Do riverine heatwaves impact ecosystem metabolism?

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Abstract

In response to climate change, research on extreme conditions is accelerating. One such condition is the aquatic heatwave. With an expected rise in the occurrence, severity, and span of heatwaves, aquatic ecosystem processes will be affected, but the impacts are understudied and uncertain. This study addressed the effects of aquatic heatwaves on gross primary production (GPP), ecosystem respiration (ER), and their difference defined as net ecosystem metabolism (NEM) in a riverine ecosystem. Using long-term data from a site in the James River, water temperature time series were analyzed for heatwave metrics. In addition, by using dissolved oxygen time series, daily rates of GPP and ER were estimated. Of the 40 heatwaves observed during this study, 70% were of moderate severity and 30% were of strong severity, as determined based on peak temperatures. The average (± SD) frequency of heatwaves was 2 ± 2 events year $^{-1}$ and ranged up to 5 events year $^{-1}$. The average duration and maximum intensity of a heatwave was 8 ± 3 days and 5.22 ± 1.36°C. GPP was significantly higher during moderate heatwaves (1.01 ± 1.30 g O_2 m^{-2} d^{-1}, p-value = 0.003) compared to non-heatwave conditions (0.70 ± 0.96 g O_2 m^{-2} d^{-1}). GPP significantly declined during strong heatwaves (0.49 ± 1.13 g O_2 m^{-2} d^{-1}) relative to moderate heatwaves (p-value = 0.002), which suggests unfavorable conditions for primary producers as heatwaves become more severe. ER and NEM were not significantly different during heatwave and non-heatwave conditions, nor during moderate versus strong heatwaves. Overall, these results suggest that GPP will increase with increasing water temperature until a thermal maximum is reached and then begin to decline. This may result in increased CO_2 release to the atmosphere as rivers become increasingly heterotrophic under persistent and strong heatwaves.

Acknowledgements

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Introduction

Climate change is increasing water temperatures in the global ocean (Rhein et al. 2013), as well as in inland waters (Kaushal et al. 2010; O'Reilly et al. 2015). In freshwater systems, water temperature exerts strong controls on organism distribution (Vannote et al. 1980), contaminant toxicity (Patra et al. 2015) and rates of biochemical reactions (De Stasio et al. 2009). Along with increases in annual mean water temperature are increases in discrete, extremely high-temperature events called heatwaves (Hobday et al. 2016). Hobday et al. (2016) formally defined an aquatic heatwave as a period of sustained high temperature that exceeds a local and seasonally varying long-term 90th percentile for at least 5 consecutive days. Aquatic heatwaves have been relatively well-studied in the global (Oliver et al. 2018) and coastal oceans (Lima and Wethey 2012) and lakes (Woolway et al. 2021). However, the development of aquatic heatwaves in rivers and streams has only recently been considered (Tassone et al. 2022a; Zhu et al. 2024). For lotic systems, aquatic heatwaves are associated with high air temperatures often in concert with low river discharge (Tassone et al. 2022a). As global temperatures rise, riverine heatwaves are expected to increase in frequency, as well as duration, along with achieving ever higher maximum temperatures (Tassone et al. 2022a; Zhu et al. 2024). The consequences of these changes include possible exceedance of organismal thermal tolerances and associated changes in ecosystem processes (Joint and Smale 2017; Smale et al. 2019), economic costs from the loss of resource species (Smale et al. 2019; Smith et al. 2021) and diminishing water quality (van Vliet et al. 2023).

This study explores the significance of riverine heatwaves in the context of riverine ecosystem functioning. Ecosystem metabolism is a central process governing the flux of carbon and oxygen. Metabolism is an umbrella term used to describe gross primary production (GPP), ecosystem respiration (ER), and their difference defined as net ecosystem metabolism (NEM = GPP - ER). In aquatic systems, ecosystem metabolism can be measured by considering fluxes in oxygen over the diel cycle (Odum 1956; Pace and Prairie 2005; Bernhardt et al. 2018).

Water temperature affects dissolved oxygen (DO) solubility (Zhi et al. 2023) as well as metabolic rates of aquatic organisms (Caffrey 2004; Demars et al. 2011). DO solubility declines with increasing water temperature (Zhi et al. 2023). Rates of respiration tend to increase with water temperature to a maximum (Pace and Prairie 2005; Tassone and Bukaveckas 2019). Respiration may also decline at very high temperatures, but this pattern is less well-documented for in situ conditions (although established for individual organisms; Gillooly et al. 2001). Rates of GPP follow a similar trend to those of ER, though GPP is also limited by other factors such as light availability or nutrients (Bernhardt et al. 2018; Joint and Smale 2017; Song et al 2018) but these limitations do not always occur (Demars et al. 2011). An increase in ER relative to GPP causes rivers, which are typically net heterotrophic (Cole and Caraco 2001; Mulholland et al. 2001; Demars et al. 2011), to become more strongly net heterotrophic, thereby depleting dissolved oxygen and increasing production of CO_2. This is due to the respiration of exogenous organic matter that flows into rivers from surrounding land. Aquatic heatwaves may increase CO_2 emissions from rivers by enhancing ER relative to GPP (Demars et al. 2011; Bernhardt et al. 2018; Song et al. 2018).

The effects of water temperature on the components of metabolism (GPP, ER, NEM) also differ with seasonality such that the greatest rates of GPP and ER occur during summer and the lowest rates occur in winter (Caffrey 2004; Tassone and Bukaveckas 2019; Munn et al. 2023). In the case of heatwaves, the most severe riverine heatwaves tend to take place during winter (Tassone et al. 2022a). Metabolic dynamics in winter differ from those in warmer conditions, such that heatwaves might further push rates of ER above GPP, since GPP can be especially limited in winter by light, nutrients, and other factors (Joint and Smale 2017).

