The importance of time and space in biogeochemical heterogeneity and processing along the reservoir ecosystem continuum

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Abstract

Globally-significant quantities of carbon (C), nitrogen (N), and phosphorus (P) enter freshwater reservoirs each year. These inputs can be buried in sediments, respired, taken up by organisms, emitted to the atmosphere, or exported downstream. While much is known about reservoir-scale biogeochemical processing, less is known about spatial and temporal variability of biogeochemistry within a reservoir along the continuum from inflowing streams to the dam. To address this gap, we examined longitudinal variability in surface water biogeochemistry (C, N, and P) in two small reservoirs throughout a thermally-stratified season. We sampled total and dissolved fractions of C, N, and P, and chlorophyll-a from each reservoir's major inflows to the dam. We found that time was generally a more important driver of heterogeneity in biogeochemical concentrations than space. However, dissolved nutrient and organic carbon concentrations had high site-to-site variability within both reservoirs, potentially as a result of shifting biological activity or environmental conditions. When considering spatially explicit processing, we found that certain locations within the reservoir, most often the stream-reservoir interface, acted as 'hotspots' of change in biogeochemical concentrations. Our study suggests that spatially explicit metrics of biogeochemical processing could help constrain the role of reservoirs in C, N, and P cycles in the landscape. Ultimately, our results highlight that biogeochemical heterogeneity in small reservoirs is driven more by seasonality than longitudinal spatial gradients, and that some sites within reservoirs play critically important roles in whole-ecosystem biogeochemical processing.

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ABSTRACT: Globally-significant quantities of carbon (C), nitrogen (N), and phosphorus (P) enter freshwater reservoirs each year. These inputs can be buried in sediments, respired, taken up by organisms, emitted to the atmosphere, or exported downstream. While much is known about reservoir-scale biogeochemical processing, less is known about spatial and temporal variability of biogeochemistry within a reservoir along the continuum from inflowing streams to the dam. To address this gap, we examined longitudinal variability in surface water biogeochemistry (C, N, and P) in two small reservoirs throughout a thermally-stratified season. We sampled total and dissolved fractions of C, N, and P, and chlorophyll-a from each reservoir's major inflows to the dam. We found that time was generally a more important driver of heterogeneity in biogeochemical concentrations than space. However, dissolved nutrient and organic carbon concentrations had high site-to-site variability within both reservoirs, potentially as a result of shifting biological activity or environmental conditions. When considering spatially explicit processing, we found that certain locations within the reservoir, most often the stream-reservoir interface, acted as 'hotspots' of change in biogeochemical concentrations. Our study suggests that spatially explicit metrics of biogeochemical processing could help constrain the role of reservoirs in C, N, and P cycles in the landscape. Ultimately, our results highlight that biogeochemical heterogeneity in small reservoirs is driven more by seasonality than longitudinal spatial gradients, and that some sites within reservoirs play critically important roles in whole-ecosystem biogeochemical processing.

Keywords: biogeochemical hotspot, carbon, nutrients, primary productivity, spatial variability, temporal variability

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Introduction
Of freshwater ecosystems, reservoirs in particular play a disproportionately large

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role in global biogeochemical cycles, transforming and burying large amounts of carbon (C), nitrogen (N), and phosphorus (P; Harrison et al. 2009; Maavara et al. 2015, 2020; Powers et al. 2015; Shaughnessy et al. 2019). Reservoirs receive a much higher quantity of nutrients (N, P) and organic C than many naturally-formed lakes due to their high watershed-to-surface area ratio and corresponding large terrestrial drainage area, making them important for biogeochemical processing within the landscape (Thornton et al. 1990; Harrison et al. 2009; Hayes et al. 2017).

Within a reservoir, multiple processes interact to control the biogeochemical cycling and fate of C, N, and P. Due to longer residence times in reservoir basins than incoming streams (Nilsson et al. 2005), organic matter and nutrients which enter the reservoir are altered via biotic transformation (e.g., uptake by organisms, decomposition; Harrison et al. 2009; Shaughnessy et al. 2019) or deposited within reservoir sediments as they travel downstream (Syvitski et al. 2005; Tranvik et al. 2009; Clow et al. 2015). Altogether, the balance of these physical and biogeochemical processes results in major changes in the quantity and quality of material leaving the reservoir and directly drives the stoichiometry of C, N, and P exported to downstream ecosystems (Maranger et al. 2018; Wang et al. 2018, Carey et al. 2022a). Consequently, reservoirs can either act as nutrient and C sources (i.e., production within the waterbody) or sinks (i.e., burial in the waterbody or emission to the atmosphere; Harrison et al. 2009; Powers et al. 2015; Maranger et al. 2018). However, because most studies focus on biogeochemical processing at a single location within a reservoir, typically the deepest site (e.g., the U.S. Environmental Protection Agency National Lake Assessment), less is known about the spatial variation in reservoir biogeochemistry which may occur between headwaters and the reservoir dam.

Reservoirs are physically heterogeneous ecosystems, which likely drives changes in biogeochemistry along the reservoir continuum. Here, we define "reservoir continuum" as the spatial gradient from the headwaters to the reservoir dam. Thornton et al. (1990) proposed a heuristic model that described the reservoir continuum as a longitudinal gradient within a reservoir consisting of riverine, transitional, and lacustrine zones, each with distinct physical, chemical, and biological characteristics. Broadly, Thornton et al. (1990) posited that nutrient availability should decrease from the riverine to transitional to lacustrine zone because of decreasing water velocity, lower allochthonous inputs of sediment and organic matter, and increasing sedimentation of particulate fractions (Fig. 1a). According to this heuristic model, photosynthetic biological activity, or by proxy, chlorophyll-a (chl-a), should peak in the transitional zone (Fig. 1a) due to relatively high nutrient and light availability for primary production (Fig. 1a).

Empirical studies examining the spatial heterogeneity of biogeochemical variables in reservoirs have found inconsistent support for Thornton et al. (1990)'s heuristic model (Fig. 1b-d). Some studies have observed peak concentrations of nutrients and chl-a occasionally following Thornton et al. (1990)'s model (Fig.

1b-d; Borges et al. 2008; Rychtecky and Znachor 2011; Soares et al. 2012), but often showing no clear pattern (Fig. 1b-d; Borges et al. 2008; Varol et al. 2012; Woldeab et al. 2018; Carneiro and Bini 2020) or patterns contrary to expectations (Fig. 1b-d; Scott et al. 2009; Soares et al. 2012; Woldeab et al. 2018). Observed discrepancies in spatial patterns of chl-a and nutrient concentrations among reservoirs may result from reservoir specific characteristics (e.g., morphology, land-use, management, age, etc.), as well as differences in the behavior of varying solutes (e.g., NO_3 vs. NH_4, as well as total vs. dissolved fractions), and other biogeochemical processes which were not accounted for in Thornton et al. (1990)'s original model. Ultimately, differences in observed patterns of water chemistry and chl-a among reservoirs suggest that more research is needed to characterize reservoir biogeochemical cycling across space and through time.

While Thornton et al. (1990)'s heuristic model does not directly predict organic C concentrations or types along the reservoir continuum, it does propose patterns for the sedimentation of different types of organic C. Specifically, Thornton et al. (1990)'s heuristic model predicts sedimentation of allochthonous C to be highest in the riverine region of the reservoir due to terrestrial material transported from the reservoir inflow. In contrast, autochthonous C sedimentation would be highest in the transitional zone, where chl-a is expected to peak, due to the contribution of algal biomass to autochthonous C production and sedimentation. These expectations regarding C sedimentation imply changes in organic C quantity and quality along the reservoir continuum are likely also occurring, potentially affecting multiple ecosystem processes including light penetration (Schindler et al. 1996; Solomon et al. 2015), and C lability (Guillemette et al. 2013), which is a critical control of decomposition rates (Strauss and Lamberti 2002; Jane and Rose 2018). However, to the best of our knowledge, only one study has examined longitudinal trends in reservoir organic C quality. Marcé et al. (2021) identified a transition from terrestrially-derived organic C to autochthonous organic C along the continuum of Sau Reservoir in Catalonia, Spain. Their findings suggest high rates of organic C processing within the reservoir from the one sampling day of the study, which motivates the need for more data over a longer period of time to examine the consistency of these spatial patterns, for both organic C and other biogeochemical variables.

