

THESIS

ANALYZING LONGITUDINAL PATTERNS OF RIVER METABOLISM IN FIVE  
DISTINCT RIVERS

Submitted by

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## ABSTRACT

### ANALYZING LONGITUDINAL PATTERNS OF RIVER METABOLISM IN FIVE DISTINCT RIVERS

The River Continuum and Serial Discontinuity Concepts are two common frameworks or theories to describe river ecosystem structure and function. While these concepts help explain how rivers should behave, the reality is that aquatic ecosystems are being changed and degraded due to dams which regulate flow and changes to land use and land cover that can negatively impact aquatic ecosystems. Ecosystem metabolism is an increasingly common way to monitor and assess river health and functioning. This analysis is a data synthesis to examine longitudinal coherence in productivity patterns and identify the strongest controls that disrupt coherence. I find that between discharge, dissolved oxygen, and metabolism, metabolism is the least predictable variable going downstream regardless of land use and river characteristics, but at the same time did show patterns consistent with the expected patterns of the River Continuum Concept or other theories of river function variation. This lack of coherence and predictability in river metabolism across sites within rivers highlights effects monitoring methods, river-specific characteristics, and the overall lack of satisfactory theories for how larger rivers behave, despite an abundance of riverine theories.

## ACKNOWLEDGEMENTS

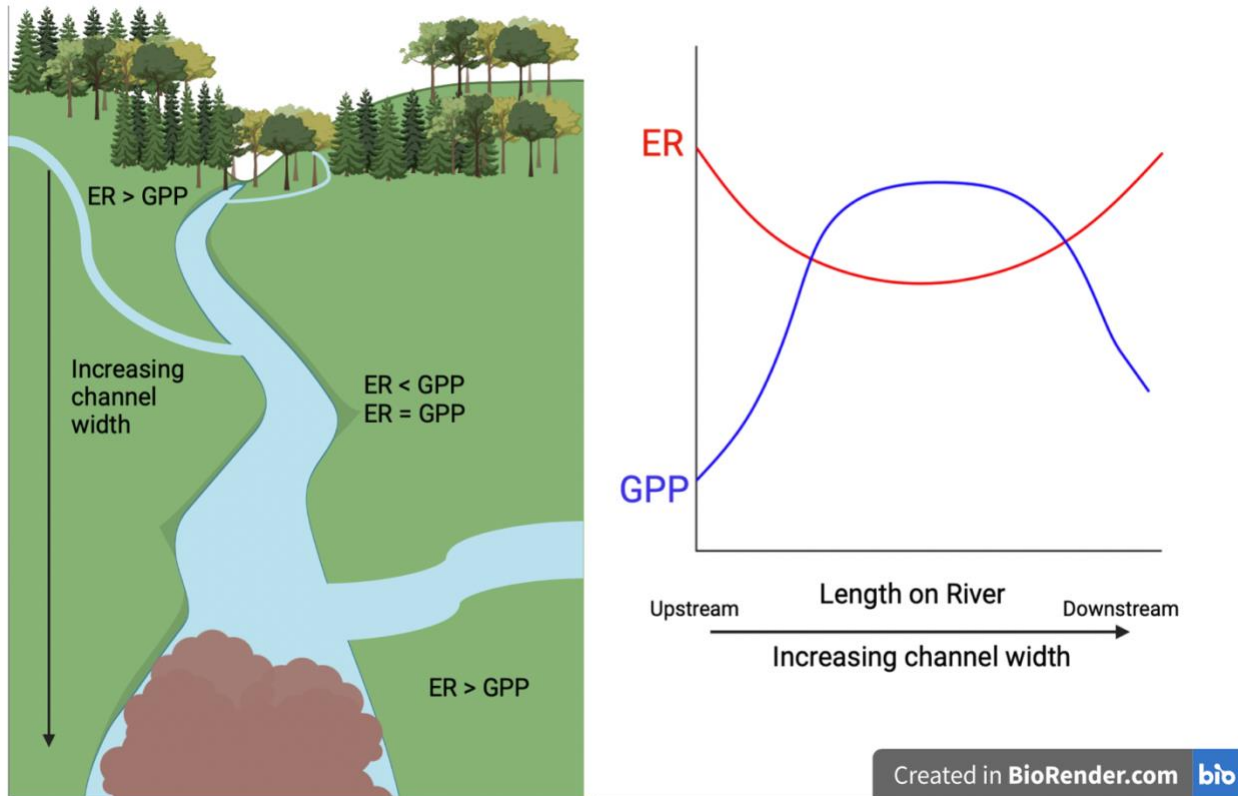
I would first like to thank my advisor, Matt Ross for all his help and mentorship throughout this analysis and grad school as a whole, as well as my committee, Kelly Wrighton and Tim Covino, for their insight and knowledge. I also want to thank the Graduate Degree Program in Ecology, Natural Resource Ecology Laboratory, and Ecosystem Science and Sustainability communities for help and friendship in this analysis, fieldwork, and general support. I am also extremely grateful for the scientists who contribute to, support, and maintain the StreamPULSE data repository which I used to carry out this analysis- all metabolism related datasets were provided by the StreamPULSE Network, with funding provided by the National Science Foundation Macrosystems program (NSF Grant EF-1442439). Finally, I want to thank my family for all their help and support in whatever I pursue.

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## Introduction

One of the most foundational theories in river ecology is the river continuum concept (RCC), which makes predictions about river functions like primary productivity and respiration based on river width, geomorphology, and consequently, light availability in the water column and benthos (Vannote et al., 1980, fig. 1). According to the RCC, headwaters are shaded by riparian vegetation, limiting both water-column (pelagic) and riverbed (benthic) primary productivity and so in these small streams, the primary source of carbon (and therefore energy) in the system doesn't come from autochthonous primary producers (Feminella et al., 1989; Lamberti & Steinman, 1997) but instead is transported into streams and rivers from riparian and hillslope vegetation (Covino, 2017; Pacific et al., 2010; Stieglitz et al., 2003). These streams then have respiration rates that exceed primary production rates, making them heterotrophic systems that are almost always supersaturated in the products of aerobic respiration, CO<sub>2</sub> (Cole et al., 2007). The RCC predicts that as a stream flows through the landscape and tributaries contribute more water, the channel grows and becomes wider. These mid-sized rivers sections experience higher light penetration due to wider channels and decreased shading, providing conditions for higher primary production rates, which eventually exceed respiration rates (McTammany et al., 2003) flipping the system to one dominated by external, allochthonous carbon inputs to one where most of the energy comes from autochthonous carbon production (Kautza et al., 2016). Finally, the RCC predicts that as mid-sized streams continue to flow down the landscape, they continue to pick up debris, eventually reaching much wider widths but also entraining large amounts of sediment which blocks light, preventing high rates of primary productivity, switching the system to one dominated again by external inputs and respiration (Gardner et al., 2020).



**Fig 1.** What the river continuum concept (Vannote et al., 1980) predicts productivity to be longitudinally.

Selected supporting citations:

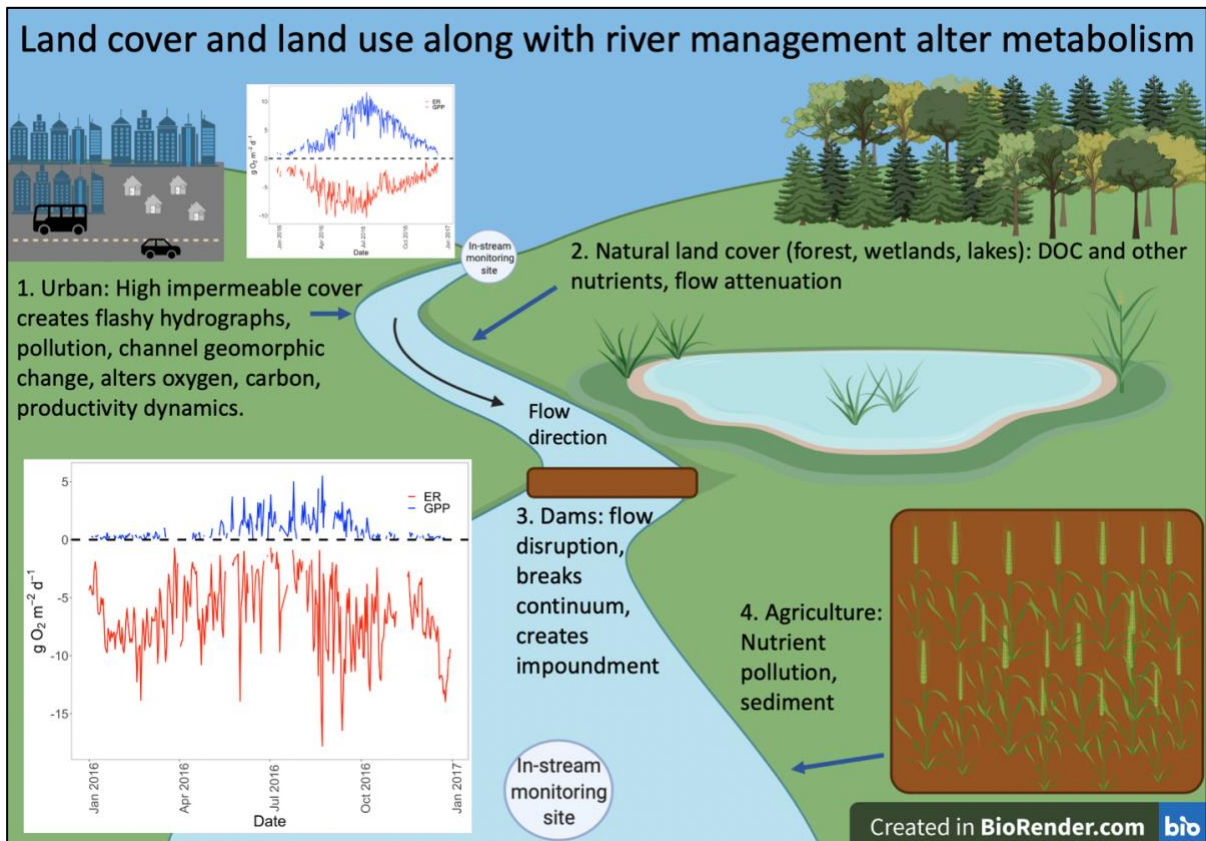
1. ER > GPP in headwaters due to shading and terrestrial carbon: Feminella et al., 1989; Lamberti & Steinman, 1997; Covino, 2017; Pacific et al., 2010; Stieglitz et al., 2003
2. ER < GPP or ER = GPP in middle reaches due to channel widening and less shade: McTammany et al., 2003; Kautza et al., 2016).
3. ER > GPP downstream due to tributary contributions: Gardner et al., 2020

This basic framework is useful for assessing patterns of ecosystem functioning, for example whole-ecosystem metabolism. River metabolism, the balance between the rates of GPP (gross primary production) and ER (ecosystem respiration) are measured in  $O_2$  in  $g\ m^2\ d^{-1}$ . Early measurements of river metabolism (Odum, 1956) involved sampling rivers every 2-4 hours and manually analyzing dissolved oxygen (DO) patterns to extract metabolic rates. This is much easier now, with advances in data collection and modeling, making it much possible to analyze metabolism patterns at scale (Appling, Hall, et al., 2018). Metabolic rates and regimes in river ecosystems are constrained by light, temperature, flow regimes, and allochthonous inputs, and

these are all parameters that can be affected by land cover and dams in a river. Combining understanding of ecosystem metabolism and the RCC has paved the way for additional work on the relationships between channel size, light regimes, and consequent patterns in productivity, highlighting the importance of spatial scale and temporal scale. Specifically, simulations of river network primary production have highlighted that despite predictions from the RCC, small streams can dominate whole-river network-scale productivity (Koenig et al., 2019), because they cover so much more area than large rivers. Additional data synthesis of rivers covering a large spatial scale have uncovered distinct metabolic regimes in the spring and summer related to stream geography such as temperature, watershed area, and discharge (Savoy et al., 2019). Advancements in modeling have affirmed, and built on these concepts, by examining the dynamic shading impacts of canopy cover (Savoy et al., 2021) and how sediment and turbidity interact with shade regimes to control primary productivity (Savoy & Harvey, 2021).

