**Key message:**

* Stream productivity is dictated by light; stream recovery post-disturbance is dictated by bed scour.
* Post-disturbance springs quickly rebound to baseline with disturbance severity having no influence. Once the light regime was regained, primary productivity returned to baseline in-tandem.
* This case study highlights the importance of both light and bed scour in dictating lotic metabolic regime. The “amplitude” of productivity is dependent on light availability, but lotic resilience is largely determined by the degree of bed scour, and the remaining primary producer’s post-event.

**Abstract:**

Florida spring-runs are typically perceived as chemostatic systems due to stable thermal, hydrologic, and chemical conditions. However, they can experience flood-like disturbances, known as backwater floods, due to interactions with downstream river stage fluctuations. These disturbances range from high-stage events (slow flow) to brownouts, where downstream river water mixes with spring-run water, and flow reversal, where spring water is displaced by river water. These floods impact benthic light availability by altering water depth and clarity, influencing spring-run gross primary production (GPP) and ecosystem respiration (ER). To understand these impacts on spring-run productivity and resilience, we measured metabolism and CO2 dynamics in five spring-runs along a reversal frequency gradient. Elevated stage that maintained clear water clarity supported higher GPP and ER resulting in a net decrease in NEP (GPP+ER) but maintained baseline dissolved oxygen (DO) and CO2 concentrations. Spring-runs enduring prolonged backwater floods experienced reduced GPP, increased ER, anoxic conditions, and elevated CO2 levels. However, GPP, ER, DO, and CO2 returned to normal as fast, or faster, than hydrological conditions, indicating resilience. These findings highlight the significant impact of flood events on spring-run metabolism and the creation of ecological bottlenecks through extended hypoxic conditions. While spring-run ecosystems differ from typical river floods due to slower or reversed flow, the observed effects on metabolic regimes likely extend to other systems. This suggests that spring-run ecosystems encompass a range of flow regimes, from chemostatic spring-runs to those vulnerable to highly consequential flooding. This research highlights the importance of both light and bed scour in dictating the lotic metabolic regime. Lotic productivity is dependent on light availability, but resilience is largely determined by the degree of bed scour and the remaining autotrophs post-event.

Author’s Note: I tried to improve my thesis’s “flow” (hehehe). I felt the thesis was a bit wordy.

**Introduction:**

Stream metabolism is a key ecosystem function serving as the basis of lotic food webs, carbon cycling, and water quality. Metabolism in flowing waters varies in response to a host of energetic, hydrologic, and ecological drivers (Bernhardt et al., 2018). The patterns of temporal metabolic variation – specifically in gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP = GPP + ER) – describe the metabolic regime, reflecting the idea that lotic ecosystems subject to known drivers yield predictable inter- and intra-annual metabolic patterns. The dominant controls on metabolic regimes in flowing waters appear to be energy inputs (light, organic matter) and disturbance (Bernhardt et al. 2022) with light availability being the dominant control on GPP (Kirk et al., 2021. Light limitation via canopy cover or flow-related changes in water depth and clarity unanimously results in a decline of GPP (Bernhardt et al., 2019; Hall et al., 2015; Julian et al., 2008; LeRoy Poff et al., 1997). Dually, organic matter (OM) supply impacts ecosystem heterotrophs and in turn, ER in flowing waters, with both autochthonous and allochthonous sources controlling OM availability and bioavailability, (Bertuzzo et al., 2022).

Author’s note: I placed greater emphasis on disturbance/flow than in my thesis. To me, the springs are a case study to see how flow-impacting disturbances alter metabolism. Light is occluded, and OM is increase/altered just like in a typical flood but it’s the slowing of flow in springs that make this research… and why I chose to emphasis flow more.

Disturbance is a key driver of stream metabolism, rapidly altering ER and GPP through changes in flow regime. Generally, discharge and productivity are inversely related, with meandering streams exhibiting higher NEP, while rapid flow velocity suppresses GPP (Acuña et al., 2011; Bernhardt et al., 2018). Depending on its frequency, duration, and severity, disturbance can cause lasting shifts in metabolic regimes (Baker & Walford, 1995; Heffernan, 2008), with floods, in particular, presenting a significant risk. Flood events typically increase discharge, resuspending sediment and reducing water clarity; accelerating OM export and altering OM supply; modulating nutrient availability; and increasing bed scour, which removes benthic biota essential for metabolic functions (Acuna et al., 2005; Bernhardt et al., 2018). Rivers with stable flow regimes generally exhibit more consistent metabolic processes and higher GPP compared to those frequently experiencing flow disturbances (Bernhardt et al., 2019, 2022). However, the specific roles of reduced light availability, OM influx, and bed scour in driving the impacts of flow-related disturbances on lotic metabolic regimes remain poorly understood.

Author’s Note: I removed the aspect of “chemostatic springs.” I think it was relevant for the SRWMD but too specific for the pub.

North Florida’s spring-fed rivers are among the most productive lotic ecosystems in the world (Duarte et al., 2010; Odum, 1956). Water from upper Floridan aquifer is delivered with low temporal variation in flow or chemical composition (Fernald & Purdum, 1998; Jawitz & Mitchell, 2011) and exceedingly high clarity and low dissolved organic matter (DOM) (Duarte and Canfield 1990), yielding conditions famously referred to as chemostatic (Odum, 1957). These relatively stable conditions support dense benthic vegetation and sustain high GPP rates, seemingly lacking pulse disturbances. However, despite the absence of traditional floods, North Florida springs experience unique "backwater", blackwater events. Many springs discharge into downstream tannic rivers, and during backwater events, rising river stages reduce the elevation difference between the spring vent and the confluence. This hinders discharge or, in severe cases, causes backwater floods, where tannic river water intrudes into the spring-run. Backwater floods alter spring dynamics by raising the spring stage (reducing light penetration), slowing or halting flow (decreasing gas diffusion), and increasing OM supply, fundamentally shifting the energy base of these ecosystems (Hall et al., 2016; Hall & Ulseth, 2020; Heffernan & Cohen, 2010). These events span a spectrum from high-stage conditions, where aquifer water persists at greater depth and reduced velocity, to brownouts, where tannic river water mixes with spring water, and flow reversals, displacing clear, alkaline aquifer water with dark, acidic, tannic river water (Brown et al., 2014; Hensley et al., 2015; Hensley & Cohen, 2017). Flood magnitude, and spring-runs susceptibility, is dependent on a spring’s distance from the river, run length, and spring-river hydraulic gradient with near-river springs being the most at risk (Donsky, 2023).