Changes in discharge also alter riverine ecosystem metabolism (Bernhardt et al. 2018; Tassone and Bukaveckas 2019; Munn et al. 2023). During high-flow conditions, primary production is limited often due to elevated turbidity that reduces light availability (Bernhardt et al. 2018; Bukaveckas et al. 2020; Munn et al. 2023). Similarly, low-flow conditions may limit primary production due to lost habitat and the resulting dry conditions (Bernhardt et al. 2018; Munn et al. 2023). Drought can also amplify temperatures (Tassone et al. 2022a; van Vliet et al. 2023), which again may affect metabolism. Thus, I expected that discharge would impact heatwaves and, consequently, metabolism.

This study aimed to uncover whether riverine heatwaves impact rates of riverine GPP, ER, and NEM beyond expected increases due to temperature. I hypothesized, based on a general review by De Stasio et al. (2009), that rates of ER would increase with increasing heatwave severity relative to non-heatwave conditions. Additionally, I hypothesized that GPP might increase during moderate heatwaves due to being in a more thermally optimal temperature range, however, as heatwaves become more severe, GPP would decrease due to thermal stress on primary producers (De Stasio et al. 2009). The net effect of these changes would be an unchanged NEM during moderate heatwaves whereas rivers would become significantly more heterotrophic during stronger heatwaves. This study is among the first to examine heatwave impacts on ecosystem processes in rivers and is currently the only study of riverine heatwaves for a Virginia river.

Methods

Study Site

For this study I used long-term data from the United States Geological Survey (USGS) monitoring station James River at Cartersville (USGS Site ID: 02035000) in Cumberland County, VA (Figure 1). This site is located in the lower freshwater section of the James River which stretches about 540 km (Smock et al. 2005) and runs through central Virginia, ultimately draining into the Chesapeake Bay. The watershed upstream from the Cartersville station is mostly forested (76.51%) and has a drainage area of 16,187 km^2 (USGS StreamStats). Between 1911 to 2023 the average depth of the James River at Cartersville was 1.47 ± 1.04m.

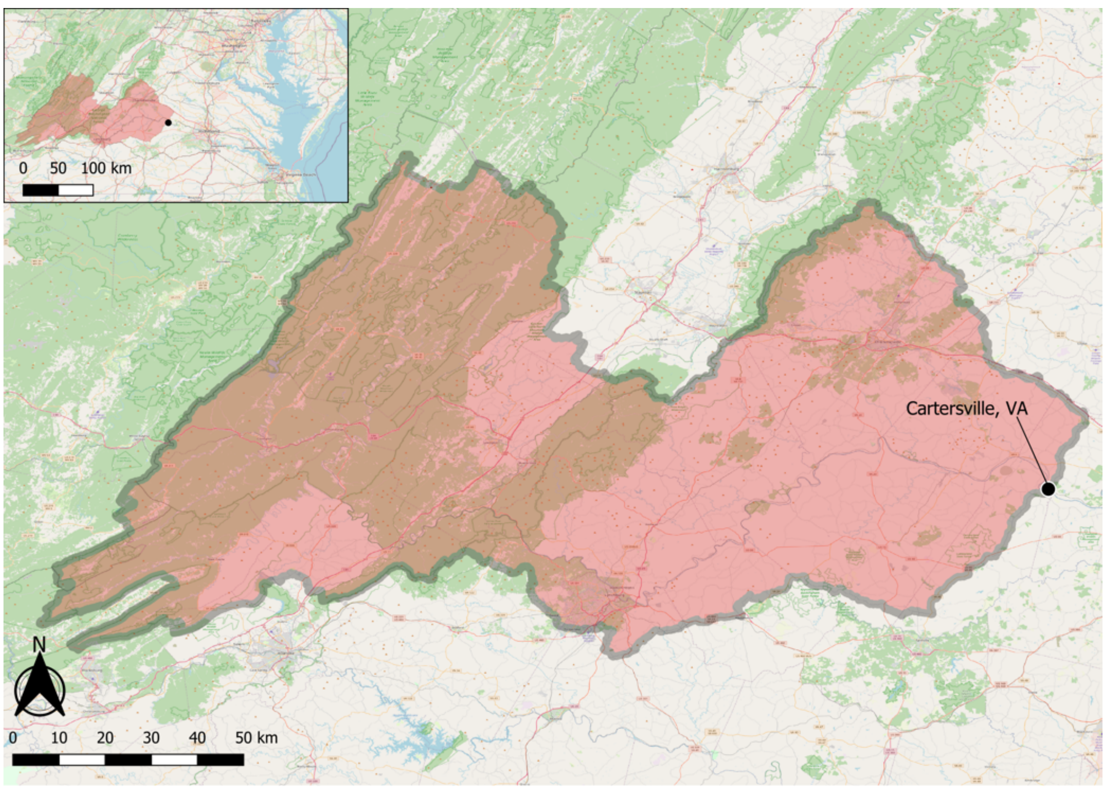

Figure 1. Map of study-site watershed (red area). Black dot indicates the sampling location for data analyzed in this study - "James River at Cartersville" USGS station.

Data & Data Manipulation

For the heatwave analysis I used high frequency (i.e., 15-minute) water temperature observations collected over a 16-year period (Oct 2007- Sept 2023). The water temperature time series were accessed using the dataRetrieval R package version 2.7.13 (De Cicco et al. 2023) and further analyzed using the R environment for statistical computing (R Core Team 2023). While the length of this data is on the lower end of the acceptable range for calculating heatwaves, sensitivity studies show that 10 years of data is acceptable for this type of analysis (Schlegel et al. 2019). Missing data from the high frequency time series was filled by linear interpolation for gaps ≤ 6 hours. Daily means were derived from the high frequency observations when ≥ 75% of a day's observations were available. Linear interpolation was then performed on the low frequency (i.e., daily) data for gaps ≤ 2 days.

