbances caused by higher flows disrupt ecosystem processes by moving the stream bed or reducing transient storage. However, insight into the mechanisms behind C-Q and P-Q dynamics across flow is limited when we view one without the other; physicochemical parameters influence, and are influenced by, in-stream biology. To understand ecosystem responses at different flows, we must integrate the interactions between flow, ecosystem process, and C-Q dynamics into our analyses of stream function. By coupling C-Q and P-Q relationships, we can better understand how ecosystems respond to, influence, and recover from the many physical and chemical changes that occur with altered flow.

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Chapter Three: Resistance and resilience of stream metabolism to high flow disturbances

B. O'Donnell^{1*}, E. R. Hotchkiss¹

¹Department of Biological Sciences, Virginia Tech

*Corresponding author: Brynn O'Donnell (brynnmodonnell@gmail.com)

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Abstract. Streams are ecosystems organized by disturbance, and one of the most frequent disturbances to a stream is elevated flow. Yet, our knowledge of how stream processes, such as stream metabolism, respond to higher flow events is limited. Stream metabolism is the fixation (gross primary production; GPP) and respiration (ecosystem respiration; ER) of carbon within an ecosystem. We still lack a general predictive framework for understanding controls on within-site variation of metabolic responses to flow disturbances. Using five years of high-frequency dissolved oxygen data from an urban- and agriculturally-influenced stream, we estimated GPP and ER across 15 isolated high flow events. Metabolism is dynamic from day to day, even at low flows. Thus, we quantified metabolic resistance as the magnitude of departure from the antecedent, dynamic equilibrium at lower flows, and calculated resilience as the days until metabolism returned to dynamic equilibrium. We evaluated how characteristics of each high flow event (such as size), antecedent conditions, and time since last flow disturbance correlated with metabolic resistance and resilience. ER was both more resistant and resilient than GPP. GPP was typically suppressed following flow disturbances, regardless of flow disturbance intensity. However, ER magnitude of departure increased with intensity of flow disturbance. Additionally, GPP was less resilient and took longer to recover (0 to >9 days, mean = 2.2) than ER (0 to 2 days, mean = 0.6). Because of the projected increase in storms, the flashy nature of altered streams, and the substantial effect of flow on ecosystem function, it is essential that we

understand how GPP and ER respond to flow disturbances of various magnitudes and across multiple seasons and environmental conditions.

1 Introduction

Disturbance is a key driver of stream ecosystem function, influencing everything from carbon and nutrient export to energy flow (Stanley et al. 2010). Stream biogeochemical processes can be altered via long-term, ‘press’ disturbances, such as land use change (Plont et al., in review), or by episodic ‘pulse’ disturbances, such as transitory changes in allochthonous inputs (Bender et al. 1984, Dodds et al. 2004, Seybold and McGlynn 2018). Disturbance creates patterns in stream processes (Resh et al. 1988, Stanley et al. 2010), generating oscillations that form a pulsing steady state (*sensu* Odum et al. 1995). Here, we use the definition of disturbance from White and Pickett (1985): “any relatively discrete event in time that disrupts the ecosystem... and changes resources, substrate availability, or the physical environment”. Disturbances to streams come in many forms, including: spates or rapid increases in the volume of water, drought, substratum movement, and anthropogenic alterations of channel morphology, flow, or solute chemistry (Resh et al. 1988).

Elevated flow is one of the most pervasive, frequent disturbances to streams. Flow disturbances can scour the benthos, increase turbidity, and reduce light – all of which can negatively impact stream function (Hall et al. 2015, Blaszczyk et al. 2018). However, flow is an inherent characteristic of streams and may influence stream function along a “subsidy-stress” gradient (*sensu* Odum et al. 1979). Excessively high flows can stress stream biota and induce conditions unfavorable for biotic processes, whereas ‘normal’ flows can stimulate internal biogeochemical transformations by flushing in subsidizing inputs of limiting nutrients or organic matter (Lamberti and Steinman 1997). Whether flow subsidizes or stresses the stream can

depend on a variety of factors, including the ecosystem process of interest, but ultimately flow is a disturbance when it exceeds some certain threshold.

Stream metabolism is an integrative whole-ecosystem estimate of the carbon fixed and broken down by autotrophs and heterotrophs within a stream, and is most commonly estimated via diel changes in dissolved oxygen (Hall and Hotchkiss 2017). Autotrophs produce oxygen via gross primary production (GPP), and both auto- and heterotrophs consume oxygen during ecosystem respiration (ER). Together, ER and GPP are opposing processes with respect to carbon balance and sum to net ecosystem production (NEP), which can elucidate whether a stream is a net producer (autotrophic; $GPP > ER$) or consumer (heterotrophic; $ER > GPP$) of carbon. Ecosystem metabolism is increasingly used to understand the health of streams (Young et al. 2008) and ecosystem responses to disturbance (e.g., Arroita et al. 2019), and is tightly coupled with other ecosystem processes (e.g., nitrogen uptake, Hall and Tank 2003).

Metabolism is influenced by many abiotic and biotic factors. GPP increases with light (Mulholland et al. 2001, Roberts and Mulholland 2007), nutrient availability (Grimm and Fisher 1986, Mulholland et al. 2001), temperature (Acuna et al. 2004), and transient storage (Mulholland et al. 2001). ER often mirrors GPP (e.g., Griffiths et al. 2013; Roley et al. 2014) and is consequently controlled by the same physicochemical conditions as GPP, as well as organic matter availability (Demars 2018). These drivers vary daily and seasonally, inducing temporal variation in metabolism that creates a pulsing steady state or dynamic equilibrium (e.g., Rosemond et al. 2000; Roberts and Mulholland 2007). Additionally, these metabolic drivers also fluctuate in response to disturbances (e.g., Uehlinger 2000).

The subsidy-stress relationship between flow and ecosystem function may create a range of metabolic responses to flow changes. Both GPP and ER may decline during high flows

(Uehlinger 2006, Roley et al. 2014, Reisinger et al. 2017); however, flow changes can also stimulate metabolism. Ultimately, the capacity of stream metabolism to withstand a flow disturbance and not be reduced or stimulated outside of its pulsing steady state constitutes its *resistance*. However, resistance is only one feature of a response to a disturbance, and captures the instantaneous reaction of metabolism to a flow disturbance. One way to quantify post-disturbance ecosystem response is through estimates of *resilience*: the time it takes for a process returns to equilibrium following a disturbance (Carpenter et al. 1992). Resilience of stream metabolism following a flow disturbance can take anywhere from days to weeks (e.g., Uehlinger and Naegeli 1998; Smith and Kaushal 2015; Reisinger et al. 2017), depending largely on seasonality and the magnitude of disturbance (Uehlinger 2006, Roberts et al. 2007). Overall, stream metabolism frequently exhibits low resistance to flow disturbances, but high resilience (Uehlinger and Naegeli 1998, Reisinger et al. 2017).

GPP and ER respond differently to flow disturbances (O'Donnell & Hotchkiss, in review). The major differences between patterns in ER versus GPP resistance and resilience may be due to the heterogeneity of the stream benthos, and because of where the microbes controlling these processes can be found (e.g., Uehlinger 2000, 2006). Autotrophic reliance on light for energy creates a stream bed commonly dominated by photoautotrophic algal communities and associated heterotrophs. Many heterotrophs, on the other hand, are established within the substrata and hyporheic zone, which can create increased resistance and resilience of ER relative to GPP (Uehlinger 2000, Qasem et al. 2019). Further, flow can carry organic matter from the catchment into the stream, increasing ER at higher flows (Beaulieu et al. 2013, Roley et al. 2014, Demars 2018).

Antecedent conditions (e.g., time since last flow event, season, antecedent light and temperature, antecedent medians of GPP and ER) may play a role in the variability of ecosystem responses to flow (McMillan et al. 2018; Uehlinger and Naegeli 1998). Additionally, the characteristics of the flow event (e.g., magnitude of flow event, time of day of event, peak discharge) may guide recovery dynamics. A flow event of lesser magnitude may yield higher resistance and resilience for both GPP and ER, as it may supply subsidizing, limiting nutrients and organic matter from the terrestrial landscape without inducing extreme scouring events. Quantifying the potential for different antecedent conditions to induce variable responses from GPP and ER is critical to furthering our understanding about stream ecosystem response to flow disturbances.

We propose an integrated framework for assessing ecosystem *resistance* and *resilience* in a single stream over the course of many high flow events to examine controls on within-site variability in metabolic response. To understand what influences response and/or recovery dynamics of stream metabolism, we address the question: What antecedent conditions or disturbance characteristics influence resistance and resilience of GPP and ER? We analyzed response and recovery dynamics (i.e., resistance and resilience) relative to a pulsing equilibrium for 15 isolated flow events across 5 years in a flashy urban- and agriculturally-influenced stream. We had three primary hypotheses (Figure 1): (H1) ER will be more resistant than GPP to flow disturbances, given the location of heterotrophs within the more protective streambed; (H2) there will be a stimulation of GPP and ER at intermediate flow disturbances due to an influx of limiting nutrients; and (H3) metabolic resistance and resilience will change with the size of the event, with larger flow disturbances inducing more stress due to enhanced scour in the system. By addressing these three hypotheses, and incorporating the concept of the pulsing equilibrium

into our quantification of recovery dynamics, we aim to improve our understanding of the relationship between metabolism and flow disturbance.

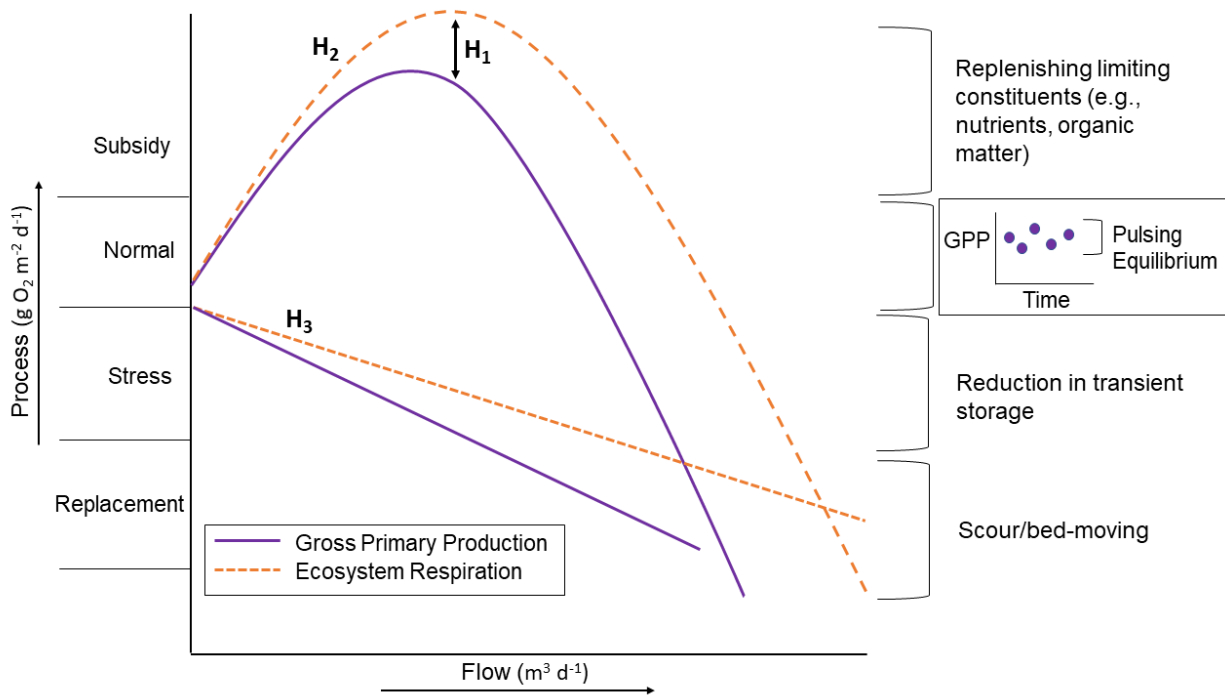


Figure 1. Potential metabolic responses along a subsidy-stress gradient controlled by stream flow (adopted from Odum et al. 1979). Flow is on the x-axis. The y-axis represents rates of ecosystem metabolism (i.e., gross primary production (GPP) and ecosystem respiration (ER)), and is broken into four categories defined by Odum et al. (1979): subsidy (when subsidization dominates and metabolism increases), normal (periods of metabolic pulsing equilibrium under ambient flow), stress (when ecosystem processes are repressed by disturbance) and replacement (when there is a severe reduction in metabolism and communities are scoured or replaced). The inset graph next to the ‘normal’ bracket depicts GPP over time, delineating how ambient rates are best represented by a pulsing equilibrium rather than a fixed point of stability (*sensu* Odum et al. 1995).

2 Methods

2.1 Study site

Stroubles Creek is a third-order, urban- and agriculturally-influenced stream draining a 15km² sub-watershed of the New River in Southwest Virginia in the United States. Stroubles Creek is a gravel bed, riffle pool stream, underlain by silty loam with a limestone bedrock (Yagow et al. 2006). The catchment's average annual precipitation is 40.43 inches, with a majority (52.6%) of that precipitation falling in May-October (Yagow et al. 2006). The average annual temp is 51.5°F (Yagow et al. 2006). The catchment draining into our study site is approximately 87% developed, 11% agriculture, and 3% forest (Homer et al. 2015). Due to the extent of anthropogenic development, Stroubles Creek is listed on the EPA's 303(d) impaired list for excessive sediment (Wynn et al. 2010). Our study site is a part of the Stream Research, Education, and Management Lab (StREAM Lab, <https://vtstreamlab.weebly.com/>), and has been monitored by Virginia Tech researchers for over 10 years.

2.2 Sensor data collection

High temporal resolution sensor data were collected from 2013-01-08 and 2018-04-14. Dissolved oxygen (DO) (mg L⁻¹), turbidity (nephelometric turbidity unit, NTU), conductivity (ms cm⁻¹), pH, and temperature (°C) data were collected at 15-minute intervals by an *in-situ* YSI 6920V2 sonde. Because a freeze event impaired DO measurements from the YSI sonde, we gap-filled with data from a PME MiniDOT installed at the same time to estimate metabolism from 2017-09-01 to 2018-04-14. Prior to the freeze event, DO data from the MiniDOT and YSI were nearly identical (Supplemental Figure 1). We obtained light and pressure measurements via a Campbell Scientific CS300 from a local weather station. A Campbell Scientific CS451 pressure

transducer recorded stage measurements every 10 minutes. A stage-discharge relationship was created in 2013 and confirmed in 2018. Velocity and width measurements were taken over multiple years to create a relationship with stage. Sensors were calibrated every 2-4 weeks.

To remove data that may have occurred due to sensor error prior to analyses, we excluded values below the 1% and above the 99% quantile for physicochemical parameters that were heavily skewed (i.e., turbidity and conductivity). We removed physicochemical measurements we knew to be unreasonable (e.g., turbidity was cut off at zero). We calculated daily medians for the physicochemical parameters for all days that had at least 80% of measurements over the course of the day. We then merged physicochemical values for days that had values for all physicochemical parameters.

2.3 Ecosystem metabolism

We estimated GPP, ER, and K (air-water gas exchange) from diel O₂, light, and temperature data using an inverse modeling approach (Hall & Hotchkiss, 2017). We selected the *streamMetabolizer* R package for our analyses, which uses Bayesian parameter estimation and a hierarchical state space modeling framework to generate daily estimates of GPP, ER, and K that create the best fit between modeled and observed DO data (Appling et al., 2018a ; Equation 1; Table 1).

$$mO_i = mO_{i-\Delta t} + \frac{GPP * PAR_t}{z * \sum PAR} + \frac{ER}{z} \Delta t + K_O (O_{sat(i-\Delta t)} - mO_{i-\Delta t}) \Delta t \quad [\text{Equation 1}]$$

Table 1: *Terms Used in Equation 1*

Term symbol	Term description (units)
mO	Modeled O_2 ($g\ O_2\ m^{-3}$)
Δt	Interval (d)
GPP	Gross primary production ($g\ O_2\ m^{-2}\ d^{-1}$)
ER	Ecosystem respiration ($g\ O_2\ m^{-2}\ d^{-1}$)
z	Depth (m)
K_o	Air-water gas exchange of O_2 (d^{-1})
O_{sat}	Oxygen at saturation ($g\ O_2\ m^{-3}$)
PAR	Photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$)

We used most of the default model specs for *streamMetabolizer*. We ensured a proper number of burn-in steps (500) based off the model convergence visualized via *traceplot* in the *rstan* package (Stan Development Team 2018) and specified 2000 saved steps. We chose to model GPP, ER, and K with both observation error and process error. Additionally, to decrease the chances of equifinality between GPP, ER, and K estimates (Appling et al., 2018b), we binned K according to discharge. We divided discharge measurements across each year into six bins, which the hierarchical modeling framework of *streamMetabolizer* then used to create $K \sim Q$ relationships to constrain K estimates (Appling et al., 2018b). We used nighttime linear regression of DO as another way to estimate the range in K in Stroubles (Hall & Hotchkiss, 2017) and used these estimates of K to quality check the range in modeled K from *streamMetabolizer* (Supplemental Figure 2).

We removed all metabolism estimates that were biologically impossible, such as negative GPP or positive ER (ER is modeled as a negative flux of O_2 consumption). Next, we used

diagnostics from *fit()* in *stan* to remove values resulting from poor model fit or lack of convergence (Stan Development Team 2018). Poor model convergence was indicated when *Rhat* exceeded 1.1, and poor model fit when *N_eff* (effective sample size) ended at or exceeded the product of the number of chains and the number of saved steps specified for our model. Additionally, to avoid using biased estimates of metabolism, we removed K values below the 1% (< 3.38 d⁻¹) and above the 99% (> 27.21 d⁻¹) quantile. 246 days were ultimately removed due to these QA/QC criteria, resulting in 1375 days (of 1621 total from 2013-01-08 to 2018-04-14) of metabolism estimates for further analyses. Here, we also report the mean standard error derived from the mcmc distributions of the mean GPP and ER of each date from the 4 chains (Appling et al. 2018c)

2.4 Selection of isolated flow events

To identify flow events for our analyses, we calculated percent change of cumulative daily discharge (Q) relative to the day prior (Eqn 2).

$$\% \Delta Q = \frac{(Q_i - Q_{i-1})}{Q_{i-1}} * 100 \quad \text{[Equation 2]}$$

To analyze metabolic response and recovery, we selected isolated flow events that had a greater than 50% Q change relative to the antecedent cumulative daily Q. We defined isolation as a period of three days before and three days after a high flow event where no other flow events exceeding 10% Q change occurred. In total, there were 15 isolated flow events across all 5 years that met our criteria for isolated flow events and had quality-checked metabolism estimates.

Hydrographs and metabolism time series for each isolated flow event analyzed are available in Supplement Figures 3 - 17.