Backwater floods in North Florida springs differ significantly from typical floods in flowing waters, particularly in their flow dynamics. In spring-run backwater floods, flow interruptions manifest as slowing, halting, or reversing, rather than the rapid flows characteristic of typical stream floods. While both types of floods reduce light and alter energy inputs through increased water depth and diminished clarity, a key distinction lies in the retention of benthic biomass and OM in spring-runs, compared to the loss of these components through bed scour in streams. This absence of bed-scour during backwater floods is atypical of rivers and streams, yet the transient interactions between river and spring water under such conditions remain largely understudied.

Given the variability in disturbance regimes across spring-runs and the significant role disturbances play in regulating their metabolic function, we aimed to enhance understanding of spring metabolic regimes along a gradient of flood impacts by testing five interrelated hypotheses:

1. GPP decreases, and ER increases with rising stage and reduced flow velocity, irrespective of light clarity.
2. Spring metabolism declines with increased light attenuation, even in the absence of bed scour.
3. Backwater flood magnitude (duration and stage change) positively correlates with longer metabolic recovery times and greater reductions in metabolism (higher ER and lower GPP).
4. Frequently disturbed springs exhibit greater metabolic variability than rarely disturbed springs.

By examining how flood disturbances influence metabolic functions in springs, this study sheds light on overlooked variability in these iconic ecosystems and quantifies the implications of shifting flood disturbance patterns in all flowing waters.

**Methods:**

Author Notes: I tried to correct the tone and tighten the section… idk if I was successful.

Study Sites:

Author Notes: Do I need to include a paragraph about Suwannee and Santa Fe?

To evaluate the impacts of backwater floods on metabolic regimes, GPP and ER were measured in spring-runs spanning a gradient of flood frequency and severity. Each selected spring featured a sufficiently long run (>300 m) in order to apply two-station metabolism method, with the spring vent and confluence serving as boundaries. Flood risk was assessed based on proximity to the receiving river and the elevation difference between the spring vent and confluence. The study sites included two springs that frequently flood (Allen Mill Pond – AM, Otter Springs – OS), three that infrequently flood (Little Fanning – LF, Gilchrist Blue – GB, and the downstream reach of the Ichetucknee River – ID), and one spring that rarely floods (the upper Ichetucknee – IU) (Figure 1). The Santa Fe River's sink-rise system buffers GB and other nearby springs from flow reversals (where river water displaces spring water) and attenuates backwater mixing and high-stage events (J. D. Gulley et al., 2014). In contrast, the Ichetucknee River, though also connected to the Santa Fe River, lies closer to the confluence with the Suwannee River, allowing floods from the Suwannee to propagate upstream and create backwater floods in springs along the lower Santa Fe River.

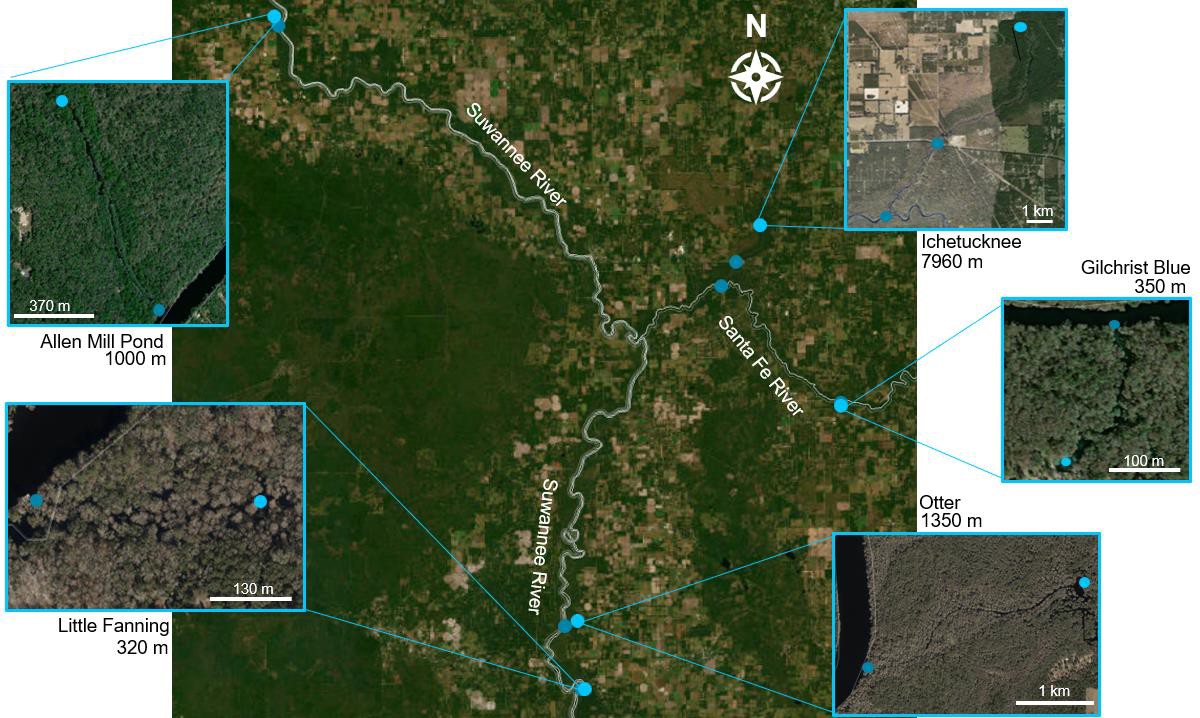


Figure 1: A map of sites along the Suwannee and Santa Fe River. Five spring-runs were selected spanning gradient of river reversal frequency. The least disturbed sites included Ichetucknee Up, Gilchrist Blue (GB), Ichetucknee Downstream (ID), and Little Fanning (LF). More disturbed sites included Otter Spring (OS) and Allen Mill Pond (AM).

**Stream Metabolism:**

High-frequency Sensor Observations:

High-frequency data for dissolved oxygen (DO) and stage were collected in each spring using optical DO sensors (Onset HOBO U26-001, Onset Computer Corporation, Massachusetts, USA) and high-resolution pressure transducers (Onset HOBO U20-001-04) deployed at the confluence of the spring run and its receiving river. These sensors logged data hourly under both flood-disturbed and non-disturbed conditions. The sole exception was IU, where publicly available data from the USGS National Water Information System (NWIS) portal were used for the same period.