Some of this work highlights a central problem in the river continuum concept, which operates on the assumption that rivers are an uninterrupted continuum, ignoring the fact that for the past 100-plus years rivers have been altered by dams for water supply (Song et al., 2021) and have long been undergoing watershed land cover change (fig. 2), affecting water quality (Stets et al., 2020) and hydrology (Schilling et al., 2008). Additional impacts to river function include other factors like climate change and population growth (Vörösmarty et al., 2000). For example, in the U.S., there are an estimated 91,000 dams, including about 75,000 large dams, impounding 600,000 mi (970,000 km) of river or about 17% of U.S. rivers (National Wild and Scenic Rivers System, n.d.; U.S. Army Corps of Engineers, 2007).





**Fig 2.** The reality of river ecosystems: changes to watershed land use and land cover as well as dams affect metabolism patterns in rivers.

Selected citations:

1. Urban: Walsh et al., 2005; Blaszcak et al., 2019; Kaushal & Belt, 2012; Larsen & Harvey, 2017
2. Natural land cover: Jones, 2010; Euliss et al., 2004; Lottig et al., 2013; Roebuck et al., 2019; Bunn et al., 2003
3. Dams: Song et al., 2021, Ward & Stanford, 1983; Davis et al., 2012; Engel et al., 2019; Carter et al., 2021
4. Agriculture: Carpenter et al. 1998; Dubrovsky et al. 2010; Griffiths et al., 2013; Hagen et al., 2010

River ecologists have long understood that these dams disrupt longitudinal connectivity and have conceptualized dam impacts to river function in a variety of ways including the Serial Discontinuity Concept (SDC, (Ward & Stanford, 1983)). This theory highlights that dams have the potential to have a major effects on river biological, chemical, and physical processes. For example, dams trap sediment, which decreases downstream turbidity and allows for increased light penetration and therefore primary productivity downstream of dams (Davis et al., 2012).

They can also prevent coherent longitudinal patterns in river metabolism (Engel et al., 2019), or can blur the separation between lotic and lentic settings, slowing water down enough to prevent aeration and induce hypoxia in reaches impacted by dams (Carter et al., 2021).

In addition to changes in the river itself, the watersheds that these rivers drain also experience human-induced change and impacts from the natural environment—in fact, specific land-cover types likely require specialized concepts and frameworks to account for the unique impacts and deviance from the RCC. For example, urbanization in watersheds consistently results in river degradation, known as the “urban stream syndrome”, with symptoms including flashy hydrographs due to increased impervious surfaces, increased import of nutrients and other pollutants, and channel geomorphic change, which leads to decreases in species richness, and increases in species that are tolerant to the changes in the ecosystem (Walsh et al., 2005). These symptoms have been shown to have detrimental impacts in river ecosystems: flashy hydrographs and the low flows afterwards between storm events, together with river channel morphology, have been shown to control oxygen patterns by 1) inducing hypoxia because of low and stagnant flows in low-slope, pool-like reaches or 2) flushing out photosynthetic organisms during flashy events, in both cases decreasing primary productivity (Blaszczak et al., 2019). Urbanization creates a unique continuum that deviates from the assumptions in the RCC because it can’t account for important interactions between urban hydrologic infrastructure and the natural environment, and efforts in developing an urban-specific theory exists as the urban watershed continuum (Kaushal & Belt, 2012). This theory provides a framework of how hydrologic networks in urban areas have a combination of engineered and natural flow paths which can impact carbon and nutrient cycling, transport, and storage throughout the watershed. Specific to metabolism, it has been found that ER is limited due to intense flashy flows that act as a disturbance and flush allochthonous carbon out of the system (Larsen & Harvey, 2017).

Additionally, agricultural land use can also have effects on ecosystems, depending on management practices: nitrogen and phosphorus-rich fertilizers travel via soil erosion to water bodies and this nutrient loading encourages eutrophication, the excess production of algae that is followed by periods of hypoxia, which can result in fish kills and water quality concerns

(Carpenter et al. 1998). Nutrient pollution and management has long been an issue for freshwater ecosystems: a report from the U.S. Geological Survey found that as of 2004, nutrient concentrations in streams and other water sources exceed standards set for human health and aquatic life and highlighted the need for regulation and monitoring (Dubrovsky et al. 2010). With respect to ecosystem functioning, the impacts from agricultural land use has been shown to change the magnitude of metabolism, increasing the rates of both GPP and ER due to open canopy, increased nutrient concentrations, and flashiness depending on the intensity of agricultural use and the composition of other land cover in the area (Griffiths et al., 2013; Hagen et al., 2010).

Natural variation in land cover also plays an important role in river ecosystem function, and the differences in hydrologic connectivity and longitudinal variation in land cover needs to be integrated into the RCC (Jones, 2010). For example, as rivers move through landscapes rich in wetlands or lakes their metabolism and other ecosystem functions can be altered by the physical hydrology and chemistry associated to these specific land cover types. For example, wetlands can be rich in organic matter, altering the light regimes of even large rivers, a fact that the RCC does not account for, and lakes can also affect the timing and magnitude of carbon transport in systems with lakes (Euliss et al., 2004; Lottig et al., 2013; Roebuck et al., 2019). In desert and arid systems, there is little riparian vegetation, so streams rely on autochthonous carbon sources, which has been largely ignored by the RCC (Bunn et al., 2003).

With all these potential anthropogenic and natural changes to rivers as they flow from mountains to sea, it is not surprising that the RCC and other theories break down in their ability to predict river function. This is true in larger rivers that accumulate these impacts in complex, variable hydroscaapes. As such, we need more research approaches that don't analyze rivers at discrete, disconnected points, but as integrated wholes. Commonly used monitoring efforts involve surveys which cover large areas but happen sporadically throughout the year, creating temporally discontinuous datasets (Read et al., 2017; Ross et al., 2019). With advancements in sensor technology, it is now possible to install monitoring instrumentation in a network configuration that takes temporally high-frequency, and continuous measurements, at discrete

points in space (Rode et al., 2016). These types of monitoring networks allow for a deeper understanding of dominant controls on things like river metabolism (Appling, Hall, et al., 2018; Appling, Read, et al., 2018; Bernhardt et al., 2018; Savoy et al., 2019), colored dissolved organic matter (Hosen et al., 2021) and light – sediment conditions (Savoy et al., 2021). When sensors are arranged longitudinally in a basin, they can provide insight into how river ecosystems respond to human alterations such as land use and land cover changes or the construction of dams. Having this data is essential for monitoring efforts by different agencies, governments, academic institutions, and nonprofits, and is crucial in developing water quality and ecosystem models for decision-making about water resources management (Pellerin et al. 2016, Rode et al. 2016).

In this paper, I focus on analyzing longitudinal patterns of dissolved oxygen, discharge, and river metabolism, because these variables allow us to explore coherence, or lack thereof, more deeply in longitudinal patterns of riverine ecosystem function. It is becoming increasingly important to understand metabolism because of how valuable a tool it could be: metabolism gives useful insight to ecosystem stress, carbon storage, food webs, and even greenhouse gas emissions and dynamics for freshwater ecosystems (Bernhardt et al., 2018) and with further development in modeling, support for data collection and dissemination, and research involving data synthesis and experiments to identify how ecosystems respond to disturbance or pollution, metabolism has the potential to be a powerful tool for monitoring and management (Jankowski et al., 2021). To contribute to the understanding of metabolic dynamics in rivers and how they are linked to river structure, function, and disruptions, I used publicly accessible data from a variety of sources and selected five rivers across the U.S. representing unique ecosystem types to answer my overarching question: *Do rivers have consistent and predictable longitudinal patterns in productivity and respiration and if not, what are the strongest controls that disrupt these patterns?*

## Methods

## Data Collection and River Selection

### StreamPULSE and river data

I leveraged the StreamPULSE data repository for this study (Appling, Hall, et al., 2018) and identified rivers in the contiguous U.S. that had at least four monitoring sites, with each of those sites having at least one year of data including dissolved oxygen (DO), discharge (Q), and modeled metabolism. For ease of analysis along with availability of data, I only used data from 2016 for five rivers and if needed, dropped sites that were tidally influenced or more than 100 km from any upstream gage. Site arrangement within rivers is such that the most upstream site is labeled “1”, with as many numbers used for the downstream sites until all sites are labeled. Rivers were chosen to represent a range of climatic and physiographic settings, and metabolism patterns (Fig. 3, table 1). StreamPULSE metabolism model data includes GPP and ER, as well as discharge and DO so I did not undertake any additional metabolism modeling, but did remove values that are biologically impossible by setting  $GPP < 0$  and any  $ER > 0$  to NA for analysis, similarly to what was done in Savoy et al., 2019. USGS discharge, DO (if available), and the site characteristic of channel widths were collected using the “dataRetrieval” R package (de Cicco et al., 2018) to ensure data completeness. Turbidity data was the same as used in Savoy & Harvey 2021.

### River Selection

All river pictures in figures 3.2-3.5 are courtesy of the U.S. Geological Survey.

Au Sable: The Au Sable River (fig. 3.1) was chosen to represent the Northern Lakes and Forests ecoregion, located in northern Michigan and is a tributary to Lake Huron. The Au Sable River and watershed characteristics have been heavily influenced by Pleistocene glaciation and subsequent outwash resulting in permeable sand and gravel, facilitating groundwater discharge which maintains flows during periods of drought and during the summer. Flowing west to east, there are several dams in this reach, with one section 23 miles long between hydroelectric dams

Mio and Alcona designated as Wild and Scenic under the Wild and Scenic Rivers Act. Soils are nutrient-poor and land cover is dominated by coniferous and northern hardwood forests (Michigan Department of Natural Resources., n.d.; United States Environmental Protection Agency, 2013)

North Canadian: The North Canadian River (fig. 3.2) is in the Cross Timbers ecoregion. This river starts in New Mexico, flows west to east and is a confluence with the Canadian River, and the study reach is in Oklahoma City, Oklahoma area. This ecoregion is a transition between prairie and wheat-growing regions in western Oklahoma and the forested, hilly eastern Oklahoma. This ecoregion is not as arid as the plains in the area, and dominant land cover includes native vegetation, rangeland, and pastures. The study reach has several dams and flows through areas of high urban development (North Canadian River Watershed Study Area | OK EPSCoR., n.d.; United States Environmental Protection Agency, 2013)

Russian: The Russian River (fig. 3.3) flows north to south, and is in northern California, representing the Central California Foothills and Coastal Mountains ecoregion. This ecoregion is a Mediterranean climate of hot dry summers and cool moist winters. Much of this ecoregion is in ranching areas, and grazing is one of the dominant land uses in the open, low mountains and foothills. The Russian river experiences flow diversions for irrigations for agriculture and for municipal water use in surrounding counties, resulting in low summer and fall flows and higher flows in winter and spring. (Center for Western Weather and Water Extremes., n.d.; United States Environmental Protection Agency, 2013) There is one dam in the study reach.

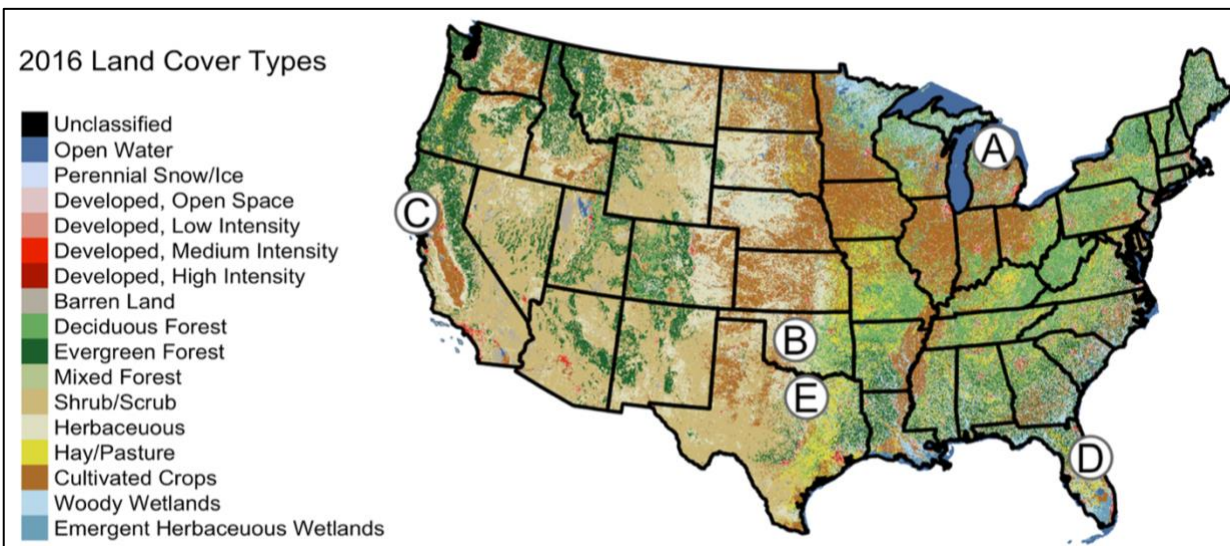
St. Johns: The St. Johns River (fig. 3.4) is the longest river in Florida and represents the Southern Coastal Plain ecoregion in the southeastern U.S. St. Johns is the lowest elevation of all study rivers with a low slope, located in an ancient intracoastal lagoon system. The river flows from south to north and flow direction is influenced by tides which can reverse flow. Wetlands are the dominant watershed land cover and while the study reach has no dams, there are several lakes, and the river is characterized as a blackwater river due to high tannin concentrations from

decaying plant matter (St. Johns River Water Management District, n.d.; United States Environmental Protection Agency, 2013).