2.5 Characterizing metabolic resistance and resilience

To acknowledge the pulsing, day-to-day variability of GPP and ER, we used metabolism from three days prior to create a range of antecedent metabolism for each isolated flow event. We quantified metabolic responses to flow disturbances by comparing this range with event and post-event metabolism. To assess resistance, we estimated metabolic magnitude of departure (M) during events to quantify the resistance of GPP and ER to disturbance. We calculated M per isolated flow event by comparing the difference between GPP and ER to the nearest value of the antecedent range (Equation 3; Figure 2),

$$M = 1 - \frac{X_{event}}{X_{prior}} \quad \text{[Equation 3]}$$

where X_{event} is either GPP or ER ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) on the day of the isolated flow event. X_{prior} is the maximum or minimum value of GPP or ER from the antecedent range, depending on if the isolated flow event resulted in a stimulated (increased) or repressed (reduced) metabolic response. For instance, if GPP was repressed during a flow event, M was calculated as the difference between GPP for the isolated flow event and the minimum value from the antecedent 3-day range (Figure 2). If the estimate of GPP or ER on the event day does not fall outside of the antecedent range, the magnitude of departure is zero, thus indicating high resistance. A negative magnitude of departure (M) represents a suppression, and a positive M a stimulation, where GPP or ER increase relative to the antecedent equilibrium.

To quantify recovery intervals (RI) and thus resilience of GPP and ER, we counted the number of days until metabolism returned to within the range of values of the three days prior, signifying a return to antecedent dynamic equilibrium (Figure 2). If metabolism from the isolated flow event does not fall outside of the antecedent range and M is zero, RI is NA. An event cannot recover if it never shifts outside of the range of normality. Given the flashy nature of our study stream, there may be events where metabolism does not recover before another flow event occurs. To ensure these additional flow events did not obscure the recovery interval of GPP or ER, we stopped counting recovery intervals the day before the next event (i.e., if a flow event happened four days out, we stopped counting RI at 3 days), and have noted this in our results as days+ and used different symbols in data figures. To test for statistically significant differences between RI_{ER} and RI_{GPP} and M_{ER} and M_{GPP} , we ran Welch's t-tests in R (R Core Team, 2017).

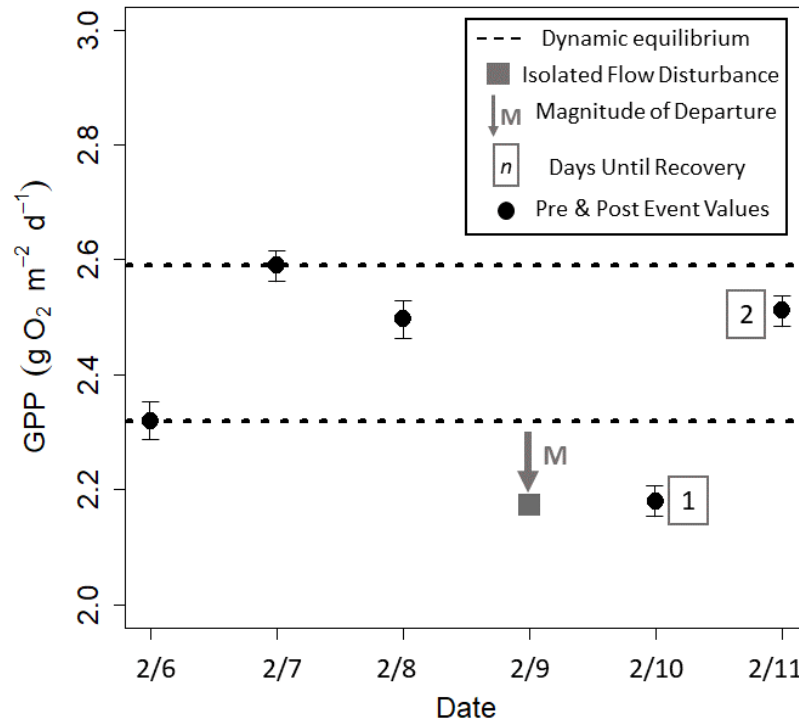


Figure 2. Example calculations of metabolic resistance (M) and resilience (RI). Daily gross primary production (GPP) was estimated for the three days before, one day during (grey square), and two days following an isolated flow event that occurred on 2017-02-09. Dashed horizontal lines represent the maximum and minimum GPP estimates from three days prior to the flow event. In this case, GPP was repressed, and the magnitude of departure (M with grey arrow) is the difference between minimum GPP estimate from the antecedent range (bottom dashed line) and GPP during the event. After this flow event, GPP recovered to antecedent range in 2 days; recovery interval days (RI) are represented by the grey boxed numbers next to GPP estimates.

2.6 Testing predictors of metabolic resistance and resilience

To determine drivers of metabolic response and recovery dynamics of each isolated flow event, we examined three categories of potential predictors: antecedent conditions, characteristics of the isolated flow event, and characteristics of the most recent, prior flow event.

Antecedent conditions included antecedent median GPP, ER ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), turbidity (NTU), water temperature ($^{\circ}\text{C}$), and PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). Flow event characteristics included flow magnitude (% change of cumulative daily discharge; $\text{m}^3 \text{ d}^{-1}$; Equation 2), time (HH:MM) of peak discharge ($\text{m}^3 \text{ s}^{-1}$), and environmental conditions (e.g., light, temperature, turbidity, season) on the event day. Antecedent medians for turbidity were estimated from seven days prior due to missing sensor data. For all other variables, we estimated median values from three days prior to the flow event for correlations between metabolism M and RI. Characteristics of the most recent flow event included the days since and magnitude of the last flow event (Table 3). We visually identified the most recent flow event (% change in cumulative daily discharge > 50) prior to each isolated flow event analyzed. We ran bivariate correlation analysis using the *cor.test* function in R to extract the Pearson correlation coefficient and the p-value (R Core Team 2017) to quantify the strength and directions of linear relationships between predictor variables and metabolic resistance and resilience (Figure 7; Table 4). All analyses were conducted in R Studio (R Core Team 2017).

3 Results

3.1 Flow and metabolism

Stroubles Creek is a hydrologically flashy stream, with frequent high flow events (Figure 3). Cumulative daily discharge for date with quality-checked metabolism estimates ranged from 66 to 114,408 $\text{m}^3 \text{ d}^{-1}$, with a median of 6,230 $\text{m}^3 \text{ d}^{-1}$. The 15 isolated flow events selected for analyses were within the mid-high range (Figure 3) of all cumulative daily discharges (Table 2), and were of magnitudes that occurred multiple times a year. We used a percent change equation to identify isolated flow events of interest, so changes in cumulative daily discharge are proportionate across seasons. GPP ranged from 0.002 to 17.3 $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with a median of 4.0.

ER ranged from -0.1 to $-27.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with a median of -9.6 (Figure 4). Stroubles was heterotrophic ($\text{NEP} < 0$), except for 38 days (3%) where $\text{GPP} > \text{ER}$, all of which occurred in spring except for one day in the fall.

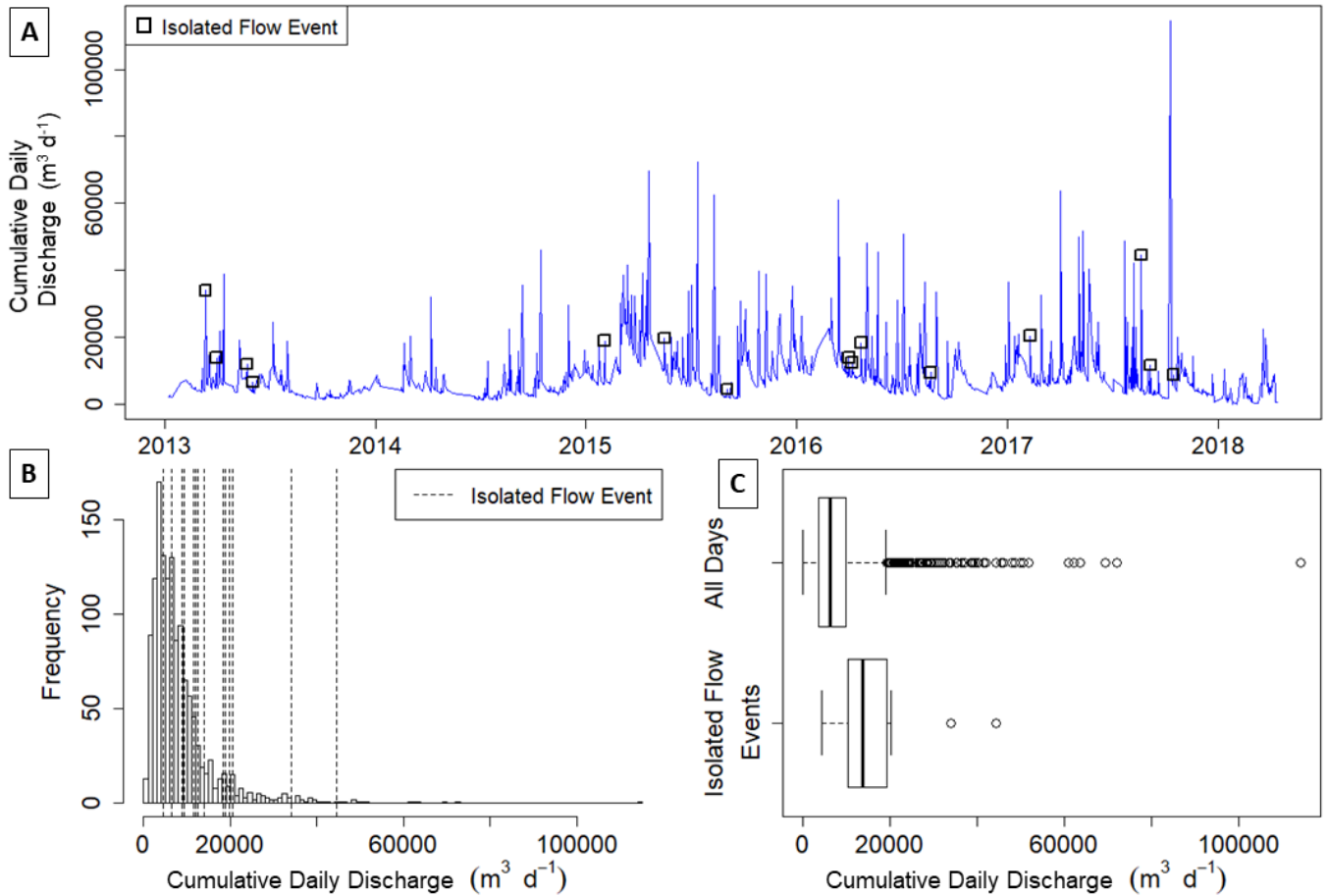


Figure 3. (A) Time series of cumulative daily discharge ($\text{m}^3 \text{ d}^{-1}$) on all days with quality-checked metabolism estimates from 2013-01-08 to 2018-04-14. The 15 isolated flow events analyzed for metabolic responses to higher flow are represented by open squares. (B) Frequency distribution of cumulative daily discharge for days with quality-checked metabolism estimates. Vertical dashed lines denote the cumulative daily discharge values of the 15 different isolated flow events. (C) Box plots of cumulative daily discharge ($\text{m}^3 \text{ d}^{-1}$) for all days with metabolism estimates versus from isolated flow event days that fit our criteria for analyzing metabolic resistance and resilience.

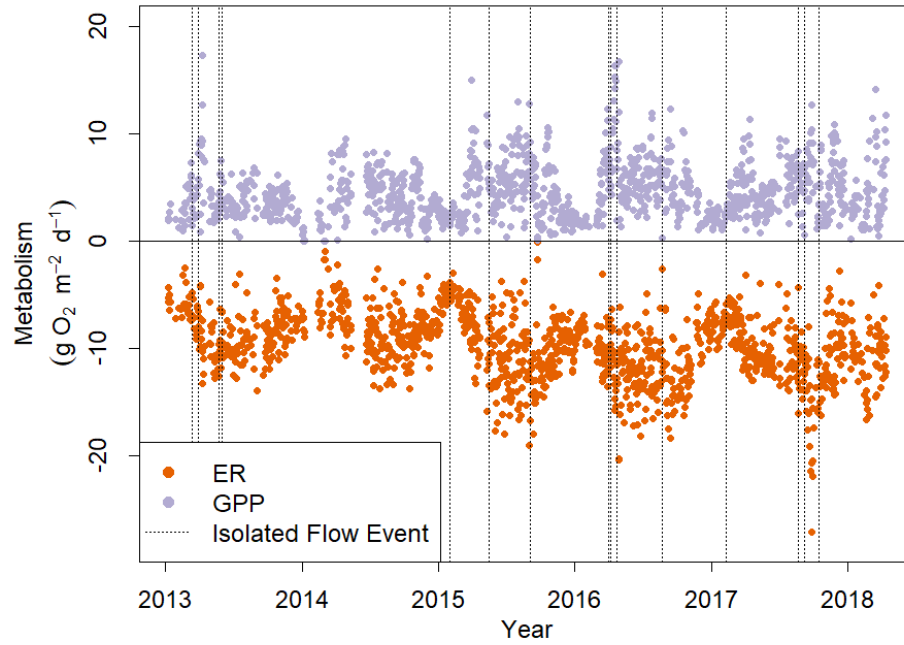


Figure 4. Gross primary production (GPP, top) and ecosystem respiration (ER, bottom) in Stroubles Creek, VA from 2013-01-08 to 2018-04-14. ER is represented here as a negative rate because it is the consumption of oxygen. Dashed vertical lines mark the isolated flow events that fit our criteria for analyzing metabolic responses to flow change (Figure 3).

Table 2: Cumulative daily discharge (Q), metabolism (gross primary production (GPP), ecosystem respiration (ER)), and air-water gas exchange (K) of isolated flow events analyzed for metabolic recovery

Date of isolated flow event	Cumulative daily Q ($m^3 d^{-1}$)	% change in cumulative daily discharge relative to day prior	GPP ($g O_2 m^{-2} d^{-1}$) $\pm$ standard error	ER ($g O_2 m^{-2} d^{-1}$) $\pm$ standard error	K (d^{-1}) $\pm$ standard error
2013-03-12	33969.8	713.0	1.5 ± 0.01	-4.8 ± 0.02	9.0 ± 0.04
2013-03-31	13848.8	187.5	2.4 ± 0.01	-8.0 ± 0.02	13.0 ± 0.03
2013-05-23	11923.0	68.6	3.7 ± 0.01	-12.6 ± 0.03	15.2 ± 0.03
2013-06-02	6544.9	92.5	3.2 ± 0.01	-10.6 ± 0.02	13.1 ± 0.03
2015-02-02	18841.9	210.3	1.4 ± 0.00	-4.7 ± 0.02	20.9 ± 0.06
2015-05-17	19682.7	93.6	7.2 ± 0.02	-13.5 ± 0.03	15.9 ± 0.03
2015-09-03	4447.0	119.9	6.5 ± 0.02	-11.2 ± 0.04	12.8 ± 0.04
2016-04-01	13868.5	67.2	4.8 ± 0.01	-7.6 ± 0.01	13.9 ± 0.02
2016-04-07	12478.0	52.8	5.0 ± 0.01	-9.7 ± 0.02	19.2 ± 0.03
2016-04-22	18340.2	114.0	1.9 ± 0.01	-10.4 ± 0.03	13.0 ± 0.03
2016-08-21	9418.2	93.5	0.3 ± 0.01	-2.6 ± 0.02	4.8 ± 0.03
2017-02-09	20382.8	148.5	2.2 ± 0.00	-7.4 ± 0.02	17.6 ± 0.03
2017-08-21	44543.0	1104.7	2.5 ± 0.01	-4.3 ± 0.02	4.1 ± 0.02
2017-09-06	11599.8	269.3	0.6 ± 0.00	-12.1 ± 0.04	17.3 ± 0.05
2017-10-16	8760.9	53.8	3.4 ± 0.01	-11.4 ± 0.05	17.8 ± 0.07

3.2 Metabolic resistance and resilience

GPP most often declined following an isolated flow event, whereas ER rarely deviated from the antecedent equilibrium during higher flows. The magnitude of departure for GPP

(M_{GPP}) ranged from -0.92 to 0.09, with a median of -0.14 (Table 3; Figure 6). GPP was inhibited in 11 of 15 analyzed isolated flow events, and stimulated during two events. The magnitude of departure for ER (M_{ER}) ranged from -0.59 to 0.22, with a median of 0. There were 3 of 15 analyzed isolated flow events that stimulated ER, 5 that resulted in repression of ER, and 7 events where ER did not deviate from the antecedent equilibrium (i.e., M_{ER} was 0). Overall, the direction of ER response to elevated flow was more variable than that of GPP.

Although GPP exhibited stronger responses across isolated flow events than ER, M_{GPP} and M_{ER} were positively correlated ($R^2 = 0.39$, $p = 0.007$, Figure 6) and not significantly different ($p = 0.06$, $\alpha = 0.05$). M_{GPP} was less than M_{ER} for nearly all of the isolated flow events, except for one event in which M_{GPP} and M_{ER} were both zero, and two events where both M_{GPP} and M_{ER} were small. The isolated flow event that induced the greatest stimulation of GPP ($M_{GPP} = 0.09$) also stimulated ER ($M_{ER} = 0.05$). The other two events that stimulated ER had no response from GPP ($M_{GPP} = 0$) or had a minor GPP reduction ($M_{GPP} = -0.06$). Similarly, the only other event that stimulated GPP ($M_{GPP} = 0.03$) had no ER response, suggesting that stimulation may cause a minor, brief decoupling between GPP and ER at our study site.

Table 3: *Magnitude of departure (M, unitless) and recovery intervals (RI, days) of gross primary production (GPP) and ecosystem respiration (ER) during and after fifteen isolated flow events between 2013-01-08 and 2018-04-14. A negative magnitude of departure (M) represents a suppression, and a positive M a stimulation, where GPP or ER increase relative to the antecedent equilibrium.*

Date of isolated flow event	M _{GPP}	RI _{GPP} (d)	M _{ER}	RI _{ER} (d)
2013-03-12	-0.76	3+*	-0.31	1*
2013-03-31	-0.44	1	0.00	n/a
2013-05-23	0.09	1	0.05	1
2013-06-02	-0.05	1	0.00	n/a
2015-02-02	-0.14	1	0.00	n/a
2015-05-17	0.00	n/a	0.22	2
2015-09-03	0.00	n/a	0.00	n/a
2016-04-01	-0.14	1	-0.05	1
2016-04-07	-0.03	2	0.00	n/a
2016-04-22	-0.83	4+*	-0.07	1*
2016-08-21	-0.92	1	-0.58	1
2017-02-09	-0.06	2	0.002	1
2017-08-21	-0.64	9+*	-0.59	1*
2017-09-06	-0.87	1	0.00	n/a
2017-10-16	0.03	6+*	0.00	n/a *

* Days in which GPP did not recover before the next flow event, and are not included in recovery interval correlation analyses

Both GPP and ER typically recovered from flow-related stimulation or disturbance in less than three days (Table 3). There were many isolated flow events where GPP took multiple days to recover but ER never departed from the antecedent dynamic equilibrium (i.e., $M = 0$; Figure 6). For events where M_{GPP} and M_{ER} both > 0 , ER recovered faster than GPP for nearly all of the flow events. RI_{GPP} ranged from 1-9+ d, with an average of 2.5 d (Table 3). RI_{ER} ranged from 1-2 d, with an average of 1.1 d. There was only one isolated flow event where GPP recovered before ER. While ER always recovered before another flow event occurred, there were 4 of 15 analyzed isolated flow events where GPP did not recover before another flow event occurred. Excluding these events, recovery intervals for GPP and ER were not correlated (Figure 6) or significantly different ($p = 0.12$, $\alpha = 0.05$).