For the metabolism analysis I also used high frequency water temperature data in addition to high frequency dissolved oxygen (mg L^{-1}), depth (m), and discharge ($m^3 s^{-1}$) data from USGS for an 11-year period (Apr 2012– Sept 2023). Additionally, photosynthetically active radiation (PAR) data were needed for the metabolism analysis, which were obtained from the National Estuarine Research Reserve System (NERRS) Taskinas Creek station which is ~130 km from Cartersville (NOAA 2024). While these PAR data are relatively far from Cartersville, they represent the closest and best PAR time series that is publicly available. PAR data flagged as "suspect" were removed prior to analysis. PAR data were accessed using the NERRS Centralized Data Management Office's Data Export System (https://cdmo.baruch.sc.edu/). Similar to the water temperature data from the heatwave analysis, linear interpolation was performed over gaps ≤ 6 hours on the dissolved oxygen, depth, discharge, and PAR data.

While USGS provides a continuous measure of gage height at Cartersville, depth is needed for the metabolism model (described below). To estimate depth at 15-minute intervals, a second order polynomial regression model was created from the relationship between historic gage height and depth (channel area divided by channel width) data provided by USGS (Figure 2). This model was then applied to the continuously monitored gage height at Cartersville to create a continuous depth time series.

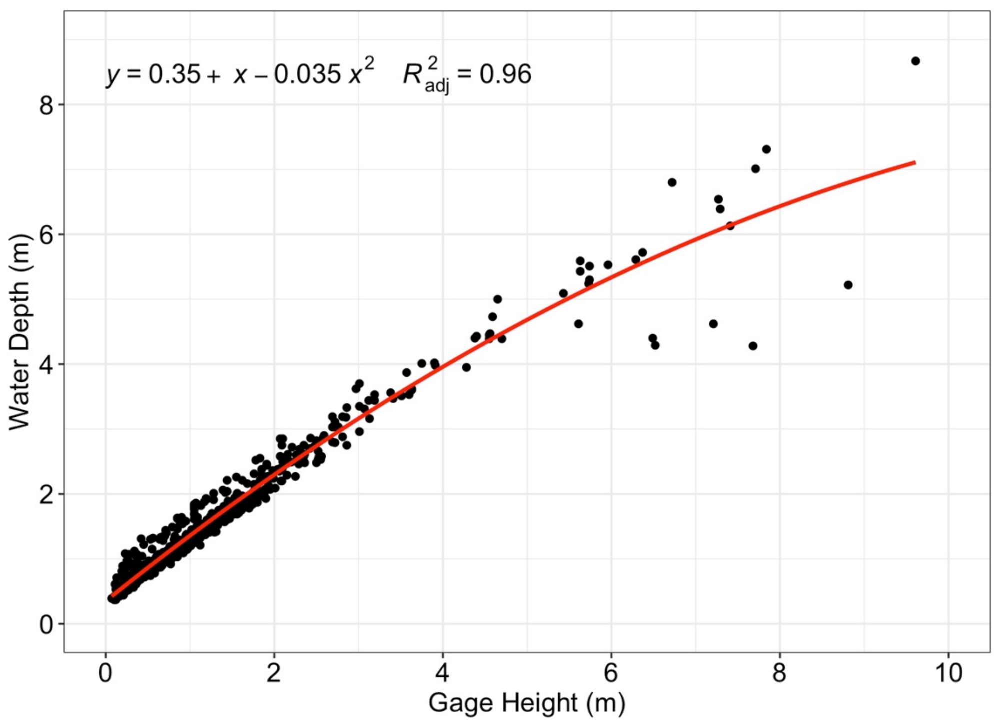

Figure 2. Model used to determine depth (m) using historic depth and gage height (m) data from the USGS Cartersville station. This equation was applied over the time series to estimate water column depth from directly measured gage height.

Heatwave Analysis

The R package heatwaveR (version 0.4.6) was applied to identify riverine heatwaves and their characteristics (i.e., total number of heatwaves per year, heatwave duration, and heatwave magnitude; Schlegel and Smit 2018). This package identifies heatwaves according to the Hobday et al. (2016) definition as periods in which daily mean water temperature is > the 90^{th} percentile for ≥ 5 days. The package also defines heatwave characteristics for each event, including severity. Heatwave severity ranges among moderate, strong, severe, and extreme and is determined using the peak magnitude of water temperature during the heatwave and by multiples of the difference between the climatological norm and the 90^{th} percentile (Hobday et al. 2018). Each identified heatwave was further classified according to the season in which it occurred (i.e., summer = June to August, fall = September to November, winter = December to February, and spring = March to May), in accordance with similar studies (Caffrey 2004; Lau and Nath 2012; Tassone et al. 2022b).

To account for departures from normal seasonal variability in discharge, I determined the residual discharge for each day. Daily mean values for discharge were downloaded for the same 16-year period (Oct 2007- Sept 2023) as water temperature. There were no missing values in this dataset, eliminating the need to perform interpolations on the daily mean discharge data. Residual discharge was determined as the difference between expected discharge and observed discharge, where expected discharge was derived using the heatwaveR package in R (according to methods in Tassone et al. 2022a).