Trinity: The Trinity River (fig. 3.5) is in Texas and is the largest watershed in the state, flowing from Dallas south to the Galveston Bay. This river is in the East Central Texas Plains and represents the southern U.S. This ecoregion is a transitional ecoregion where many areas have a dense, underlying clay layer affecting water movement and available moisture for plant growth. Pasture and range are the dominant land cover in the watershed, and the most upstream sites are in a more urbanized part of the watershed (United States Environmental Protection Agency, 2013). There are four dams in the study reach.

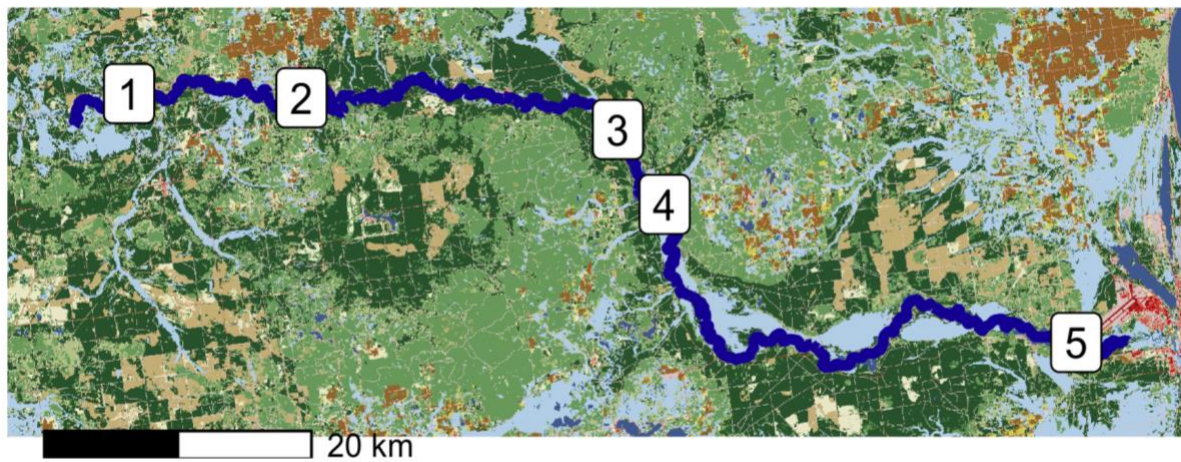
**Table 1.** Watershed characteristics for each study river. Elevation, watershed area, slope, mean discharge, and stream order calculated for most downstream site in each river.

River	EPA Region	Level 3 Ecoregion	Elevation (m)	Watershed Area (km <sup>2</sup> )	Slope	Mean discharge (cfs)	Stream order
Au Sable	5	Northern Lakes and Forests (50)	184	4324	2.76E-04	39	5
North Canadian	6	Cross Timbers (29)	325	35398	1.00E-05	10	6
Russian	9	Central California Foothills and Coastal Mountains (6)	24	3465	1.00E-05	38	5
St. Johns	4	Southern Coastal Plain (75)	1	8793	1.00E-05	82	5
Trinity	6	East Central Texas Plains (33)	94	21054	2.74E-04	103	6



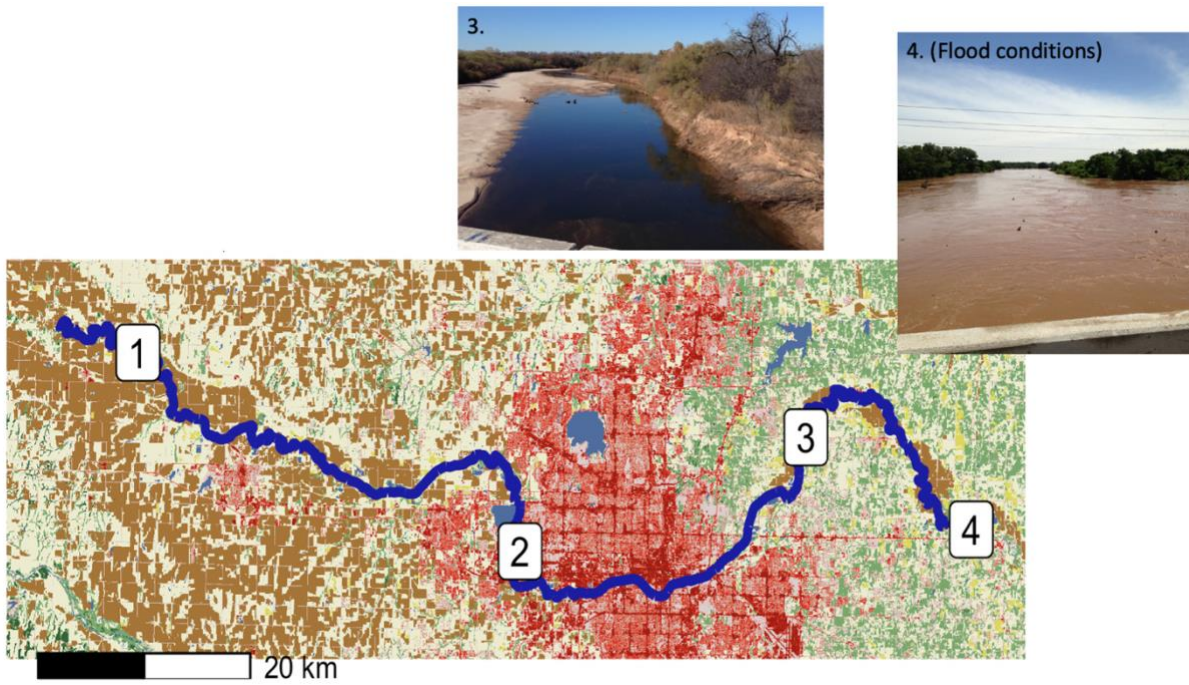
**Fig 3.** Map of chosen study rivers. Legend applies to figures 3.1-3.5.

A. Au Sable, MI



**Fig 3.1.** Map of Au Sable River in northern Michigan. Site 1 is most upstream site.

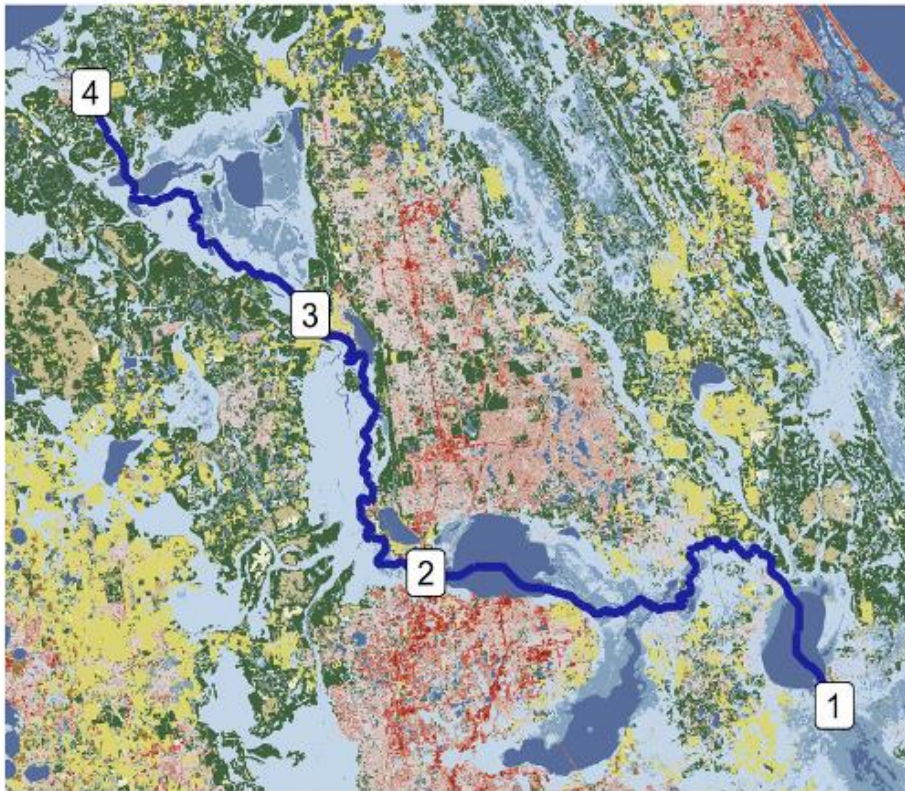




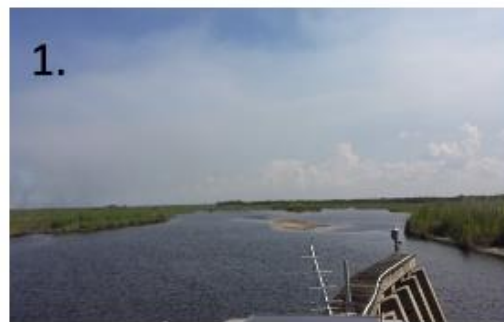
**Fig 3.2.** Map of North Canadian River near Oklahoma City. Site 1 is most upstream site.



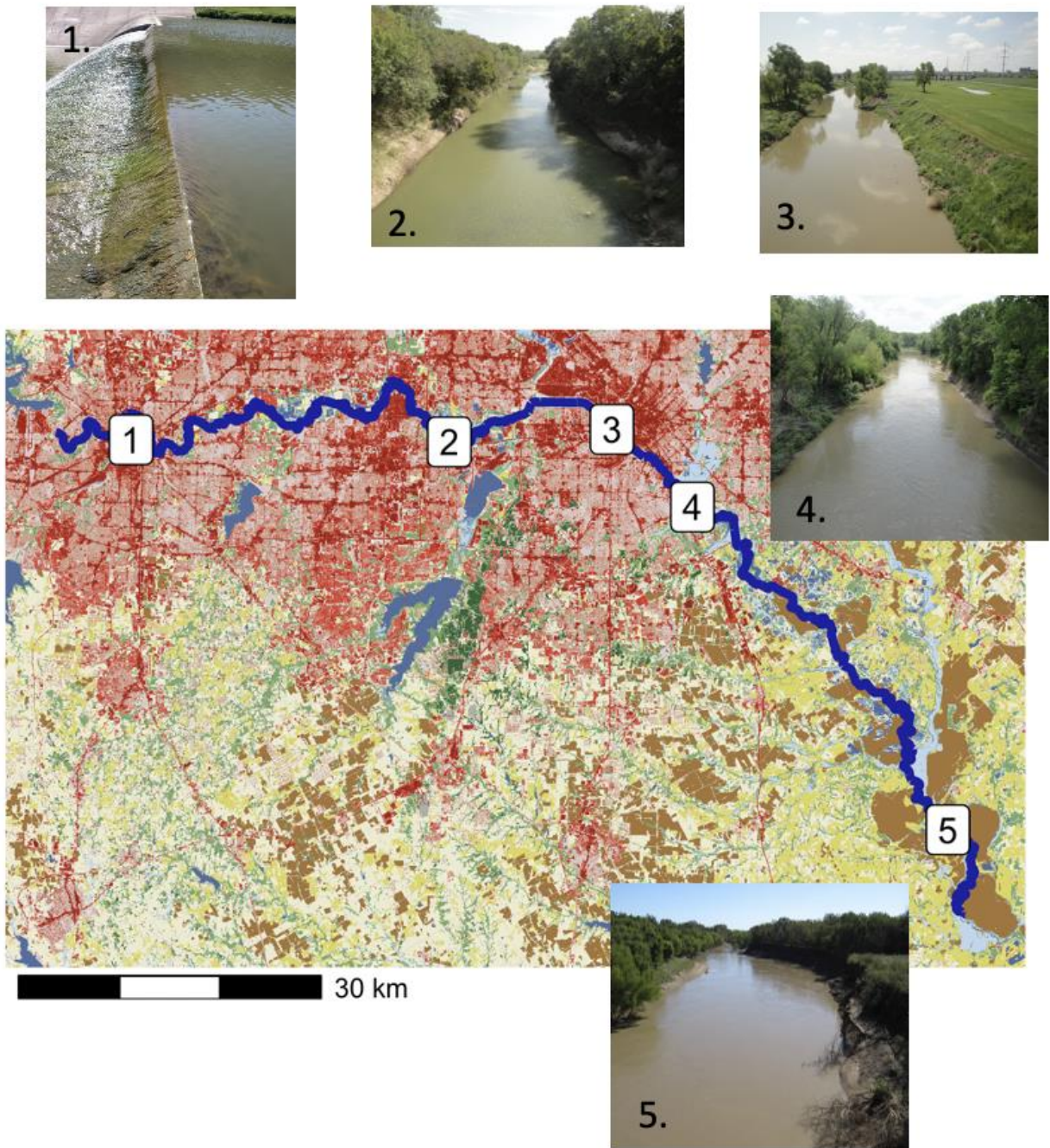
**Fig 3.3.** Map of Russian River in northern California. Site 1 is most upstream site.