To account for the distinct differences between the tannic, acidic river floodwaters and the clear, alkaline aquifer waters of the spring-runs, additional sensors were deployed to monitor source-water characteristics and distinguish between undisturbed periods, high-stage events, and backwater floods. These included a specific conductivity (SpC) sensor (Onset HOBO U24-001), and pH sensor (Onset HOBO MX2501), placed alongside the DO and PT sensors. SpC was particularly critical in detecting source-water changes due to the stark contrast between the low-conductivity floodwaters and the highly conductive, carbonate-rich spring water.

Additionally, a dissolved CO2 sensor (Eosense eosGP, Eosense Inc., Dartmouth, NS) was co-deployed with the DO sensor to gather data on ER and metabolic fluxes, providing insights into source-water changes and the role of anaerobic processes. It is important to note that the IU time series did not include CO2 measurements.

Two-station Metabolism:

Four pathways influence DO dynamics, and thus the inference of GPP and ER: 1) aquatic autotrophs releasing oxygen (GPP), 2) O2 consumption via respiration (ER), 3) exchange of O2 with the atmosphere (Din), and 4) groundwater influence accrual (Ac) (Demars et al., 2015; Kirk, 2020; Odum 1957; Reichert et al., 2009; Riley & Dodds, 2013). Changes in DO concentrations yield the following equation for NEP:

Where dCDO /dt is the change in DO concentration over time (g O2 m-3 hr-1), and z is mean water column depth (m). The atmospheric gas exchange flux, Din (g O2 m-2 hr-1), is the product of the gas exchange velocity (K, m hr-1) and the DO saturation deficit (CSat.Deficit = Csat - CDO, g O2 m-3), the above equation can be rearranged to:

For one-station metabolism, Δt is time step, and CDO(2i) - CDO(1i) is the change in DO over each time step. For two-station metabolism, Δt represents travel time, accounting for stream surface area, between an upstream and downstream location, and CDO,2i-CDO,1i represents the change in DO between two locations (a constant upstream boundary condition CDO,1i). Metabolic reactions that generate O2 contribute to a positive NEP (GPP+ER), whereas reactions that consume DO and produce CO2 result in a negative NEP.

Author’s Note: I included that final GPP and ER estimates were an average of one station and two station methods.

A combination of two-station and one-station stream metabolism methods was used to estimate ER and GPP. For the two-station method, the DO concentration difference between an upstream station (spring vent) and a downstream station (confluence) was calculated as CDO(2i) - CDO(1i). In the one-station method, the DO concentration difference at a single location over an hour was calculated as CDO(2i) - CDO(1i). The two-station approach is generally preferred in these spring-runs as it isolates the metabolic signal of a specific reach, with the upstream boundary condition (spring vent) often well below saturation, which a one-station model might incorrectly interpret as high respiration (Demars et al., 2015). However, the validity of the two-station method is contingent on the reach length (L) between stations; if L\*3< 0.4uk-1 (u= velocity m h- 1; k = gas constant h-1) or L\*0.3>0.4uk-1 , the two stations are assumed independent, and one-station metabolism assumptions are viable (Reichert et al., 2009; Riley & Dodds, 2013). At OS, this two-station length threshold was consistently violated due to slow flow velocity. Additionally, during flood disturbances, when velocity decreased significantly, AM, LF, and GB also exceeded the threshold, necessitating reliance on the one-station method.

To minimize potential bias between the methods, we averaged their outputs for the final analysis. Under normal, undisturbed conditions, the results from both methods were comparable. However, during disturbances, the two-station method yielded more pronounced impacts, whereas the one-station method produced more conservative estimates (Appendix, Figure 1).

The two-station metabolism model was implemented in R following protocols from Demars et al. (2015), Kirk (2020), Marzolf et al. (1994), Odum (1956), and Young et al. (1998). The one-station method was estimated using the streamMetabolizer package in R, employing Bayesian parameter pooling of the reaeration coefficient (k600) as a function of discharge (velocity\*width\*stage) (Appling et al., 2018; github.com/USGS-R/streamMetabolizer).

Sensors were serviced biweekly, during which a DO sensor was deployed at the spring vent to measure boundary condition concentrations. Under normal flow conditions, groundwater at the spring vent was assumed chemically constant, allowing vent-water DO concentrations CDO(1i) to serve as boundary values for the two weeks between field servicing.

Estimating Gas Exchange:

The gas exchange velocity, K (m/d) or k (d-1; K divided by depth), quantifies how gases move between the water and atmosphere (Hall and Ulseth, 2019). To estimate the gas flux, k was multiplied by the CSat. Deficit and daily stage, then normalized using Schmidt scaling coefficients, to attain K for two-station metabolism modeling (Hall & Ulseth, 2020; Kirk, 2020). K600 was empirically estimated using floating domes conducted biweekly at each site (Copeland & Duffer, 1964). The floating dome is an inverted plastic container yielding a head-space volume of 15.5 L equipped with a high frequency (1 sample per minute) CO2 sensor (deployed in the headspace) tracking CO2 concentrations over time following a pulse to increase headspace internal concentrations far above river water concentrations. Stream surface water velocity (u) was measured adjacent to the gas dome using an orange.

Following Khadka et al., (2014) and McDowell & Johnson, (2018), kCO2, the reaeration coefficient for CO2, was estimated by fitting a linear regression between time and the partial pressure of CO2 (pCO2). The flux in CO2 (ppm min-1), or ΔCO2 was converted to mol day-1 using the ideal gas law:

Here n/T (mol/time) is CO2 mols per day, ΔCO2 is the slope of pCO2 vs time, R is the ideal gas constant (0.0821 L atm K-1 mol-1), and T is air temperature (K). kCO2 was then solved with:

Where FD is the floating dome footprint (m2), KH is Henry’s law constant adjusted for temperature (moles per atmosphere), pCO2, water is the pCO2 of the water column during the experiments (ppm) and pCO2, air is the peak concentration of CO2 within the gas dome. kCO2 was converted to k600 (d- 1) with Schmidt scaling (~ 585):

Using our field measurements, a rating curve for stage (h) versus velocity (h) and the ratio of u/h versus k600 (1/day) was developed to enable continuous estimates of gas exchange. First, the relationship between field-measured u and h, derived from PT sensor data, was regressed to estimate velocity from continuous stage measurements. Next, we regressed the ratio u/h against measured k600 ​ to capture the continuous variation in gas exchange at each site, which was then incorporated into the metabolism models (Appendix, Figure 2). During flow reversals (u<0), the absolute value of u was used to estimate k600 ​, reflecting the dynamics of gas exchange under reverse flow conditions. To validate the representativeness of the k600 ​ rating curve, we compared its estimates with outputs from established models, including those of Raymond et al. (2012), John et al. (2006), and Knight (1980) (Appendix, Figure 3).

