**Key message:** Stream productivity is dictated by bed scour. Post-disturbance springs quickly rebound to pre-disturbance productivity with disturbance severity having noinfluence; once the light regime was regained, primary productivity returned to baseline. This case study in the springs 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.

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).Light availability is 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 them unique… and why I chose to emphasis flow more.

Disturbance is a key driver of stream metabolism, rapidly altering ecosystem respiration (ER) and gross primary productivity (GPP) through changes in flow regime. Generally, discharge and productivity are inversely related, with meandering streams exhibiting higher NEP, while rapid discharge suppresses GPP. Depending on its frequency, duration, and severity, disturbance can cause lasting shifts in metabolic regimes (Baker & Walford, 1995; Heffernan, 2008), with flooding, 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 (UFA) 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 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 flow reversals, 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 full 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 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 for their future metabolic regimes.

**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 the 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) to apply the 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 2-1). 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 (Figure 1), allowing floods from the Suwannee to propagate upstream and create backwater floods in springs along the lower Santa Fe River.

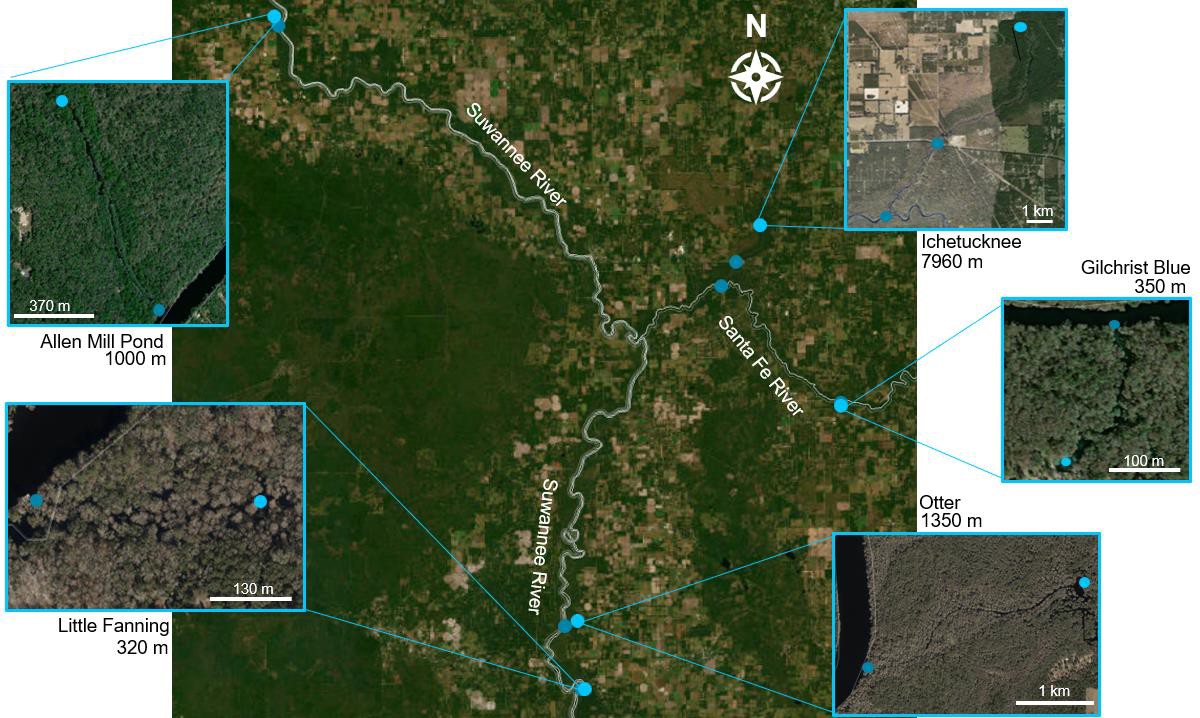


Figure 1: A map of sites along the Suwannee and Santa Fe River. Five spring-runs were selected spanning gradient of river reversal frequency. The least disturbed sites included Ichetucknee Up, Gilchrist Blue (GB), Ichetucknee Downstream (ID), and Little Fanning (LF). More disturbed sites included Otter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

**Ecosystem 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), a pH sensor (Onset HOBO MX2501), and a fluorescent dissolved organic matter (FDOM) sensor (Cyclops-7F, Turner Designs, Inc., San Jose, CA), 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 water sources 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 represent 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 2).