20 km



**Fig 3.4.** St. Johns river in east central Florida. Site 1 is most upstream site.



**Fig 3.5.** Trinity River in north central Texas. Site 1 is most upstream site.

## NHD Flowlines

Using the individual site coordinates along with the “NHDPlusTools” R package (Blodgett, 2019), river flowlines were extracted from the National Hydrography Dataset (NHD, USGS (U.S. Geological Survey), 2016). I collected flowlines starting at the most downstream site to the most upstream site and added several km to the most upstream to ensure completeness. For ease of analysis, I excluded tributaries and only used the mainstem flowlines—the lines that sites appear on, and lines that connect the sites. I also collected watershed area (km<sup>2</sup>) from NHD, which is analogous to the drainage area for each individual site.

## Land Cover and Dams

Using the individual NHD flowline comids (identifiers for river flowline segments), I then used the EPA StreamCat database (Hill et al., 2016) to collect catchment and watershed percent land cover and percent impervious cover, extracted from the 2016 National Land Cover Dataset (fig. 4). Catchment here refers to the local area around a stream, and watershed refers to the entire watershed until that point. For analysis, like land cover types for both the watershed and catchment were aggregated and/or renamed to agriculture (hay and crops), forest (deciduous, conifer, and mixed forest), developed (open, low, medium, and high intensity developed), herbaceous (grassland), open (barren land and shrub/scrub), wetland (woody wetland and herbaceous wetland), and water (open water and ice/snow). Dam data were collected from the Army Corps of Engineers National Dam Inventory (U.S. Army Corps of Engineers, 2007) for each state that contained a river I was using for this study, and located through first buffering NHD flowlines, then identifying intersecting flowlines and dams. Only dams located on the main stem of the river were included (fig. 4).

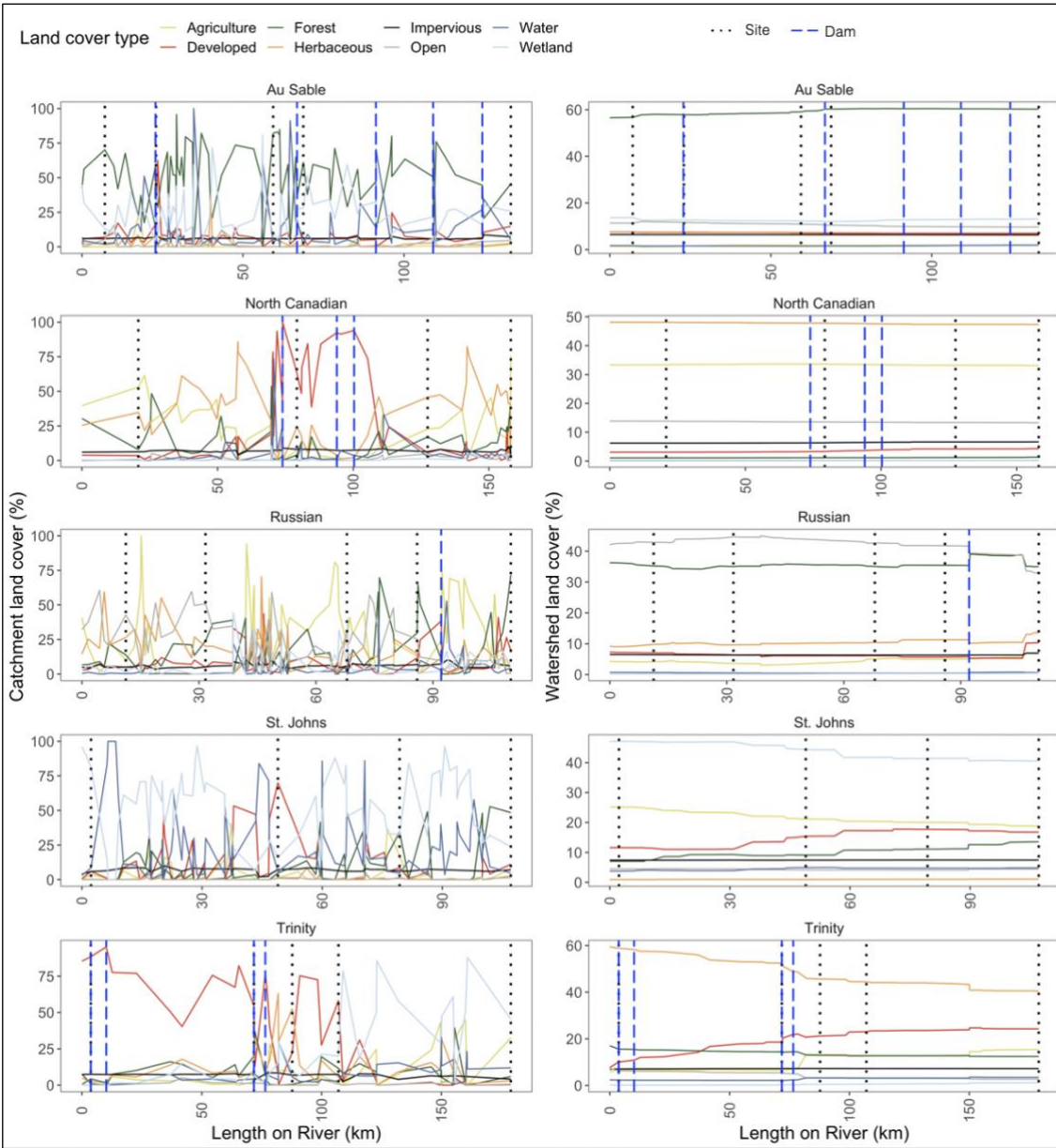
## Analysis

### Within-River Site Correlations

Pearson correlations for discharge, dissolved oxygen, GPP, and ER between sites within the same river were done to identify patterns and relationships between upstream and downstream sites. This analysis step was meant to help guide my thinking on longitudinal variation and patterns and how they map onto existing theories by examining how much an upstream site may be controlling the dynamics of a downstream site. I would expect to see a gradual decrease in positive correlation moving downstream, and so if there were a sharp difference or a negative correlation, I would be able to closely examine the setting of the river and the presence of dams or specific land cover types and gain clarity regarding the drivers of longitudinal heterogeneity. All analysis done in R version 4.0.2 (R Core Team, 2020).

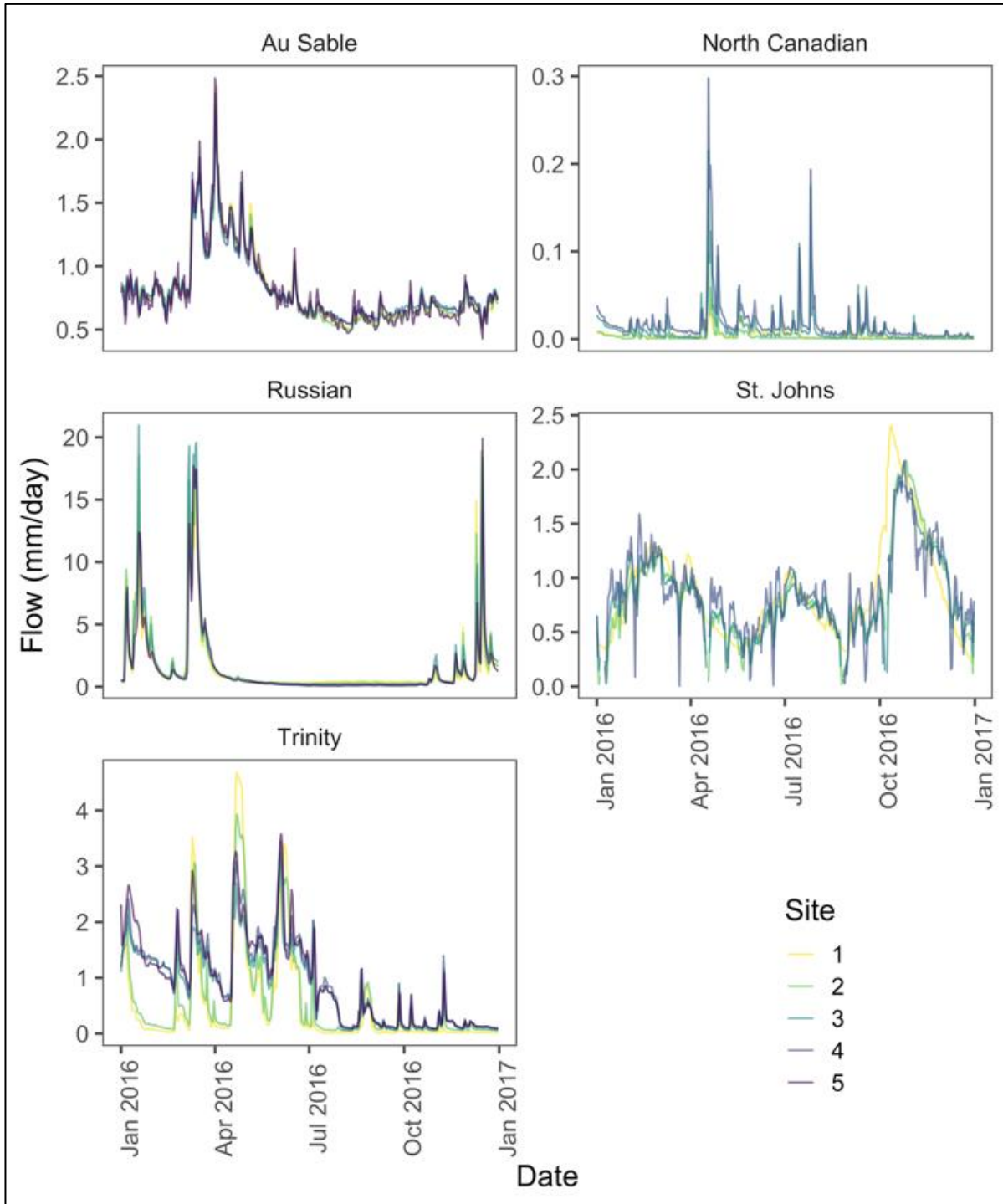
# Results

## Land Use and Dams



**Fig 4.** Catchment (left column) and watershed (right column) land cover percentages for the length of each study reach in each river. 0 km is most upstream, and each site is represented by a dotted black line.