Temporal changes may play an equal or even more important role than spatial gradients in driving biogeochemical heterogeneity within reservoirs. For example, seasonal changes in hydrology may be an important driver of biogeochemical heterogeneity (Williamson et al. 2021), both directly via loading or dilution of biogeochemical variables (Woldeab et al. 2018), as well as indirectly via reservoir residence time, which will vary throughout the year (Soares et al. 2012). Seasonality in air temperature and solar radiation alters biogeochemical processes such as mineralization, nutrient uptake, and biological growth rates (Wetzel 2001; Weathers et al. 2021) and can increase thermal stratification, resulting in decreased oxygen concentrations in reservoir bottom waters and increased release of certain nutrients from sediment in the summer (Nürnberg 1988; Rydin 2000; Bostr m et al. 1988). Temporally variable storm events can

alter rates of primary production and respiration (Jennings et al. 2012; de Eyto et al. 2016; Kasprzak et al. 2017), as well as disrupt thermal stratification, mixing nutrient-rich hypolimnetic water into the surface. Changes in both allochthonous and autochthonous C are driven by seasonal dynamics, often with an influx of allochthonous material during snowmelt or autumn leaf senescence, and autochthonous C (e.g., phytoplankton and macrophytes) typically peaking in spring or summer (Sommer et al. 1986). Indeed, numerous studies examining seasonal variation in reservoirs have found significant trends in biogeochemical variables over the course of a year (Torres et al. 2007; Varol et al. 2012; Woldeab et al. 2018; Klippel et al. 2020). Despite the many impacts of seasonality on biogeochemical variables, the relative importance of time and space in driving biogeochemical heterogeneity in reservoirs remains unknown.

Analyzing trends in spatial variability of biogeochemical variables may help identify important sites where reservoir processing disproportionately occurs (i.e., biogeochemical hotspots, McClain et al. 2003 or control points, Bernhardt et al. 2017). Hotspots of biogeochemical processing often occur at ecosystem interfaces due to the occurrence of gradients, which either deliver limiting nutrients or provide substrate for chemical reactions (Mcclain et al. 2003; Sadro et al. 2011; Hotchkiss et al. 2018). Within a reservoir, the inflowing stream-reservoir interface may be a critical point for processing incoming biogeochemical variables (Marcé et al. 2021). However, it is likely that the importance of this ecosystem interface may vary over time. Studies documenting spatial hotspots of biogeochemical processing in reservoirs are rare (although see Marcé et al. 2021), and none exist which examine hotspots across seasons or compare the relative importance of spatial heterogeneity to seasonal (or temporal) heterogeneity.

In this study, we examined the spatial and temporal heterogeneity of chl-a, C, N, and P along a reservoir continuum in two small, eutrophic reservoirs. Both reservoirs are located within ~3 km of each other, with similar age, geology, weather, and land-use, allowing us to constrain external driving factors in biogeochemical heterogeneity. We sampled surface water along a longitudinal gradient from stream inflow to the reservoir dam and outflow in both reservoirs every month from April to October. Our main questions were: 1) How do concentrations of biogeochemical variables change along the reservoir continuum? 2) What is the relative importance of space and time in driving heterogeneity along the reservoir continuum? and 3) Are there "hotspots" of biogeochemical processing along the reservoir continuum?

Methods

Study sites

Falling Creek Reservoir and Beaverdam Reservoir are both small (FCR: 0.119 km^2; BVR: 0.39 km^2), shallow (maximum depth FCR: 9.3m; BVR: 11m at the time of this study) dimictic reservoirs owned and operated by the Western Virginia Water Authority as drinking water supplies (Fig. 2). Both reservoirs

are located in Vinton, Virginia, USA (FCR at 37.30325, -79.8373; BVR at 37.31288, -79.8159). BVR has an outflow pipe installed at an upstream site (B2) which delivers a small volume of water via an underground tunnel to the FCR watershed, feeding the inflow stream which enters FCR on the northeastern side of the reservoir (site FS2, Fig. 2b). This transfer of water from BVR to FCR occurs when water levels in BVR are <6.0 m below full pond, which occurred during the first three sampling events of this study (April-June 2019). There are two major inflows to FCR, which we sampled immediately before they entered the reservoir at site FS1 located on a forested stream, and site FS2 located on a wetland-stream complex (Fig. 2b). BVR has multiple inflow streams, but we chose to focus on two major forested inflows in the western (site BS1) and eastern (site BS2) arms, which represent the sub-watersheds with the largest contributing area within the major western and eastern arms, respectively (Fig. 2b, Text S1). In addition, we monitored discharge, but not water chemistry, at the spillway of FCR (FS3) to estimate the volume of water leaving the reservoir. Drinking water was not regularly extracted from either reservoir during the time of the study, so the primary export of water from FCR was via the surface spillway (site FS3), whereas BVR's primary export was via a stream draining below site B4. Consequently, the primary flow of water in both reservoirs was from the inflowing streams to the dam, as is typically found in run-of-river reservoirs.

Within each reservoir, we chose sites along a gradient from the stream inflows to the reservoir dam, resulting in 4 reservoir sites in FCR (F1, F2, F3, and F4 in order of increasing distance from the inflow streams) and 5 reservoir sites in BVR (B1a in the western arm, B1b in the eastern arm, B2, B3, and B4 in order of increasing distance from the inflow streams). We also monitored one site within each inflowing stream to FCR (n = 2) and BVR (n = 2) just upstream of the reservoir-stream interface, resulting in a total of 14 monitoring sites, 9 sites within each reservoir, 4 inflowing stream sites, and one stream site downstream of FCR (Fig. 2b).

Field sampling

We sampled all sites in both reservoirs (Fig. 2) on the same day once every month from April to October 2019 (n = 7 sampling days), which allowed us to capture broad spatial and temporal changes in reservoir biogeochemistry. On each sampling day, we sampled surface water from downstream to upstream (e.g., from F4 to F1 and then onto the stream sites).

We measured a suite of surface physico-chemical variables (water temperature, dissolved oxygen, and specific conductance) using a handheld YSI and conductivity probe (Carey et al. 2022b). Additionally, water samples were collected from the surface at all sites and analyzed for chl-a, dissolved organic C (DOC), total N and P (TN, TP), and dissolved N and P (ammonium: NH_4; nitrate: NO_3; soluble reactive phosphorus: SRP) and DOC quality via excitation emission matrices (EEMs; Fellman et al. 2010). EEMs measure the natural fluorescence of dissolved organic matter to characterize DOC quality (Fellman et al. 2010);

here, we specifically focused on metrics correlated with allochthonous vs. autochthonous origin of DOC. Water for dissolved analysis (DOC, dissolved N and P) was immediately filtered through GF/F (0.7 µm) filters into acid-washed 125-mL HDPE bottles and unfiltered water was collected for total N and P analysis in acid-washed 125-mL HDPE bottles (Carey et al. 2021). Water for EEMs analysis was filtered separately through ashed GF/F (0.7 µm) filters directly into ashed 20-mL glass scintillation vials (Hounshell et al. 2021). All samples for chemical analyses (total and dissolved N and P, DOC, and EEMs) were transported on ice back to the lab, where they were frozen immediately for subsequent chemical analysis. Water for chl-a analysis was collected in 2-L amber bottles, stored at ~4°C in a refrigerator, and filtered within one day, following the methods described by Carey et al. (2022b).