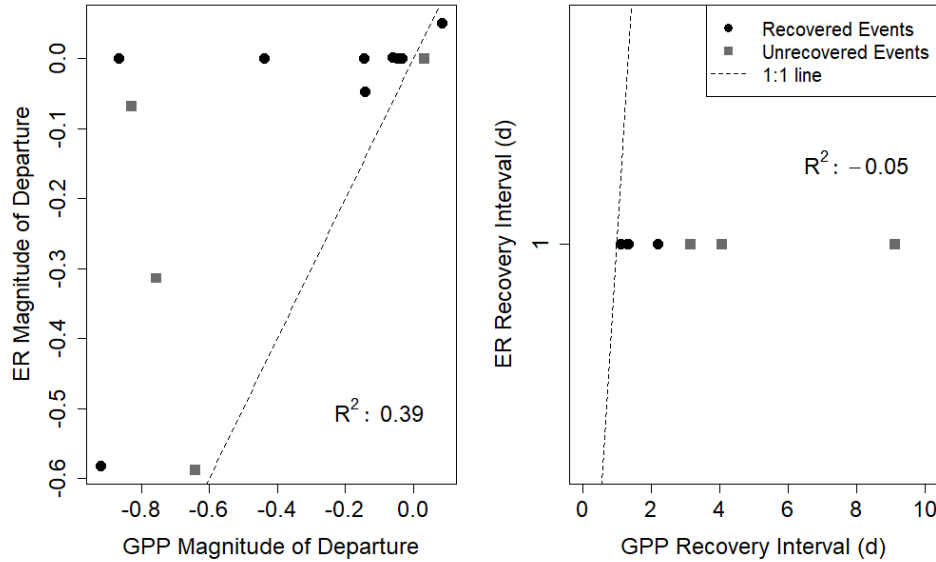


Figure 6. (A) Resistance (i.e., magnitude of departure; left) and (B) resilience (i.e., recovery interval; right) of gross primary production (GPP) versus ecosystem respiration (ER) in Stroubles Creek, VA. Dashed lines are 1:1 lines. Black circles are isolated flow events that did recover to antecedent equilibrium, or were unresponsive (i.e., $M = 0$). Grey squares are the isolated flow events that did not recover to antecedent equilibrium before another flow event occurred. RI values (right) are jittered along the x-axis, meaning that the points are slightly scattered around their value to visualize overlapping values; each recovery interval is calculated at the daily scale.

3.3 Correlation analysis of predicted controls on metabolic resistance and resilience after a flow disturbance

Although GPP and ER are inherently linked, predictor variables with moderate or stronger relationships ($r > 0.50$) differed between ER and GPP (Table 4; Figure 7). There were no predictors with moderate or stronger relationships for both M_{GPP} and RI_{GPP} . Because the median RI_{ER} was zero, bivariate correlations could not be ran to determine potential predictor variables for resilience of ER. Peak discharge of the flow event ($m^3 s^{-1}$) was a significant

predictor of M_{ER} ($r = -0.59$). The magnitude of each disturbance, characterized by the % change in cumulative daily discharge, was negatively correlated with M_{GPP} ($r = -0.46$, $p = 0.08$) and significantly negatively correlated with M_{ER} ($r = 0.66$, $p = 0.01$, $\alpha = 0.05$) (Figure 8), but was not significantly correlated with RI_{GPP} ($p = 0.54$; $\alpha = 0.05$). Overall, there were multiple environmental controls on metabolic resistance or resilience that were strongly correlated with either GPP or ER, but no significant drivers of both GPP and ER resistance and resilience.

Table 4: *Pearson correlations (r) between predicted drivers of gross primary production (GPP) and ecosystem respiration (ER) magnitudes of departure (M) and recovery intervals (RI) of isolated flow events. Predictor variables with moderate or stronger relationships ($r > 0.50$) are bolded.*

Predictor variables (units)	RI _{GPP} r	M _{GPP} r	RI _{ER} r	M _{ER} r
Isolated flow event of interest				
Daily median PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-0.26	0.16	n/a	-0.17
Daily peak discharge ($\text{m}^3 \text{s}^{-1}$)	-0.03	-0.32	n/a	-0.59
Daily median temperature ($^{\circ}\text{C}$)	-0.46	-0.11	n/a	-0.28
Event median discharge ($\text{m}^3 \text{s}^{-1}$)	0.00	-0.21	n/a	0.03
% discharge change during event	-0.24	-0.46	n/a	-0.66
Season	-0.42	-0.16	n/a	-0.18
Time of peak discharge (HH:MM)	-0.65	-0.12	n/a	-0.10
Turbidity (NTU)	-0.21	-0.41	n/a	-0.18
Most recent flow event				
Days since last event (d)	0.23	0.15	n/a	0.10
Last event cumulative daily discharge ($\text{m}^3 \text{d}^{-1}$)	0.59	0.40	n/a	0.21
% discharge change of last event	0.55	0.51	n/a	0.47
Antecedent conditions				
Antecedent median K (d^{-1})	0.26	-0.04	n/a	-0.08
Antecedent GPP ($\text{g O}_2 \text{m}^{-2} \text{d}^{-1}$)	0.02	-0.48	n/a	-0.12
Antecedent ER ($\text{g O}_2 \text{m}^{-2} \text{d}^{-1}$)	0.16	0.25	n/a	0.09
Antecedent median PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-0.31	0.12	n/a	0.04
Antecedent median discharge ($\text{m}^3 \text{s}^{-1}$)	0.08	0.34	n/a	0.40
Antecedent median water temperature ($^{\circ}\text{C}$)	-0.32	-0.14	n/a	-0.29
Antecedent median turbidity (NTU)	-0.23	0.13	n/a	0.00

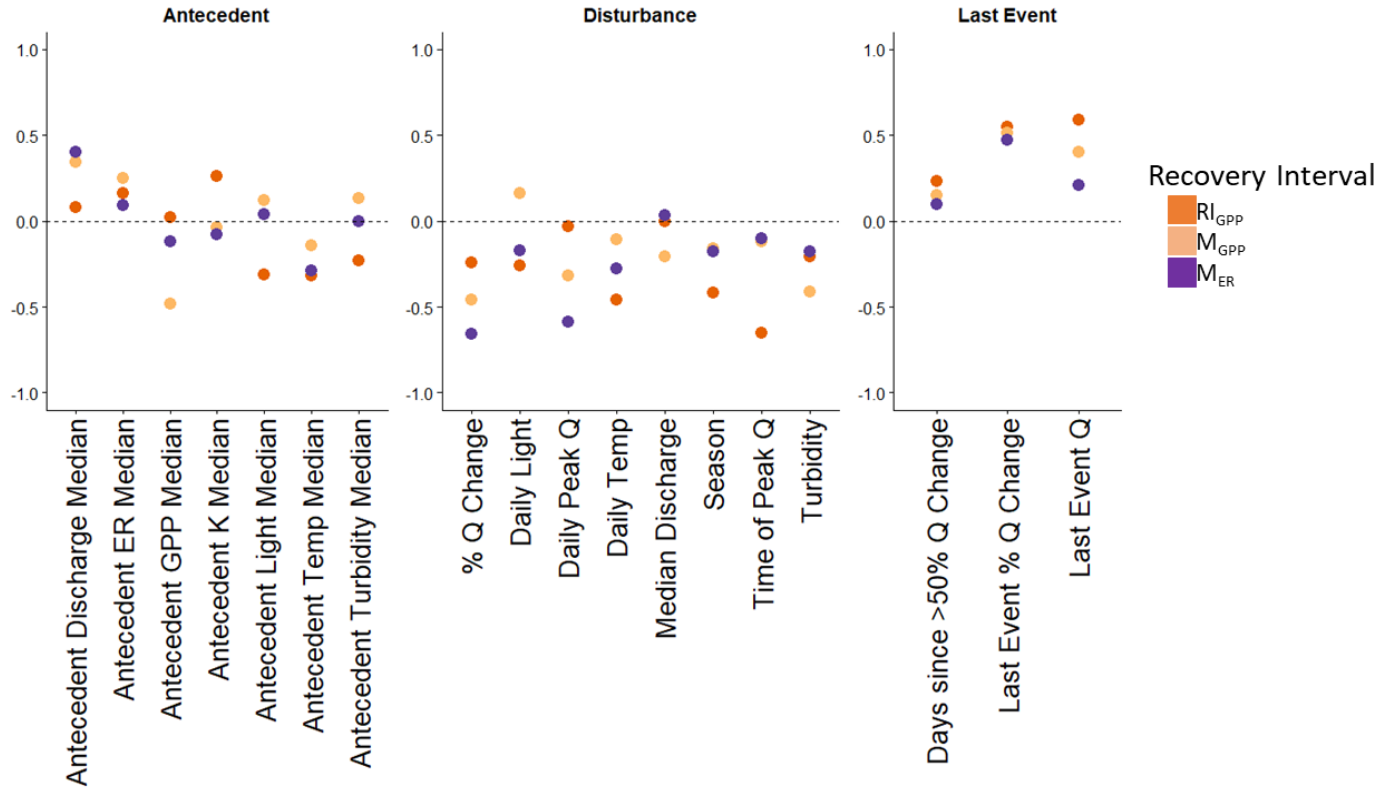


Figure 7. Pearson correlation coefficients for all recovery metrics: ecosystem respiration (ER) magnitude of departure (M), gross primary production (GPP) M and recovery interval (RI) of GPP. Potential predictor variables are divided into three groups (left-right): antecedent conditions, disturbance characteristics, and characteristics of the most recent flow event. For units of variables, see Table 4.

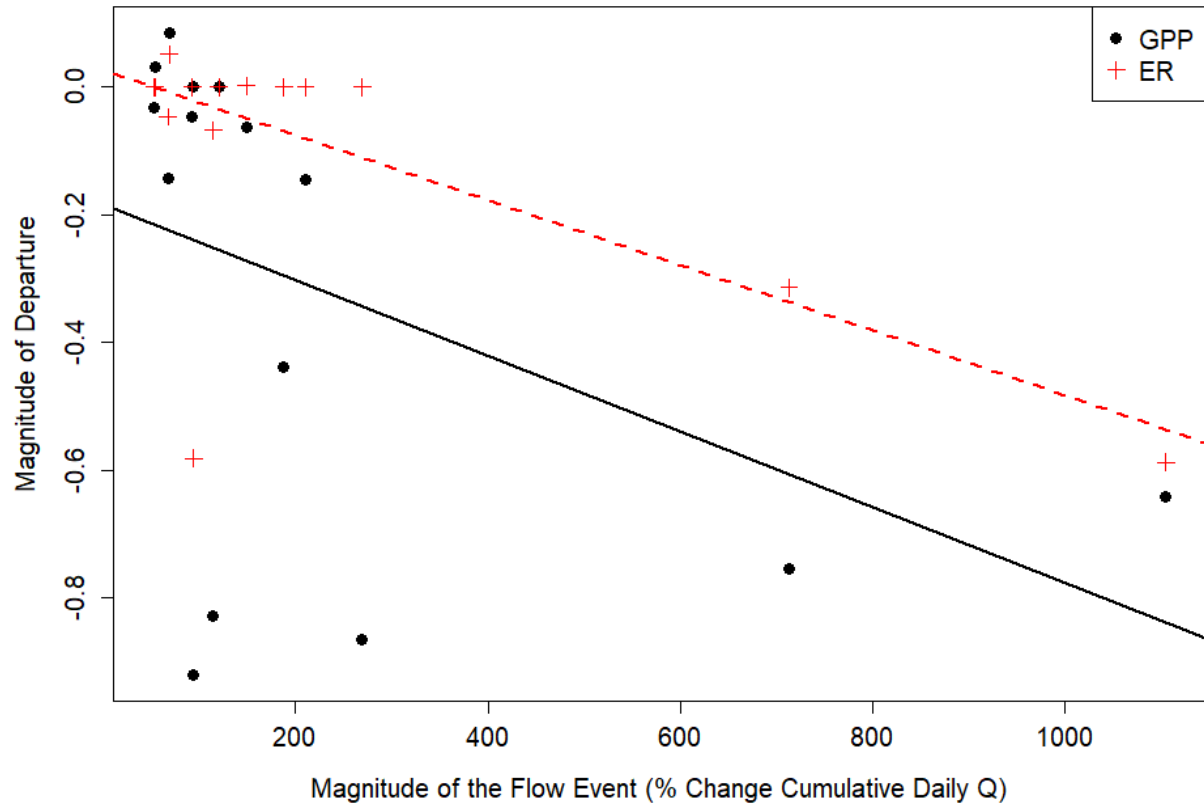


Figure 8. The magnitude of the flow event (% change in cumulative daily discharge relative to the day prior) is negatively correlated with magnitude of departure (M) for gross primary production (GPP; $R^2 = 0.15$, $r = -0.46$, $p = 0.08$) and ecosystem respiration (ER; $R^2 = 0.39$, $r = -0.66$, $p = 0.01$, $\alpha = 0.05$). The solid black line is the regression for the relationship between M_{GPP} and % change in discharge, while the dashed red line is the regression for the relationship between M_{ER} and % change in discharge. % change in cumulative daily discharge was significantly negatively correlated with M_{ER} , but not significantly correlated with M_{GPP} .

4 Discussion

4.1 Metabolic resistance and resilience

Despite the inherent links between GPP and ER in streams, we found marked differences in their responses to isolated flow events (Figure 6). Notably, ER was more resistant than GPP,

supporting our first hypothesis (Figure 1). For many of the events analyzed, ER did not shift out of the range of antecedent equilibrium (i.e., $M = 0$), whereas GPP was reduced (Figure 6; Table 3). Decreased GPP can decrease ER because autotrophs respire and also provide a labile organic matter (OM) source for heterotroph growth and respiration (Kaplan and Bott 1982, Uehlinger and Naegeli 1998). Yet, the potential negative consequences of flow on heterotrophic activity are balanced with the possibility for flow-induced stimulation of respiration caused by increased DOC concentrations from allochthonous sources (Demars 2018), more labile DOC (Mulholland et al. 1990). Further, GPP can be stimulated via influxes of limiting nutrients (Beaulieu et al. 2013). However, in our study system, three events stimulated ER, whereas there were two instances of minor GPP stimulation (Table 3). Flow-induced stimulation of GPP may have been caused by the replenishment of a limiting nutrient (Lamberti and Steinman 1997).

ER was also more resilient than GPP. Across all flow events, ER recovered on average much faster than GPP (Table 3; Figure 6). ER returned to antecedent rates within one day after flow events for all but one event, whereas GPP recovery ranged from 1-9+ days. Resilience differences between ER and GPP (i.e., RI_{ER} and RI_{GPP}) are likely a result of flow-induced changes to physicochemical parameters (e.g., turbidity), which can alter GPP more than the impacts of flow would alone (O'Donnell & Hotchkiss, in review). For instance, sustained periods of high turbidity following a disturbance can prolong the recovery of GPP by inhibiting light attenuation (Blaszczak et al. 2018). In contrast, faster average resilience of ER is likely a function of both OM stimulation of ER, and the greater resistance of ER to disturbances (i.e., smaller M ; Table 3). The greater resistance of ER to disturbances indicates potentially less biomass scoured than primary producers, and therefore more capacity for greater resilience (i.e., smaller RI). The correlation of M_{GPP} and M_{ER} , but a lack of correlation between RI_{GPP} and RI_{ER}

(Figure 6), suggests that the instantaneous responses of GPP and ER to flow disturbances align, while metabolism becomes temporarily decoupled while recovering. Ultimately, flow-induced changes can disproportionately negatively impact GPP relative to ER.

4.2 Controls on metabolic resistance and resilience following a flow event

The characteristics of a flow disturbance (i.e., % change in cumulative daily discharge, larger peak event discharge) were significantly related to M_{ER} but not M_{GPP} , suggesting that while GPP may respond similarly to flows regardless of magnitude, ER has greater resistance to flows of smaller magnitudes. Our hypothesis that isolated flow events of greater magnitudes (i.e., larger % change in cumulative daily discharge) would result in less resistance and a higher M_{GPP} and M_{ER} due to increased scouring was supported only for M_{ER} . Flow events of greater magnitude were weakly correlated with M_{GPP} ($r = -0.46$; Table 4; Figure 8), supporting the idea that GPP may have low resistance to flow disturbances, regardless of magnitude (Reisinger et al. 2017; Roley et al. 2014). The different responses of GPP and ER to variable flow can potentially be attributed to the differences in energy source and residence within the streambed of the autotrophs and heterotrophs (Uehlinger 2000, 2006). The surface of the stream bed is dominated by primary producers who reside in exposed areas because of their need for light for photosynthesis. The exposed surfaces are more vulnerable to scour than the locations of the heterotrophic biofilms tucked within, and protected by, the substrata and hyporheic zone (Uehlinger 2000). However, higher flows may reduce metabolism in deeper sediments. Indeed, M_{ER} was significantly negatively correlated with % change in cumulative daily discharge ($r = -0.66$, $p = 0.01$; Figure 8). We tried to examine the effect of four of the five flow characteristics defined by Poff et al. (1997) (magnitude, frequency, rate of change, timing; Table 2; Fig 5), yet

we were unable to ask how the fifth flow characteristic – duration – impacts metabolism. Do sustained, higher flows impact GPP and ER in the same way as a more instantaneous, intense flow event would? Overall, geomorphology and disturbance regimes may control spatial metabolic resistance dynamics across sites (Uehlinger 2000, Blaszcak et al. 2018), but within-site, temporal variability of M_{ER} may be controlled by the particular characteristics of each flow event.

Flow disturbances may have a more substantial impact on M after a certain resistance threshold is crossed. Neither of the subsidy-stress responses hypothesized to influence metabolic responses to flow change (Figure 1; H2, H3) were supported. At small-intermediate sized flow disturbances, there was not a clear stimulation nor stress on ecosystem metabolism. Rather, the response of metabolism was variable, with the greatest range of stimulations and reductions observed at smaller flow changes (Figure 8). Therefore, it may be more likely that either H2 (a stimulation) or H3 (no stimulation, just stress response) can result during smaller flow disturbances. After a resistance threshold is crossed with increasing intensity of flow disturbance, stress and replacement may indeed scale with intensity. Prior to crossing that threshold, other predictor variables, such as light, temperature, or turbidity may control the variability in metabolic response to smaller flow disturbances.

Contrary to our predictions, the size of the most recent antecedent flow disturbance had a positive relationship with M_{GPP} and M_{ER} . M_{GPP} was smaller, and GPP more resistant, when the most recent flow events were larger (i.e., the magnitude of the last event was strongly positively correlated with M_{GPP} ; $r = 0.51$; Supp Fig 18). Similarly, the % change in cumulative daily discharge from the last event was positively correlated with M_{ER} ($r = 0.47$). Stream metabolism can be influenced by the most recent event because the stream may still be recovering and

regenerating biomass lost from scour and algal taxa might respond differently to flow events depending on successional stage (Peterson and Stevenson 1992). We speculate that the positive correlation between M_{GPP} , M_{ER} and % change in cumulative daily discharge from the last event may be a result of biomass growth stimulation from the preceding larger event, which was subsequently limited by some chemical constituent until the next event (i.e., the isolated flow event we analyzed) supplied the limiting nutrients for that enhanced biomass. We ultimately do not know what caused the unexpected negative relationship between the magnitude of the most recent event and M_{GPP} , M_{ER} in Stroubles Creek, and further research incorporating biomass assessments at the flow event scale may elucidate this interesting relationship.