Author’s Note: Is this something we want to include in the publication? It’s cool but it feels like a lot of content. I wonder if it would be worth it being its own paper, and including the Bradford in the mix (confined vs unconfined; surficial gw vs deeper gw fed)

Spring Stoichiometry

Ecosystem production and consumption of DO and CO2 on a molar basis are generally expected to yield concentrations that covary along the -1:1 slope. The stoichiometric quotients for photosynthesis (PQ) and respiration (RQ) are broadly assumed to be 1.0, even though evidence has accumulated for values that can depart significantly. Given the broad expectation of 1:1 coupling, plots of the temporal patterns of O2 vs. CO2 can be used to infer biogeochemical functions about ecosystems (Vachon et al., 2020), including sources of water, which can decouple concentrations of DO and CO2, mineral dissolution reactions, which can consume or produce CO2 without affecting DO, or anaerobic respiration, which yields CO2 without consuming DO. We plotted O2 and CO2 departure from atmospheric equilibrium (Bernal et al., 2022; Vachon et al., 2020) yielding “cloud points” of hourly changes in O2 (mol L-1) in relation to CO2 (mol L-1); to visualize the effects of floods, and to further assess the coupling of these metabolic gases with changes in flood conditions. DO mg L-1 and CO2 ppm were converted to mol L-1 using the molar mass of 16 g mol-1 and ideal gas laws, respectively. DO saturation based on water temperature was calculated in R using streamMetabolizer. Daily slopes of DO vs. CO2 coupling were calculated using dataEllipse (https://rdrr.io/cran/car/man/Ellipses.html). Days with positive slopes were removed.

**Reduction, Recovery, and Stability of Flood Stage Metabolism:**

Flood effects of ER and GPP include changes in fluxes in response to flood magnitude, and persistent effects after the flood has abated (i.e., relative recovery times). To assess these metabolic responses to flood stage conditions, we calculated the changes in ER and GPP, the recovery times to return to pre-flood metabolic rates after peak-disturbance, and the overall temporal stability of the metabolic regime.

GPP and ER Reduction:

Author’s Note: I removed the section about using histograms and its bimodal peaks to distinguish between high stage and backwater floods. I believe Carter’s feedback that my delineation was largely subjective proved correct. Truthfully, I placed more stake in using my first-hand observations of water clarity, DO (did it spike or not during peak stage), and SpC- sometimes pH when it was working. I feel that this suffices, especially with the accompanying time series, but can be persuaded differently.

I also changed how I found GPP/ER reductions. First, I found the average GPP and ER during the peak of the flood (5 days post stage reaching its maximum). Prior, I was finding the GPP and ER minimum across the disturbed periods. I can return to these methods, but I believe our story would be consistent. During high stage events where water clarity was retained, there was no impact on spring metabolism (if anything, we saw an improvement) and therefore, we should not see a change in GPP and ER. However, by taking the minimum… we do and it’s not representative- I think it skews the results.

Changes in productivity were assessed by categorizing spring stage conditions into two main categories: normal baseflow and disturbed periods. The distinction between "normal" and "disturbed" was based on significant deviations from the stage average (Appendix, Figure 4). Disturbed periods were further divided into high stage events, brownouts (mixing of spring and river water), and flow reversals (displacement of spring water by river water), based on data from DO, SpC, and pH sensors, as well as first-hand observations of water clarity. If pH and SpC measurements indicated tannic, river water characteristics (pH < 5, SpC < 200) and the spring run exhibited visible browning, the disturbance was classified as a backwater flood. Backwater floods were then differentiated into brownouts and flow reversals based on the response of DO during peak stage: a spike in DO indicated flow reversals, while hypoxia signaled a brownout (Figure 5 and 6).

Each disturbance event was isolated from the time-series, and mean GPP and ER during peak flooding (at the peak and 5 days after) were averaged (GPPdisturbance). The relative change in GPP was estimated as 1- (GPPnormal / GPPdisturbance) (Reisinger et al. 2017). This was repeated for ER, and across every disturbance, tracking the magnitude of each flood based on the stage excursion from normal condition. To test whether disturbance magnitude significantly impacted GPP and ER, we regressed change in stage (Δh) against the GPP and ER percent reduction.

GPP and ER Recovery:

Quantifying patterns of metabolic recovery were inspired by Martí et al., (1997) and Reisinger et al., (2017). First, disturbance events, and two weeks prior and after, were isolated from the time-series. The stage, GPP, and ER for the ~7 days before the reversal were averaged and considered baseline metabolic activity. Disturbance stage, GPP, and ER were divided by baseline stage, GPP, and ER creating a disturbance ratio for each day where 1 equals pre-disturbed GPP or ER. These were then smoothed by applying a rolling means function in R (rollapply) that calculated the mean for every four consecutive days. Once each component’s time-series reached ~1 or plateaued, the component was deemed recovered. A linear regression was fitted between the disturbance ratios versus time to determine the recovery rate, resulting in a y=mx+b equation. Using the y=mx+b equation, y=1 and solved for x to approximate how many days would be required for full recovery. To test whether disturbance magnitude significantly impacted spring recovery, we regressed change in stage (Δh) against the recovery ratios. Flood disturbance that did not experience a decline in GPP or an increase in ER, such as high stage events where water quality is maintained, were exempt from recovery analysis.

Author’s Note: Changed to emphasis springs (no bed scour) versus typical flowing waters w/ bed scour.

Metabolic Stability:

To assess the role of disturbance on spring-run metabolic regime, the stability of each sites metabolism was estimated by using autocorrelation patterns for 1 and 10 day lags (i.e., AR(1) and AR(10)). Autocorrelation was calculated using the corrplot package in R. We compared the autocorrelation patterns between the springs as a function of flood vulnerability, and additionally, compared our sites versus river metabolic stability obtained from a national river metabolism data set (Appling et al. 2018). Specifically, AR(1) and AR(10) for ER and GPP was calculated from 74 and 50 streams (respectively), reflecting those streams with minimal data gaps. This comparison allowed us to explore how the absence of bed scouring floods may dictate metabolic recovery and resilience.

**Results:**

Author’s Note: I removed details I no longer thought were relevant. For instance, I removed sentences that mentioned 2023 was dry period… it was but our sample size captures spring disturbance regime.