We measured discharge at all stream sites (FS1, FS2, FS3, and BS1, BS2) using either a salt slug or flowmeter method, depending on the stream site (see Carey et al. 2022c for a detailed description of discharge measurement methods). Discharge data were used to calculate the transport of solutes from upstream to downstream and to calculate mass balance estimates. Because we did not have a sampling location at the spillway of Beaverdam Reservoir, we calculated outflow using a mass balance approach based on modeled inflow and reservoir volume (Text S3).

In addition, we collected data for other environmental variables which might be associated with spatial and temporal heterogeneity, including whole-reservoir water residence time (Fig. S1), meteorological variables (air temperature, precipitation, Fig. S2), surface water temperature and dissolved oxygen (Fig. S3), and thermal stratification metrics (thermocline depth and Schmidt stability, Fig. S4). Thermal stratification metrics were calculated at the deepest site of each reservoir (F4 and B4) using full water column temperature profiles which were collected as part of both reservoirs' routine monitoring programs (Carey et al. 2022d, 2022e). Water residence times were calculated by dividing the total reservoir volume by the summed inflow to the reservoir for a given day (following Gerling et al. 2016). Thermocline depth and Schmidt stability were calculated at the deepest site using the R package rLakeAnalyzer (Winslow et al. 2019). Distance between sites within each reservoir were measured using GPS points and the Measure Tool in ArcGIS Pro (2018).

Chemical analyses

All chemical analyses were conducted within six months of collection following the standard methods outlined by Carey et al. (2020), Carey et al. (2021), and Hounshell et al. (2021). In brief, TN and TP were analyzed colorimetrically using a flow injection analysis (Lachat ASX 520 Series, Lachat Instruments, Loveland, CO, USA) following persulfate digestion. NH_4, NO_3, and SRP were also analyzed using a flow injection analysis. DOC was analyzed using the persulfate catalytic method on an Elementar Vario TOC Cube (Hanau, Germany). EEMs samples were analyzed for absorbance using a Shimadzu UV-1800 spectrophotometer (Kyoto, Japan) and fluorescence using a Horiba FluoroMax-3

spectrofluorometer (Kyoto, Japan). We used traditional peak-picking methods to identify broad types of autochthonous and allochthonous DOM within the EEMs (i.e., Fellman et al. 2010; Gabor et al. 2014), specifically focusing on Peaks T (Excitation: 275, Emission: 340) and A (Excitation: 260, Emission: 400-460). These two metrics represent microbial-like and humic-like fractions of dissolved organic matter, which have been correlated with autochthonous-like (e.g., algal-derived) or allochthonous-like (e.g., terrestrial-derived) DOC, respectively (Fellman et al. 2010; Gabor et al. 2014). Chl-a was analyzed using a UV-Vis Spectrophotometer (UV-Vis 1601, Shimadzu Scientific Instruments, Durham, NC, USA) after extraction in 96% buffered ethanol. We used analytical limits of quantitation for nutrient and carbon analyses to interpret ecologically meaningful differences in concentrations (Table S3).

Examining biogeochemical distributions along the reservoir continuum

We first compared concentrations of nutrients and chl-a at each sampling site to expected spatial patterns of nutrients and chl-a from the riverine to the lacustrine zone according to Thornton et al. (1990)'s model. We limited this visual analysis to variables which were included in Thornton's model (i.e., chl-a and nutrients: TN, TP, NH_4, NO_3, SRP). We also compared temporal variability in concentrations of all biogeochemical variables (i.e., chl-a and nutrients: TN, TP, NH_4, NO_3, SRP, as well as DOC and carbon quality: Peaks T and A) across sampling days. Lastly, we examined nutrient stoichiometry to estimate the relative availability of N, and P, which influences phytoplankton nutrient limitation, among other ecosystem processes (Klausmeier et al. 2004; Hessen et al. 2013, Sterner and Elser 2002). Specifically, we calculated molar ratios of TN:TP, DIN:SRP (dissolved inorganic nitrogen to SRP), SRP:TP, and DIN:TN. We calculated DIN as the sum of NH_4 and NO_3.

Drivers of heterogeneity

To determine the relative importance of space and time in driving heterogeneity within the reservoir continuum, we used the coefficient of variation (CV) as a metric of heterogeneity (following Sadro et al. 2012; Soares et al. 2012). We calculated CV across both space (CV_{space}) and time (CV_{time}). CV_{space} was calculated across all sites within each individual reservoir (e.g., F1-4, B1-4, dark brown circles on Fig. 2) on a given sampling day separately for each of the n=7 sampling days. In contrast, CV_{time} was calculated individually for each reservoir site (n = 4 sites at FCR, n = 5 at BVR; i.e., dark brown circles on Fig. 2) across all 7 sampling dates. As a result, we calculated 7 values of CV_{space} for FCR and 7 values of CV_{space} for BVR, and 4 values of CV_{time} for FCR and 5 values of CV_{time} for BVR. We report the mean, minimum, and maximum of these distributions in Table S4.

We compared CV_{time} to CV_{space} across both reservoirs to estimate the relative importance of space and time in driving heterogeneity. Additionally, we compared CV_{time} and CV_{space} between FCR and BVR to estimate differences between reservoirs. All comparisons were made using unpaired Wilcoxon tests

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(Alboukadel 2020).

Spatially explicit processing of biogeochemical variables

When analyzing reservoir biogeochemical processing, many studies calculate the mass balance of solutes coming into and out of a waterbody, thereby estimating whether the waterbody as a whole was a sink (retention of nutrients/carbon) or source (release of nutrients/carbon) for a given analyte (e.g., Vollenweider 1975; Torres et al. 2007; Brett and Benjamin 2008; Keys et al. 2019). However, because processing may not occur uniformly along a longitudinal gradient, we extended the mass balance approach to calculate a spatially explicit metric of change in biogeochemical mass along the stream-reservoir continuum in the surface water, $_{var}$, using Equation 1:

$$_{var} = \frac{[var]_d * Q_d}{\text{sp cond}_d} - \frac{[var]_u * Q_u}{\text{sp cond}_u} \text{ Eq. 1}$$

where $[var]_d$ is the concentration of a given variable at the downstream reservoir site in units of g/L, mg/L, or RFU (relative fluorescence units) depending on the analyte (see Table S3); Q_d is the discharge at the downstream site (m^3/s), and sp cond$_d$ is the specific conductance at the downstream reservoir site (S/Cm), included here to account for unobserved intrusions of solutes into the reservoir which may occur between sites (more detail below); $[var]_u$, Q_u, and sp cond$_u$ are similarly defined but at the upstream site. Q_u was calculated for each stream site on each sampling day.

Using this method, we calculated $_{var}$ both for the whole reservoir ($_{var}$WR) and along the reservoir continuum from one site to the next ($_{var}$Site) in BVR and FCR. As a result, $_{var}$WR represents the traditional mass balance approach of estimating solutes coming into and leaving the whole reservoir, whereas $_{var}$Site represents the same metric of solutes entering and leaving the surface water within a given location, but estimated at multiple locations along the reservoir continuum. In the case of $_{var}$WR, the upstream site is the reservoir inflow(s), and the downstream site is the reservoir outflow; whereas for $_{var}$Site, the upstream and downstream sites are determined along the flow path of the reservoir continuum (e.g., when calculating $_{var}$Site between F1 and F2, F1 is the upstream site and F2 is the downstream site). As a result, positive values indicate that the reservoir or site acted as a source of a given biogeochemical variable downstream, whereas negative values indicate that the reservoir or site acted as a sink. By comparing $_{var}$WR for a given day to $_{var}$Site throughout the reservoir, we can identify locations within the reservoir which disproportionately contribute to whole-reservoir biogeochemical processing reservoir, and serve as potential hotspots.

For most reservoir sites, $_{var}$Site was calculated as the difference between the single upstream and single downstream sites. However, when there were two upstream stream sites (e.g., at F1 when both FS1 and FS2 flow into FCR; Fig. 2b), the solute mass at both sites was summed to calculate the total input. At site B3, where the western and eastern arms of BVR converge, we calculated a

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weighted average of the mass of the two incoming sites, B2 and B1b, based on a weighted average of the incoming discharge rates.