Environmental conditions on the day of isolated flow events that intuitively promote fast biomass growth, such as high light and temperature, were not significant predictors of ER or GPP recovery intervals. Conditions of the days following the flow event – rather than the day of the flow event itself – may have stronger relationships with metabolic recovery, although we did not test these here; however, since metabolism recovered so rapidly, we predicted GPP would recover faster with high temperature and light even on the flow event day. Accordingly, metabolic recovery trajectories often increase with temperature and PAR (Uehlinger and Naegeli 1998, Uehlinger 2000), and consequently also display a seasonal component, with faster recoveries in spring and slower recoveries in winter (Uehlinger 2000, 2006). Here, we found a negative relationship between RI_{GPP} and both temperature and season ($r = -0.46, -0.42$ respectively), suggesting that under colder conditions and in winter months, GPP takes longer to recover (Supp Fig 19). However, as we could not test what drives recovery intervals of ER, multiple factors may play critical roles in the recovery of ER. For one, more labile OM inputs may induce a faster RI_{ER} (Roberts et al. 2007). Combining OM lability measurements at the

event scale with metabolic recovery intervals could yield insight into whether lability of OM alters ER recovery.

4.3 Future Work

Metabolism is innately pulsing, which can affect the quantification of metabolic responses to disturbance. Across the literature, resistance of stream metabolism is often quantified as percentages of reductions or stimulations relative to an antecedent average (e.g., Reisinger et al. 2017; Roley et al. 2014). As resistance is usually quantified as a deviation from a fixed point, there are no recorded flow events that have yielded total resistance and no change (i.e., there's always been some sort of response). When calculated in this way, every new metabolism estimate results in some sort of reduction or stimulation, which creates the potential of quantifying just about anything as a 'disturbance', even though metabolism has an inherently pulsing nature (Bernhardt et al. 2018). We found some of the shortest metabolic recovery intervals recorded in the literature (Fig. 9; Supplemental Table 1), either because we assessed smaller flow events or because we acknowledged the dynamic equilibrium of metabolism. Incorporating the pulsing equilibrium of metabolism and standardizing calculations of metabolic recovery dynamics would enable more robust, cross-site comparisons of this complex ecosystem response.

Looking forward, there are opportunities to extend our current understanding of stream metabolism and its response to flow. We are just beginning to characterize metabolic regimes (e.g., Bernhardt et al. 2017; Savoy et al. 2019), and there are still many responses that are unexplained at base flow (e.g., declines in GPP and ER even with a constant, low flow (Uehlinger 2006)). Higher flows pose even more of a challenge. The often short timeframes

between high flow events make isolating and quantifying their functional response very difficult. As records of metabolic data sets increase and modeling tools improve, however, we may be able to find enough isolated events to discern patterns, even potentially assessing impacts of multiple, sequential high flow disturbances that did not meet our criteria for isolation.

Land use, geomorphology, and disturbance regime may affect site differences in metabolic resistance and resilience (Figure 9; Supplemental Table 1; Uehlinger 2000, Blaszcak et al. 2018). Limiting constituents have the potential to drive resilience, as high inputs of otherwise limiting nutrients from agricultural fields or DOC from wetland rich areas may help induce faster metabolic recovery (Uehlinger 2006). Sites that have more extensive hyporheic zones, and thus more refugia for heterotrophs, may be more resistant to flow disturbances, although this merits further research (Uehlinger 2000). Additionally, reaches that have access to their floodplains may display less response from GPP and ER, as floodplains may mitigate the role that extreme flow events play in regulating metabolism (Roley et al. 2014). As sensors become cheaper and modeling software increasingly accessible, more long term, high frequency datasets of metabolism estimates will be generated. Such data offers new opportunities to understand both within- and across-site controls on metabolic resistance and resilience. Consequently, although characterizing metabolic flow regimes may become easier, understanding metabolic response to flow disturbances still poses a unique challenge.

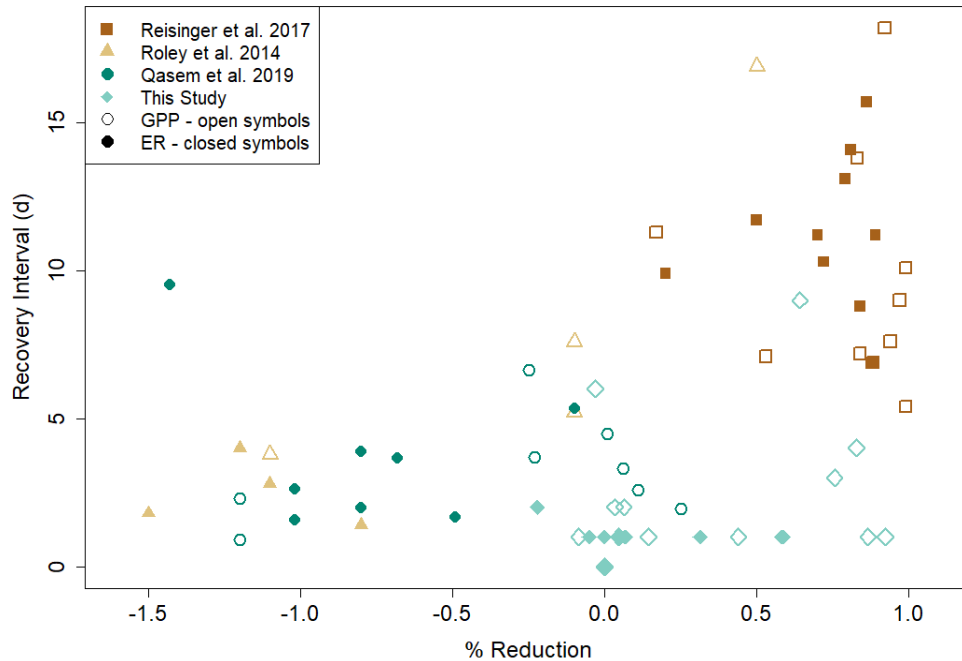


Figure 9. Published metabolic recovery intervals (days) and % metabolic reduction of gross primary production (GPP) and ecosystem respiration (ER) in response to flow disturbances. Open symbols represent GPP response, and closed symbols signify ER response. A negative % reduction is a stimulation. Included in Supplemental Table 1 are additional studies that have reported either recovery intervals, or % metabolic reduction in response to flow disturbances, but not both, and consequently could not be graphed here.

4.4 Conclusion

Metabolic regimes are punctuated by high flow events that create frequent pulses of stimulated or repressed GPP or ER (e.g., Uehlinger 2006, Beaulieu et al. 2013; Bernhardt et al. 2018). As such, flow events play an influential role in driving daily trends and variability in metabolism. Differences between ER and GPP response and recovery may be a result of increased resistance and resiliency of ER relative to GPP. Within this study, our prediction that ER would be more resistant than GPP to flow disturbances was supported, as ER frequently did

not even deviate from the antecedent equilibrium (Table 3; Figure 6). However, ER had less resistance to events of greater magnitude: M_{ER} had a negative, strong relationship with the % discharge change of the flow event, whereas M_{GPP} did not, suggesting that GPP responded similarly to changes in flow regardless of flow magnitude (Figure 8). Metabolic response to small and intermediate flow disturbances was variable, and resulted in both stimulations and reductions in GPP and ER. Therefore, there may be a resistance threshold to flow disturbances, where below this threshold other controls (light, season, or turbidity) might drive metabolic response. Quantifying a resistance threshold of processes to flow disturbances, such as using segmented process-discharge relationships (O'Donnell & Hotchkiss, in review), would enable a more extensive understanding of metabolic response to flow disturbances. Ultimately, we are entering an era of metabolic data opportunity. The increasing prevalence of metabolism datasets will enable: further regime characterization (Savoy et al. 2019), the adoption of metabolism as a bioindicator of health (Young et al. 2008), and the use of metabolism as a proxy for biotic change (Arroita et al. 2019). Correct interpretation of metabolic regimes requires an understanding of their relationship to frequent flow disturbances.

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Chapter Four: 'Ghost streams' sound supernatural, but their impact on your health is very real'

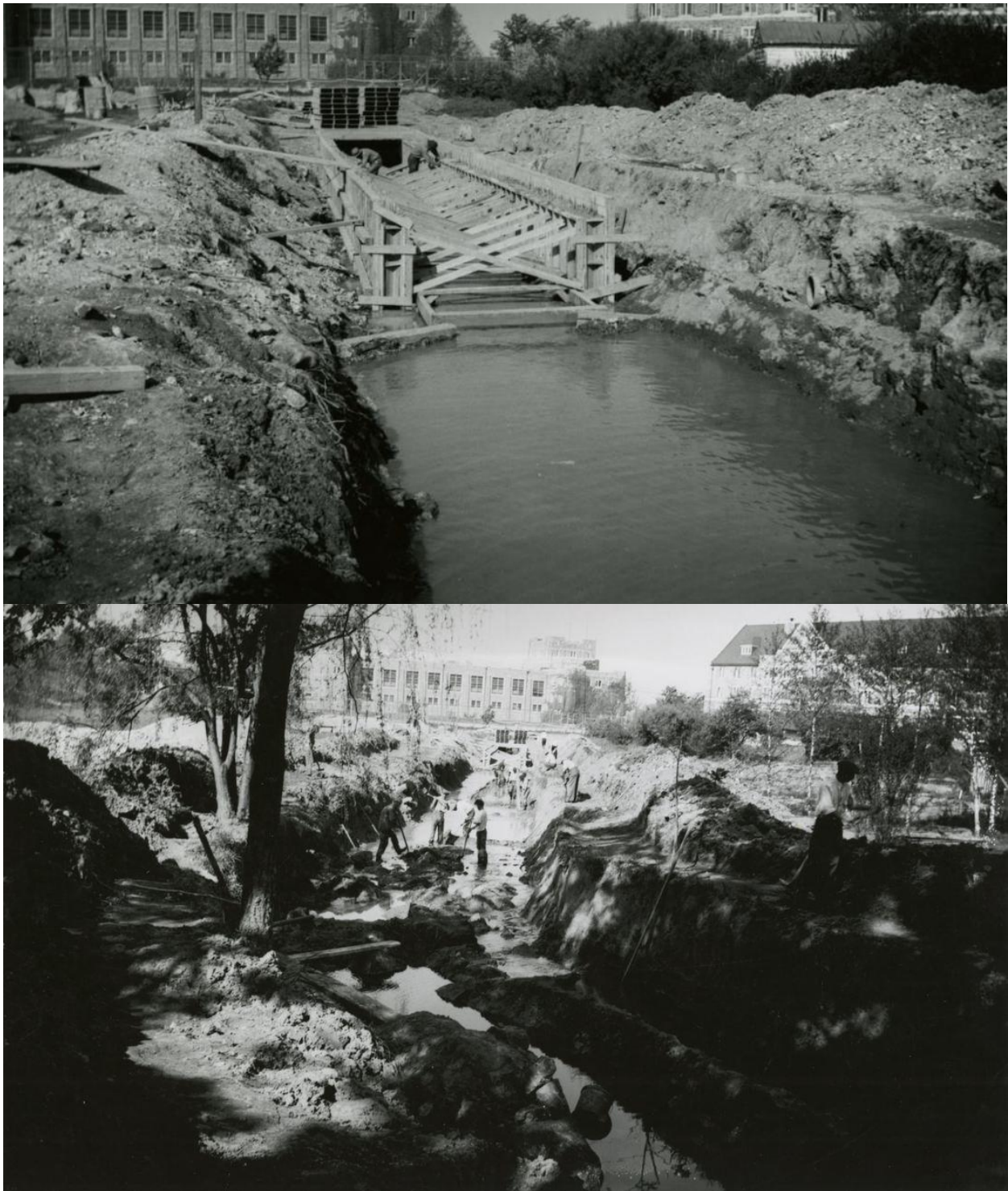
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Across the country, buried beneath the pavement you walk on, an invisible network of waterways flows through the darkness. These are ghost streams, and they're haunting us.

In their former lives, they wound through natural landscapes above ground; it's only through decades of development that humanity has relegated them beneath the earth's surface, enclosing the waterways in tombs of concrete and iron. The effects, decades later, plague us. Without a natural habitat to snake through, these streams carry downstream an excessive amount of pollutants (like salt and sediment) and nutrients (like nitrogen and phosphorus) because they can't shed these materials into their surrounding environment.

Here's how ghost streams happen: Civilizations grow near water sources, clustering around lakes, rivers, and springs that provide the resources required for drinking, bathing, and irrigating. As we industrialized drinking water infrastructure and outsourced water sources to larger, distant reservoirs and aquifers, most towns stopped using the smaller springs that originally drew them to a place. With that shift, many of the original freshwater sources go untapped. Without relying on them for drinking water or irrigation, they become nothing but nuisances to development. If you want to build on a piece of land, the stream that threads through it has got to go. But streams

are formidable obstacles; you can't just demolish them and move on. Water needs to flow, so when we construct on land traversed by a stream, we bury it.



Images of the burial of Stroubles Creek in the 1930's, underneath the Virginia Tech campus in Blacksburg, VA. Photos borrowed from VT-Facilities, scanned by VT-Digital Imaging and Archiving, and made available by C. Hession.

The move isn't a recently devised trick. The western world has been moving streams underground since the Roman Empire. Between then and now, our stream burial technology has not undergone any revolutions, aside from separating stormwater and raw sewage and using different pipe materials.

Most people are not aware of the historic streams that have been buried—except for the curious few who wonder, for instance, why the street in downtown New York City is named “Canal.” In fact, we've buried streams all across the nation—in Los Angeles, D.C, and more. The U.S.'s Environmental Protection Agency estimates that we've buried 98 percent of the streams that once crossed through Baltimore's urban core.

Although we've buried these streams, we haven't put them to rest. They are still flowing, and still take in all the things we shed, spill, drop, and leak into our landscape. As rain runs over paved streets and sidewalks, it sweeps everything from the urban world directly into the nearest waterbody. Urban runoff makes its way to these hidden streams.

Unpiped, healthy streams naturally filter much of the water that flows into them. Smaller streams are mediators of human effluent: receiving the waste discharged from point sources (like industrial pipes and wastewater treatment plants) and from nonpoint sources (like runoff from streets and agricultural activities) and using tools like microbes, algae, rocks, and soil to slowly unload and transform excess nutrients and pollutants. Unwittingly tasked with filtering chemicals and solutes, natural streams are very important to human health. And when we bury streams, we rob ourselves of our natural purifiers.

Streams typically teem with life: algae, fish, and invertebrates. A stream is home to microbes that require light, nutrients, and a natural stream bottom. These microorganisms are the power players that remove those excessive nutrients. But most ghost streams don't host much life at all. When we bury a stream underground, we cut it off from light and the stream bottom. Only nutrients remain, which are funneled downstream, mixing city runoff with fresh water in the nearest river.

"Nutrients" sound good, but they can wreak havoc in downstream waterbodies, polluting waterways, feeding thick blooms of toxic cyanobacteria, and creating coastal dead zones

Luckily, towns are beginning to acknowledge the importance of these buried streams in an effort to reduce the terrors of urban runoff. Simply letting locals know a stream exists beneath them, and that the stream receives everything, untreated, that goes down the drain, encourages people to keep their waste out of the secret streams.

For example, small frog statues adorn city drains in Blacksburg, Virginia, marking the drains directly above the local ghost stream. It's a callback to the Ancient Romans, who marked their buried streams with shrines to "Cloaca Maxima" or the sewer goddess. Baltimore stencils its storm drains, and Richmond, Virginia and Dayton, Ohio want to do the same using the work of local artists. Entry points to waterways are embellished with paintings of fish, octopuses, and otters encircled by cautionary reminders like "all water drains to the sea" and "only rain should go down the drain." Other storm drain murals are decorated with landscape paintings of scenic

wildlife, images of kelp with plastic and litter for companions, or paintings of fish where grated drains act as mouths.

Some places are going further, ripping up pavement, shattering pipes, and hammering away the concrete to exhume ghost streams. Daylighting, as the procedure is called, opens the streams up to the sun and restores the adjacent land connection. This begins the process of healing, re-growing vegetation, and encouraging microbes and algae to come back. It's great, but unburying a stream is expensive and requires strong community backing, and community support for daylighting a stream can't be mustered if residents aren't aware of the buried stream itself. Art is a great first step.

By recognizing ghost streams and getting locals engaged, we can work toward healing the waterways by limiting the pollutants poured into them, and even eventually unearthing them from the ground.

Chapter Five: General Discussion: Integrating disturbance into our current understanding of metabolism and stream health

What does a healthy stream look like? Regardless of whether you're a water quality practitioner, resource manager, or an ecologist, visions of a healthy stream likely converge on similar characteristics – geomorphic heterogeneity with a mix of riffles and pools; riparian connection with thriving plants; access to a moderate amount of sunlight, filtered through a canopy; relatively clear water with a mix of species swimming about. Historically, stream health has been monitored and characterized via such structural metrics (Palmer and Febria 2012). However, as advances in technology (e.g., dissolved oxygen sensors) have made quantifying functional metrics easier, there has been a shift away from considering what a healthy stream might *look* like, to deliberating what a healthy stream *does*. Does it remove more nutrients? Have a more stable streambed? Support more productive fisheries? Notably, there has been less consideration of things like point measurements of oxygen concentration, and more emphasis placed on biologic oxygen demand and production in the form of stream metabolism (Palmer and Febria 2012).

Stream metabolism is increasingly being applied as a metric used to quantify stream health (Young et al. 2008), the response of a stream to a disturbance (e.g., Reisinger et al. 2017; Chapter 2), and stream recovery following restoration (e.g., Arroita et al. 2019). Some of the benefits of using metabolism as a bioindicator are well outlined by Young et al. (2008): (1) metabolism represents the carbon transformations of a whole reach; (2) the ratio of productivity to respiration can illuminate the balance between energy supply and demand; (3) short time-scales are needed to estimate metabolism; and (4) metabolism is intimately connected to the more long-standing health metric of oxygen concentration. Additionally, stream metabolism

influences other ecosystem processes; namely, metabolism is related to nutrient uptake (Hall and Tank 2003), which is critical to the ecosystem service of nitrogen removal (Pataki et al. 2011), as well as consumer secondary production (Marcarelli et al. 2011).

One notable consideration of applying metabolism as a bioindicator missing from past discussions is that daily metabolism responds rapidly to disturbances. This is beneficial if trying to ascertain instantaneous ecosystem response; however, the rapid response of metabolism to disturbance means that metabolism, and the ecosystem services it is intimately connected to, can be considerably impacted by flow events – one of the most frequent stream disturbances. With this in mind, here I discuss: (1) the need to differentiate between stream health and stream function; (2) the importance of quantifying resistance and resilience of stream metabolism to frequent flow disturbances; and (3) my recommendations for the future applications of stream metabolism as a metric of health.