Incidence of High Stage Events:

During the two-year study, six distinct flood periods were distributed across seasons (08/2022, 02/2023, 06/2023, 09/2023, 12/2024, and 05/2024), and all sites experienced at least one flood with LF, GB, OS, and AM experiencing at least one flow reversal. Each site exhibited the expected disturbance regime with AM being the most flooded followed by OS, LF and GB being moderately flooded, and IU and ID only experiencing high stage events (Table 1). While the spring run at GB shares a similar length with LF and OS, it only experienced a single flow reversal and only two high stage events. This infrequency in flooding can be attributed to its location along the lower Santa Fe River. The storage in the sink-rise system of the Santa Fe River attenuates high stage and mixing events, buffering GB and other Santa Fe springs from the effects of regular floods (J. D. Gulley et al., 2014). Ichetucknee, situated closer to the confluence of the Suwannee River, experiences backwater floods from the Suwannee River that propagate upstream to create high-stage events at ID and other springs along the lower Santa Fe River.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Site | Mean Stage (m) | Mean Reach (m) | Mean Discharge (m3 day-1) | Study Period | hhigh | hbrown | hreversal | Total floods | Recorded floods |
| **IU** | 1.1 | 4950 | 303 | 07/20/23 - 09/20/23 | 3 | 0 | 0 | 3 | 3 |
| **ID** | 1.2 | 2900 | 668 | 07/20/23 - 09/20/23 | 7 | 0 | 0 | 7 | 7 |
| **GB** | 0.5 | 350 | 141 | 07/10/22 - 09/20/23 | 2 | 0 | 1 | 4 | 3 |
| **LF** | 0.5 | 320 | 58 | 07/12/22 - 09/07/23 | 4 | 0 | 2 | 7 | 6 |
| **OS** | 1.0 | 1350 | 165 | 07/20/22 - 09/07/23 | 2 | 4 | 2 | 13 | 8 |
| **AM** | 1.4 | 1000 | 516 | 07/20/23 - 09/20/23 | 8 | 4 | 2 | 14 | 14 |

Table 1: Backwater flood occurrences among sites on the Suwannee and Santa Fe River (Figure 2-1). “Total floods” designates how many flood events occurred during the study, while “Recorded floods” designates floods for which I obtained viable DO time series.

Velocity exhibited significant variations over time and showed a strong correlation with changes in stage. The backwater flooding events became evident due to the consistent negative relationship between velocity and stage observed at all sites. However, the degree of coupling between stage and velocity differed significantly among sites, making it challenging to establish a uniform representation of flood magnitude based solely on-stage variations. For instance, GB and LF had comparable stage variation, but their velocity response was substantially different (3-fold difference in fitted slopes) (Appendix, Figure 2). This was largely attributed to varying flood regimes on the downstream river adjacent to each of the springs, as well as different geomorphic conditions of the spring (height above the river). According to these rating curves, velocity neared zero during floods, consistent with field observations.

Temporal variation in stage and velocity impacted the gas exchange rates, both estimated and measured. Overall, gas dome measurements were more conservative than Raymond et al. (2012), John et al. (2006), and Knight (1980) models with slightly lower values, and less sensitivity to stage and velocity variation but lies within the various estimates (Appendix, Figure 2). As expected, k600 increased with decreasing stage (when velocity increased), and was lowest during flow reversals. GB experienced the largest range in k600, ranging from an extremely low 1 day-1 during high stage periods and reaching 20 day-1 at low stage.

Chemical Time Series with Flood Events:

The sensors for the main solutes of interest (DO, CO2, pH, and SpC) all recorded data across a spectrum of flood severity despite significant deployment challenges. The time series of solutes varied distinctly and predictably with fluctuating stage. DO and CO2 were strongly inversely coupled, both at the daily scale (diurnal variation) and over longer timescales (Figure 2). During every backwater-induced flood, both brownouts or flow reversals, hypoxic conditions (DO < 2 mg/L) prevailed for some duration (11-24 days) (21-46% of the disturbance), and CO2 reached its maximum.

Other solutes that trace the change in source water, including, pH, and SpC, remained unchanged during low severity high-stage events but were clearly altered during backwater flood events (Figure 2). The shift towards river water resulted in more acidic pH whereas SpC significantly decreased reflecting river water. A strong decreasing shift in conductivity occurred during flow reversals, indicating the replacement of aquifer water in the spring- run with Suwannee River water. During brownouts, SpC was only modestly changed which may arise as waters of different density result in a poorly mixed water column from which sensor deployed near the benthic surface sampled only the denser aquifer water.

During modest floods, the rise in stage and decline in velocity leads to declines in both the mean DO and the diurnal amplitude (Fig. 2, High Stage Event), a pattern that is inversely matched by the dynamics of CO2. At more significant floods (e.g., the brownout shown in Fig. 2, Brownout), the diurnal DO amplitude is eliminated, indicating the loss of primary production, and a prolonged period of hypoxia occurred (~20 days). Notably, the most extreme floods yielded a different pattern. AM experienced a reversal during which tannic river water was observed displacing aquifer water, (Fig. 2, Flow Reversal) with negative flow velocities (-0.005 m s-1) and associated declines in specific conductance. During the height of this reversal, spring oxygen levels spiked, signifying the entry of river water with higher average DO than spring water. Note that while OS also experienced a backwater flood during the 02/2022 period, DO did not spike-and-fall, indicating that OS only experienced a brownout. The relative impact of brownouts versus flow reversals remains unclear, but while reversals are hypothesized to be a more ecologically harmful since they usually last longer and completely shift the water source in the spring-run, the persistence of hypoxia was far longer during the brownout, which may have especially important detrimental consequences for ecosystem function (Hensley et al., 2019; Hensley & Cohen, 2017, Donsky 2023).