Given the availability of data for this study, our spatially explicit mass balance approach provided a robust metric of spatial variability in reservoir biogeochemical processing with some caveats. First, given limited resources for monitoring discharge at within-reservoir sites, we used the same Q_d for all sites within a given reservoir on each day, measured at the outflow of the reservoir on each sampling date. Second, we strategically chose to monitor inflow streams to the reservoirs which contributed the most watershed area (Text S1), given limited resources for stream monitoring. This method assumed that the majority of incoming water was delivered through the streams we monitored, and additional sources of water and associated solutes were negligible. We accounted for any unmonitored intrusions of solutes (e.g., groundwater intrusion or smaller tributaries which were not monitored) through the use of specific conductance, which can be used as a conservative tracer due to limited biological uptake relative to C, N, or P at each site (Baker and Webster 2017; e.g. Triska et al. 1989; Casas-Ruiz et al. 2017). Third, while this method does not partition out the specific abiotic or biotic processes which may have occurred, it allowed us to estimate ecologically meaningful changes in biogeochemical variables along the reservoir continuum.

All analyses were conducted in R 4.0.3 (R Core Team, 2020), all code to recreate the analyses is available in the Zenodo repository (Woelmer, 2022), and all field and laboratory data are published with extensive metadata in the Environmental Data Initiative repository (Hounshell et al. 2021, Carey et al. 2020, Carey et al. 2021, Carey et al. 2022b, Carey et al. 2022c, Carey et al. 2022d, Carey et al. 2022e, Carey et al. 2022f).

Results

Distribution of biogeochemical variables along the reservoir continuum

In general, our observations of nutrients and chl-a (Fig. 3) did not follow the predicted patterns of Thornton et al. (1990)'s model of the reservoir continuum (Fig. 1a). Total nutrients (TN, TP) did not show a predictable decrease along the reservoir continuum in either reservoir, as was expected by Thornton et al. (1990)'s model (Fig. 3a-b, d-e). Similarly, dissolved nutrients (NH_4, NO_3, SRP) did not show a consistent pattern of decreased concentrations along the continuum in either reservoir (Fig. 3g-l). In FCR, we observed a marked increase in both NH_4 and NO_3 along the continuum (Fig. 3j-k), contrary to expectations, whereas BVR's patterns were more inconsistent (Fig. 3g-h). Lastly, we did not observe the expected peak in chl-a in the transitional zone within the reservoir, and concentrations remained relatively unchanged through the reservoir (Fig. 3c, f), except in BVR in later months when concentrations increased at upstream reservoir sites (Fig. 3c). Overall, FCR exhibited concentrations that were similar or higher than BVR for all biogeochemical variables. As a result, we focused our comparisons of spatial and temporal variability among

sites within a single reservoir, rather than comparing between FCR and BVR.

For TN and TP, both BVR and FCR showed inconsistent spatial variability over time, with peak concentrations occurring in different regions of the reservoir in different months (Fig. 3a-b, d-e). Spatial variability, as estimated by differences in concentrations across sites, increased throughout the season with the largest range in concentrations across sites in BVR occurring in October for TN (258.5 g/L) and in September for TP (11.6 g/L). Similarly, the largest range in concentrations across sites in FCR occurred in September for TN (435.5 g/L) and October for TP (14.8 g/L). In both BVR and FCR, sampling days later in the year (August – October) tended to have higher (>2× in FCR) concentrations than earlier sampling days (April – July, Fig. 3a-b, d-e).

Chl-a was relatively constant across space on all sampling days in FCR (Fig. 3f; max. range = 5.7 g/L in August, min. range = 0.2 g/L in April), with relatively similar concentrations throughout the reservoir. Chl-a in BVR was similarly homogenous over space (Fig. 3c; max. range = 7.6 g/L in October, min. range = 0.5 g/L in June), with the exception of September and October, when chl-a was higher in the riverine areas of the reservoir. Chl-a increased over the study period in both reservoirs, with the highest concentrations observed in September and October.

Dissolved N, P, and organic C were generally more variable over both space and time than total nutrients (Fig 3). Both NH_4 and NO_3 were variable across space in FCR (Fig. 3j-k), showing peak concentrations of both variables in the most downstream location near the dam. NO_3 and NH_4 in BVR and SRP in both reservoirs varied both across space and time, but most observed values were below the limits of quantitation and therefore should be interpreted with caution (Table S3). Finally, DOC was highly variable over both space and time in BVR (Fig. 3m), with the largest range across sites occurring in July (2.4 mg/L), and the smallest range occurring in October (0.7 mg/L). While FCR did exhibit some spatial variability in DOC (Fig. 3p), the trend was inconsistent over time.

Over our sampling sites and dates, autochthonous (Peak T) and allochthonous (Peak A) C varied more over time than space (Fig. 3n-o, q-r), with relative fluorescent intensities increasing throughout the year. The one exception to this pattern was in August in BVR, when Peak T increased at the most downstream site B4 (range across sites = 0.10 RFU). Given that both autochthonous (Peak T) and allochthonous (Peak A) metrics showed very little change along the reservoir continuum, our data do not support a clear shift between autochthonous C and allochthonous C sources among sites in our reservoirs. Overall, there was greater fluorescent intensity for both Peaks A and T in FCR as compared to BVR across both time and space, reflective of higher DOC concentrations observed in FCR.

Nutrient stoichiometry was also highly variable over space and time (Fig. S5). Molar ratios of TN:TP at reservoir sites in FCR and BVR were typically above

Redfield ratios of 16:1 (Redfield 1934), indicating potential P limitation in both systems (mean ratio of 28.9 ± 14.6, 1 SD). However, these ratios were variable over space, with no consistent increase or decrease observed along the continuum. Molar DIN:SRP was similarly variable over space and time, but showed a consistent increase along the reservoir continuum in FCR, on average from 1.3 at the most upstream site to 3.8 at the dam (Fig S5). This pattern did not occur in BVR, which ranged from a ratio of DIN:SRP of 2.0 and 3.7 at the most upstream sites (B1a and B1b, respectively) to 2.1 at the dam. Across FCR and BVR, mean molar DIN:TN ratios were 0.04 (±0.02), indicating that the particulate fraction of N dominated the total N pool. In contrast, SRP:TP ratios were 0.6 (± 0.45) in both reservoirs.

Ancillary environmental variables showed expected seasonal trends. Discharge at all four stream sites showed a clear decreasing trend over the course of the study period from April to October (Fig. 4a). Specific conductance, which we used as a conservative tracer in our study, increased over time throughout the year at all study sites. In addition, specific conductance showed very little variation over space within the reservoir (Fig. 4b), except for lower specific conductance (on average by 8.4 S/cm) in reservoir sites than stream sites. Following Eq. 1, which used specific conductance as a conservative tracer throughout the reservoir, this difference in specific conductance had a negligible effect on $_{var}$Site, and may have resulted in under-estimation of biogeochemical processing at the stream-reservoir interface (Fig. S7). Over our study period, water residence times were approximately $3\times$ longer in BVR than FCR, with a mean water residence time of 475±301 (1 SE.) days for FCR and 1300±335 days for BVR. The longest residence times occurred during October (Fig. S1), which were $8\times$ longer in BVR and $73\times$ longer in FCR than the shortest residence times in April. Text S2 includes a description of meteorological variables (air temperature and precipitation, Fig. S2), surface water temperature and dissolved oxygen (Fig. S3), and thermal stratification metrics (thermocline depth and Schmidt stability, Fig. S4) over the study period.