Metabolism Analysis

Diel dissolved oxygen (DO) dynamics were used to estimate rates of ER and GPP. During the day, DO rises due to photosynthesis exceeding respiration. At night, DO declines due to respiration in the absence of photosynthesis. This oscillation continues daily but DO concentration and magnitude of the cycle may vary between days. The loss of DO at night (ER_n) is used to estimate respiration over the 24-hour period. GPP is estimated by the accumulation of DO during the day plus ER_n.

To determine ecosystem metabolism, the streamMetabolizer R package (version 0.12.1) was utilized (Appling 2018a). This program requires time series input data (described below) in addition to prior values for GPP and ER. I used the default, minimally informative prior values found in the sample code provided by the streamMetabolizer R package for the sample dataset (Appling et al. 2018a), which were: GPP = 3 ± 2 g O_2 m^{-2} d^{-1} and ER = -7.1 ± 7.1 g O_2 m^{-2} d^{-1}. These values are referred to as prior probabilities and are used with the measured input data to apply the Bayesian method where estimates of GPP and ER are obtained from the posterior distribution, which is proportional to the probability of the measured input data considering the prior estimates (Hobbs and Hooten 2015; Hall et al. 2016; Tassone and Bukaveckas 2019).

The Bayesian model estimates GPP and ER for each day using observed oxygen concentrations, oxygen saturation determined from water temperature, light determined from PAR, and depth estimated from the gage-height to depth relationship. The model's fundamental equation from Appling et al. (2018b) solves for the rate of change of oxygen over time by determining the combination of GPP, ER, and gas exchange (K600) that fit the daily cycle of oxygen as follows:

$$dO_{id}/dt = (GPP_d/z_d \times (PAR_{id}/PAR_d)) + (ER_d/z_d) + f_{id}\,(K600_d)(Osat_{id} - O_{id}) \quad [1]$$

where dO_{id}/dt is the rate of change of oxygen concentration with respect to time at any time step i (15 minutes in my study) for a specified day d; GPP_d and ER_d are the daily estimated values in g m^{-2} d^{-1}; z_d is the daily mean river depth in meters; PAR_{id} is the photon flux over the time step

(i) of the specified d in mmol m^{-2} sec^{-1}; PAR_d is the average photon flux in the same units over the day; $Osat_{id}$ is the oxygen saturation if air and water are in equilibrium, K600 is the gas exchange coefficient in meters per day, and f (K600) is a function to determine gas exchange with respect to oxygen and temperature (Appling et al. 2018b). The three unknowns, GPP, ER, and K600, are estimated using a Hamiltonian Monte-Carlo method to determine the best fit for measured and modeled oxygen over the daily cycle (Appling et al. 2018a,b). The fitting process used 1000 burn-in steps and 500 saved steps for each daily estimation (Appling et al. 2018a,b).

Statistical Analysis

The metabolism analysis produced daily estimates of GPP and ER. Consistent with other studies, some estimates produced negative rates of GPP and positive rates of ER, which are theoretically impossible (Appling et al. 2018b; Pace et al. 2021). Of the 3722 metabolism values estimated by streamMetabolizer, 24% of GPP and 15% of ER values were non-real numbers. These values occur because diel cycles of oxygen are altered by rapidly changing river conditions such as shifting discharge and/or storm passage. Non-real numbers from the metabolism data output were removed based on conditions used in other studies (Appling et al. 2018b); GPP values $-0.5 < x < 0$ were converted to 0 and GPP values < -0.5 were converted to NAs. Similarly, ER values $0.5 > x > 0$ were converted to 0 and ER values > 0.5 were converted to NAs (Appling et al. 2018b).

One obvious outlier was flagged from the respiration data output (-73.03 g O_2 m^{-2} d^{-1}), as it was almost three times higher than the next greatest value (-25.54 g O_2 m^{-2} d^{-1}). This extreme ER value occurred during a flooding event, and while it may represent a true value, it was 20 standard deviations greater than the mean and was therefore removed to avoid skewing the data.

After suspect data removal, daily NEM was calculated, where ER is expressed as a positive value (Eq. 2).

$$NEM = GPP - ER \qquad [2]$$

To test for the effects of heatwaves on metabolism, data were organized into categories (non-heatwave, moderate heatwave, severe heatwave). One-way ANOVA and Tukey post-hoc tests were performed to test if metabolism parameters (GPP, ER, NEM) were significantly (p-values < 0.05) different among heatwave categories. Linear regressions were conducted for daily mean water temperature vs log transformed GPP and ER and log transformed daily mean discharge vs log transformed GPP and ER.

Results

Heatwaves

There were 40 heatwaves over the 16-year span of this study (Oct 2007- Sept 2023; Figure 3). The average (± standard deviation) frequency of heatwaves was 2 ± 2 events year^{-1} and ranged up to 5 events year^{-1}. Similarly, the average duration and max intensity of a heatwave was 8 ± 3 days and 5.22 ± 1.36 °C. Only moderate and strong heatwaves were observed, comprising 70% and 30% of the total observed events, respectively. Overall, 28 moderate heatwaves were observed for a total of 187 days and 12 strong heatwaves were observed for a total of 115 days. The majority of heatwaves occurred in the summer (32%), followed by winter (28%), fall (25%), and spring (15%). There were no statistically significant linear trends for the annual total heatwave days per water year or annual frequency of heatwaves per water year (both p-values > 0.05).