Within-River Site Correlations and Data  
Discharge



**Fig 5.** Time-series of discharge in mm/day for all rivers January – December 2016. Site 1 is most upstream.

Time series discharge data is shown in fig. 5 and within-river correlations are shown in fig. 6 for this section. Au Sable showed strong correlations in the downstream direction in



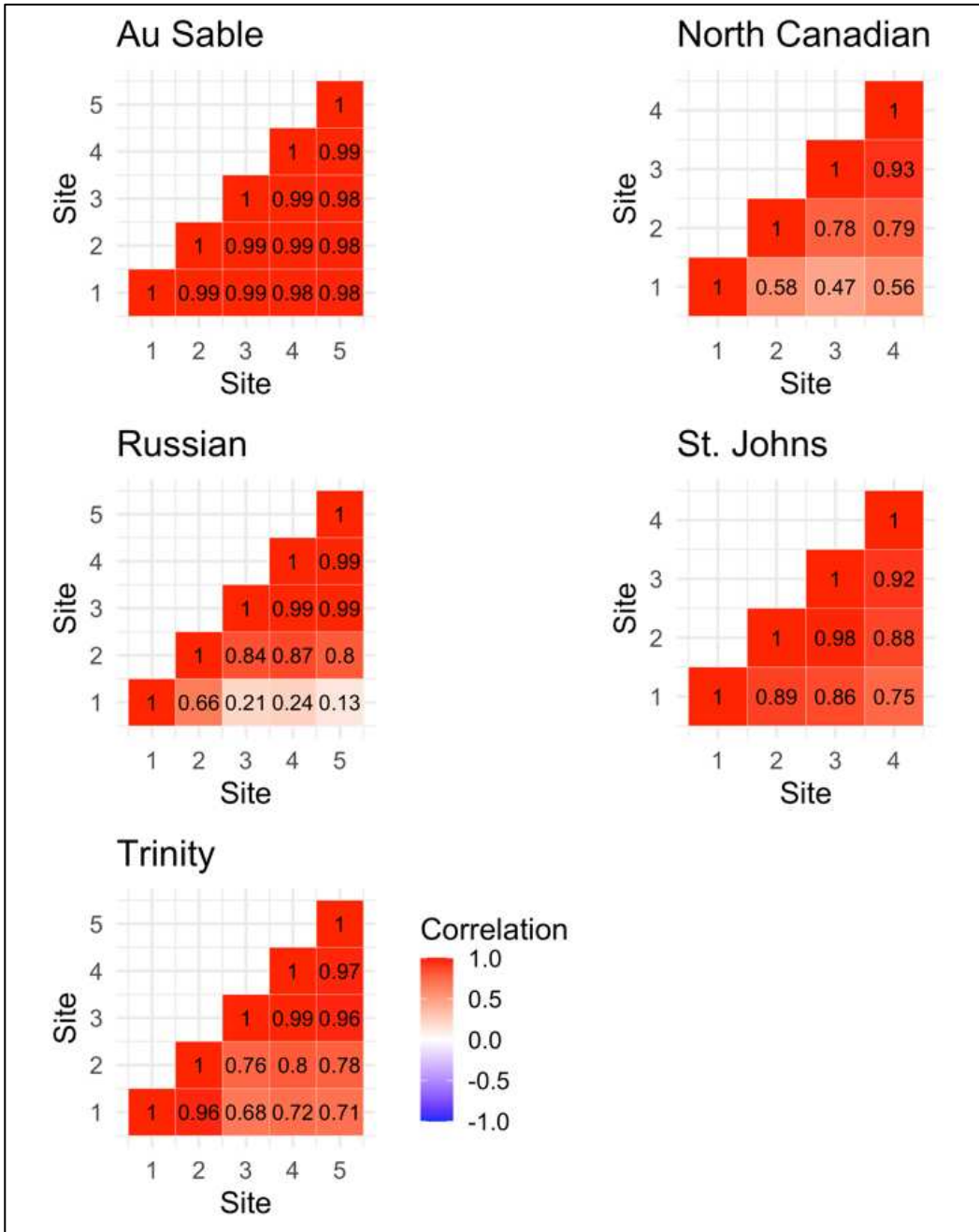
discharge. Despite Au Sable having five dams in the reach of concern, including a dam 0.1 km upstream of site 2 and 2 km upstream of site 4 (second-to-last site in the study reach), consecutive correlation coefficients were very similar and there is no evidence of major disruption in discharge patterns going downstream, possibly due to the dams maintaining flows instead of holding water back and releasing. Au Sable also generally had less than 25% urban land cover and low impervious cover, with forest land cover being the dominant land cover type for the watershed and forest and wetlands being the dominant catchment land cover types.

In contrast, the North Canadian and Trinity rivers, both of which has several dams like Au Sable but flow through a highly developed area for anywhere between 50 to over 100 km. In the North Canadian river, there is one dam 5 km upstream of site 2, and two dams between site 2 and site 3 (27 and 33 km upstream of site 3), and an increase in urban land cover – shortly upstream of site 2, catchment urban land cover does not exceed around 25%, but between sites 2 and 3 ranges between 50% and over 75% which introduces flow variability. These characteristics decrease the correlation by 42% from site 1 to site 2 ( $r = 0.58$ ), however there is a stronger correlation between sites 2 and 3 ( $r = 0.78$ ), indicating that dams or land cover are not affecting all downstream sites in the same way. This is a similar pattern to the Trinity river, another river with multiple dams that flows through developed areas. Trinity has a dam located on site 1 and shortly downstream, and on site 2 and shortly downstream. Sites 1 and 2 also have a high percentage of urban land cover, exceeding 75%, which makes them more like each other than the other sites due to flow controls from dams and variability from urbanization. Coherence starts to change between site 2 and 3: there is a dam 11 km upstream of site 3 and sites 2 and 3 are less correlated ( $r = 0.76$ ) than sites 1 and 2 ( $r = 0.96$ ). Additionally, there is a distinct switch from urban to wetlands being a dominant catchment land cover around site 4.

The Russian river has the least coherent pattern of all the rivers. This river only has one dam, about 18 km upstream of site 5. The breakdown in coherence between site 1 and 2 ( $r = 0.66$ ), as well as the downstream sites match the sharp increases in catchment agricultural land cover, so is most likely attributed to canals drawing water out of the river. These withdrawals are evident in the time series where there is very low flow during the summer months and times

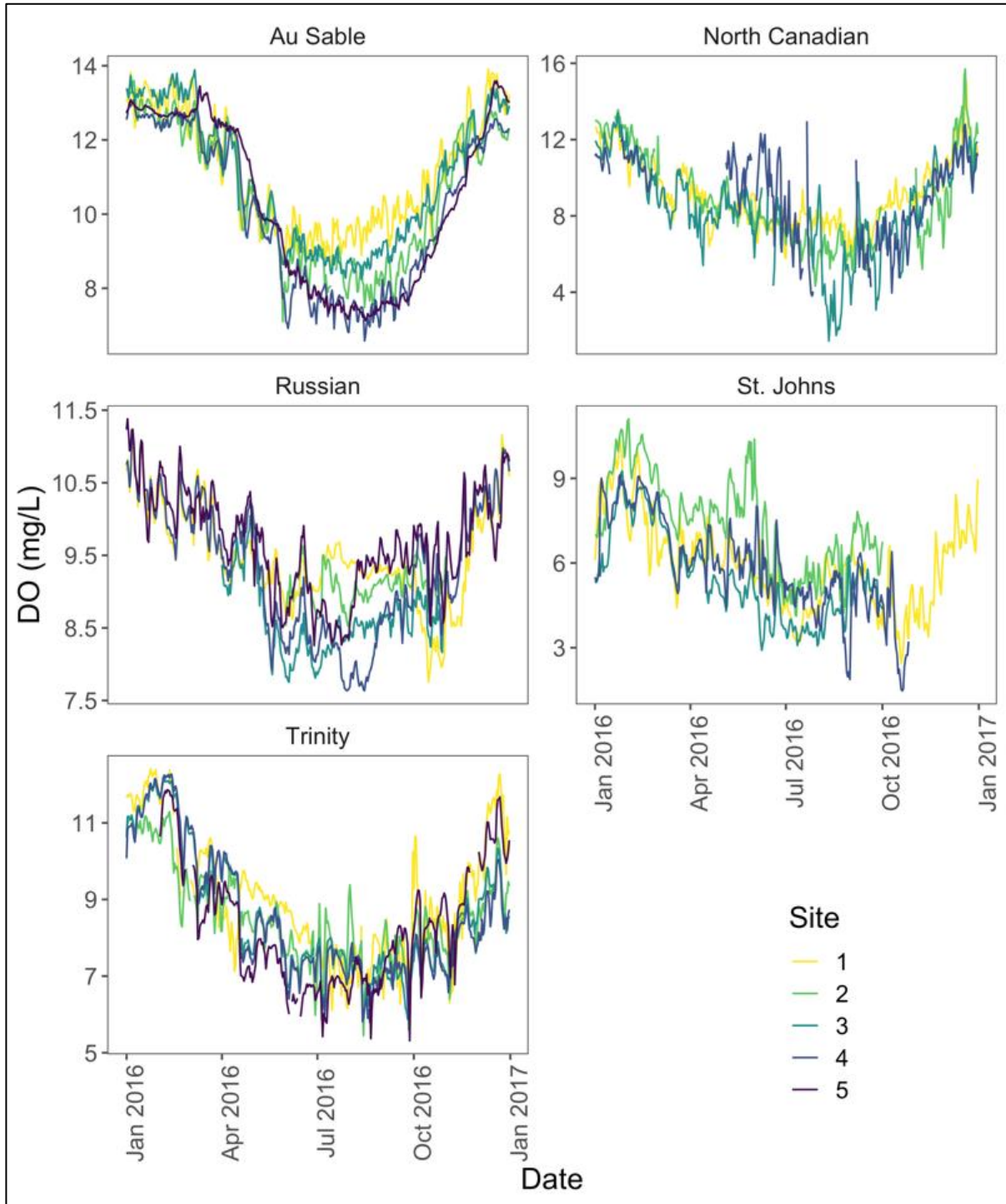
when downstream sites have lower flow than upstream. This land and water use characteristic make it so downstream sites are more related to each other because of effect of canals and agriculture ( $r = 0.84$  between 2 and 3,  $r = 0.99$  between 3, 4, and 5).

St. Johns, like Au Sable, generally shows coherence but the major difference is that this river has no dams, instead all sites have the potential for tidal influence due to proximity to the ocean, with site 4 being the most influenced as it is the most downstream ( $r = 0.56$  between 1 and 4). Though site 2 is directly downstream of a large lake, it seemed to have negligible impact on the flow relationship between sites 1 and 2 ( $r = 0.89$ ).



**Fig 6.** Within-river Pearson correlation coefficients for discharge in mm/day. Site 1 is most upstream.

Dissolved Oxygen



**Fig 7.** Time-series of dissolved oxygen concentrations in mg/L for all rivers January – December 2016. Site 1 is most upstream.

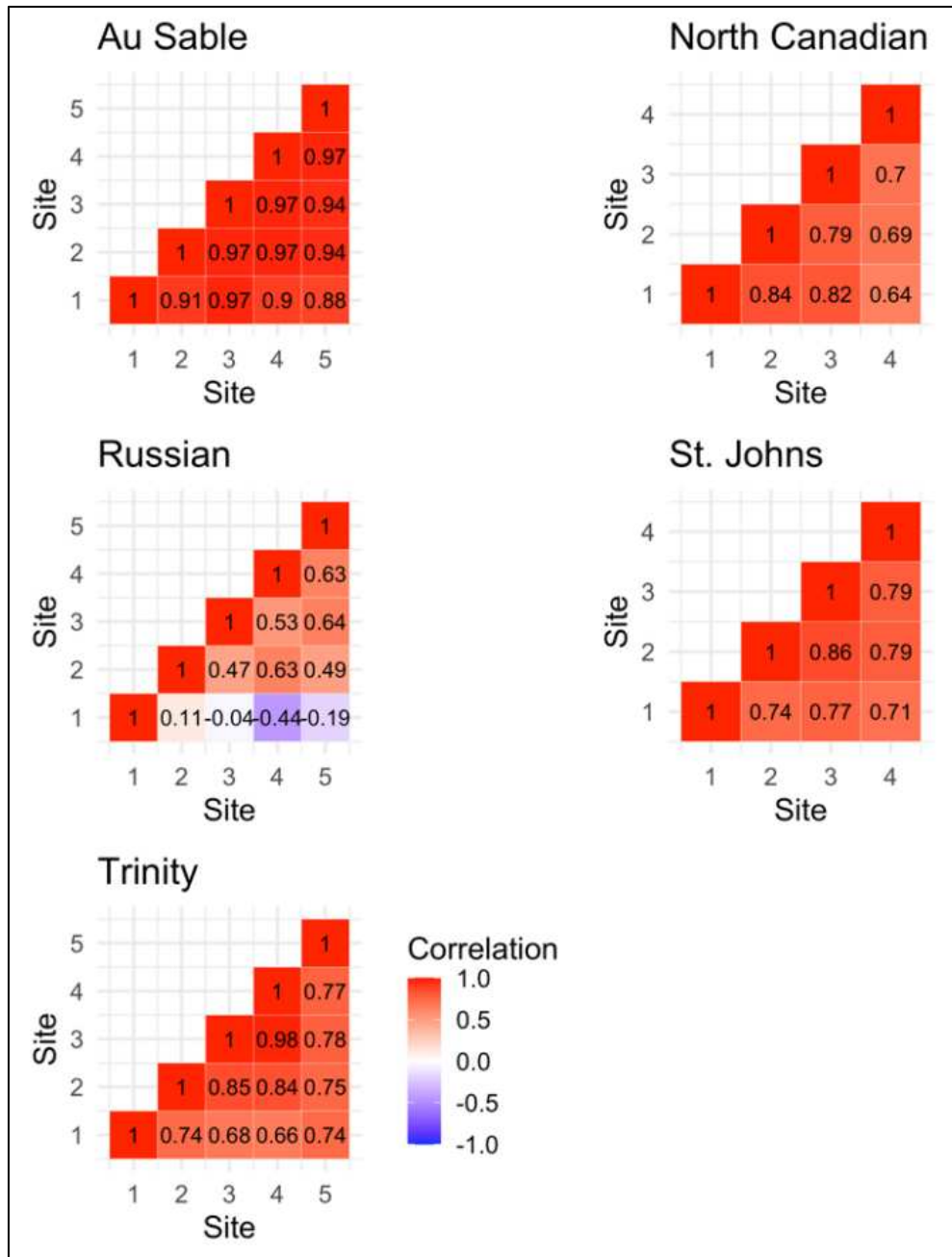
Time series dissolved oxygen data is shown in fig. 7 and within-river correlations are shown in fig.8 for this section. Similar to discharge patterns, the Au Sable River generally shows a strong coherence going downstream. However, there is a slight difference in that sites 2, 4, and 5 are more correlated to each other, with  $r$  values greater than 0.94, than sites 1 or 3 with  $r$  values of 0.91 and 0.90. These sites are directly downstream of dams (0.1, 2, and 9 km respectively), which could be having a similar effect between different sites. Additionally, there is a clear seasonal pattern in that beginning in late spring, lasting through early fall, DO concentrations decrease in the downstream direction, with consistent declines in summer DO across all sites and increasing seasonal amplitude as the river flows downstream. The downstream most site has highly reduced diel variation in DO, suggesting low primary productivity.