Heterogeneity across space and time

Across both reservoirs, heterogeneity over time (CV_{time}) was significantly higher than heterogeneity across space (CV_{space}) for TN, TP, Chl-a, SRP, Peak T, and Peak A (Fig. 5a-c, f, h-i; SRP p = 0.046; all others p < 0.0001). For the remaining variables (NH_4, NO_3, and DOC; Fig. 5d-e, g), there was no significant difference in heterogeneity across space and time. FCR and BVR were significantly different from each other in heterogeneity of both space and time for most biogeochemical variables (Fig. 5). FCR was significantly more temporally heterogeneous than BVR for several variables: TP, NH_4, NO_3, DOC, Peak T, and Peak A (Fig. 5b, d-e, g-i). In contrast, BVR was significantly more temporally heterogeneous than FCR only for chl-a (mean CV_{time} BVR = 0.84; mean CV_{time} FCR = 0.75; Table S4). Over space, FCR was not significantly more heterogeneous than BVR for any variable, and BVR was more heterogeneous over space than FCR for chl-a only (mean CV_{space} BVR = 0.21; mean CV_{space}

FCR = 0.1; Table S4, Fig. 5c).

CV_{space} and CV_{time} were not significantly different from each other for the nutrient ratios, with the exception of SRP:TP, which was more heterogeneous over time than space (Fig. S6, $p < 0.05$). Similarly, BVR and FCR were not significantly different in the magnitude of heterogeneity for any variables, except for CV_{space} for SRP:TP.

Spatially explicit processing of biogeochemical variables

When calculating spatially explicit processing between sites ($_{var}$Site), we found that the highest rates of processing typically occurred at the inflowing stream-reservoir interface (Fig. 6). This pattern is exemplified by peak values of $_{var}$Site in the regions between the stream sites and the most upstream reservoir sites in both reservoirs (i.e., between FS1/FS2 and F1; BS1 and B1a; BS2 and B1b). We found that the stream-reservoir interface disproportionately contributed to whole-reservoir dynamics, in which the magnitude and direction of the whole-ecosystem processing (as indicated by $_{var}$WR) matched that of $_{var}$Site at these locations. For example, the $_{var}$Site data for DOC in BVR highlight that a majority of changes in DOC occurred between the inflowing stream sites and upstream areas of the reservoir, with negligible change occurring in the down-stream areas of the reservoir. Consequently, the upstream areas of the reservoir were primarily responsible for the magnitude and directionality of $_{var}$WR, which shows that BVR was a source of DOC on most days (Fig. 6m; e.g., between BS1 and B1a and BS2 and B1b, Fig. 2b), despite some sites in the intermediate area of the reservoir (e.g., sites B2 and B3) functioning as a small sink of DOC on some days, especially in April.

This pattern where the stream-reservoir interface disproportionately impacted whole-reservoir ($_{var}$WR) dynamics, as exhibited by large values $_{var}$Site at the stream-reservoir interface, was exhibited by TN, TP, Chl-a, NH4, DOC, and Peaks T and A in BVR, and almost all biogeochemical variables in FCR, with the exception of DOC. The changes along the reservoir continuum in $_{var}$Site for Peak T (a metric of autochthonous organic C) indicates an increase in autochthonous sources of C between the incoming stream and upstream reservoir sites for both reservoirs, with the exception of some months (July in BVR and June in FCR, Fig. 6n, q). Interestingly, $_{var}$Site for peak A (a metric of allochthonous C) followed a similar pattern, with an increase in allochthonous sources of C (peak A) between incoming stream sites and upstream reservoir sites, except for July in BVR, and June and August in FCR. Overall, patterns of DOC, Peak A, and Peak T were similar across days and sites in BVR.

Despite that the stream-reservoir interface often dominated whole-reservoir dynamics, there were some biogeochemical variables and sampling days for which sink-source dynamics changed throughout the reservoir, indicating that the reservoir functioned as both a sink and a source at different locations. These variables included TN in both reservoirs (Fig. 6a, d), NO_3 and SRP in BVR (Fig. 6h-i), and Peaks T and A in FCR (Fig. 6q-r). For example, changes in

$_\text{var}$Site of Peak T were variable along the reservoir continuum in FCR, with some sampling days showing decreases from site to site in the intermediate region of the reservoir (e.g., site F2). Values of $_\text{var}$Site for SRP in BVR were also spatially variable, in which the reservoir exhibited source dynamics at upstream sites, sink dynamics in the intermediate sites of the reservoir, and source dynamics again near the dam on a single sampling day (e.g., April, August, October). This variability over both space and time highlights that likely multiple interacting mechanisms were driving the processing of these biogeochemical variables along the reservoir continuum.

Further, the presence of large values of $_\text{var}$Site at sites throughout the reservoir (e.g., NO_3 in BVR, which exhibited numerous fluctuations between sink and source dynamics, Fig. 6h) were more common in BVR than in FCR, where large $_\text{var}$Site values were primarily found in upstream areas of the reservoir. Variability in the location of peak values of $_\text{var}$Site as well as increases in the magnitude of $_\text{var}$WR were more common in FCR during April, when the discharge into the reservoir was $>4\times$ higher than any other sampling days. This result indicates that our metrics of processing were sensitive to large changes in hydrology and emphasizes the importance of time-discrete changes in the location of processing 'hotspots.'

According to the whole-reservoir metric of processing, $_\text{var}$WR, BVR and FCR acted similarly as a sink of both NO_3 and TP at the whole-reservoir scale, and both reservoirs acted as a source of TN, DOC, and chl-a on most or all days (Fig. 6). On all days, BVR was a sink for NH_4, and on most days FCR was a sink or passive transporter (meaning no substantial change between the inflow and outflow) for NH_4, but acted as a source of NH_4 in April. Sink-source dynamics of SRP differed between FCR and BVR, with FCR primarily serving as a sink of SRP, whereas BVR switched from a sink to a source through time.

Discussion

Our study demonstrates that in two small reservoirs, time is a more important driver of heterogeneity than space for multiple biogeochemical variables. While the two reservoirs did show substantial spatial variability in surface water biogeochemistry, these patterns were inconsistent over time, contrary to Thornton et al. (1990)'s heuristic model which describes distinct and consistent longitudinal zones along a reservoir continuum. Moreover, we observed "hotspots" of processing along the reservoir continuum where biogeochemical variables consistently and substantially changed, indicating that some locations disproportionately contributed to changes in biogeochemistry within a reservoir. For multiple variables we found that this hotspot location was frequently the interface between the stream and the reservoir, supporting other studies which posit that ecosystem boundaries or transitions often result in "hotspots" of biogeochemical processing (McClain et al. 2003, Bernhardt et al. 2017, Marcé et al. 2021). Ultimately, our analysis emphasizes the importance of examining spatial patterns and biogeochemical processing along the reservoir continuum.

Spatial and temporal variability in biogeochemistry along the reservoir continuum

BVR and FCR exhibited substantial variability in biogeochemistry across the reservoir continuum (space) and throughout the study period (time) (Fig. 3). However, spatially, most variables either showed inconsistent longitudinal variability over different sampling dates (e.g., NH_4 and DOC in BVR, SRP in FCR) or patterns contrary to previous expectations (e.g., NH_4 and NO_3 in FCR, chl-a in BVR). Ultimately, our results provide limited support for Thornton et al. (1990)'s model that biogeochemical variables change predictably along the reservoir continuum (following Fig. 1). However, a major caveat of Thornton et al.'s (1990) model is the absence of an explicit time-dynamic component, which may be a key factor constraining the generality of their proposed trends. Our findings follow other studies that found inconsistent or divergent trends in reservoir spatial dynamics (Carneiro and Bini 2020, Borges et al. 2008, Varol et al. 2001, Woldeab et al. 2017, Scott et al. 2009, Soares et al. 2012), adding to a body of work examining longitudinal biogeochemistry in reservoirs.