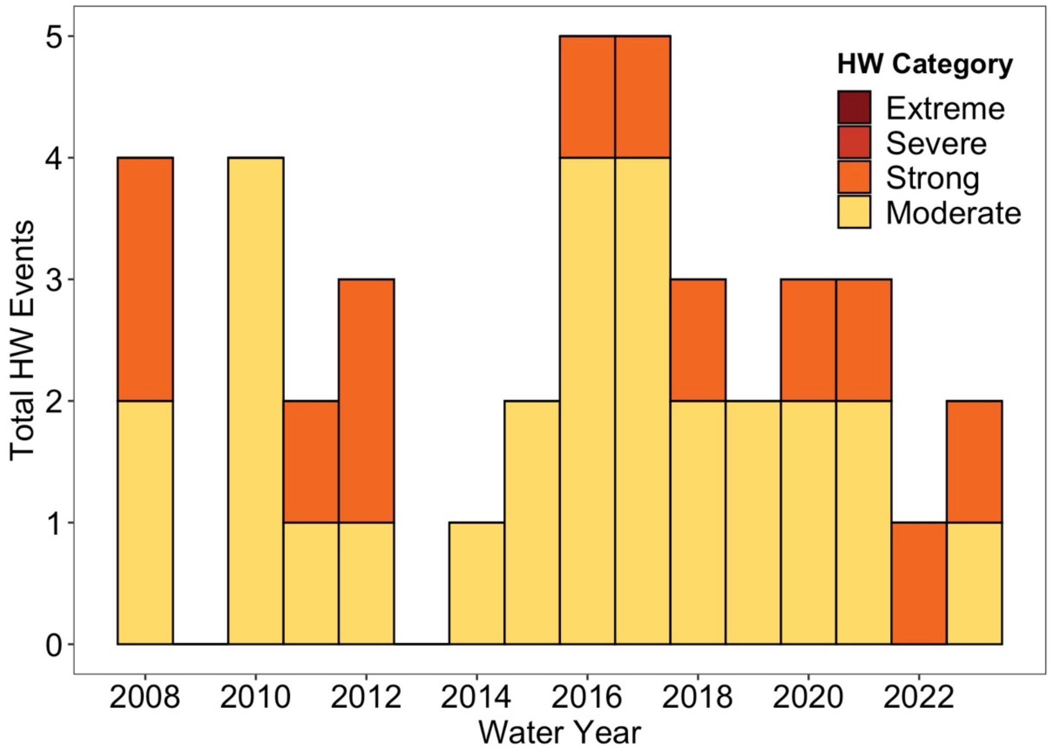

Figure 3. Total number of heatwave (HW) events per water year. Yellow bars represent moderate heatwaves and orange bars represent strong heatwaves. Extreme and severe heatwaves were not observed in this study. No heatwaves occurred in the years 2009 and 2013.

Residual discharge was calculated to determine if heatwaves are more likely to occur during periods of low discharge compared to expected discharge conditions. For all months except January, the median residual discharge during heatwaves was less than zero and for most months the upper 95th percentile of the distribution was below zero. Thus, heatwaves tend to occur during low discharge except in November through January (Figure 4).

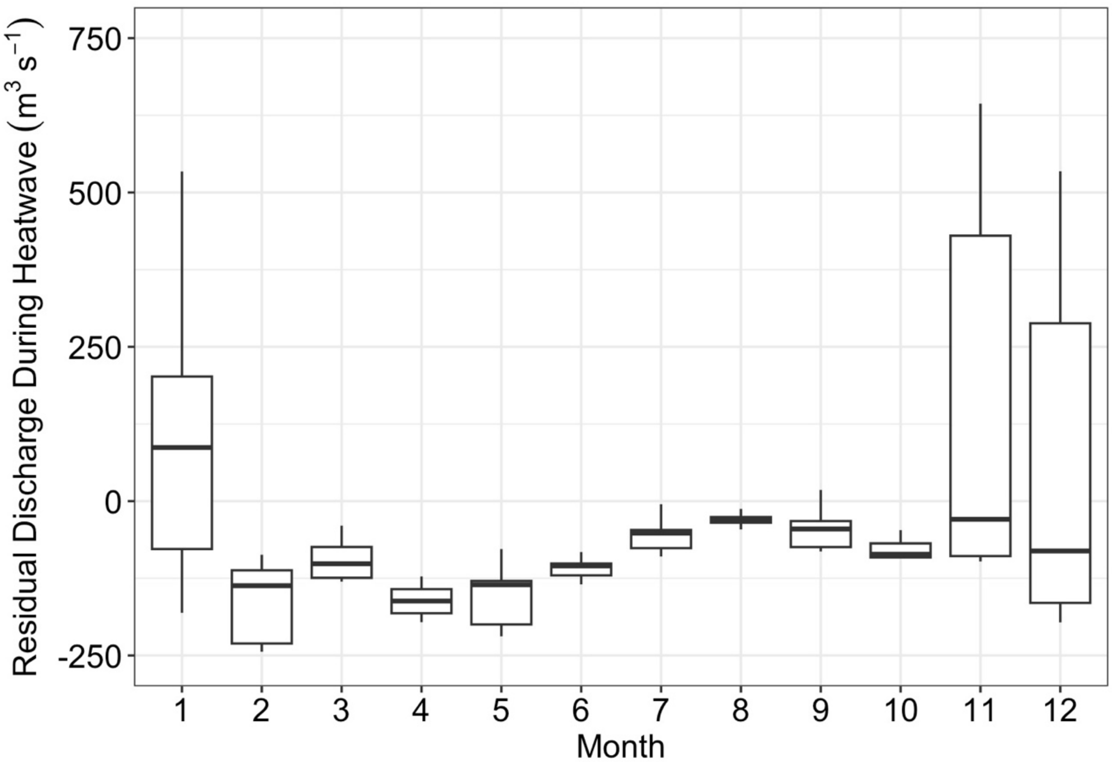

Figure 4. Daily average residual discharge during heatwave events. The median value is the dark line within the distribution, box ends are the 25th and 75th percentiles, and lines extending from the boxes indicate the 5th and 95th percentiles.