Many ecologists have adopted the mindset, either explicitly or implicitly, that the health of a stream is related to its likeness to a less altered, reference stream (Boulton 1999, Palmer and Febria 2012), and this mentality has spilled over into metabolism. One of the most highly cited papers promoting metabolism as a metric of stream health splits its study sites into two groups for health characterizations: reference and impacted (Young et al. 2008). Reference sites, and thus sites with assumed better health, have lower GPP and ER (Young et al. 2008). Although Young et al. (2008) acknowledge that low metabolism equating to better health is not a universal rule, this notion can create conflicting ideas of stream health between ecologists and water quality practitioners by creating a divergence between health and potential function.

Ecological understanding of the relationship between metabolism and health is impaired by the idea that low GPP and ER represent a healthier system, as this separates the idea of health

and function. The function of a stream, and the ability to remove nutrients and also metabolize to provide the basis of energy for food webs, is often greater in impaired, classically ‘unhealthy’ systems. Forested reference streams are characterized by typically lower rates of GPP and ER. Therefore, high rates of GPP and ER typically reflect poor stream health; however, streams with high metabolic rates can have much higher function, and are indicative of either certain types of catchments (e.g., open canopy grasslands) or of impairment to the catchment, such as the excessive loading of nutrients from agricultural fields. Additionally, rates of GPP and ER that are low enough to be categorized as from ‘healthy’ systems according to Young et al.’s criteria have been recorded in ecosystems ranging from 73-90% developed (Reisinger et al. 2017); we know these ecosystems are not ‘healthy’ in that they have been severely altered, and yet they are considered healthy according to this criteria. When assessing the health of the stream, we should also consider the potential for higher rates of functional metrics.

Low rates of metabolism and likeness to reference streams should not drive our assessments of metabolism in regard to stream health; instead, we should adopt an understanding of the relationship between metabolism and stream health that incorporates its potential for function, and more closely aligns with other functional metrics of stream health, which include, but are not limited to, pollutant removal rates and nutrient cycling rates (Palmer & Febria 2012). When ecologists talk about the hidden dangers of excessive nutrient loading and alterations to stream morphology, we typically warn about the potential for excessive downstream export - causing the downstream accumulation of biomass, depletion of oxygen, and consequential harm to biota. Streams with greater function and higher rates of metabolism control nutrient uptake and retention (Hall and Tank 2003), ultimately alleviating downstream export (Bernhardt et al. 2003). Less function and consequently lower rates of metabolism in a stream loaded with high

levels of nutrients would mean that more nutrients are exported downstream. If we adopt a more ecosystem-service centric metric of metabolism for understanding health, as we should to ensure that metrics of ecosystem health align between ecologists and water quality practitioners, then lower rates of metabolism in impaired streams should be considered to be less beneficial for ecosystem health, as they have less potential for in-stream nutrient removal. However, deeming higher rates of metabolism and greater function as healthier should be considered in the context of the ability for nutrient removal, and should be used carefully, as high GPP and ER in some conditions can result in a build-up of unconsumed primary producers, leading to algal blooms and/or hypoxia. We do not suggest that the inverse of Young's criteria is the better route (high rates of metabolism are healthy and low are unhealthy); rather, we caution against using metabolic rates as metrics of health overall, without also incorporating a consideration for how this reflects the functional capacity of the stream.

Elevated flows have disproportionate impacts on stream metabolism and the export of nutrients (Raymond and Saiers 2010, Inamdar et al. 2015, Bernhardt et al. 2018). Consequently, we should account for how the transformative potential of metabolism is altered from flow disturbances through incorporating an understanding of metabolic resistance and resilience across sites. Resistance is the capacity of a stream process to withstand a disturbance. If resistance to elevated flows are higher, the large influx of nutrients from the catchment at higher flows may be mediated to some extent. However, if the resistance is low – as is often seen in urban, impaired streams with channelized and altered geomorphology – the ability to potentially offset that nutrient influx is severely hindered. Resilience is the speed at which a process returns to equilibrium (Carpenter et al. 1992). Metabolic resilience represents how quickly equilibrium rates of metabolism are resumed following a disturbance. If resilience is low and metabolic

recovery is prolonged, the full capacity for metabolism to enhance nutrient uptake is not achieved, and an opportunity for lessening nutrient export is missed. Understanding the extent and duration of metabolic impairment following elevated flows – the most frequent stream disturbance – is critical to our understanding of the utility of metabolism as a component of stream health in regard to mitigating excessive nutrient loading. Stream health should encompass multiple functional metrics; if metabolism is to be used and considered in the context of its ability to mitigate excessive loading from the catchment, then increased resistance and resilience of GPP and ER are important, and may even play a disproportionate role in lessening nutrient export over baseflow rates of metabolism.

To begin incorporating the concepts of resistance and resilience into our understanding of metabolism and stream health, we must first find the best ways to quantify them. Most studies examine event-scale metabolic responses to flow disturbances, where resistance is calculated via a percent reduction relative to an antecedent average, and resilience is defined as the rate of recovery to that antecedent average (e.g., Reisinger et al. 2017; Uehlinger 2000). These studies typically examine only a handful of flow disturbances at one site, focusing on characterizing resistance and resilience drivers spatially. Within Chapter 3 of this thesis, I addressed temporal, within-site variability of GPP and ER resistance and resilience, examining their responses across 15 different flow disturbances. I found that the low resistance/high resilience trends typically found for urban stream metabolism (Reisinger et al. 2017) were supported within this research, and both GPP and ER typically recovered within a few days. I also tested which antecedent conditions or disturbance characteristics drive recovery dynamics of GPP and ER, and found that the size of the flow disturbance only strongly mattered to ER, and GPP responded similarly regardless of magnitude.

It is possible to quantify metabolic resistance to flow disturbances without looking at event-scale response. Resistance of processes can be quantified via statistically-derived changes of slope across discharge in P-Q (process-discharge) relationships, as demonstrated in Chapter 2. When segmenting P-Q relationships within the second chapter, metabolism did exhibit changes across low and high discharges. ER and NEP had significant changes across flow, whereas the slope change for GPP was not significant. The slope change for ER and delayed slope change for GPP illuminates the potential for divergent responses of ER and GPP at higher flows, and the potential for different levels of process resistance to flow changes. Additionally, there are other methods for quantifying metabolic resistance and resilience that were not addressed in this thesis. Namely, kernel density plots of metabolism that represent the metabolic fingerprint of a site can be used to examine metabolic resistance or resilience (Bernhardt et al. 2018). The expansion or contraction of the metabolic fingerprint would enable us to move away from looking at singular point estimates of metabolism with confounding environmental controls, such as land use or nutrient concentration, towards instead evaluating the metabolic regime response to a change (Hall 2016).

In sum, evaluating the impacts disturbances have on stream ecosystem health requires a clear, contextual definition of health. Low metabolism may be more consistent across forested reference streams, but lower metabolism in anthropogenically altered systems indicate less potential for nutrient removal, and consequently more downstream export of excessive nutrients and pollutants. We should move away from suggesting low rates of metabolism are ‘healthy’. Additionally, incorporating measurements of resistance and resilience via the novel frameworks outlined in this thesis would make the understanding of the relationship between stream metabolism and health more complete. In the face of increasing anthropogenic changes, the

effective restoration and conservation of our streams relies on our comprehensive understanding of the changes that occur to streams following disturbances, and how that may relate to overall ecosystem health.

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Appendix

Supplement Chapter 1

Supporting Information for: Biogeochemical Consequences of Stream Flow Changes: Coupling Concentration- and Metabolism-Discharge Relationships

Contents of this file

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Additional Supporting Information (Files available upon request)

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Introduction

Supplementary materials below cover the following: text and figures to support our data quality checks, figure of seasonal process discharge (P-Q) variation, concentration- and process-discharge graphs and table from segmentation at median flow, additional K_{600} figures, results showing robustness of segmentation method, and statistical results for chemostatic trends.

Additional supporting information, contained within the uploaded files, includes our dataset used for C-Q and P-Q analyses, code for specs for metabolism, and code for the C-Q and P-Q analysis.

Text S1.

To ensure we were not capturing sensor error, we first removed the values we knew to be unreasonable. Dissolved oxygen was constrained to within 4 and 20 mg/L. pH was limited to above 5 and below 14. Turbidity was cut off at zero. Conductivity values below 0.1 ms/cm were removed, as these values likely converged on sensor error (Figure S4). Additionally, we removed below the 1% and above the 99% quantile for parameters that were heavily skewed (turbidity and conductivity) to be conservative in our analyses and ensure these extremes were not a function of sensor error (Figure S3 & S4).

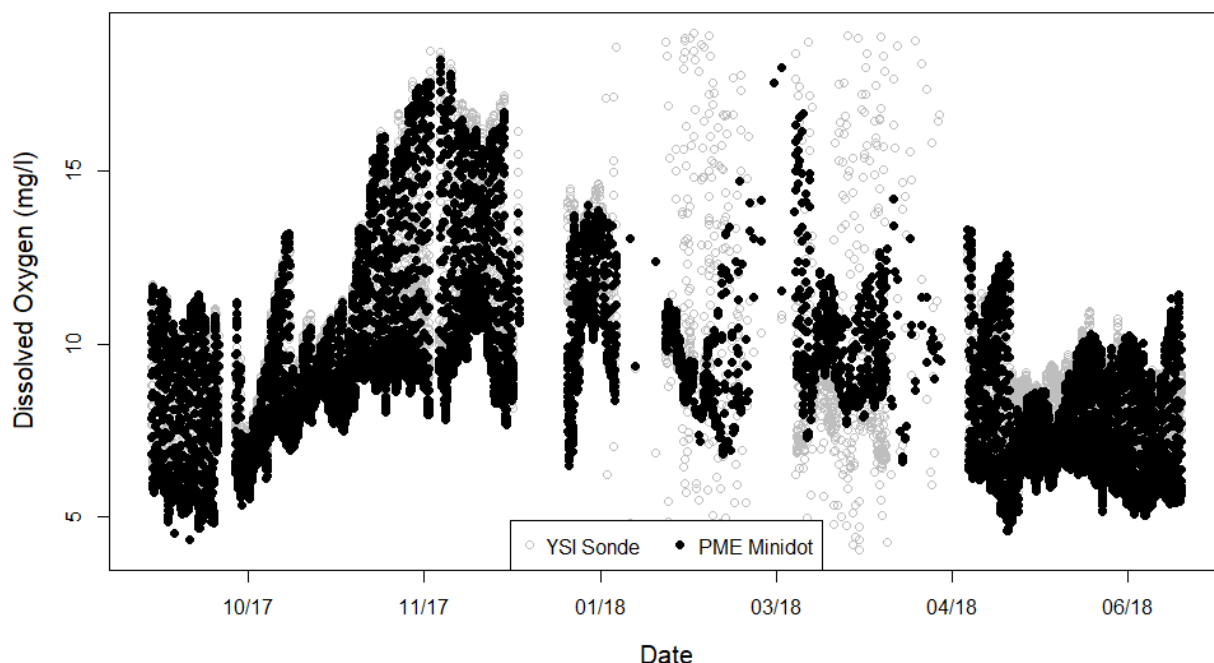


Figure S1. Dissolved oxygen measurements from two sensors at our study site. The spread of YSI Sonde values spanning from the end of January to mid-April is likely a result of a freeze event impacting the sensor.

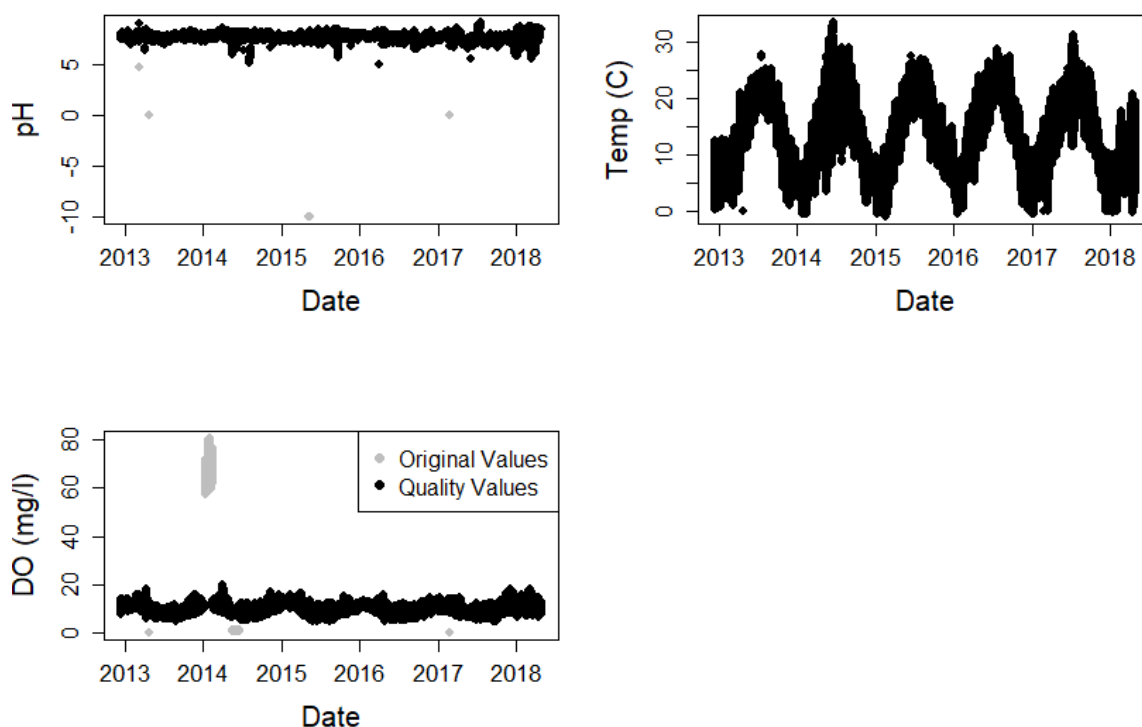


Figure S2. Plots of pre- and post-quality checked pH, temperature (Temp), and dissolved oxygen (DO) sensor data recorded at 15-minute intervals. Grey points are all original values. Black points are the ones used for our analyses.

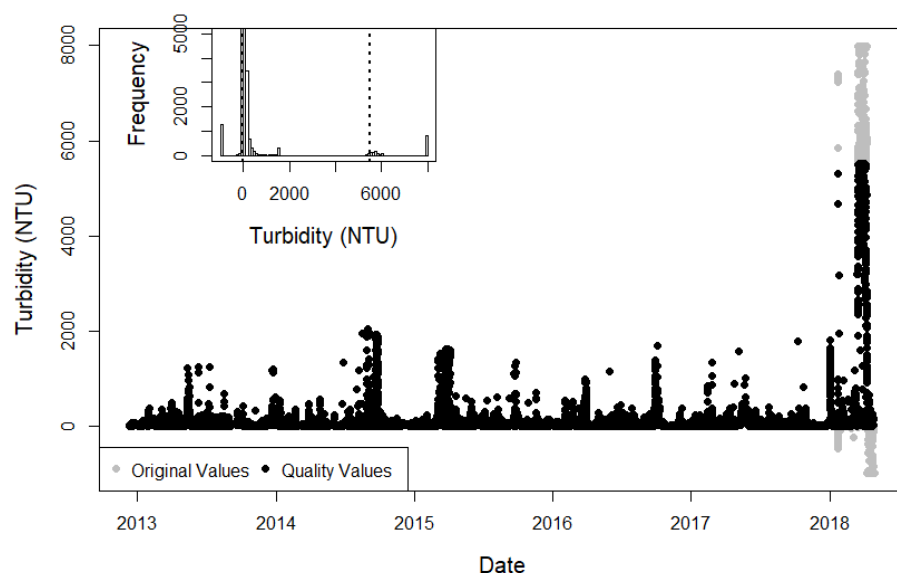


Figure S3. Plots of pre- and post-quality checked turbidity. To be conservative in our analyses, we eliminated impossible values and cut at the 1 and 99% quantile, which are shown by dashed lines in the histogram inset.

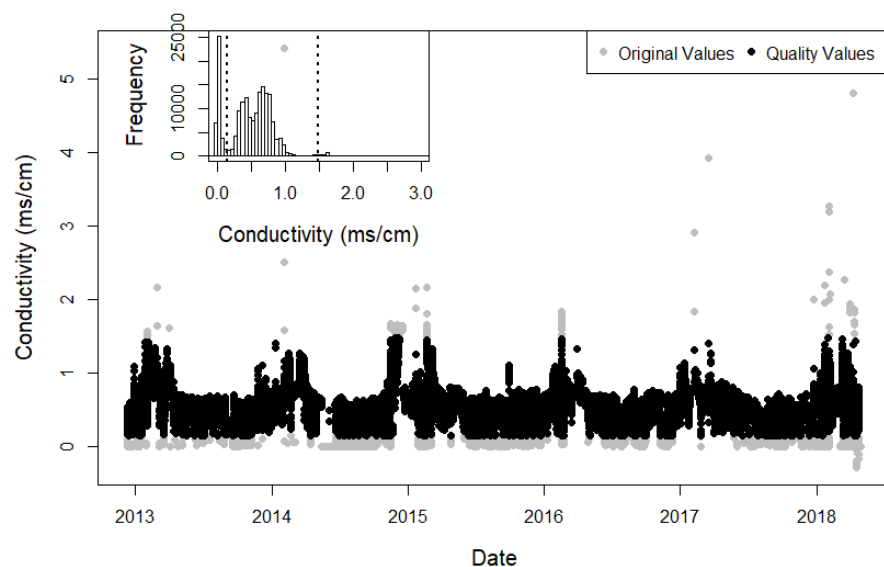


Figure S4. Plots of pre- and post-quality checked conductivity. To be conservative in our analyses, we eliminated impossible values and cut at the 1 and 99% quantile, which are shown by dashed lines in the histogram inset.

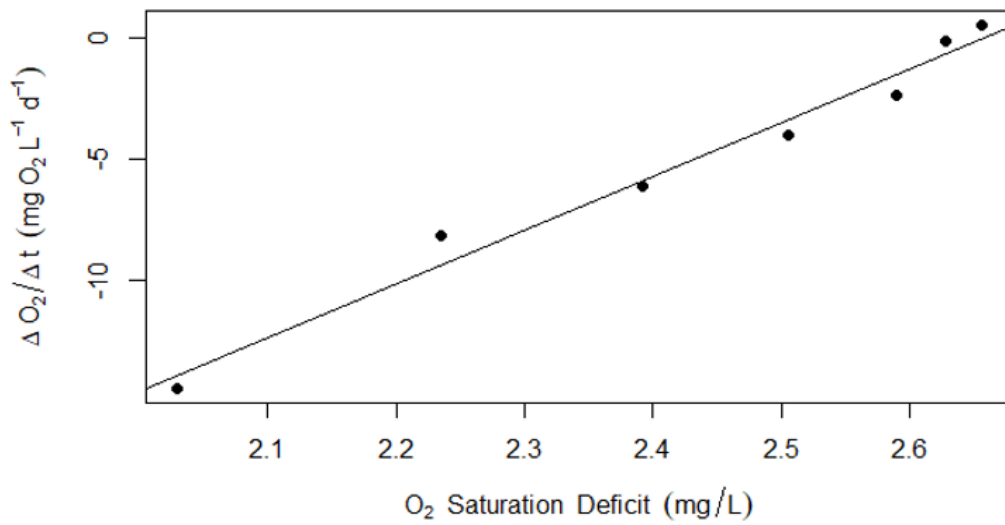


Figure S5. Example of data used for the nighttime regression method for calculating K_{600} (d^{-1}) to confirm modeled K . The value for K_{600} for 9/4/2017 is 22.10 d^{-1} . The nighttime regression method takes into consideration the influence of daytime photosynthesis shifting the concentration of O_2 in the stream out of equilibrium with the air-water gas exchange (Hall & Hotchkiss, 2017).