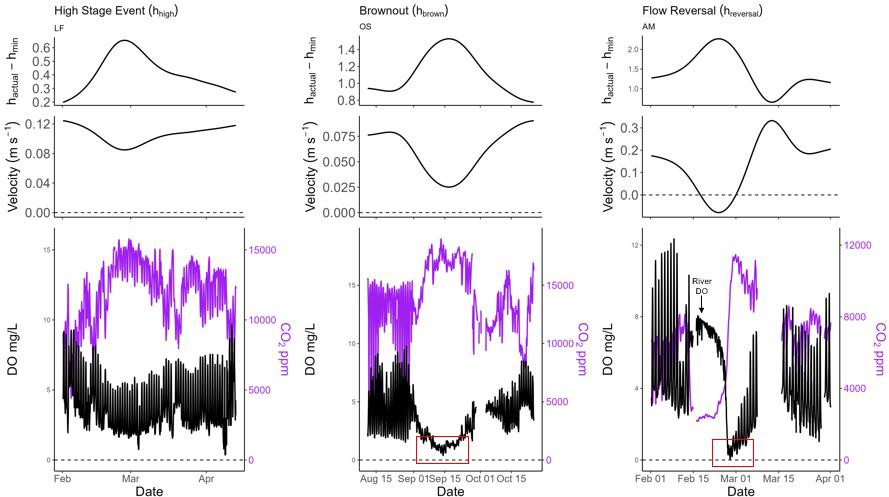


Figure 2: Time series of DO (black) and CO2 (purple) through high-stage events of varying severity. In all cases, as stage rises, DO amplitude decreases, DO levels decrease and CO2 concentrations increase implying strong coupling. At the peak of a flow reversal in AM (right panel), DO spikes and CO2 declines as river water completely displaces aquifer water in the spring-run. Hypoxic conditions (DO < 2 mg L-1) (red squares) that persist during brownouts, and after reversals are of ecological significance.

Metabolic Responses to Flood Events:

Overall, including normal and high stage, sites were heterotrophic with a GPP ~ 5 g O2 m-2 d-1 and an ER ~ −12 g O2 m-2 d-1 (IU, ID, AM, and OS) (Appendix, Figure 7). LF had the greatest variation despite no river water influence. IU, the chemostatic spring-run, had the least variability in its metabolic regime, remaining near a GPP ~ 5 g O2 m-2 d-1 with fluctuating stage.

Author’s Note: Outline is not written in academic publication vernacular/voice

* Surprisingly, if water clarity was maintained within the spring run but stage increased, Δh (stagei-stageminimum) had a positive relationship with both ER and GPP (p<0.005).
* However, the magnitude of increase ER was often greater than GPP resulting in an overall negative relationship between NEP (GPP+ER) and Δh (Figure 3) (p<0.005).
* During backwater flood events, when light was occluded by river water, GPP was significantly reduced, and ER increased, resulting in a sharp decline in NEP and creating an overall arch-shaped relationship between stage and the spring-run's metabolic constituents.
* The exception to this relationship was ID, which experienced a net increase in NEP with increasing stage (Figure 3-ID). ID is located at the confluence of the Ichetucknee and, due to its geomorphic characteristics, rarely experiences backwater flooding, and has an extensive floodplain that likely contributes to its total productivity during high-stage periods.
* The rate and extent in which each metabolic signal changed varied among the sites without obvious pattern (Figure 3, and Appendix, Fig. 5) indicating spring-runs metabolic regime is dependent on its disturbance regime.

A screen shot of a computer

Description automatically generated

Figure 3: Site-specific patterns of GPP (green), ER (red), and NEP (blue) were observed in response to changing stage (Δh), reported here as departure from minimum stage. When water clarity was maintained, GPP and ER exhibited a positive relationship, yet overall causing a net decrease in NEP. However, once light was occluded by river water, GPP halted, causing NEP to plummet.

CO2-O2 Stoichiometry:

To analyze the stoichiometric response of springs, the hourly deviations of CO2 and O2 from their atmospheric equilibrium were analyzed (Appendix, Figure 14). Across all sites, an increase in stage corresponded to a shift towards greater CO2 production and O2 consumption.

* This change was noticeable even during high stage events. However, note that although high-stage events shifted spring stoichiometry towards CO2 production, it did not reach the extent and magnitude seen during backwater floods.
* During spring-run floods (high stage events and backwater periods), the gas coupling exhibited variations in direction and magnitude across sites. Both LF and ID had slopes that significantly decreased with increasing stage, although the change at ID was quite small (Δslope = -0.09).
* In contrast, during flood conditions at LF, the slope significantly decreased, approaching ~ -1. For GB, AM, and OS, under flood conditions, a significant increase in slope (p < 0.001) occurred. Notably, in OS and AM, the larger floods led to the entrainment of Suwannee River water into the spring-runs.

GPP and ER Reduction During Floods:

A diagram of a graph

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Figure 4. Proportional metabolic responses (i.e., reduction in GPP (green) and ER (red) compared with normal flow conditions) as a function of the magnitude of discrete flood events, measured as the maximum stage increase. Disturbed GPP and ER has no correlation with disturbed stage. During backwater floods, most GPP reached near 0 while ER response was unique to each site.

Author’s Note: I only expect the top figure to make it into the publication but for the sake of the outline….

* Reflecting trends portrayed among GPP and ER vs stage, high stage events experienced minor changes in ER and GPP with few flood even experiencing an increase in metabolic productivity (Figure 4).
* Among the disturbances that had a decline metabolic productivity, high stage event saw a 34% decrease in GPP and 32% increase in ER,
  + An 89% decrease in GPP and a 22% increase in ER during brownouts (mixing of spring and river water),
  + and a 69% decrease in GPP and12% decrease in ER during flow reversals (river water displacing spring water)
* Note, modeling stream metabolism during flow reversals should be approached with skeptism. During these events, a spike in DO occurs as river water displaces spring water (essentially deep groundwater) within the run. In stream metabolism models, this spike is often interpreted as an increase in spring-run productivity (an increase in GPP and a decrease in ER). However, the shift in source water results in modeling the metabolism of the river rather than that of the spring-run. Consequently, direct GPP and ER estimates during flow reversals do not accurately capture the spring-run’s metabolic response. To provide a more accurate depiction of flood-metabolic impacts, further exploration of recovery time is necessary.

Our hypothesis that disturbance magnitude will be reflected in spring-runs’ metabolic response with GPP and ER decreasing with increasing disturbance magnitude is partly correct.

* During each backwater flood, GPP was significantly reduced (>50%) and during the most severe floods, reached near 0.
* ER, overall, was increased during floods but with no significant trend.
* Similarly, flood frequency did not have a significant trend between GPP decreases and ER increases during disturbance.
* Flood frequency exhibited a slight positive trend with disturbed GPP reductions (p=0.029) and a slight negative trend with disturbed ER increases (p=0.027). These patterns suggest that backwater floods—where river water intercepts and mixes into the spring—have more severe metabolic impacts than high-stage events, during which stage is elevated but water clarity remains intact.

Flood Recovery:

To determine whether disturbance magnitude influenced spring recovery, we estimated the time for GPP, ER, and stage to recover to pre-flood conditions following a flood event. The recovery ratio (Recoverystage / Recoverymetabolic) had values >1 when metabolism recovers faster than stage, and values <1 when metabolism recovers more slowly.