Physical, Chemical, and Hydrological Site Conditions

Discharge is variable in the James River at Cartersville with flood (or high discharge events) occurring episodically, and low discharge typically associated with the warmest periods of the year (Figure 5). In contrast with discharge, water temperature, dissolved oxygen, and light have pronounced and regular seasonal cycles (Figure 5). The inverse pattern of water temperature and dissolved oxygen reflects the greater solubility of oxygen in cold water (Zhi et al. 2023). Similarly, water temperature is inversely related to discharge. Discharge is generally lower during summer months due to increased rates of evapotranspiration resulting in lower run-off (Bukaveckas 2009).

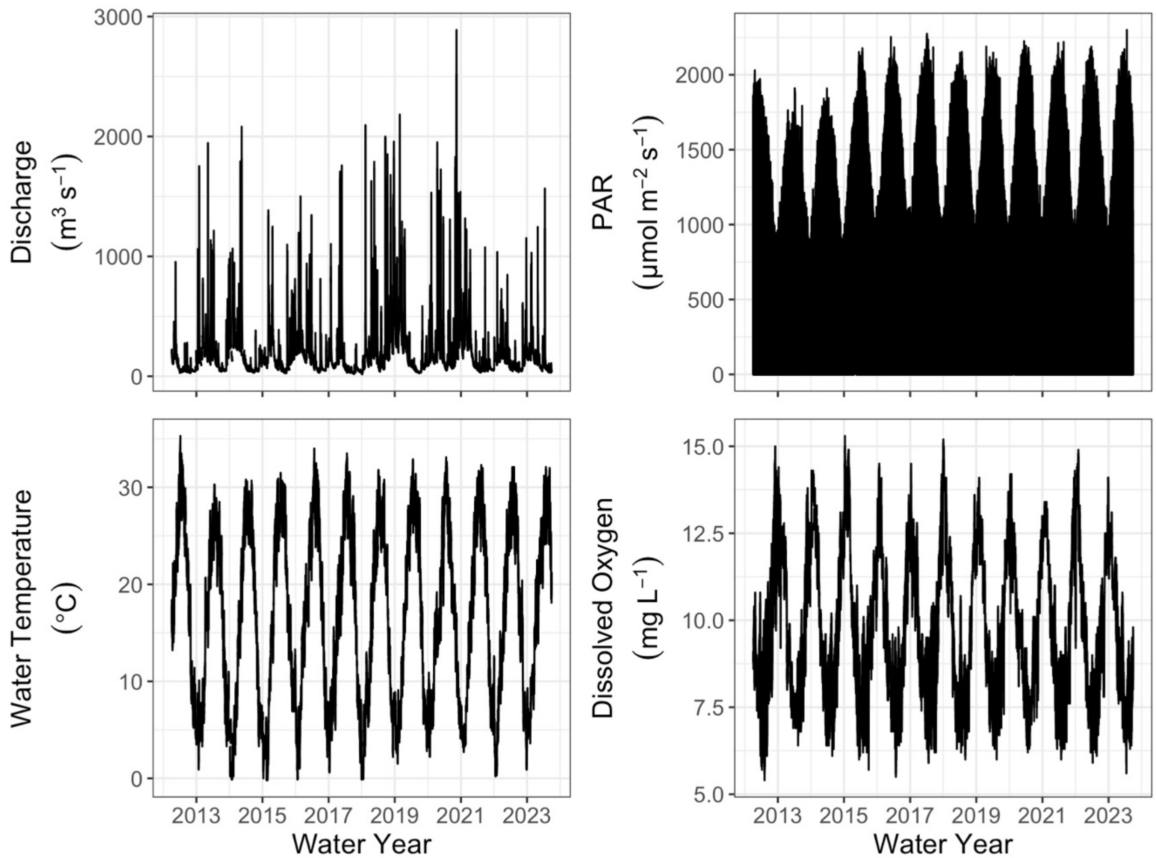

Figure 5. High-frequency observations of discharge (top left), water temperature (bottom left), PAR (top right), and DO (bottom right) over the water years of 2012 to 2023.

Are Metabolic Rates Different During Heatwaves?

GPP and ER followed seasonal patterns in water temperature and PAR (Figure 6). Daily rates of ER were on average 3x greater (mean = -3.14 ± 2.92 g O_2 m^{-2} d^{-1}) than GPP (mean = 0.70 ± 0.98 g O_2 m^{-2} d^{-1}; Table 1). Note that ER represents oxygen consumption, so it is expressed as a negative number. The standard deviation was approximately the same magnitude as the mean, indicating substantial variability of the rates (Table 1). Ranges were also large especially for ER and NEM (Table 1). Daily average NEM was -2.41 ± 2.88 g O_2 m^{-2} d^{-1} indicating this section of the James River was predominately net heterotrophic (66% of the time over the study period or 2751 days out of 4198 total days). Linear regressions between log transformed metabolic parameters (i.e., GPP and ER) and daily mean water temperature and daily mean log transformed discharge were highly significant (p-values ≤ 0.001) but had low explanatory power ($R^2 < 0.20$). Gas exchange was high for the James River at this location (mean 3.78 ± 1.99 m d^{-1}) as expected for rivers due to the quickly moving and relatively shallow water (Raymond et al. 2012).