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.

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 definition was largely subjective, and truthfully, I distinguished between the two 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.

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 3). 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 2).

GPP and ER Reduction:

Changes in productivity were assessed by dividing spring stage conditions into 1) normal baseflow and 2) disturbed periods. The categorization between “normal” and “disturbed” was dependent on significant deviations from the stage average (Appendix, Figure 3) with disturbed periods further parsed into high stage events, brown outs (spring and river water mixing), and flow reversals (river water displacing spring water) based one DO, SpC, and pH sensor readings, and first-hand observations of water clarity. If pH and SpC observations reflected tannic, river water characteristics (pH<5, Spc <200), and the spring run was visibly brown, the disturbance was considered a backwater flood. Backwater floods were lastly divided into brownouts and flow reversals depending on DO’s response during peak stage with a spike in DO representing flow reversals and hypoxia indicating a brown out (Figure 2).

Each disturbance event was isolated from the time-series, and mean GPP and ER during peak flooding (2 days before and after stage reached its maximum) 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 made some small changes that I no longer thought were relevant. For instance, I removed the aspect of 2023 being dry year because we captured 3 FR in 2024. I believe our sample size is large enough and the detail is unimportant.

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 052024), 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 | 6 | 6 | 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 (hnorm).

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 (Appendix, Figure 4). 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 02/2022 flood, 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).

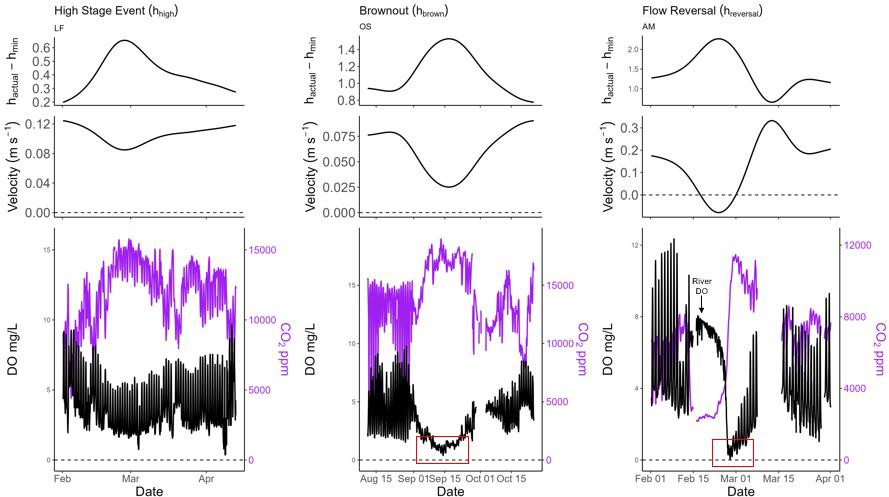


Figure 5: Time series of DO (black) and CO2 (purple) through high-stage events of varying severity. In all cases, as stage rises, DO amplitude decreases, DO levels decrease and CO2 concentrations increase implying strong coupling. At the peak of a flow reversal in AM (right panel), DO spikes and CO2 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 1 and 5). 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

* To our surprise, if water clarity was maintained within the spring run, Δh (stagei-stageminimum) had a positive relationship with both ER and GPP (p<0.005).
* However, the magnitude of increase ER was largely greater than GPP resulting in an overall negative relationship between NEP (GPP+ER) and Δh (Figure #) (p<0.005).
* During backwater flood events, when light was occluded by river water, GPP was extinguished, 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
* The rate and extent in which each metabolic signal changed varied among the sites without obvious pattern (Figure 3, and Appendix, Fig. 5) inferring a spring-runs metabolic regime is dependent on its flow and disturbance regime

A screen shot of a computer

Description automatically generated

Figure 6: 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.