Author’s Note: Remember these are not publication ready (although pretty close) because this is an *outline*. Next draft will have ready-to-publish figure drafts.

A diagram of a recovery

Description automatically generated with medium confidence

Figure 5: GPP (green) and ER (red) recover at the same rate, or often more quickly, than hydrological recession following floods. Both plots show the relationship between flood disturbance severity and the time for GPP and ER to recover to pre-disturbance levels, indexed to the time for flood recession recovery. At left, flood disturbance is measured as a function of peak stage, and in the middle, RR frequency gradient in ascending order. The plot on the right displays the distribution of recovery. There was not a significant relationship between spring-run recovery and disturbance magnitude nor its disturbance regime, suggesting spring-runs are highly resilient to flood disturbances*.*

* At most springs and disturbances, GPP and ER recovered largely along-side stage (within ~5 days) with the mean recovery ratio for ER = 1.63 and GPP= 1.68, indicating spring-run metabolic functions are resilient to flood events regardless of river influence or flood severity (Appendix, Figure 6).
* Among the sites, there was no significant correlation between flood frequency and recovery ratios. Spring-runs experiencing backwater floods two to three times a year recovered just as quickly, or faster, as rarely disturbed spring-runs that only encountered high-stage events.
* There was no obvious, nor significant, trend among disturbance metabolic impacts (GPP decreases and ER increases) with recovery ratios. Spring run rebounded to normal metabolic conditions alongside or faster than stage, no matter the severity of its disturbance impacts.
* Overall, ER and GPP recovered at the relatively same rate likely due to the microbial communities and benthic vegetation retained due to the lack of bed scour.

These results provide no support for the hypothesis that increasing disturbance magnitude will result in longer metabolic recoveries. The absence of a clear pattern between disturbance magnitude and recovery, and indeed the idea that metabolic recovery is, on average, faster than stage suggests that spring metabolic function is surprisingly resilient to these floods.

Stability:

Among sites, GPP and ER displayed autocorrelations between approximately 0.9 and 0.4 for AR1, and around 0.85 to 0.2 for AR10 (Appendix, Figure 13). As anticipated, the autocorrelation between GPP and ER was most pronounced at AR1 and significantly decreased with AR10. Notably, this autocorrelation pattern closely mirrored the disturbance frequency gradient. IU, ID, and GB exhibited the highest autocorrelation, followed by LF, OS, and AM.

* In comparison to the dataset in Appling et al., (2018), the spring-runs exhibited a similar distribution to flowing water with typical, bed-scouring events.
* Less frequently disturbed sites (IU and ID) had autocorrelations between 1 and 0.7 for AR1 and AR10 and decreased with disturbance frequency (GPP AR1~0.5 and AR10~0.3; ER AR1~0.3 and AR10~0.2 for OS AM). The only exception was AM which displayed strong autocorrelation for AR1 but sharply declined for AR10.
* This underscores that, although the absence of bed scour allowed spring-run metabolism to normalize as stage returned to baseline, disturbance remains a key driver in the metabolic regime of flowing waters, particularly through its influence on light availability.

**Discussion:**

Author’s Note: Most of this section was already written for my thesis. I tweaked it to reflect more updated data.

Light Availability is the Key Driver in Spring-Run Metabolism:

* As stage increased, spring-runs displayed elevated productivity; however, as high-stage events transitioned into backwater floods, productivity declined sharply.
* This pattern was also evident in the relationship between stage, DO, and CO2 concentrations. High-stage events had no discernible impact on DO but saw an increase in CO2 levels , whereas backwater floods led both to a rapid decrease in DO and a rise in CO2, frequently resulting in hypoxia.
* These flood impacts were consistent across all sites, however, it's important to note that each site showed varying sensitivity to flood disturbances.

In spring-runs, floods are a consequence of downstream backwater effects that elevate stage and significantly reduce flow. This alteration in flow dynamics results in reduced water clarity, primarily through increased OM inputs (Brown et al., 2014; Hensley & Cohen, 2017), and increased stage that hinders light penetration through the deeper water column (Hosen et al., 2019; Julian et al., 2008). In contrast, floods in streams also increase stage (like spring-runs), but induce bed scouring flow (LeRoy Poff et al., 1997). Unlike high flow in spring-runs, bed scour disturbs the benthic environment, increasing stream turbidity and removing organic matter and biomass from the channel, either exporting it out of the watershed or redepositing it downstream (Bernhardt et al., 2018; Hosen et al., 2019; LeRoy Poff et al., 1997; Uehlinger, 2000). Spring-run biomass is also affected by backwater floods (Albertin & Stevenson, 2007; Stevenson et al., 2004), however not to the extent of bed scour impacts.

* The increase in productivity during high-stage events, coupled with the absence of bed scour, is likely attributable to the incorporation of the floodplain, enabling floodplain vegetation and undisturbed benthic aquatic vegetation to contribute to primary productivity.
* Conversely, during backwater floods where light is occluded, photosynthesis halts while respiration is encouraged, pushing spring-runs toward hypoxia and increasing CO2 concentrations.

The absence of bed scour is a unique characteristic of spring-runs. In these environments where seasonal variations are relatively modest (Fernald & Purdum, 1998), and nutrients remain consistently available (Brown et al., 2014), this emphasizes the significance of clarity as a primary determinant of spring-run productivity.

Each of the study sites exhibited a unique relationship between flow regime and metabolism, likely influenced by site-specific geomorphic and hydrological conditions, as well as specific light constraints associated with seasonality and canopy cover. For instance, sites with similar average stage (such as IU and ID), sites with comparable velocities (like GB and OS), and sites near each other (e.g., OS and LF) all displayed significantly different relationships between their flow regime and metabolism.

* This study clearly underscores the role of clarity and flow as a determinant of spring-run metabolic regimes.

Light Availability is More Impactful on Spring-Run metabolic Regime than Source Switching:

Both types of backwater flood induced hypoxic conditions that persisted for 11 to 30 days, providing further evidence that light is the primary determining factor in spring-run metabolism. Once light availability is diminished, the increased inflow of river water has no additional influence on GPP. This suggests that both flow reversals and brownouts create similar metabolic impacts.

Consequently, brownouts (mixing), which occurred 2-3 times per year during the study period, have the potential to be more ecologically significant due to their higher frequency, as they shade the spring-run with every event, potentially having a more profound impact on the ecosystem.