DO, as with discharge, in the North Canadian and Trinity rivers show decreasing correlation in the downstream direction and the sites that are affected by dams or changes to land use, specifically urbanization. For the North Canadian, there is a short window in late summer of decreasing DO downstream pattern. Going from sites 1 to 2 ( $r = 0.84$ ) to 3 ( $r = 0.79$ ), to 4 ( $r = 0.7$ ), there is a clear decrease in correlation which may be due to the cumulative effects of dams and urban land cover. A similar correlation pattern emerges in the Trinity as well, where sites 3 and 4 correlated with each other (0.98) but not as much with 1, 2, or 5, and site 3 happens to be 11 km downstream of all the dams and most of the urban land cover. Site 4 is the least correlated with 1 ( $r = 0.66$ ) and is also downstream of the majority of urban land cover and downstream of all dams.

The Russian river shows the least coherent pattern of all the rivers, again mirroring the pattern as seen with discharge. Starting at site 1 the correlation breaks down at site 2 where the correlation with site 1 is 0.11 and downstream sites are negatively correlated with site 1. But, going consecutively downstream, correlation between consecutive sites become stronger, indicating there may be something unique about site 1 that makes DO so much different than the other sites. When canals are not diverting water, there is a pattern where the sites that have higher flow also have higher DO, and this follows the expected pattern of higher flow and higher

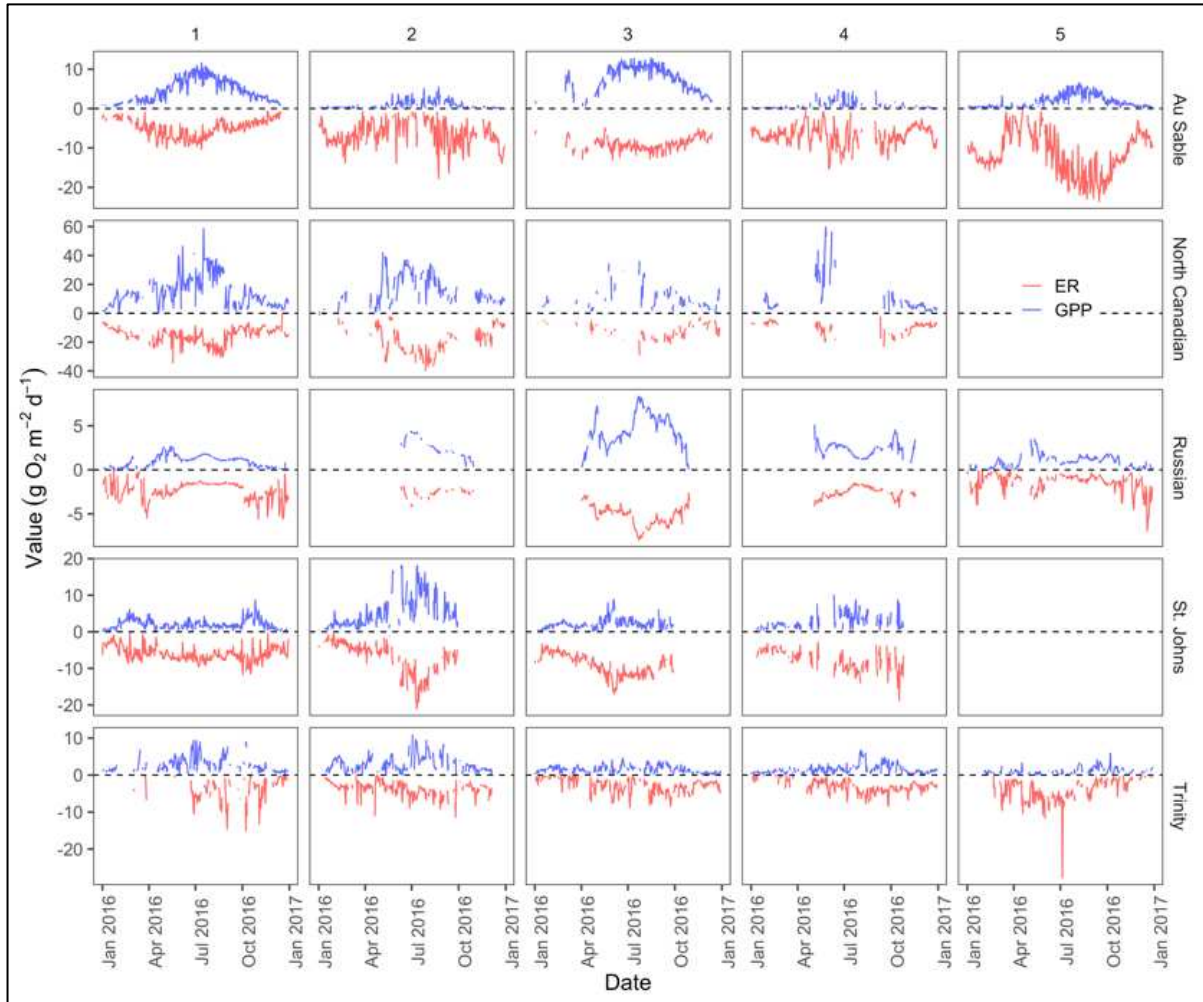
DO going downstream. But, when canals are active and drawing water in the summer, this pattern is flipped and site 1 has higher flow and DO.

St. Johns shows slight coherence but for this river, site 2 tends to have highest DO concentration. St. Johns is unique for these rivers in that not only are there no dams, but there are also several lakes that essentially function as very wide and very slow-moving reaches. Site 2 is directly downstream of one of these lakes and so there may be a lentic influence on DO patterns. Additionally, St. Johns has the lowest DO concentrations of all the rivers, but has high concentrations of tannins from wetlands which may be inhibiting primary production and therefore oxygen produced from primary production.



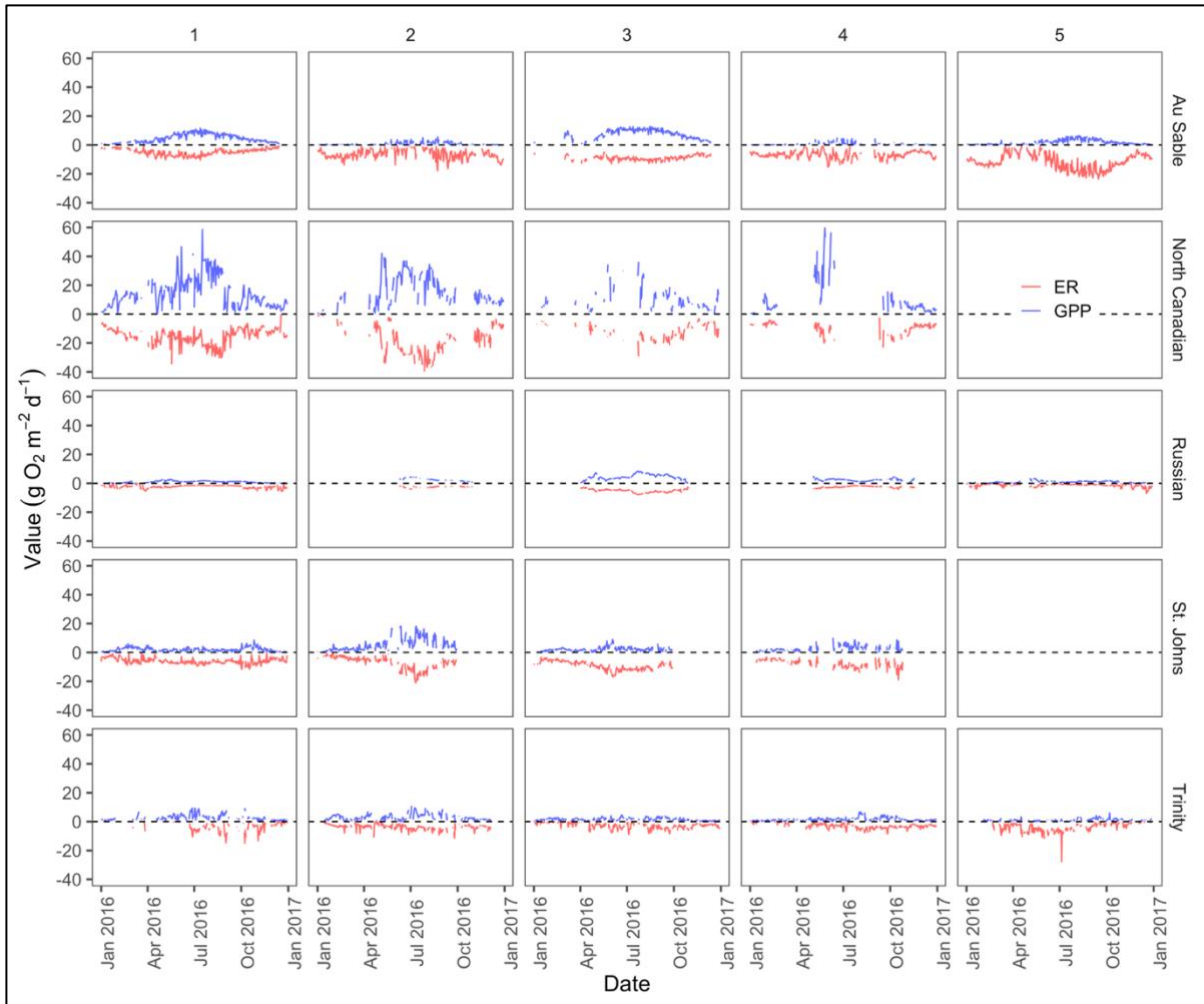
**Fig 8.** Within-river Pearson correlation coefficients for dissolved oxygen in mg/L. Site 1 is most upstream.