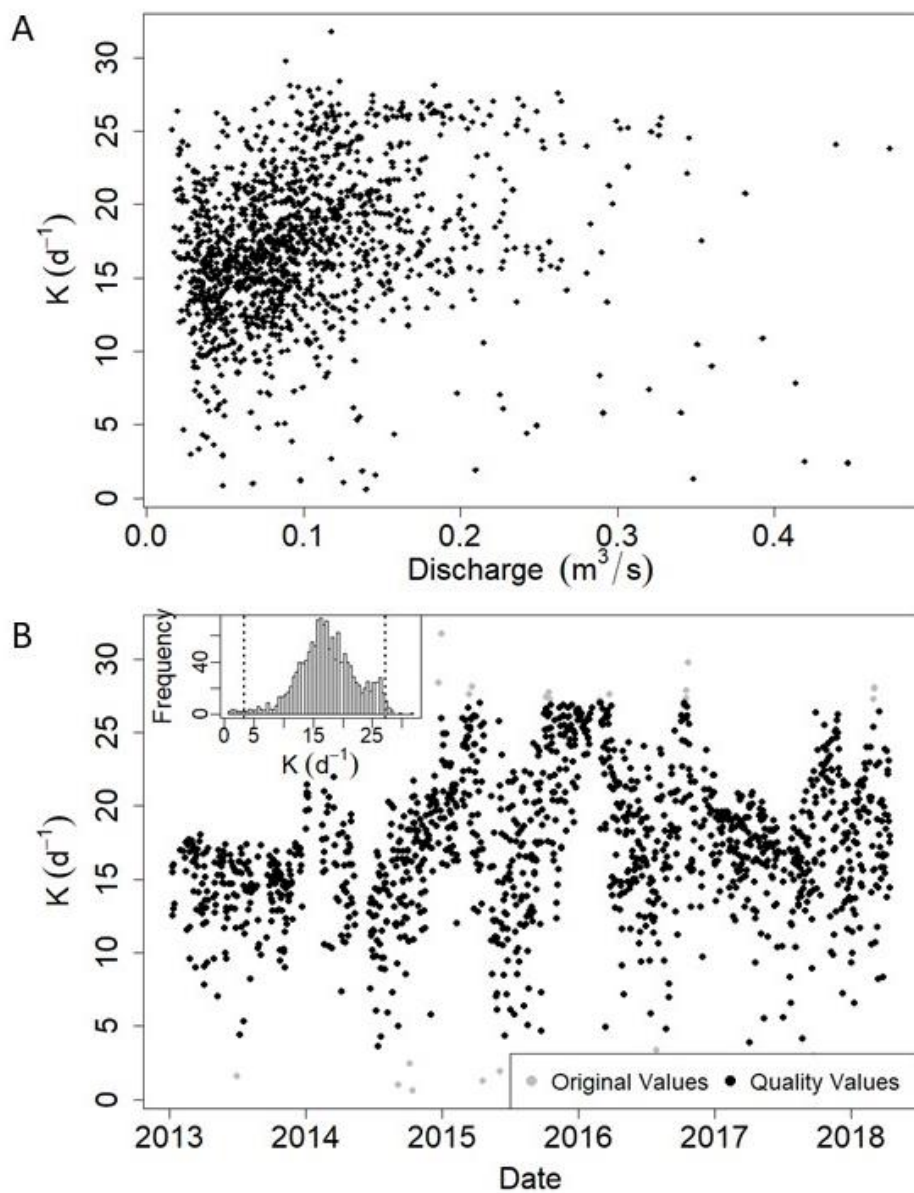


Figure S6. (A) $Q \sim K$ (discharge $\sim$ gas exchange) output from *streamMetabolizer* shown in panel A. (B) Time series and histogram (inset) of modeled K_{600} (d^{-1}) values for 2013 - 2018 at our study site.

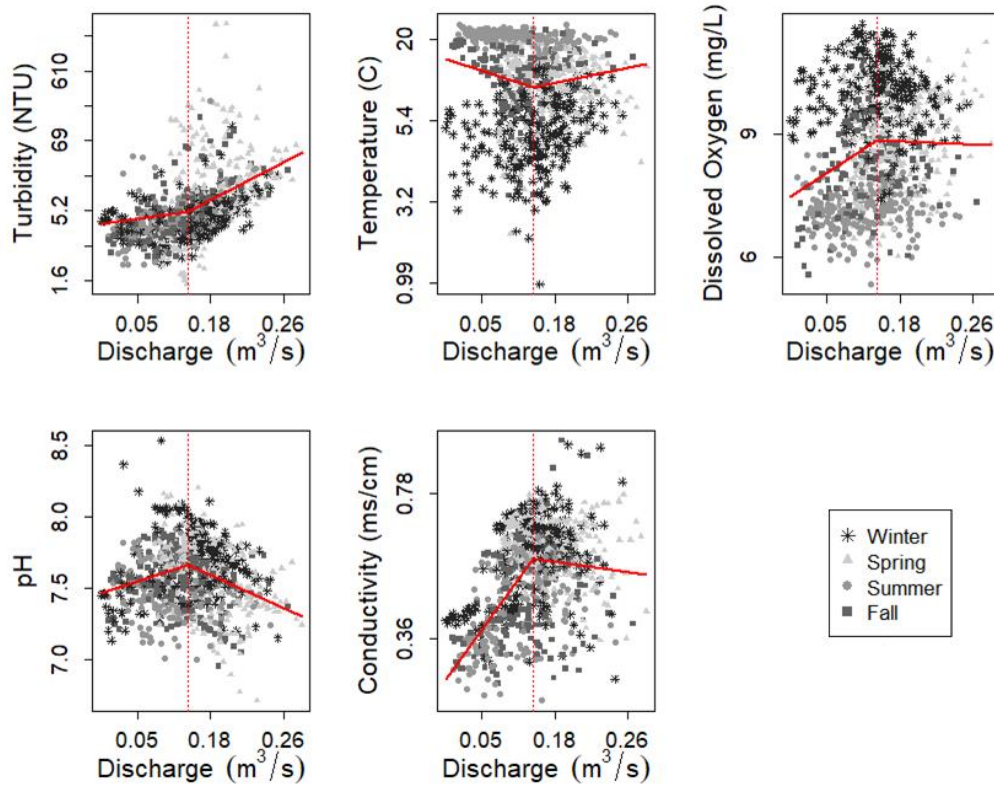


Figure S7. Concentration-discharge graphs of physicochemical parameters, natural logged and segmented at median flow instead of using a statistically-derived breakpoint (as presented in main text). The same general trends existed between segmenting at the median and from segmenting via a statistically-derived breakpoint.

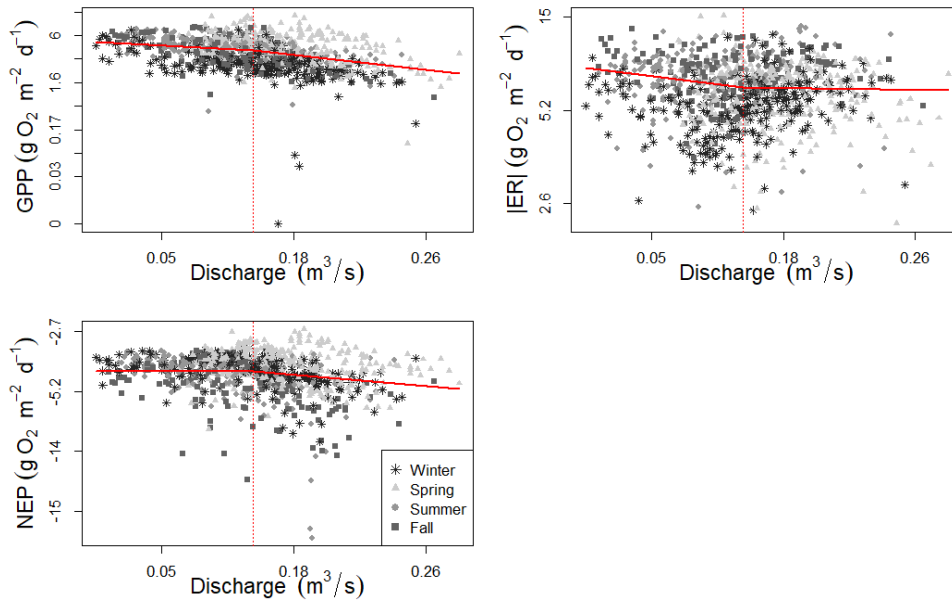


Figure S8. Metabolism-discharge graphs of gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) natural-logged and segmented at median flow instead of using a statistically-derived breakpoint (as presented in main text).

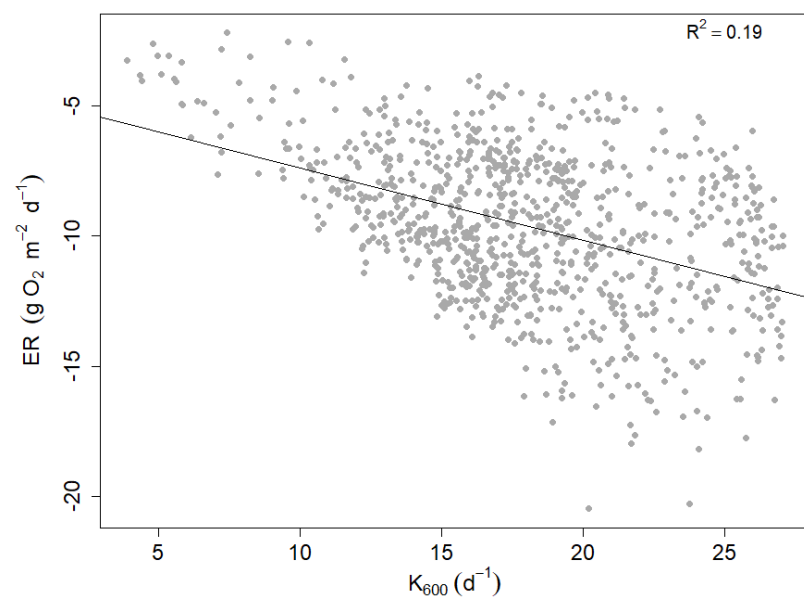


Figure S9. Modeled air-water gas exchange (K_{600} , d^{-1}) versus modeled ecosystem respiration (ER) for all days used in concentration-discharge and process-discharge analysis at Stroubles Creek.

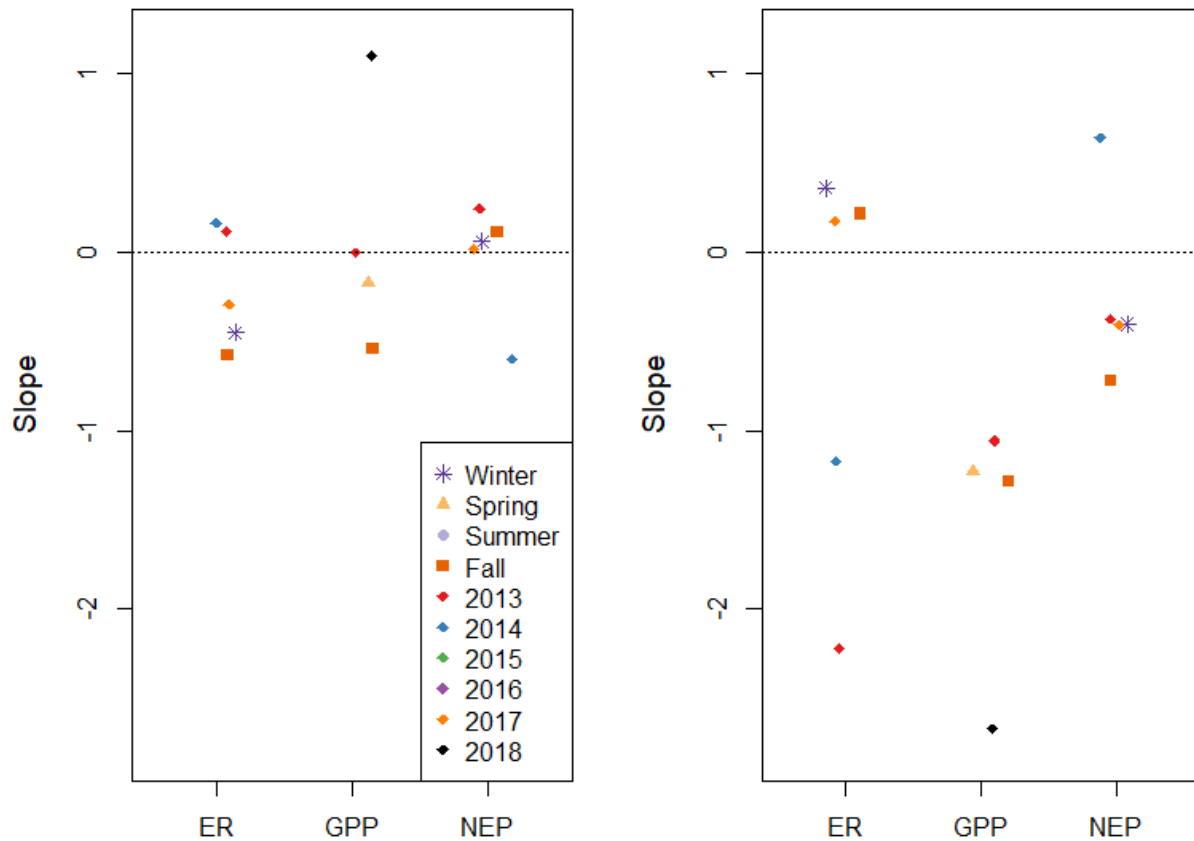


Figure S10. Seasonal and yearly slopes for below (left) and above (right) the breakpoint for the three process-discharge (P-Q) graphs: gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP). Only the scenarios where the Davies test found a significant slope break are shown. P-Q relationships exhibited inconsistent slope trends above and below the breakpoint according to year or season of data collection. Below the breakpoint, GPP response to flow was variable for scenarios where the Davies p-value was significant, exhibiting both positive and negative trends. Above the breakpoint, GPP was consistently negative for all significant scenarios. ER was variable both above and below the breakpoint. NEP increased below the breakpoint and declined above it for all significant scenarios except for 2014.

Parameter (units)	Breakpoint estimate with 25% Q quantile as starting value (standard error)	Breakpoint estimate with 50% Q quantile as starting value (standard error)	Breakpoint estimate with 75% Q quantile as starting value (standard error)
Ecosystem respiration (g O ₂ m ⁻²)	-2.67 (0.14)	-2.67 (0.14)	-2.67 (0.14)
Gross primary production (g O ₂ m ⁻²)	-1.47 (0.17)	-1.47 (0.17)	-1.47 (0.16)
Net ecosystem production (g O ₂ m ⁻²)	-2.47 (0.17)	-2.47 (0.16)	-2.47 (0.16)
Temperature (°C)	-2.22 (0.12)	-2.22 (0.12)	-2.22 (0.12)
pH	-2.30 (0.06)	-2.30 (0.07)	-2.30 (0.06)
Dissolved oxygen (mg/L)	-2.30 (0.12)	-2.30 (0.12)	-2.30 (0.12)
Conductivity (ms/cm)	-2.47 (0.04)	-2.47 (0.04)	-2.47 (0.04)
Turbidity (NTU)	-2.65 (0.09)	-2.65 (0.09)	-2.65 (0.09)

Table S1. Statistically-derived breakpoints with different input values. This table illustrates the robustness of the *segmented* package in finding the same breakpoint for our data set, regardless of initial inputs for breakpoint required to start the iterative search for a breakpoint. Each parameter was tested by inputting a starting value at the 25% discharge quantile (a natural-logged discharge of -2.617 m³/s), 50% discharge quantile (-2.307), and the 75% discharge quantile (-1.997). The breakpoint output stayed the same for each parameter across all three inputs, with slight variations in standard error.

Parameter (units)	Below median β	Below median β standard error	Above median β	Above median β standard error	P-value of β difference
Temperature (°C)	-0.29	0.09	0.19	0.07	0.0001
pH	0.16	0.03	-0.23	0.03	<0.0001
Dissolved Oxygen (mg/L)	0.15	0.03	-0.01	0.03	0.0001
Conductivity (ms/cm)	0.70	0.04	-0.07	0.04	<0.0001
Turbidity (NTU)	0.29	0.10	1.10	0.12	<0.0001
Gross primary production (g O ₂ m ⁻²)	-0.30	0.08	-0.64	0.11	0.013
Ecosystem respiration (g O ₂ m ⁻²)	-0.18	0.05	-0.02	0.05	0.036
Net ecosystem production (g O ₂ m ⁻²)	0.00	0.04	-0.20	0.06	0.007

Table S2. Summary of statistics and slopes (β) for each parameter when segmented at median flow, instead of using a statistically-derived breakpoint (as presented in main text).

Parameter (units)	ANOVA independence p-value of β below breakpoint	ANOVA independence p-value of β above breakpoint
Ecosystem respiration (g O ₂ m ⁻²)	0.01	<i>0.32</i>
Gross primary production (g O ₂ m ⁻²)	<0.0001	0.03
Net ecosystem production (g O ₂ m ⁻²)	<i>0.56</i>	<0.0001
Temperature (°C)	0.0001	0.03
pH	<0.0001	<0.0001
Dissolved Oxygen (mg/L)	<0.0001	<i>0.81</i>
Conductivity (ms/cm)	<0.0001	<i>0.377</i>
Turbidity (NTU)	<i>0.94</i>	<0.0001

Table S3. Summary of test results for slope (β) chemostasis using ANOVA test of independence for statistically-derived segmentation. p-values from the analysis of variance (ANOVA) independence test included for slopes above and below breakpoints for each parameter. Insignificant p-values ($p > 0.05$) denote that β is not significantly different from zero and are italicized. Slopes that are not significantly different from zero are considered chemostatic.

Parameter	Season	p-value from Davies ^a	Estimated breakpoint (m ³ /s)	β below breakpoint	β above breakpoint	No. of points above breakpoint	No. of points above breakpoint
Temperature (°C)	Spring	0.53	-1.35	-0.01	-0.69	293	18
	Summer	0.06	-2.14	-0.07	0.11	157	48
	Fall	<0.001	-2.55	-0.92	1.33	62	118
	Winter	0.02	-2.21	0.76	-0.95	103	134
pH	Spring	<0.001	-2.53	0.33	-0.60	94	217
	Summer	<0.001	-2.89	-0.14	0.09	61	144
	Fall	<0.001	-2.53	0.76	-0.95	21	159
	Winter	<0.001	-2.41	0.24	-0.53	90	147
Dissolved oxygen (mg/L)	Spring	0.69	-1.37	0.05	0.24	292	19
	Summer	0.005	-2.91	-0.18	0.21	58	147
	Fall	<0.001	-2.56	0.43	-0.56	62	118
	Winter	<0.001	-2.54	0.13	-0.23	167	70
Conductivity (ms/cm)	Spring	0.001	-2.58	1.08	-1.21	38	273
	Summer	<0.001	-2.55	0.69	-0.73	102	103
	Fall	<0.001	-2.51	0.70	-0.75	74	106
	Winter	<0.001	-2.33	0.57	-0.63	135	102
Turbidity (NTU)	Spring	0.17	-1.80	1.70	-1.22	231	80
	Summer	0.04	-2.21	0.38	0.81	152	53
	Fall	0.24	-2.57	0.55	0.71	60	120
	Winter	<0.001	-2.59	-0.39	1.24	178	59

Table S4. Statistical results for seasonal slopes segmentation for the five concentration-discharge (C-Q) relationships: temperature, pH, dissolved oxygen, conductivity, and turbidity. ^asegmented output for the Davies p-value.