GPP and ER Reduction During Floods:

* GPP and ER decreased during floods (GPP mean= 71%; ER mean= 39%) however the overall trend with Δh was insignificant (p= ~0.06).
* 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 diminished to 0. As for high-stage events, GPP declined with increasing stage.
* ER increased with increasing stage regardless of river influence (Figure 4).
* Flood frequency had a significant, negative trend with ER (p<0.005), with sites experiencing less frequent disturbance experiencing a greater increase in ER. GPP response to disturbance displayed no trend with disturbance regime (Figure 3-9).

A diagram of a flood impact

Description automatically generated with medium confidence

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. In all cases, GPP and ER decreased during the floods. GPP declined to zero but had negative relationship with stage during high stage events. ER had a positive relationship with the stage, regardless of river influence, and sites with more severe disturbance regimes tended to have less ER increases.

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.

* At most springs and disturbances, GPP and ER recovered largely along-side stage (within ~5 days) with the mean recovery ratio for ER = 1.55 and GPP= 1.66, indicating spring-run metabolic functions are resilient to flood events regardless of river influence or flood severity (Appendix, Figure 6).
* There was no obvious, nor significant, trend among disturbance metabolic impacts and recovery with GPP reductions and ER increases during disturbance have no correlation with recovery time or recovery ratios (p ~ 0.6). Spring run rebounded to normal metabolic conditions alongside 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 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.

* However, sites with more severe disturbance regimes tended to recover their metabolic regime faster than less disturbed sites (p=0.95) (Figure 3-11). Excluding ID’s flow reversal, an extremely rare occurrence for this site, and its subsequent high stage event, ER recovery correlation with disturbance frequency strengthens but is still insignificant (p=0.92).

Stability:

Among sites, GPP and ER displayed autocorrelations between approximately 0.9 and 0.6 for AR1, and around 0.85 to 0.2 for AR10. 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 RR 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), these spring-runs generally displayed greater autocorrelation in GPP and ER, suggesting that spring-run metabolic regimes are comparatively more stable than those in typical flowing waters. It's worth noting that, unlike Appling et al. (2018), the decline in autocorrelation for GPP and ER over time in spring-runs was relatively small.

**Discussion:**

High Stage Events Consistently Impact Spring-Run Metabolism:

As both stage and disturbance magnitude increased, I observed decreases in GPP and increases in ER, resulting in a significant decrease of NEP (Figure 3-5). Additionally, rising stage led to a significant increase in CO2 concentrations while DO concentrations significantly decreased (Figure 3-4). These flood impacts were consistent across all sites, including high-stage events (hhigh), which also exhibited significant effects. 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/or 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 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 and stage as a primary determinant of spring-run productivity.

During the study period, I observed that DO concentrations fluctuated in tandem with stage variations, offering preliminary evidence that spring-run metabolism could be inferred with stage (Figure 3-4). However, it's important to note that evaluating spring-run GPP, ER, and NEP with stage would necessitate a site-specific evaluation of spring-run sensitivity to fluctuating stage across various spring-run disturbances. Each of the study sites exhibited a unique relationship between stage and metabolism (Figure 3-5), 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 stage and metabolism. Due to below-average precipitation during the study period, I was unable to capture the full spectrum of disturbance events that these spring-runs could potentially experience. This limitation prevented me from interpolating ER and GPP data for all available records across sites. While further research is needed, this study clearly underscores the role of clarity and stage as a determinant of spring-run metabolic regimes. Moreover, it provides initial evidence of stage as a valuable tool for understanding historical spring-run metabolism.

Brownouts are More Ecologically Significant than Flow Reversals:

Both types of RRs induced hypoxic conditions that persisted for 11 to 24 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 hreversal and hbrown create similar metabolic impacts.

Consequently, hbrown, which occurred 2-3 times during the study period, are likely 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.