## Metabolism

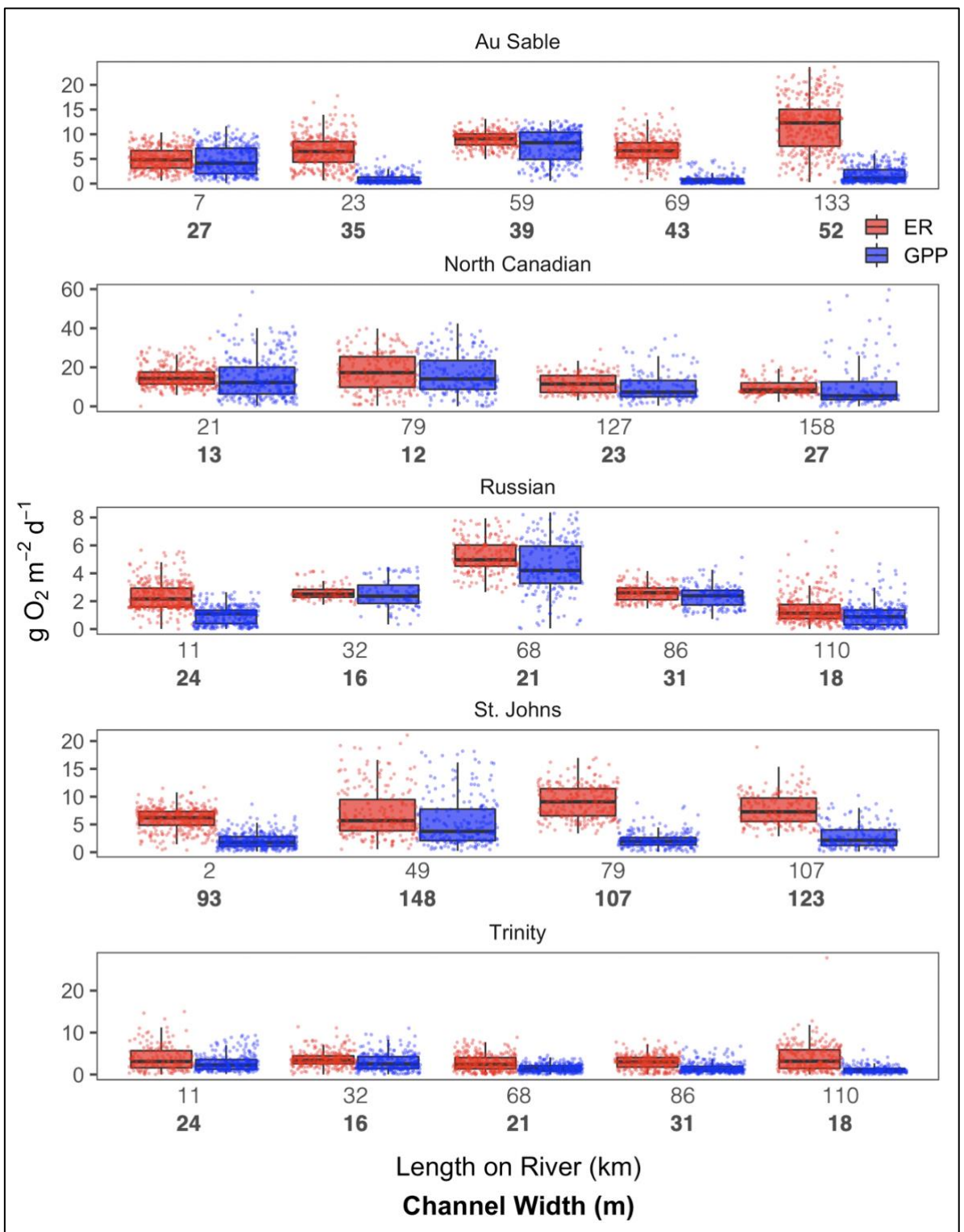


**Fig 9.** Time series of metabolism data in g O<sub>2</sub>m<sup>-2</sup>d<sup>-1</sup> per river, per site for January – December 2016. Site 1 is most upstream. Note that Y-axis scaled to values specific to each river.





**Fig 9.1.** Time series of metabolism data in  $\text{gO}_2\text{m}^{-2}\text{d}^{-1}$  per river, per site for January – December 2016. Site 1 is most upstream. Note that Y-axis scaled to values in the whole dataset, highlighting differences between rivers.



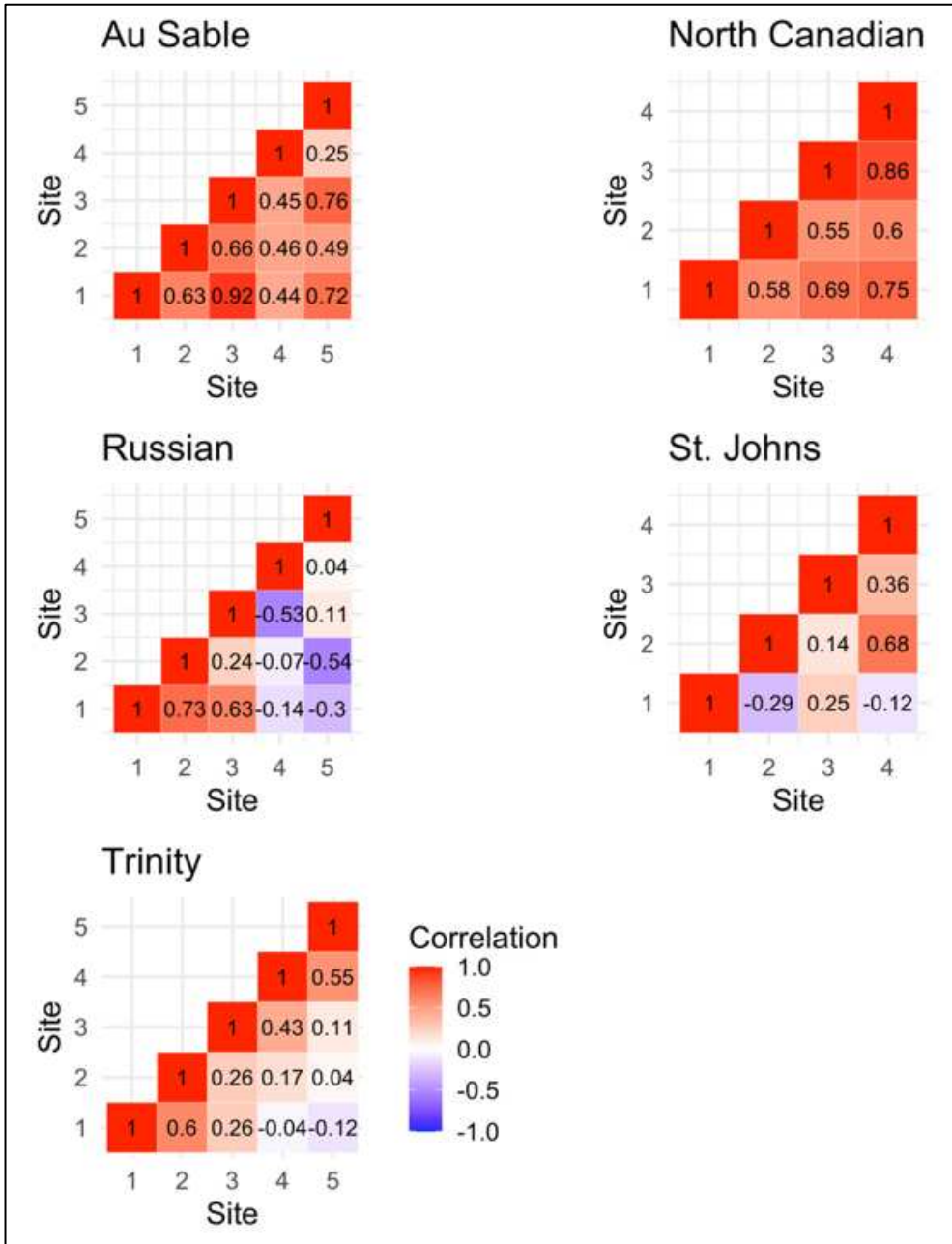
**Fig 10.** Box plots of absolute values of metabolism data in  $g O_2 m^{-2} d^{-1}$  per river, per site. Site 1 is most upstream. Note that Y-axis scaled to values specific to each river.

Time series metabolism data is shown in fig. 9 and 9.1, metabolism boxplots in fig. 10, and within-river correlations are shown in figs. 11 and 11.1 for this section. Between all the rivers, the least longitudinally correlated patterns can be found in GPP and ER. In the Au Sable River, dams have a more pronounced effect in that GPP declines immediately downstream of dams at sites 2, 4, dropping the correlation with site 1 to 0.66 and 0.44, respectively, potentially because they are immediately downstream of the dams and the dams disrupt productivity patterns. GPP at the dam sites are constrained more as compared to sites 1 and 3 and by site 3, GPP has recovered and is more similar site 1 ( $r = 0.92$ ). Site 5 has higher ER rates which is expected for most downstream sites, but overall, the patterns of GPP and ER at Au Sable don't cleanly follow any of the predictions from either the RCC or SDC, with no distinct longitudinal pattern of change.

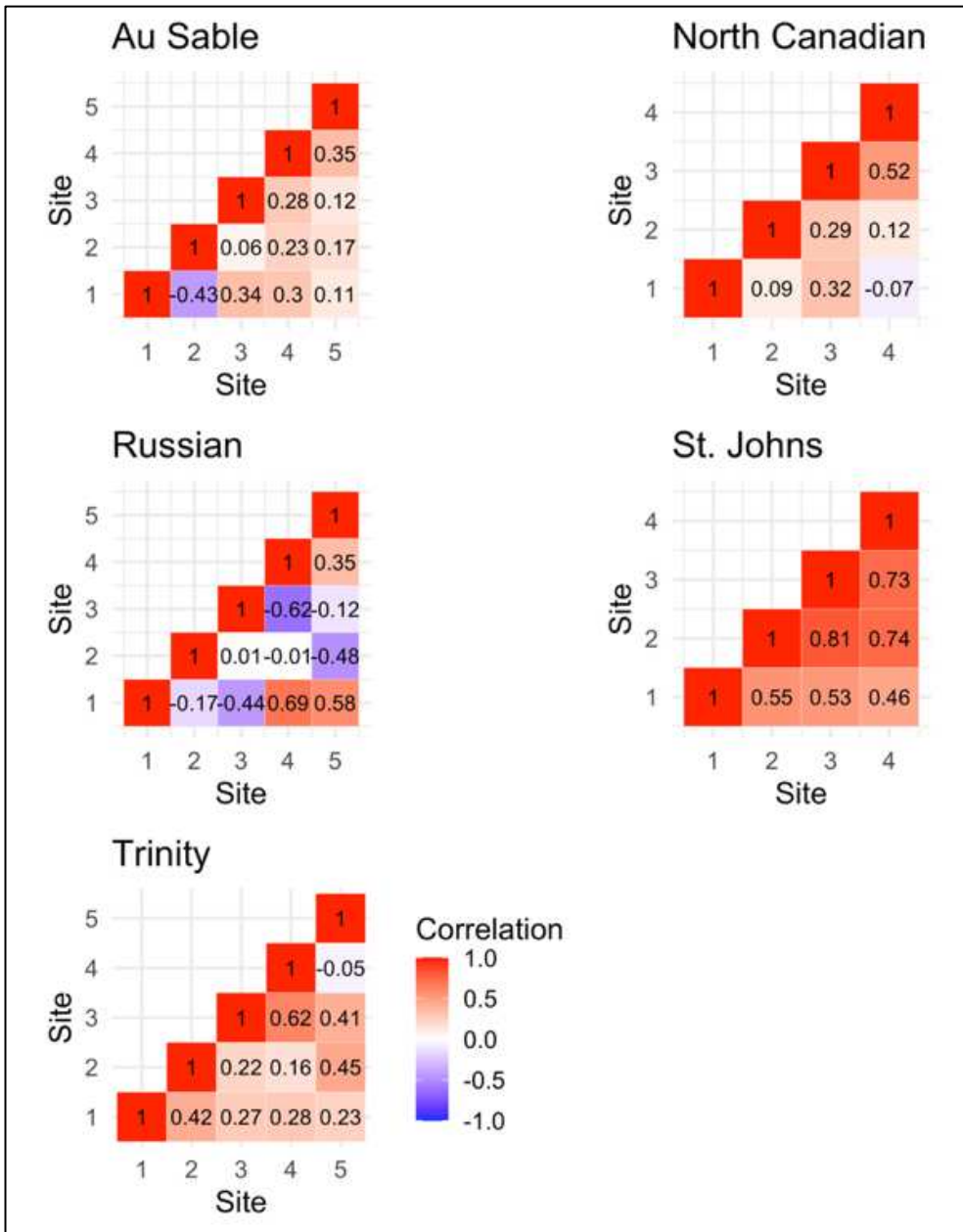
North Canadian and Trinity do not exhibit the same pattern, even though both rivers have multiple dams like the Au Sable. In the North Canadian River, site 2 is generally more variable as shown by the wider range of GPP and ER values and has a weaker correlation with site 1 ( $r = 0.52$ ). This weak relationship is most likely because of either the high urban land cover (exceeding 75%) or dam operations, releasing water, both of which can flow variation and flow is a control on metabolism dynamics. In the Trinity River, GPP correlation flips sign at site 4 when comparing to site 1 ( $r = -0.14$ ). This may also be a result of high urban land cover, as up until site 4 is high catchment urban cover (generally exceeding 50% in many places) and dams on sites 1 and 2, as well as 11 km upstream of site 3. But, despite the similar land use setting, the Trinity River does not show the same type or magnitude of variation that North Canadian does. In contrast to the North Canadian, land cover more downstream in the Trinity River changes to being more wetland-dominated and more turbid based on visual data and previously collected turbidity data, (Savoy & Harvey, 2021) which could be limiting GPP downstream. Both of these rivers show weak alignment with the RCC in that ER tends to have higher rates than GPP, but do not follow predictions of the SDC.