Supplement Chapter 2

Supporting Information for: Resistance and resilience of stream metabolism to isolated flow events of various magnitudes

Contents of this file

Figures S1, S2

Figure S3 – S17: Hydrographs and metabolism time series for each isolated flow event analyzed

Figures S18, S19

Table S1

Additional Supporting Information (Files available upon request)

Dataset S1

Metadata for Dataset S1

Supplemental Code S1

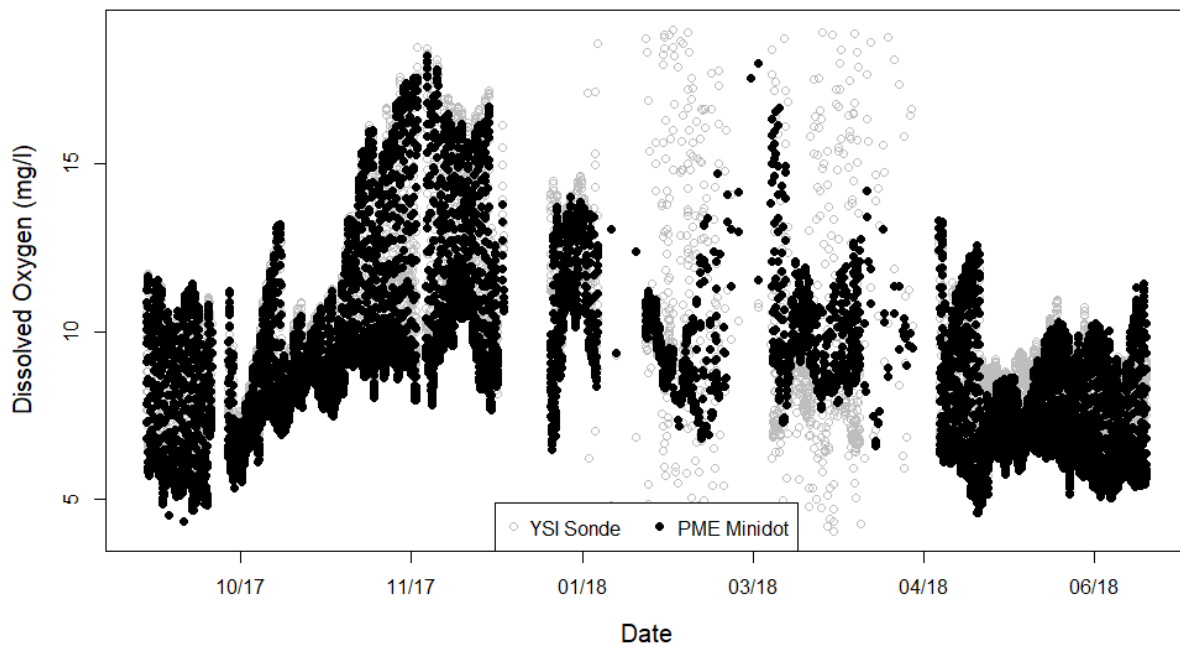


Figure S1. Dissolved oxygen measurements from the two sensors – YSI Sonde and PME Minidot - at our study site. The spread of YSI Sonde values spanning from the end of January to mid-April was likely a result of a freeze event that impacted the sensor.

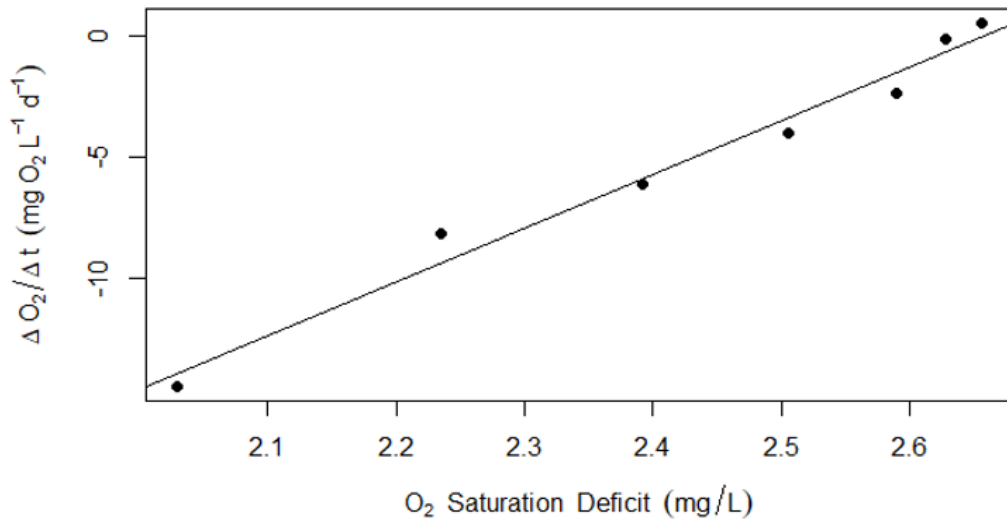


Figure S2. Example of data used to confirm modeled K_{600} (d^{-1}) using the nighttime regression. The nighttime regression method calculates K by taking into consideration the effect daytime photosynthesis has on shifting the concentration of O_2 in the stream out of equilibrium with the air-water gas exchange (Hall & Hotchkiss, 2017). For 9/4/2017, the value for K_{600} was $22.10 d^{-1}$.

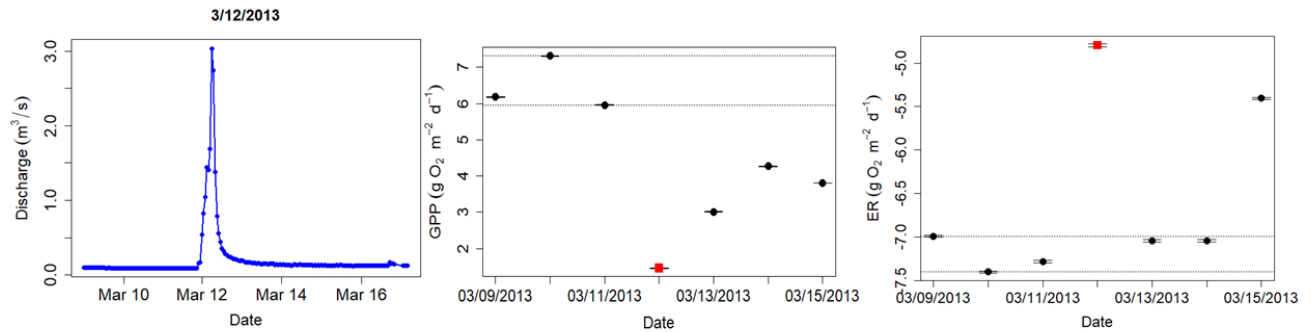


Figure S3. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2013-03-12.

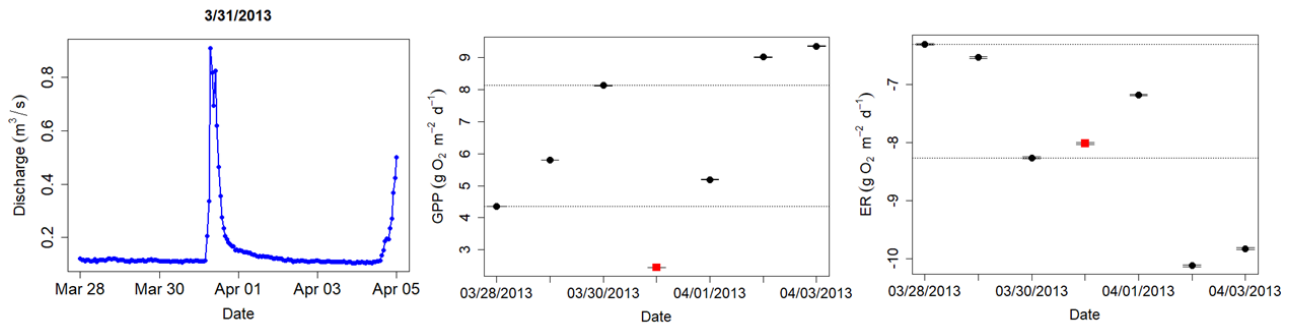


Figure S4. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2013-03-31.

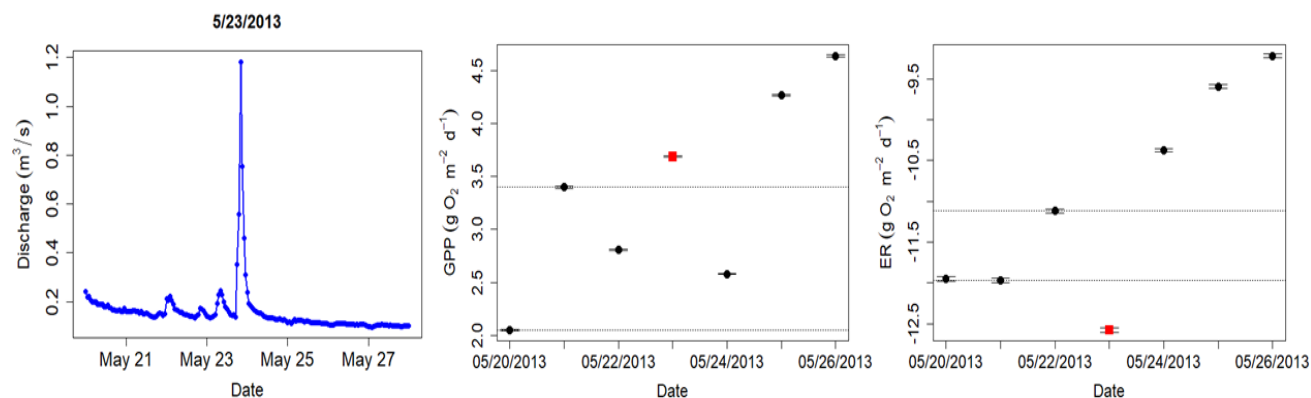


Figure S5. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2013-05-23.

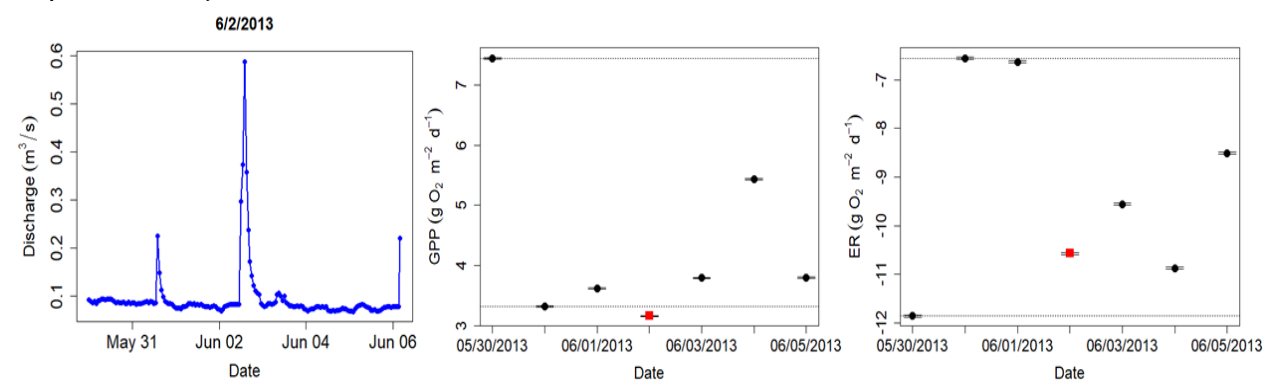


Figure S6. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2013-06-02.

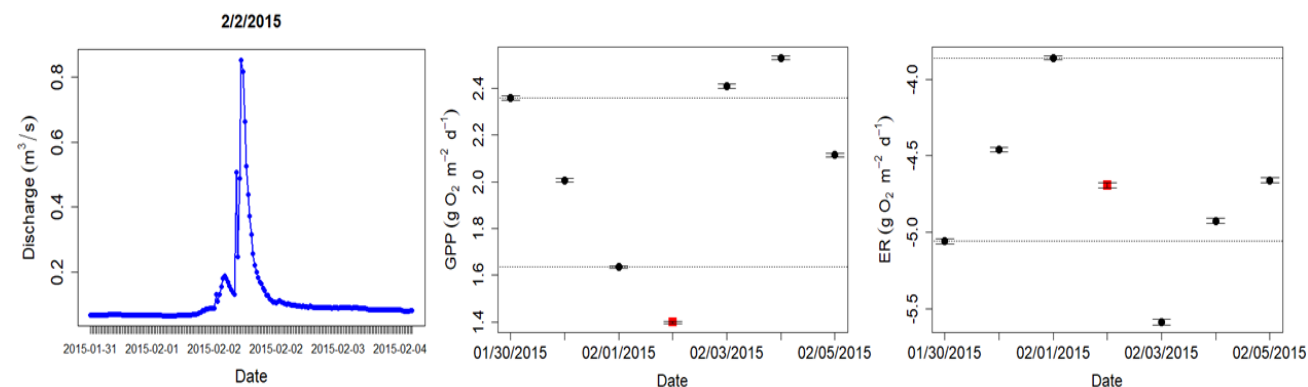


Figure S7. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2015-02-02.

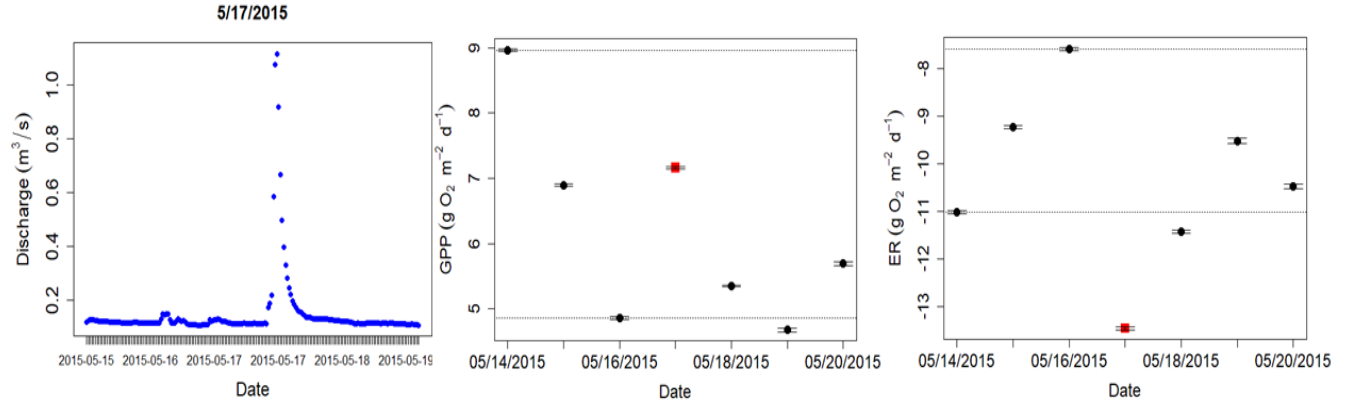


Figure S8. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2015-05-17.

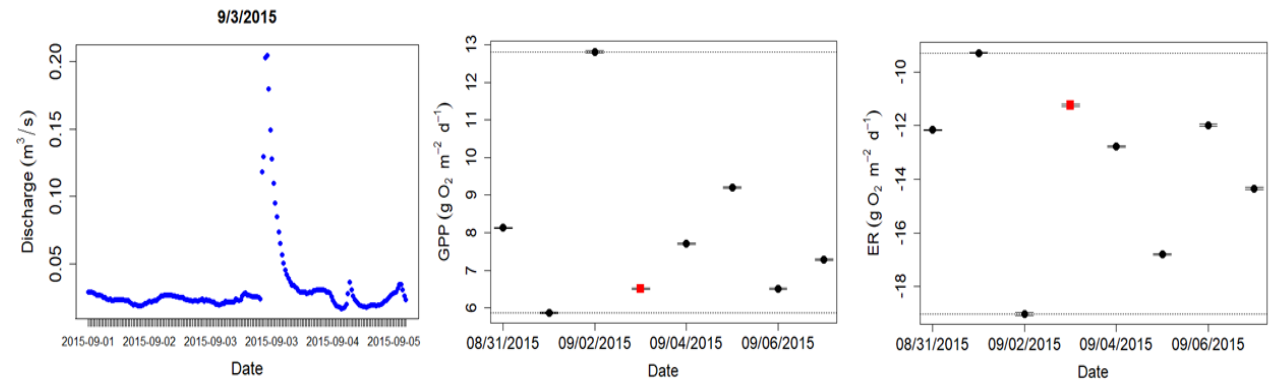


Figure S9. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2015-09-03.

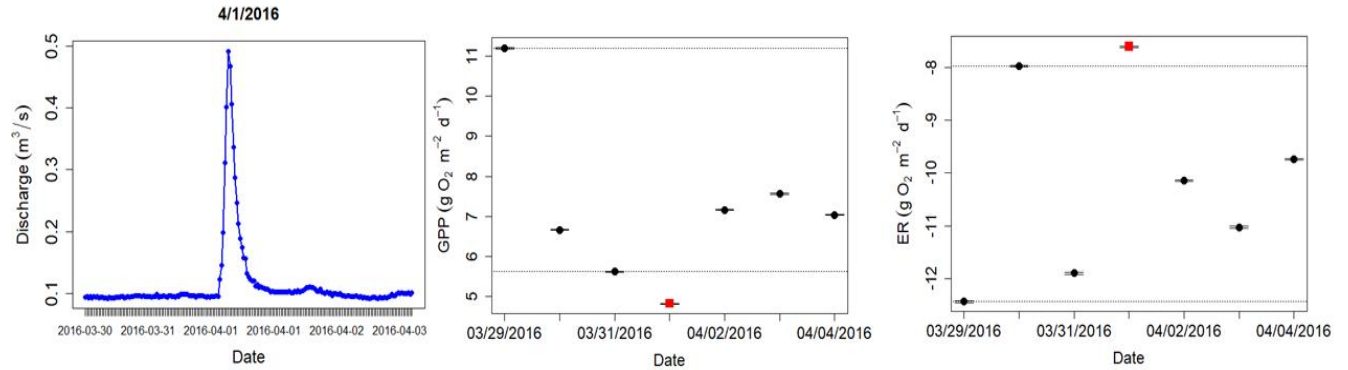


Figure S10. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2016-04-01.