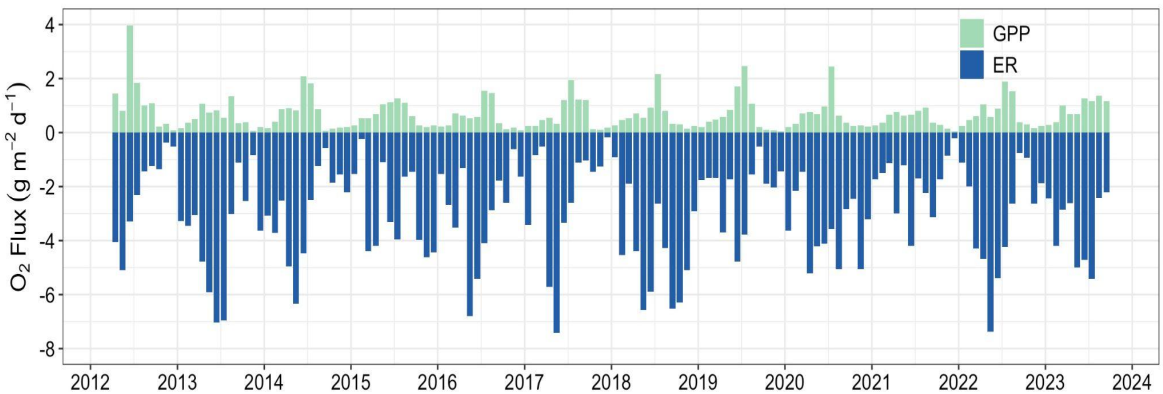

Figure 6. Average monthly rates of GPP (green, top) and ER (blue, bottom) after the outlier and non-real data were removed. ER values are generally much greater than GPP values, indicating a net heterotrophic system.

Table 1. Summary statistics for output metabolism data from streamMetabolizer. These values were calculated after the outlier and non-real data were removed. A negative mean NEM indicates the system is net heterotrophic.

Metabolism Parameter	Mean	SD	Range
GPP (g O_2 m^{-2} d^{-1})	0.70	0.98	10.63
ER (g O_2 m^{-2} d^{-1})	-3.14	2.92	25.54
NEM (g O_2 m^{-2} d^{-1})	-2.41	2.88	31.61

Daily mean GPP during non-heatwave conditions was 0.70 ± 0.96 g O_2 m^{-2} d^{-1} which was significantly lower than GPP during moderate heatwaves (1.01 ± 1.30 g O_2 m^{-2} d^{-1}, p-value

= 0.003, Table 1, Figure 7). GPP during strong heatwaves was low (0.49 ± 1.13 g O_2 m^{-2} d^{-1}) and was significantly lower than moderate heatwave conditions (p = 0.002, Figure 7) but was not significantly different from non-heatwave conditions. ER and NEM were not significantly different during heatwave and non-heatwave conditions or during moderate versus strong heatwave conditions (Figure 7).

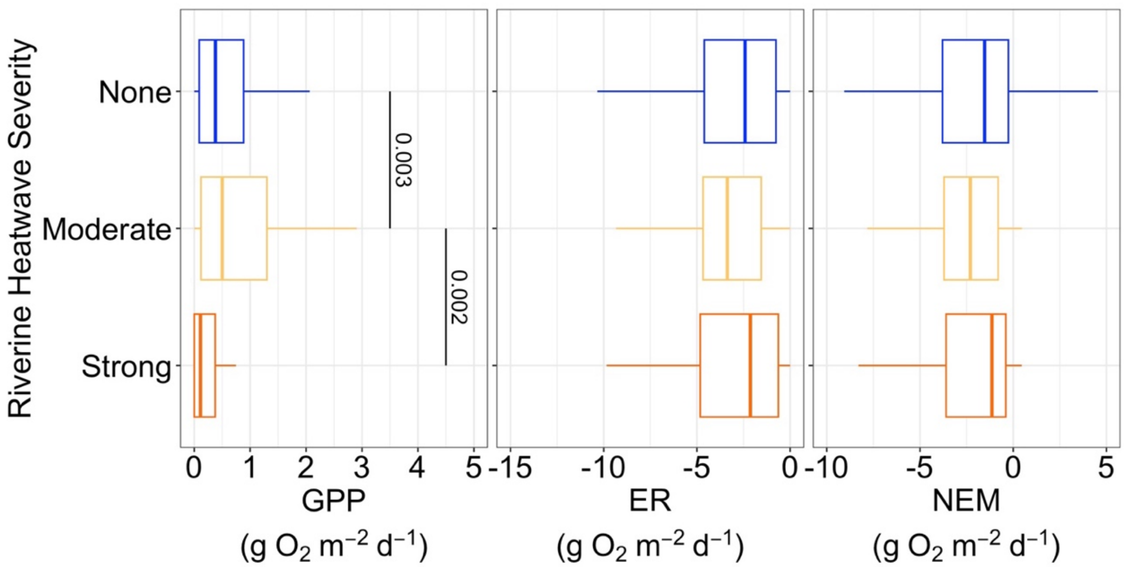

Figure 7. Riverine heatwave conditions by metabolic variable. Baseline (no heatwave) conditions are in blue, moderate heatwaves are in yellow, and strong heatwaves are in orange. GPP significantly increased during moderate heatwaves ($p < 0.05$) and significantly decreased during strong heatwaves compared to moderate heatwaves ($p < 0.05$). There were no other significant differences.