A number of reservoir-specific characteristics may influence the strength of longitudinal gradients along the reservoir continuum, and help explain why we observed differences in biogeochemical distributions between BVR and FCR. Reservoir morphology, the number and location of tributaries, and reservoir size may all influence the strength of biogeochemical gradients and the heterogeneity within a reservoir (Carneiro and Bini 2020). While BVR and FCR are of similar age and have similar land-use within their watersheds (Gerling et al. 2016), they differ in several other important characteristics. FCR is a single-arm reservoir with two main upstream inflows. In contrast, BVR's morphology is more complex, with two main tributaries feeding separate arms that converge downstream within the reservoir, potentially leading to additional hotspots at the confluence of the distinct parcels of water. Indeed, for some variables, especially chl-a, SRP, and on some days DOC and Peaks T and A, we did see that the confluence at B3 showed larger rates of processing (Fig. 6c, i, m-o), although the pattern did not occur consistently.

Additionally, BVR is typically much more strongly stratified than FCR (Fig. S4). This difference in thermal stratification strength is likely due to differences in volume, with FCR ~2 m shallower and 30% smaller in surface area (difference of 0.27 km^2) than BVR. Because BVR was more strongly stratified than FCR, internal nutrient loading from sediment fluxes may have been less likely to influence surface water concentrations in BVR than in FCR, and may have prevented increases in some nutrients downstream, such as we observed in FCR for NO_3 (Fig. 3j). Overall, these differences in morphology may have led to our observations of increased spatial heterogeneity in BVR as compared to FCR (as exemplified by greater spatial heterogeneity in NH_4, NO_3, DOC, and SRP in BVR than FCR, Fig. 3), as BVR has generally more complex morphology.

Nutrient concentrations in FCR were consistently higher than BVR. We expected to see this pattern during the periods when surface water from BVR is delivered to FCR due to both increased connectivity, leading to higher nutrients

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in downstream ecosystems (Wurtsbaugh et al. 2005, Sadro et al. 2012; Brown et al. 2008; Stachelek and Soranno 2019), as well as lower spatial heterogeneity in FCR due to shorter water residence times in cascading reservoirs (Barbosa et al. 1999; Drastik et al. 2008). While we did see shorter residence times during the first three sampling dates when BVR was connected to FCR, nutrient concentrations were higher later in the season when the reservoirs were not connected, indicating that seasonal dynamics may be more important for driving nutrient concentrations than inflow connectivity. Moving forward, examining spatial and temporal distributions of biogeochemistry across a range of reservoir ages, land-uses, morphologies, tributaries, and landscape positions will help build upon this work and inform generalizable trends in reservoir biogeochemical distributions across space and time.

Implications of time as a dominant driver of heterogeneity

Despite observing substantial spatial variation in the biogeochemistry of both BVR and FCR, time significantly dominated heterogeneity for most biogeochemical variables (Fig. 5). Seasonal succession has long been considered a critical driver of variability in freshwater ecosystems (e.g., Sommer et al. 1986; De Senerpont Domis et al. 2013). However, our study adds an important novel comparison between the relative influence of space and time in driving heterogeneity, a central question in the study of physically heterogeneous reservoirs (Thornton et al. 1990). Similar to our findings, many studies have documented that spatial heterogeneity of biogeochemistry is highly variable over time (Shaughnessy et al. 2019, Borges et al. 2008, Soares et al. 2012).

While we cannot directly parse the mechanisms driving temporal heterogeneity in our reservoirs, a number of changing seasonal dynamics could be connected. For example, Collins et al. (2019) found that both winter precipitation, which may influence delivery of organic matter and nutrients during spring runoff (Pierson et al. 2013; Brown et al. 2008), as well as summer temperature, which is directly related to biological activities such as primary production and mineralization, were able to predict lake water quality across ~11,000 U.S. lakes, highlighting the importance of temporal variation in climate variables. Another study found that seasonal changes in temperature, nutrient availability, and hydrology also directly influenced phytoplankton communities across a reservoir continuum (Lv et al. 2014). In our study, which was focused on the summer thermally-stratified period, we were unable to examine the effect of winter precipitation, but did observe that the later months with the warmest temperatures (July and August, Fig. S3) had higher concentrations of chl-a, total nutrients, and both autochthonous and allochthonous organic C indicators (Fig. 3). The highest concentrations of these variables tended to occur even later in the season (September and October) after water temperatures had begun to decline, indicating that other seasonally variable drivers such as increased residence time (Fig. S1) may also play a role.

However, we did observe that spatial heterogeneity may play a role in driving the concentrations of some variables; specifically, NH_4, NO_3, DOC showed a

non-significant difference between space and time in driving heterogeneity (Fig. 5). Thus, because neither time nor space was significantly more important in driving the heterogeneity of these variables, we infer that space may be relatively more important for driving variability in dissolved nutrients (e.g., NH_4, NO_3, DOC, SRP) than for total nutrients, metrics of C quality, and chl-a, which were significantly more influenced by time. Dissolved nutrient concentrations are generally considered more variable and harder to predict than total nutrients (Robson and Dourdet 2015; Soares and Calijuri 2021), which may be related to their increased spatial variability and rapid uptake times.

Lastly, nutrient stoichiometry, i.e., the ratios of molar N to P, as well as ratios of total to dissolved fractions of these nutrients, were highly variable over time and space (Fig. S5). We did not observe any significant differences between CV_{space} and CV_{time} for any of the ratios except for SRP:TP, indicating an important role of both space and time in driving variability of stoichiometry (Fig. S6). While most of these ratios show highly variable patterns, DIN:SRP tended to increase along the reservoir continuum in FCR, with the highest values found nearest the dam. This was strongly driven by increases in dissolved N (Fig. 3j-k, NH_4 and NO_3) which were observed in FCR and is evidence for increased P limitation in the downstream regions of the reservoir. Despite that some individual nutrient constituents did not exhibit consistent change spatially within our reservoirs (Fig. 3), the relative availability of N and P did change, with potentially important implications for controlling phytoplankton community composition (Watson et al. 1997; Downing et al. 2001). For example, greater P-limitation downstream in FCR could result in the promotion of non-N-fixing phytoplankton upstream and N-fixing cyanobacteria downstream (Vanni et al. 2011; Hamre et al. 2018).

Importance of biogeochemical processing "hotspots"

Examining spatially explicit processing suggests that along the reservoir continuum, the stream-reservoir interface can be disproportionately important for whole-reservoir biogeochemical processing. Our spatially explicit metric of processing, $_{var}$Site, highlights that the stream-reservoir interface most consistently acts as a "hotspot" of biogeochemical processing, as shown in the largest values of $_{var}$Site at the farthest upstream location in the reservoir for most variables (Fig. 6). This finding is in line with previous conceptual frameworks (McClain et al. 2003, Bernhardt et al. 2017), field experiments (Marcé et al. 2021, Sadro et al. 2011), and laboratory experiments (Lambert and Perga 2019), which also suggest that ecosystem boundaries, particularly those between stream and lake ecosystems, serve as ecosystem hotspots. This result is likely driven by multiple mechanisms. First, inflowing streams provide subsidies of nutrients and C which can be processed and transformed by organisms either via primary production or decomposition (Wetzel 2001). Second, physical processes may also play an important role. For example, if incoming stream water is much colder than reservoir surface water, the parcel of stream water may plunge to the bottom of the reservoir, resulting in delivery of organic matter and nutrients deeper

within the water column or in the sediments (Thornton et al. 1990), where they would not be measurable via our sampling method in surface waters. In FCR and BVR, it is likely that both of these mechanisms play a role in driving the importance of the stream-reservoir interface in biogeochemical processing, as the inflowing streams in FCR and BVR were 3.9°C and 4.7°C colder, respectively than the average reservoir site water temperature (Text S2, Fig. S3). Altogether, our data suggest that the stream-reservoir interface is a key location of biogeochemical processing, which can inform reservoir field monitoring programs to better understand how reservoirs function as sinks or sources of biogeochemical variables.