In addition to the systematic changes in metabolism associated with backwater floods, the magnitude of disturbance had a notable and consequential impact on GPP. GPP exhibited a significant negative trend with increasing flood stage, decreasing as disturbance magnitude increased (Figure 3-8). Notably, one exception to this trend was IU, representing a chemostatic spring-run, where GPP remained relatively stable due to minimal stage and clarity changes between normal periods (hnorm) and high-stage events (hhigh). 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),

In contrast, there was no discernible effect of disturbance magnitude on ER, suggesting that, while overall respiration increased during all floods, larger floods did not necessarily result in proportionally larger inputs frequently emerge as primary controls of ER, both having positive relationships, but the response varies depending on the ecosystem (Acuña et al., 2004; Fuss & Smock, 1996; Meyer & Edwards, 1990; Mulholland et al., 2001; Shen et al., 2015; Sinsabaugh, 1997). FDOM significantly increased between hhigh and brownouts (hbrown) (Figure 3-3), yet hhigh experienced ER increases like those observed during hbrown. Flow reversals (hreversal) showed a slight decrease in FDOM, but due to the limited data available (approximately 7 days of hreversal), drawing conclusions about hreversal impacts on ER remains challenging. 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 trend 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 FDOM during hhigh may have stimulated greater ER, while hypoxia during hbrown may have limited respiration, contributing to the lack of a significant trend in ER.

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

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 resilience is bed scour. Commonalities between RRs 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). On average, ER increased 63% during floods, whether a river reversal (RR) or hhigh. The reasons for the seemingly random yet positive ER reaction with disturbance magnitude is largely speculative. ER constraints are less clear than GPP constraints. Temperature and OM from the channel, potentially even from the watershed entirely (Hensley et al., 2019; LeRoy Poff et al., 1997). Consequently, both RRs and stream floods drive flowing waters toward hypoxia (Martí et al., 1997), with a notable difference being the absence of bed scour in RRs.

In this study, I observed that backwater floods do not significantly impact spring recovery.

Following nearly every flood event, GPP and ER rebounded faster than stage, indicating high resilience of spring-run metabolism (Figure 3-9). The exception was OS, characterized by slower flow, lacking the force to flush river water from the spring-run post-flood, which allowed metabolic impacts to persist. 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 (Figure 3-10). 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 aligns with the overarching hypothesis that Florida Springs' "chemostatic" archetype may apply to springs distant from rivers but not to those in proximity. 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. Furthermore, this research underscores the importance of considering spring ecosystems as spanning a gradient of natural flow regimes that include the large chemostatic springs that never flood, which represent the archetypal

metabolic regime often adopted for Florida’s springs, but also those springs that are subject to prolonged and highly consequential flooding that dramatically impact metabolism. Only by accurately establishing the expected metabolic regime can we hope to manage and restore the ecosystem functions of our precious springs.

Challenges and Implications:

Navigating Challenges in Modeling North Florida's Spring-Run Metabolism:

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 I had to search for the correct vents to serve as the upstream station. In the case of AM, I encountered three vents, while at LF, I found 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 (hreversal). StreamMetabolizer interprets any increase in DO as a sign of increased productivity. While this interpretation is generally valid for typical stream disturbances, during hreversal, 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 hreversal 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 hreversal at AM, where 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.

Lastly, it's worth noting that the study took place during a period of atypically dry conditions in the Suwannee and Santa Fe Basin, resulting in only one hreversal being observed. While this research clearly demonstrates the ecological significance of brownouts (hbrown) compared to hreversal, capturing hreversal conditions at sites like GB and OS would provide a more comprehensive understanding of spring- run disturbances. Nonetheless, findings offer valuable insights into the metabolic implications of river reversals (RRs).

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

Throughout the study, I 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 (hnorm), I felt confident in the estimation of GPP, ER and NEP. However, during the transitional period (hhigh < transitional period > hnorm), 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 hreversal, 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 one observed hreversal, 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, hreversal events may present unique challenges that require in-depth investigation and tailored methodologies.

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