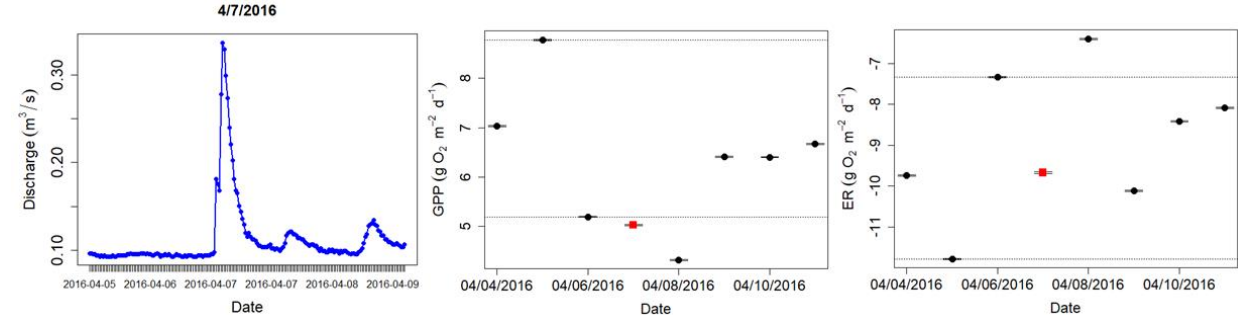


Figure S11. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2016-04-07.

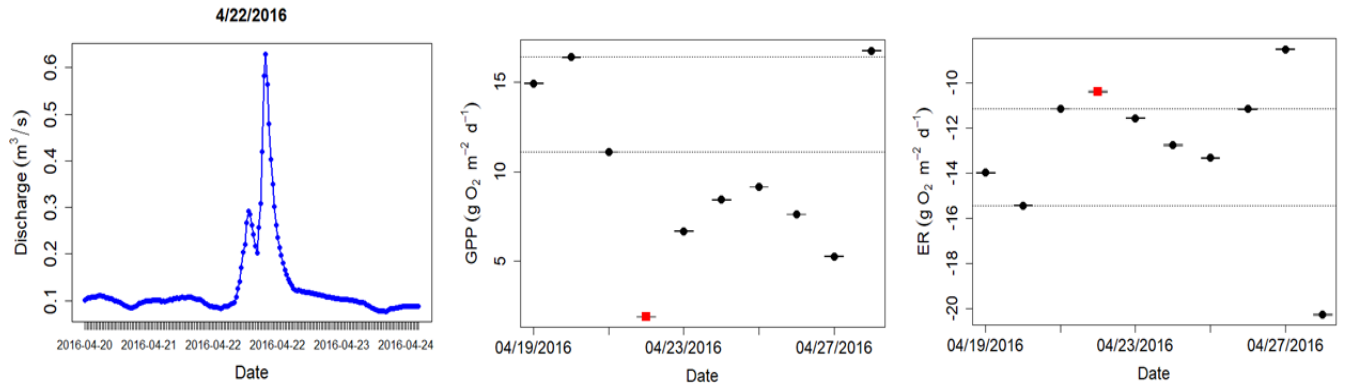


Figure S12. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2016-04-22.

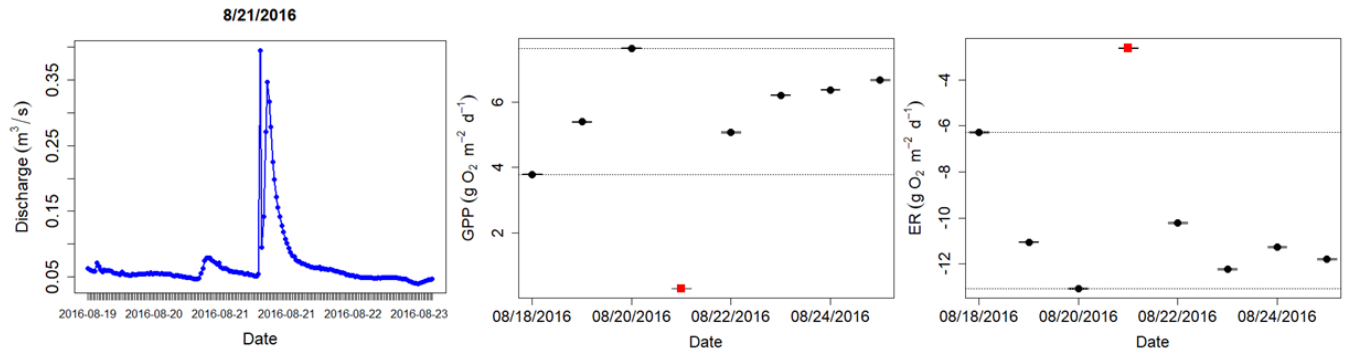


Figure S13. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2016-08-21.

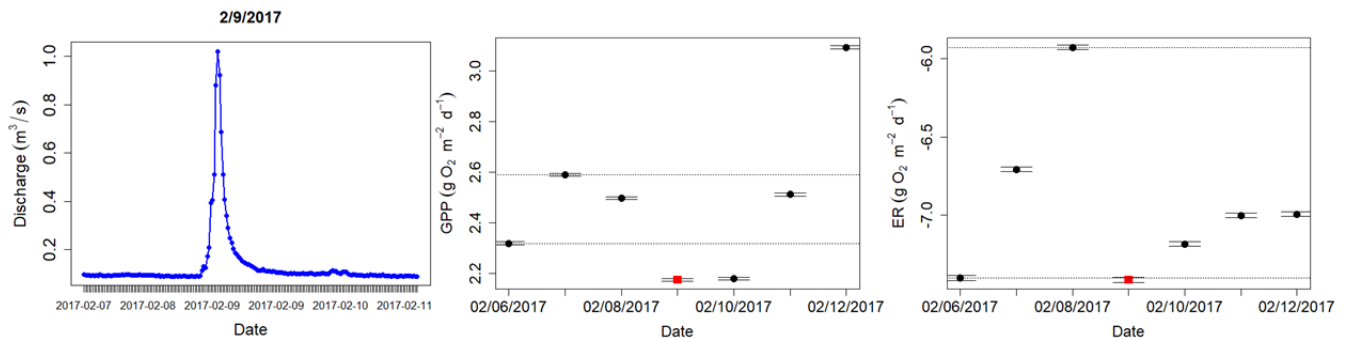


Figure S14. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2017-02-09.

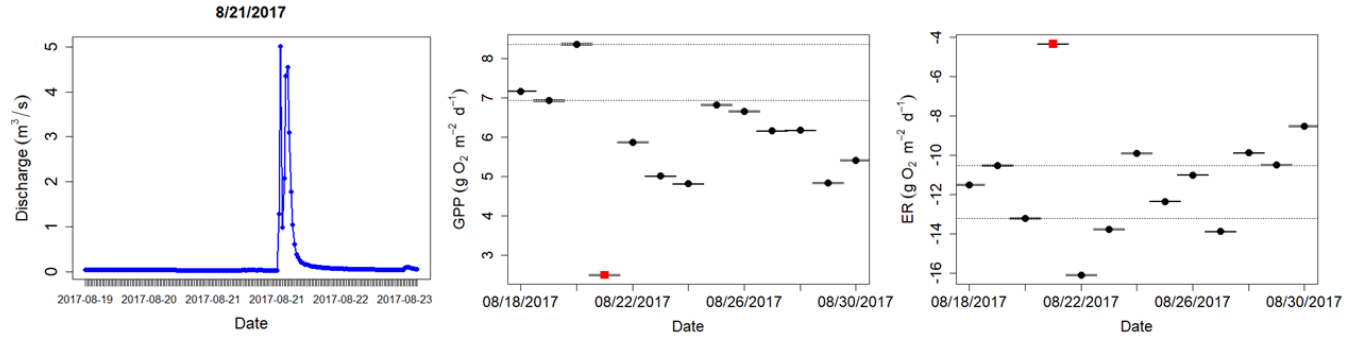


Figure S15. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2017-08-21.

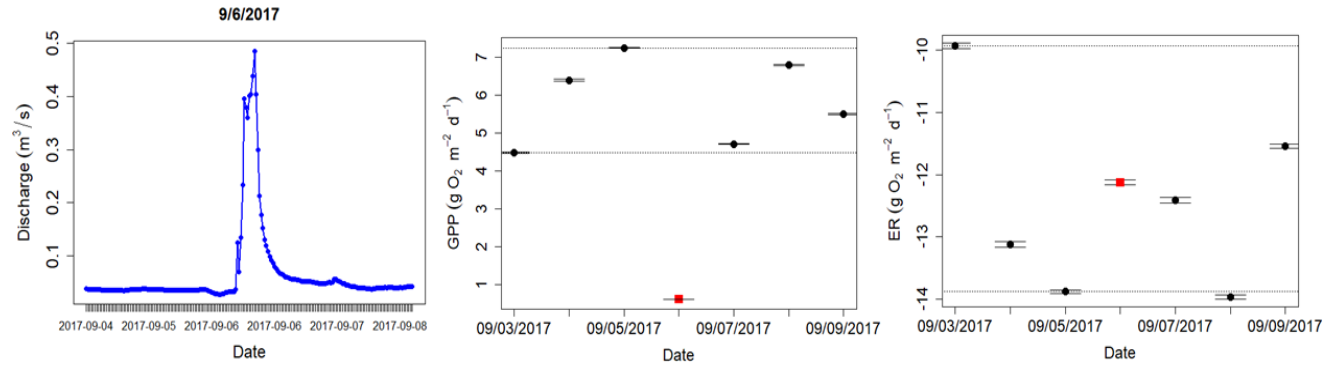


Figure S16. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2017-09-06.

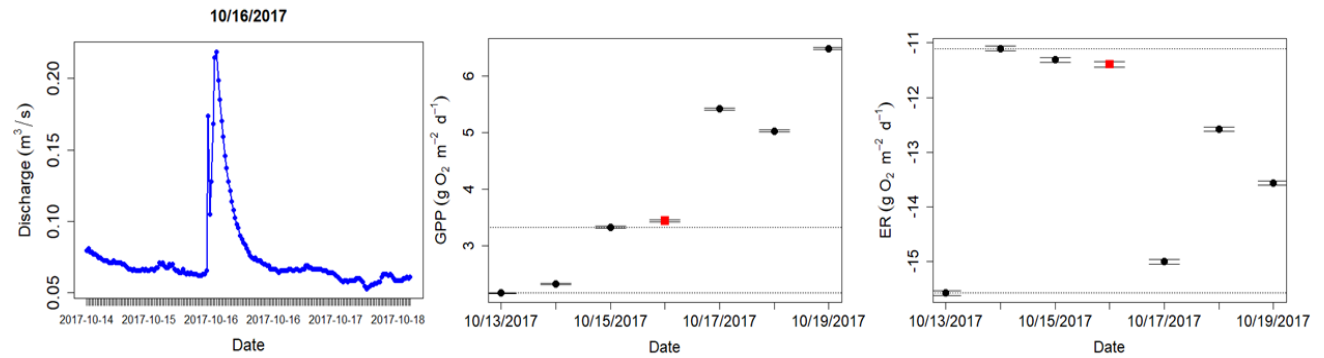
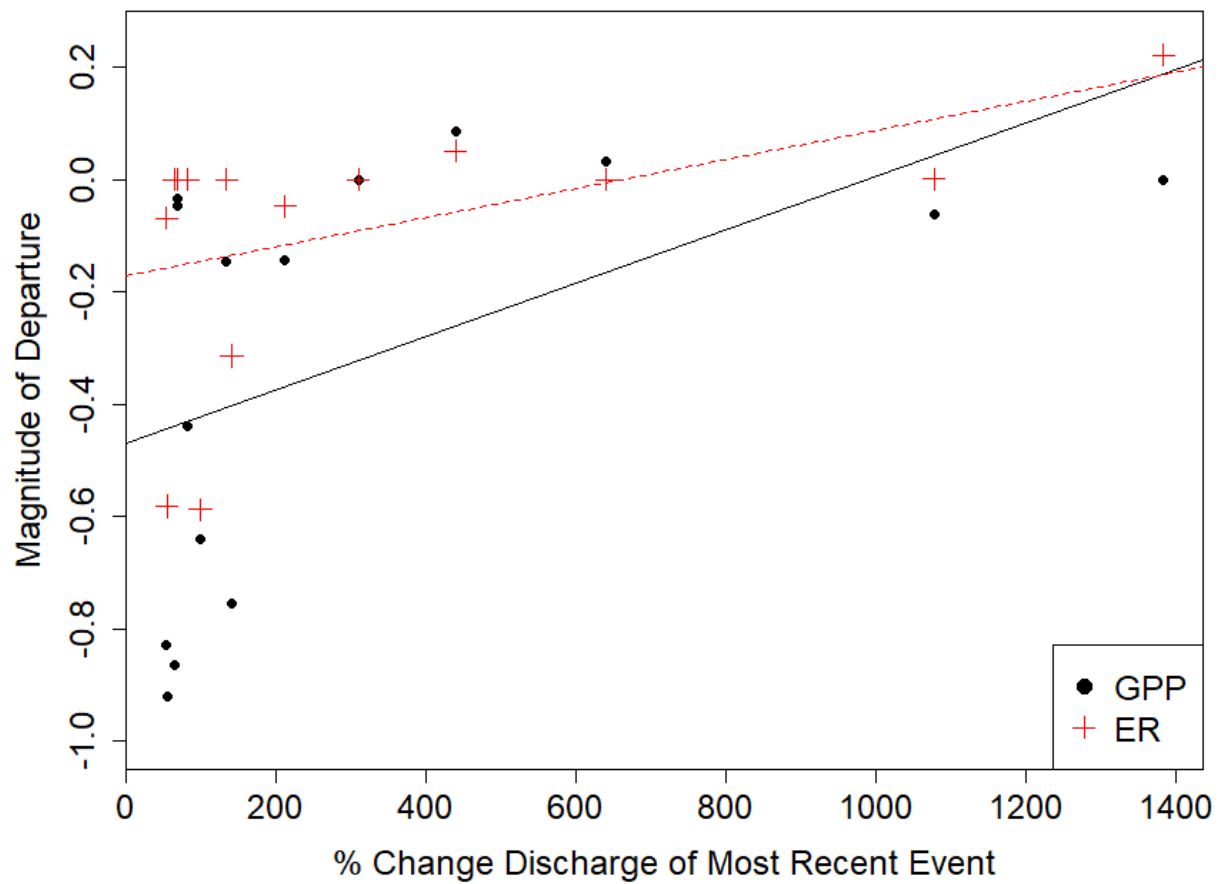


Figure S17. Hydrograph and metabolism (gross primary production; GPP & ecosystem respiration; ER) time series for the flow event on 2017-10-16.



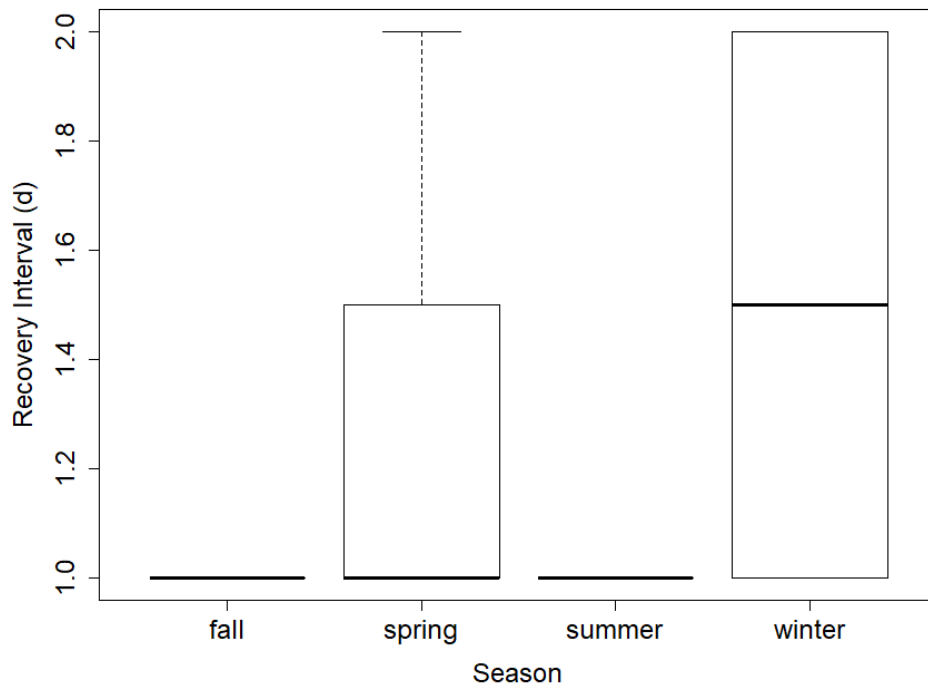


Fig S19. Relationship between recovery intervals of RI_{GPP} (days) across seasons.

Supplemental Table 1

Source	Reduction in gross primary production (%)	Reduction in ecosystem respiration (%)	Recovery interval (d) of gross primary production	Recovery interval (d) of ecosystem respiration
Uehlinger & Naegeli 1998	0.53	0.24	n/a	n/a
Uehlinger 2006	0.49	0.19	n/a	n/a
Uehlinger 2000	0.53	0.37	n/a	n/a
Uehlinger 2000	0.37	0.14	n/a	n/a
Roberts et al. 2007	0.90**	n/a	5	5
Roberts et al. 2007	n/a	n/a	4*	4
Reisinger et al. 2017	0.92	0.86	18.2	15.7
Reisinger et al. 2017	0.84	0.72	7.2	10.3
Reisinger et al. 2017	0.99	0.88	5.4	6.9
Reisinger et al. 2017	0.99	0.81	10.1	14.1

Reisinger et al. 2017	0.53	0.89	7.1	11.2
Reisinger et al. 2017	0.94	0.79	7.6	13.1
Reisinger et al. 2017	0.71	0.11	4.3	No recovery
Reisinger et al. 2017	0.88	0.7	6.9	11.2
Reisinger et al. 2017	0.97	0.84	9	8.8
Reisinger et al. 2017	0.83	0.2	13.8	9.9
Reisinger et al. 2017	0.17	0.5	11.3	11.7
Roley et al. 2014	-1.1	-1.1	3.8	2.8
Roley et al. 2014	-0.1	-1.5	5.2	1.8
Roley et al. 2014	0.5	-0.8	16.9	1.4
Roley et al. 2014	-0.1	-1.2	7.6	4
Uehlinger 2003	0.64	0.36	~1 month*	~1 month*
Smith & Kaushal, 2015	0.50**	n/a	2-3 weeks	n/a
Qasem et al. 2019	0.06	-0.49	3.3	1.68
Qasem et al. 2019	-0.25	-0.68	6.65	3.67
Qasem et al. 2019	0.01	-0.8	4.49	1.97
Qasem et al. 2019	0.25	-0.1	1.95	5.35
Qasem et al. 2019	0.11	-1.43	2.58	9.54
Qasem et al. 2019	-1.2	-1.02	2.29	1.58
Qasem et al. 2019	-1.2	-1.02	0.92	2.62

Variation presented in the literature of recovery intervals (days) and % metabolic reduction of gross primary production (GPP) and ecosystem respiration (ER) in response to flow disturbances. Averages were included when individual measurements were not recorded (Uehlinger 2000, 2006, Uehlinger & Naegeli 1998). Does not include standard deviations.

* Had to approximate days of recovery, based off of a figure

** an approximation was given