Interestingly, we did find some exceptions to the stream-reservoir interface dominating the location of processing "hotspots." These exceptions (i.e., large $_{var}$Site values) occurred inconsistently at different sites throughout the reservoir. However, they occurred more often in BVR than in FCR, and in FCR during our April sampling, when discharge was highest. These results suggest that some reservoirs may be more spatially variable than others in locations of hotspots, and that changes in stream inflow volume can influence processing rates. In larger, more morphologically variable reservoirs (e.g., with multiple inflow streams along the reservoir, higher shoreline development indices), biogeochemical processing may occur less consistently in the furthest upstream stream-reservoir interface due to additional inflow streams entering the reservoir downstream or greater influence of overland runoff. Similarly, increased inflow volumes are directly connected to shorter water residence times, which may limit processing upstream and instead favor processing occurring further along the reservoir continuum where water flows have slowed (i.e., in the transitional and lacustrine regions, as we observed in April in FCR).

Comparing values of $_{var}$Site to the traditional method of estimating whole-reservoir function, $_{var}$WR, suggests limitations of traditional whole-ecosystem mass balance approaches which tend to focus on sources into and out of the reservoir. Because most monitoring programs sample at stream sites and the deepest lacustrine sites only, current methods would provide biased estimates of reservoir functioning according to our results. For example, the estimate of whole-reservoir function, $_{var}$WR, shows that BVR was a sink of NO_3 on all sampling days. However, the reservoir was both a sink and a source of NO_3 at different locations within the reservoir on a single sampling day according to $_{var}$Site (Fig. 6). We see a similar pattern for most variables in BVR (i.e., a mismatch between $_{var}$WR and individual values of $_{var}$Site along the continuum), indicating that complex dynamics occur along the reservoir continuum which are ignored by simply measuring only one reservoir site alone.

Strengths and limitations of study design and directions for future research

Our study provides a novel examination of spatial and temporal variability of biogeochemical concentrations and processing in reservoirs, motivating future research. First, both of our study reservoirs are relatively small and shallow. While reservoirs of similar size (less than 1 km^2) make up ~99% of reservoirs

globally (Lehner et al. 2011), larger reservoirs may have more complex morphology and as a result exhibit different patterns and drivers of spatial variability. Second, BVR is mesotrophic (mean TP = 15.5 µg/L, mean chl-a = 6.35 µg/L) and FCR is eutrophic (FCR mean TP = 28.7 µg/L, mean chl-a = 8.95 µg/L; following Carlson and Simpson 1996), with algal blooms occurring regularly in FCR (Carey et al. 2022d). Research in a hyper-eutrophic lake of similar size shows that the presence of algal blooms can dramatically increase spatial heterogeneity as the blooms move from one location to another (Ortiz and Wilkinson 2021). Studies conducted in additional systems, especially those which are oligotrophic, may illuminate different patterns in spatial heterogeneity and highlight differences among systems of diverse trophic states.

Third, additional spatial data may help increase the utility of our biogeochemical processing metric, $_{var}$Site. For example, by estimating the location of the stream plunge-point (i.e., where the incoming stream water plunges into the reservoir), Marcé et al. (2021) were able to specifically pinpoint locations of processing and associated changes in dissolved organic matter composition. Because we sampled at discrete, set locations within each reservoir region irrespective of stream plunge-points, we were unable to identify the exact location where processing occurred, but rather regions within which high rates of processing likely occurred.

Fourth, because water residence time is dependent on depth and bathymetry, it is likely to change within a reservoir along the longitudinal continuum. Calculating reservoir site-specific residence times, as opposed to using the outflow of the entire reservoir, could improve our spatial processing metric. Our Eq. 1, which was based on using specific conductance to account for changing hydrology, likely resulted in more conservative estimates of $_{var}$Site processing than what actually occurred because of small differences in specific conductance between the inflowing stream and most upstream reservoir sites. Higher values of specific conductance at stream sites resulted in lower calculations of incoming nutrient and C loads for the stream component of Eq. 1, thereby resulting in smaller values of $_{var}$Site. Standardizing specific conductance at stream sites to be equal to the observed specific conductance at the first within-reservoir site (Fig. S7) indicates that our Eq. 1 calculations likely underestimated values of $_{var}$Site at the stream-reservoir interface, increasing our confidence in this region as a major site of biogeochemical processing.

Finally, collecting samples of biogeochemical variables throughout the water column, as opposed to just the surface, may also help inform some of the patterns we observed. For example, by sampling throughout the water column, we may be able to parse additional sources of nutrients within the reservoir, e.g., via sediment release or interflow. Altogether, a more detailed approach to sampling nutrients and C within reservoir continua will help inform the fate of biogeochemical variables and advance our understanding of how these variables change across ecosystems.

Conclusions

Our study informs future research on spatial and temporal heterogeneity across lentic ecosystems. While we focus on surface water effluent reservoirs, our results likely hold for reservoirs with selective water withdrawal, as well as naturally-formed lakes with surface water outflows. Given that these waterbodies are typically only sampled at their deepest point, we are likely missing important spatial variability influencing whole-ecosystem biogeochemical dynamics. Our work points to the need for more data examining the role of the stream-reservoir interface as "hotspots" of biogeochemical processing, as well as the need for understanding when and why these hotspots dominate whole-ecosystem dynamics. Finally, our study provides support for temporal sampling which occurs over multiple months in order to capture the full variability in reservoir functioning. Ultimately, a better quantification of when and where biogeochemical variables are processed within reservoirs will advance our understanding of the important role reservoirs play in global biogeochemical cycles.

Author contribution statement: WWM, AGH, and CCC co-conceived the design of the study. WMW and AGH led field sampling, with assistance from ASL, HLW, and MEL. WMW, AGH, and HLW analyzed water chemistry samples, with analytical support from DS. ASL contributed to figure design, and CCC, MEL, and DS contributed to conceptual development, which substantially improved the quality of the manuscript. WMW led the writing of the manuscript with CCC, AGH, and MEL, and all authors contributed to manuscript editing.

Availability of data and material: All data used in this study are published and available within the Environmental Data Initiative repository (Hounshell et al. 2021, Carey et al. 2020, Carey et al. 2021, Carey et al. 2022b, Carey et al. 2022c, Carey et al. 2022d, Carey et al. 2022e, Carey et al. 2022f). All code used to download data, generate data specific to this study, and conduct analyses are available in a Zenodo repository (Woelmer, 2022).

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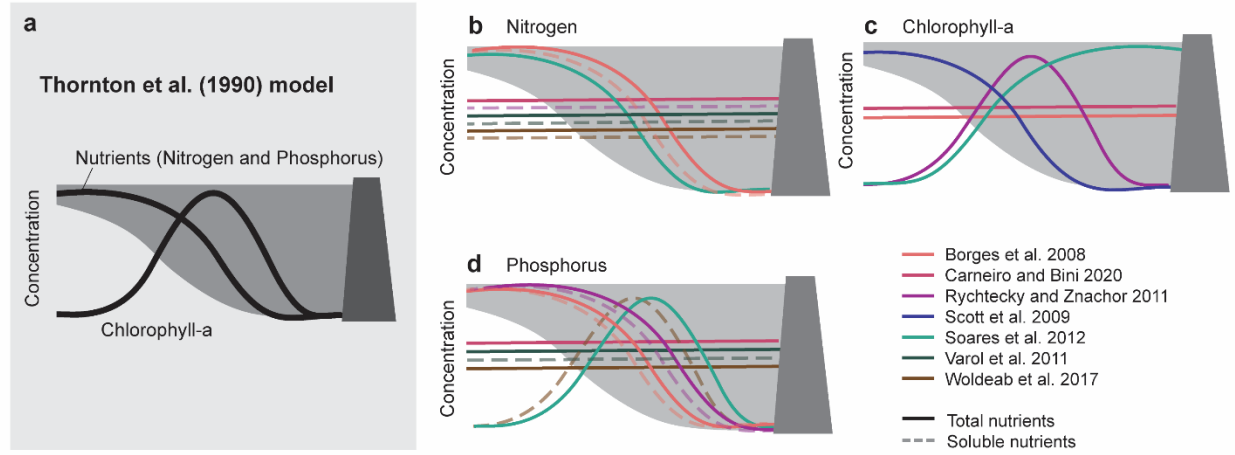
Figure Captions