The Russian River has a unique metabolism pattern in that GPP and ER increase in the middle of the study reach. Going downstream, GPP increases, but then decreases. This is the only river that has a GPP /ER pattern that resembles RCC predictions

Finally, St. Johns shows contrasting correlation patterns between GPP and ER and there are higher rates of ER than GPP in this terrestrial carbon-dominated river. Throughout the watershed, the dominating land cover is wetlands and due to these wetlands, this river has high CDOM which can enhance ER rates (Meyer & Edwards, 1990) and at the same time reduce GPP because of light attenuation (Phlips et al., 2000). As mentioned, St. Johns has no dams and several lakes which are acting as very slow and wide rivers and so there is the possibility of lentic influence, as seen with the range of metabolism rates at site 2 which is directly downstream of a lake.



**Fig 11.** Within-river Pearson correlation coefficients for GPP. Site 1 is most upstream.



**Fig 11.1.** Within-river Pearson correlation coefficients for GPP. Site 1 is most upstream.

## Discussion

### Theories of Longitudinal Variation and Observations of River Metabolism

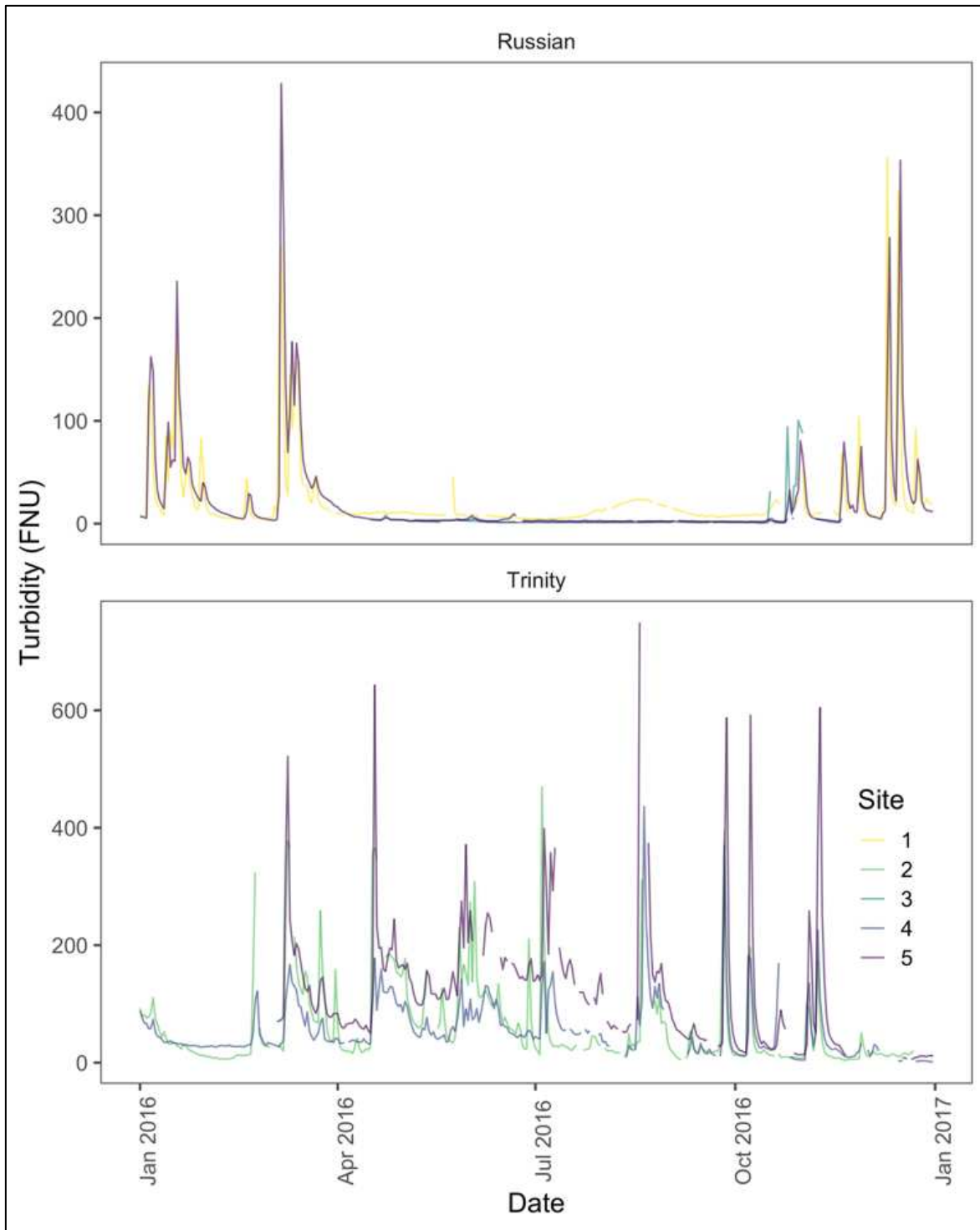
These rivers were chosen to answer my overarching research question: *Do rivers have consistent and predictable longitudinal patterns in productivity and respiration and if not, what are the strongest controls that disrupt these patterns?* In general, I did not observe results consistent with the expected patterns of the River Continuum Concept or other theories of river function variation. Nor did I observe patterns that were consistent or even predictable, even among rivers that are similar in their climate and land use settings. This lack of coherence and predictability in river metabolism across sites within rivers likely happened for several reasons.

First, most of the main-stem river observations started at larger watershed areas than conceptualized in the RCC (Vannote et al., 1980). Across all study sites but the North Canadian, minimum stream order was 5 and all of the North Canadian was 6<sup>th</sup> order, and drainage areas ranged from 3,465 – 35,398 km<sup>2</sup>. At these size watersheds and rivers, most of the sites are likely not experiencing shading by adjacent riverbanks and trees (Savoy & Harvey, 2021) with our narrowest width river being 12 m as compared to the <1 m wide rivers often categorized as headwaters in the RCC (Vannote et al., 1980). As such, primary productivity is likely higher in the "headwater" gauges (sites 1, and possibly 2 for each river) than in a true headwater which would likely experience tree shading. Other site characteristics that could introduce bias is the actual gage location at each site. Discharge and oxygen data used in this analysis were from USGS gage sites, which are installed in sections that are beneficial for collecting data needed for discharge and so are most likely in riffles rather than pools, which will have different flow velocities and oxygen patterns (Carter et al., 2021).

Secondly, while having a markedly different pattern than the other rivers in this study, more basic requirements of the RCC are not met in the strongly agriculturally dominated system,

the Russian River, where discharge declines as the river moves downstream. Water diversions take out enough water that the river has a decrease in discharge as it flows downstream, likely altering patterns of GPP and ER for this study system. But, whatever the effect of discharge, it is also possible that this pattern emerges due to 1) the channel widening enough to allow for more light, 2) the catchment agricultural land is introducing nutrients and facilitating GPP, or 3) downstream of 3 the river becomes increasingly turbid, suppressing GPP (fig. 12). This specific example reflects a truth that what many other authors have noted: rivers encounter a complex landscape of alterations due to dams and changing land use that alter their metabolism and other functions (Schilling et al., 2008). For example, the Au Sable River passes through several hydropower dams which have strong impact on primary productivity, producing river metabolism patterns inconsistent the SDC prediction that GPP will increase downstream due to sediment impoundment – in the case of the Au Sable River, GPP decreased downstream of dams. However, another river that encounters many dams, the Trinity River, shows relatively little impact from dams on primary productivity (fig. 10). And, while the Trinity River passes through a highly urbanized area similarly to the North Canadian River, it does not show the same variation in discharge and metabolism in the urbanized sites like the urbanized North Canadian sites, instead the Trinity River shows a constricted range in GPP in the downstream sites of 3-5 which are highly turbid for long stretches of the year, limiting light penetration to pelagic or benthic primary producers (fig 12). In this case, it may be useful to examine the specifics of the dams – dam type, height, times of the year they are active, and where in the impoundment water is being released from which could affect downstream measurements.





**Fig 12.** Time series of turbidity in FNU for Russian River sites 1, 3, 4, and 5; and Trinity River sites 2, 4 and 5.

Ultimately, the results of this analysis show that longitudinal patterns in productivity are sensitive to both internal and external river network characteristics. However, productivity patterns are not necessarily consistent across similar settings and therefore are difficult to predict even using longstanding frameworks (e.g., RCC or SDC). This apparent randomness in river metabolism could arise for several reasons. First, as mentioned earlier, sites are co-located with USGS gages which are installed in reaches conducive to measuring discharge. These gages and the dissolved oxygen sensors placed on or near them are not necessarily best suited to compare patterns of metabolism along a single river. Micro-variation in site characteristics may introduce large variation in GPP and ER, while also being integrated with macro-variation in the form of changing land use and land cover through the watershed, on the order of 100s of km as compared to the 100s of meters that might cover a pool-riffle sequence. Additional targeted field work would be required to disentangle these macro vs. micro-scale drivers of metabolism. Overall, the absence of predictable patterns highlights that theories predicting ecosystem function in large rivers require more work and consistent data collection.

Recent studies that attempt this kind of work have highlighted several key ideas that may guide future theories to explain longitudinal patterns in river metabolism. First, several studies focused on large, repeat synoptic surveys have highlighted the primacy of spatial variation as a dominant control of riverine function across complex and connected freshwater landscapes (Abbott et al., 2018; Dupas et al., 2019). Similarly studies that focus on sampling rivers in spatially rich manners (with flotation devices or boats) yields complementary insights (e.g., Gardner et al., 2020; Hensley et al., 2019). These studies also highlight some of the intractable logistical challenges and sampling artifacts of Lagrangian or particle-tracking sampling, particularly when ecosystem functions exhibit large short-term (e.g., diurnal) variation, such that water quality depends on both sample location and time-of-day (Ensign et al., 2017; Hensley et al., 2020). In contrast to these field-intensive approaches, there is untapped potential in synoptic surveys conducted by satellites where large-scale coherent patterns of river behavior and function are observable (e.g. patterns of river color in Gardner et al., 2021). Some combination of these synoptic and Lagrangian approaches to riverine observation will likely provide far more insight into the dominant controls on river metabolism and other functions than comparing

individual USGS gage data as I have done here. One particularly promising approach could be methods and analyses that allow for rich spatiotemporal modelling of whole river networks similar to theoretical work that Koenig et al., (2019) did, but using real sensor data to model whole networks as the USGS has been doing with river discharge and temperature in recent years (Jia et al., 2021; Rahmani et al., 2021).

For analyses such as this one, there are several areas that could be improved upon. First, I only was concerned with the mainstem of these rivers. Where available, including tributary data would be beneficial as land use can vary widely within watersheds, but also may have different management practices creating a different ecological setting than the mainstem river and serves as important links throughout the network (Milner et al., 2019). Considering the timing, magnitude, and characteristics of water being transported through tributaries is also important since tributaries can be important sources of turbidity and other constituents and contribute to dynamic flow conditions like floods (Pattison et al., 2014). Second, productivity dynamics and overall ecosystem functioning can be impacted by nutrient input, transport, and transformation, but I did not include nutrient data in this analysis, only inferred possible nutrient dynamics given the land cover and land use around the river. Third, each river is likely managed differently due to the local needs, and knowing specifics about management like flow regulation, dam type and operation, and diversions could be valuable for a more in-depth comparison across rivers and for further insight into why the patterns observed occur, even in rivers that appear similar. Lastly, for ease of analysis I only chose five rivers for one year. Including more data both spatially and temporally could be useful for understanding the patterns shown or understanding how something like changing land use, dam installation, or dam removal affect productivity.

#### Broader impacts and future directions

Building better conceptual models, and the computational models that would follow, of how rivers function as they flow downstream could have real practical benefits for water resource managers. For example, fish kills are a common problem in urban rivers, where anoxic waters can accumulate in deeper, stagnant pools (Blaszczak et al., 2019). Yet, there is no clear

theory that estimates how these riffle-pool structures might interact to constrain river metabolism and, consequently, oxygen dynamics. Ultimately, if we had better theory to make predictions about where problematic anoxic events might occur, we can design interventions to alter those structures to prevent anoxia and use that sort of knowledge to have a more holistic understanding of river dynamics that can facilitate decision making surrounding resource management.

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