Discussion

Riverine heatwaves affect gross primary production but do not impact the other components of ecosystem metabolism for the James River study site (Figure 7). There are several possibilities for the positive effect on GPP during moderate heatwaves. Higher temperatures are associated with lower discharge (Tassone et al. 2022a; van Vliet et al. 2023) and therefore greater water clarity, which could facilitate photosynthesis until it becomes light-limited by depth (Bernhardt et al. 2018). Also, low discharge facilitates the buildup of attached algae, as scouring from surfaces is reduced (Bernhardt et al. 2018). Additionally, moderate heatwaves may create an advantageous thermal range for primary producers, but as heatwaves become more severe GPP would be expected to decrease due to thermal stress on primary producers (De Stasio et al. 2009; Smale et al. 2019; Filbee-Dexter et al. 2020; Tassone et al. personal communication 2024). This hypothesis was partially supported by my results, as it was observed that GPP during strong heatwaves was significantly lower than GPP during moderate heatwaves (Figure 7). This result suggests stronger heatwaves may exceed thermal tolerances and therefore suppress GPP (Figure 7; Joint and Smale 2017). Other studies have found rising temperatures have a stronger effect on ER compared to GPP (Demars et al. 2011; Song et al. 2018), which did not occur in this case. While I did see an increase in the median rate of respiration during moderate heatwaves compared to non-heatwave conditions, this increase was not statistically significant. However, more data would be needed to confirm this difference in results. The general lack of statistically significant differences for ER and NEM could be due to the low sample size (i.e., 5844 non-heatwave days compared to 187 moderate heatwave days and 115 strong heatwave days). Other studies have suggested that strong heatwaves can negatively affect primary producers (Smale et al. 2019; Aoki et al. 2021; Filbee-Dexter et al. 2020) thereby causing aquatic systems to become net heterotrophic (Berger et al. 2020). Overall, my results provide evidence that moderate riverine heatwaves can affect aquatic metabolism by increasing rates of GPP.

Like many rivers, the James at Cartersville had a negative mean NEM (GPP < ER), signifying this system was net heterotrophic (Table 1; Figure 6; Cole and Caraco 2001; Demars et al. 2011; Munn et al. 2023). The differences between ER and GPP (NEM) were similar to those found in a study of metabolism from the James River Estuary below Richmond where phytoplankton blooms occur in summer (Tassone and Bukaveckas 2019). However, ER and GPP were lower at Cartersville, as would be expected for riverine systems compared to their wide and shallow estuarine equivalents (Tassone and Bukaveckas 2019).

Heatwaves were associated with low-flow conditions, as the monthly median residual discharge during heatwaves was < 0 for most months of the year (Figure 4). Droughts can amplify temperatures (Tassone et al. 2022a; van Vliet et al. 2023) and thus lead to heatwave conditions. January was the only month in which the median residual discharge during heatwaves was > 0. This could be because the lack of evapotranspiration in the watershed coupled with episodic heavy precipitation in winter leads to high surface and groundwater flow (Bukaveckas 2009). The large variability of residual discharge during heatwaves for November-January suggest high variability in discharge temperatures for these months.

Of the 40 observed heatwaves, 70% were of moderate severity. While strong heatwaves were also observed (30%), no severe or extreme events occurred during the years of this study at the Cartersville location, thereby limiting my ability to assess impacts of all heatwave severity classifications on metabolism (Figure 3). Other studies have considered the seasonality of heatwave events, citing that the most severe riverine heatwaves tend to take place during winter (Tassone et al. 2022a). Of the top ten percent most intense heatwaves in the present study ($n = 4$), 50% occurred in winter, 25% in summer and 25% in spring. Additionally, most heatwaves were observed in the summer, similar to prior observations (Tassone et al. 2022a). The total annual heatwave days and annual frequency do not appear to be increasing over time ($p > 0.05$) as might be expected due to climate warming (Tassone et al. 2022a; Zhu et al. 2024). However, the relatively short 16-year time series may be insufficient for observing effects of climate warming on heatwaves. Additionally, other studies have found non-significant trends in heatwave duration over time (Tassone et al. 2022b).

This study had several limitations including 1) the length of the times series for analysis of heatwaves, 2) uncertainties in metabolism estimates, and 3) the need to use data from other locations because not all the necessary data were available at Cartersville. Water temperature and DO time series only overlapped for 11 years which is a relatively short period for identifying heatwaves and associated effects on metabolic processes. While I had thousands of daily estimates of GPP, ER, and NEM, there were only 40 heatwaves over the record, with each heatwave lasting on average 8 ± 3 days. More heatwaves, including those in the severe and extreme categories, would have allowed a fuller analysis of effects on metabolism. A second concern is that metabolic estimates based on diel oxygen cycles are relatively imprecise (Appling et al. 2018a; Pace et al. 2021). Other processes besides photosynthesis and respiration affect oxygen concentrations, and these can be difficult to account for. Some examples include air-water gas exchange, photochemical oxygen consumption, unaccounted inputs and losses (e.g. lateral or hyporheic flows) and variable inputs (and losses) of oxygen relative to the measurement footprint of the sensor (Reichert et al. 2009; Pace et al. 2021). In this study I estimated air-water gas exchange by statistical fitting whereas there are process models that allow direct estimation (Dugan et al. 2016). Overall, unmeasured processes and random variation including rapid changes in river conditions that alter oxygen concentrations independent of biological production and consumption are likely to contribute to the observed negative values of GPP and positive values of ER. Regardless, more constrained and precise estimates of rates would facilitate testing for the effects of conditions like heatwaves. A third specific limitation for my study was that PAR data were not available for the study location. I used data from a site about 130 km from Carterville, which may represent the general area well but may not account for local variability in light conditions (e.g., due to variable cloud passage).

Despite the limitations of my study, a significant increase in GPP under moderate heatwave conditions is an important finding and can provide insight for how aquatic ecosystems will function under climate change. Future studies should build on this result and consider additional sites and longer times series that incorporate more heatwaves to facilitate within and among-site analysis of results. Additionally, because severe and extreme heatwave events were not observed during this study, considering systems that have a history of severe and extreme heatwaves is necessary to further understanding of how extreme climatic events will impact ecosystem functioning. Given what was found in this study, an increase in GPP during moderate heatwaves with no significant change in ER means more CO_2 will be removed from the system while inputs of photosynthetically produced O_2 will be elevated.

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