* There was no discernible effect of disturbance magnitude on GPP or ER, suggesting that, while overall respiration increased during all backwater floods and some high stage events, larger floods did not necessarily result in proportionally larger metabolic impacts.
* OM inputs, seen in the literature to have a stimulating response on ER although with varying response, seemingly increased with the introduction of tannic river water to the OM-depleted spring-run, however, the proportion of river water did not result in proportionally larger impact on ER (Acuña et al., 2004; Fuss & Smock, 1996; Meyer & Edwards, 1990; Mulholland et al., 2001; Shen et al., 2015; Sinsabaugh, 1997).
* Temperature, which influences the rate of respiration, did not significantly change with increasing disturbance magnitude, however, its impact on ER is not universally consistent across the literature (Acuña et al., 2004; Bernhardt et al., 2018; Meyer & Edwards, 1990; Sinsabaugh, 1997).
* Another possibility for the observed ER response may be related to DO becoming more limiting with increasing disturbance magnitude, hindering both GPP and ER and shifting spring-runs towards anaerobic reactions. The increase in OM during initial backwater flooding may have stimulated greater ER, while hypoxia at latter stages may have limited respiration, contributing to the lack of a significant trend in ER.
* The observed reductions in GPP during disturbances in spring-runs surpassed productivity losses seen in alpine floods and forested streams (Roberts & Mulholland, 2007; Uehlinger, 2000) and were consistent with GPP reductions observed in urban streams (Reisinger et al., 2017), however like ER, any occlusion of light by river water, whether from mixing or complete displacement, halted GPP.

Light as a Determinant of Disturbance Magnitude, While Bed Scour Shapes Lotic Recovery:

* The post-flood recovery of spring-runs provides evidence that while light may influence the response in GPP and ER, the primary determinant of lotic recovery-time is bed scour.
* Commonalities between spring-run floods and typical stream floods include channel shading, increased depths, and the introduction of organic nutrients.
* As mentioned, in streams, bed-scouring flows disturb the benthos, increase stream turbidity, and export biomass effects on ER (Figure 3-8).
* ER and GPP response to disturbance magnitude was seemingly random but overarching patterns held true: river water influences decreased GPP and increased ER.
* Both spring-run backwater floods and typical stream floods drive flowing waters toward hypoxia (Martí et al., 1997), with a notable difference being the absence of bed scour in blackwater, backwater disturbances.

We observed that backwater floods do not significantly impact spring recovery. Following nearly every flood event, GPP and ER rebounded along-side, or faster, than stage, indicating high resilience of spring-run metabolism. In contrast, streams affected by floods may require up to a decade for vegetation and taxa to recover (Woodward et al., 2015), particularly when these floods occur in close succession, potentially altering ecosystem function over time (Baker & Walford, 1995; Uehlinger, 2000). While disturbance is recognized as a fundamental aspect of flowing metabolic regimes, defining characteristics of a lotic disturbance regime remain poorly understood. Light, like stream metabolism, influences disturbance magnitude, but resilience and function are primarily governed by bed scour, involving the extensive removal of channel biomass. This suggests that spring-run productivity is not solely attributed to their chemostatic nature but also to the absence of scouring floods.

Disturbance as a Key Driver of Spring-run Metabolic Regimes and Typology:

Frequently disturbed springs exhibited higher metabolic variability compared to rarely disturbed springs, emphasizing the fundamental role of disturbance in shaping ecosystem function, especially in systems where disturbances have traditionally received less attention. These findings display the significant distinctions between frequently disturbed and rarely disturbed springs. Frequently disturbed springs tend to be located near their receiving blackwater rivers, whereas rarely disturbed springs feature longer runs that are more distant from downstream rivers. This research suggests that spring flood disturbances play a defining role in the metabolic regimes of these systems. Disturbance has emerged as a key factor in lotic metabolic regimes in general, and results suggest springs are no exception.

**Challenges and Implications**

Navigating Challenges in Stream Metabolism with Switching Source-Waters:

Along with technical challenges, modeling North Florida's spring-runs presented unique obstacles. One prominent challenge was the inadequacy of the two-station metabolism method in representing boundary conditions, particularly in porous, karst flowing waters where locating suitable headwaters for an upstream station could be quite challenging. This challenge became evident at AM and LF, where a thorough search for the correct vent to serve as an upstream station ensued. In the case of AM, three vents were discovered, while at LF, two vents, before finally settling on vents closer to sensor deployments. Conversely, for GB and Ichetucknee (IU and ID), the headspring was readily identifiable.

Additionally, it's important to note a limitation of the one-station metabolism model, streamMetabolizer, which may have led to overestimations of GPP and ER during flow reversals. StreamMetabolizer interprets any increase in DO as a sign of increased productivity. While this interpretation is generally valid for typical stream disturbances, during flow reversals, intruding river water with higher DO levels can raise DO concentrations within the reversed spring-run. Consequently, StreamMetabolizer misinterprets this DO spike as a productivity increase rather than an introduction of a new end member. Data collection during flow reversals was limited to approximately seven days. Therefore, the extent to which StreamMetabolizer overestimated GPP and ER remains unclear. Nevertheless, based on direct observations of the flow reversals at AM, OS, and GBwhere stage reached its maximum and the spring-run exhibited blackwater conditions, it is highly unlikely that primary producers were actively photosynthesizing, and the observed increases in DO were primarily attributed to the intruding river water.

Future Implications in Metabolism Modeling for North Florida Spring-Runs:

Throughout the study, we employed both two-station and one-station metabolism methods to model spring-run metabolism, depending on the prevailing conditions. The transition between these methods posed certain challenges.

* During normal flow and flood conditions, I felt confident in the estimation of GPP, ER and NEP.
* However, during the transitional period (stageflood < transitional period > stagebaseline), where stage fluctuated and chemical responses were notable, there may be some uncertainty in the accuracy of the models. This transitional phase warrants further investigation to better understand its dynamics.

Moreover, for flow reversals, where the upstream boundary shifts from the spring vent to the receiving river, complications arise when using the two-station methods. The source waters essentially reverse and DO concentrations in the river typically exceed those in the now "downstream" spring-run, potentially resulting in unrealistic ER rates.

* For the observed flow reversal, the flow velocity violated the 0.4u k-1 > L threshold, requiring one-station methods.
* Furthermore, considering the locations of the study sites at the confluence of the spring-run with the downstream river, the use of one-station methods was deemed sufficient. However, it's important to acknowledge that for sites like IU, where metabolism is modeled closer to the spring vent, flow reversals events may present unique challenges that require in-depth investigation and tailored methodologies.

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