Fig. 1 Conceptual diagram showing a) Thornton et al.'s (1990) model of the spatial distribution of chlorophyll-a and nutrients (N and P) along the reservoir continuum, as well as selected field studies which have examined the distribution of b) nitrogen (N), c) chlorophyll-a (chl-a), and d) phosphorus (P) in reservoirs across the globe. While Thornton et al. (1990) did not distinguish between N and P, or total and dissolved nutrient fractions, we delineate these pools here when possible (total nutrients in solid lines, dissolved nutrients in dashed lines in panels b and d). We note that patterns of reservoir longitudinal distributions are meant to be qualitative and only represent relative minimums and maximums. Other than Marcé et al. (2021), we were unable to find analyses of the distributions of allochthonous and autochthonous carbon across the riverine, transitional, and lacustrine reservoir zones in the literature to match Thornton et al. (1990)'s model
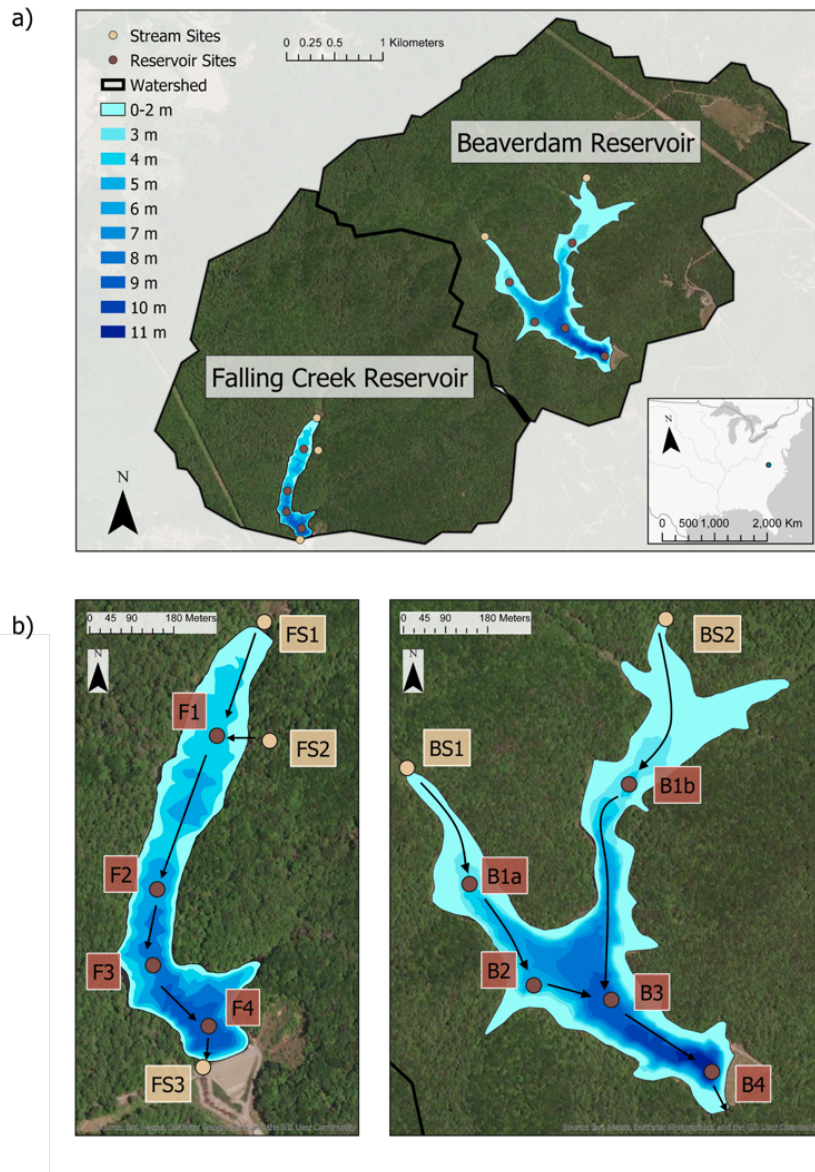
Fig. 2 Map of Falling Creek Reservoir (FCR) and Beaverdam Reservoir (BVR) with a) watershed area, and locations of stream and reservoir sampling sites and b) names of sampling sites on both reservoirs' bathymetry. Arrows in panel B indicate the approximate flow of water through the stream-reservoir continuum
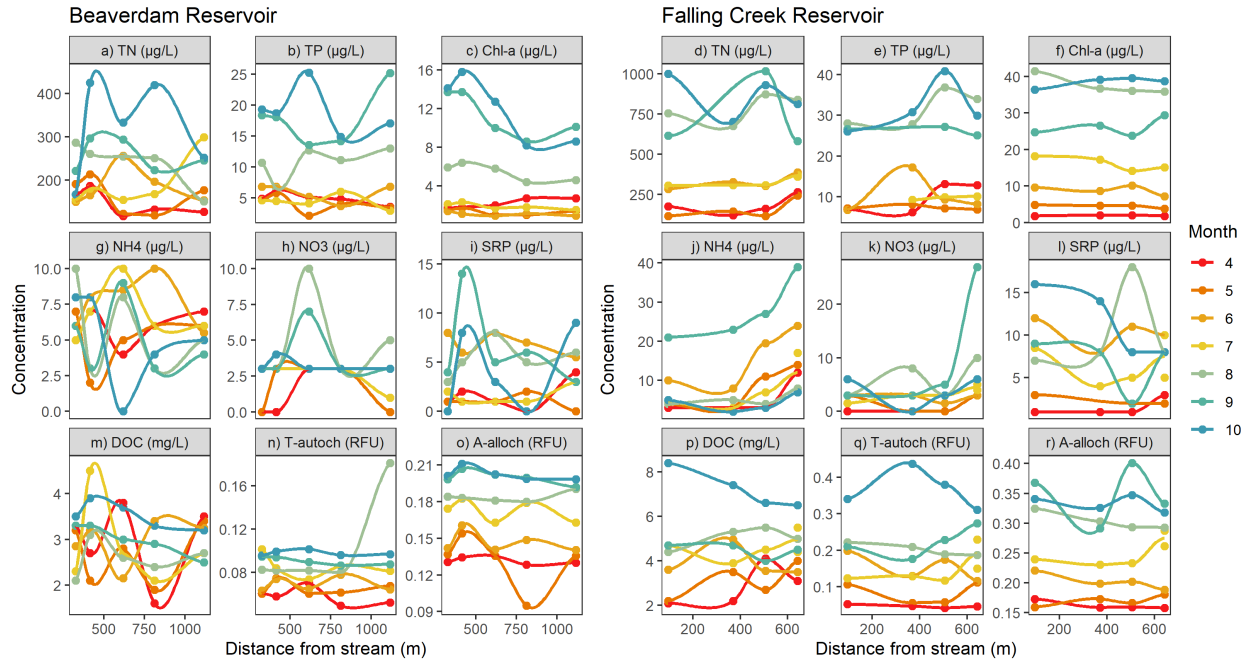
Fig. 3 Concentrations of biogeochemical variables along the reservoir continuum starting from the most upstream reservoir site of Beaverdam Reservoir (left panels) and Falling Creek Reservoir (right panels). Each panel represents a different biogeochemical variable, and colors represent the month of sampling, from 4 (April) to 10 (October). All units are denoted in each panel header. TN = total nitrogen, TP = total phosphorus, chl-a = chlorophyll-a, NH_4 = ammonium, NO_3 = nitrate, SRP = soluble reactive phosphorus, DOC = dissolved organic carbon, T-autoch = Peak T autochthonous carbon quality, A-alloch = Peak A allochthonous carbon quality
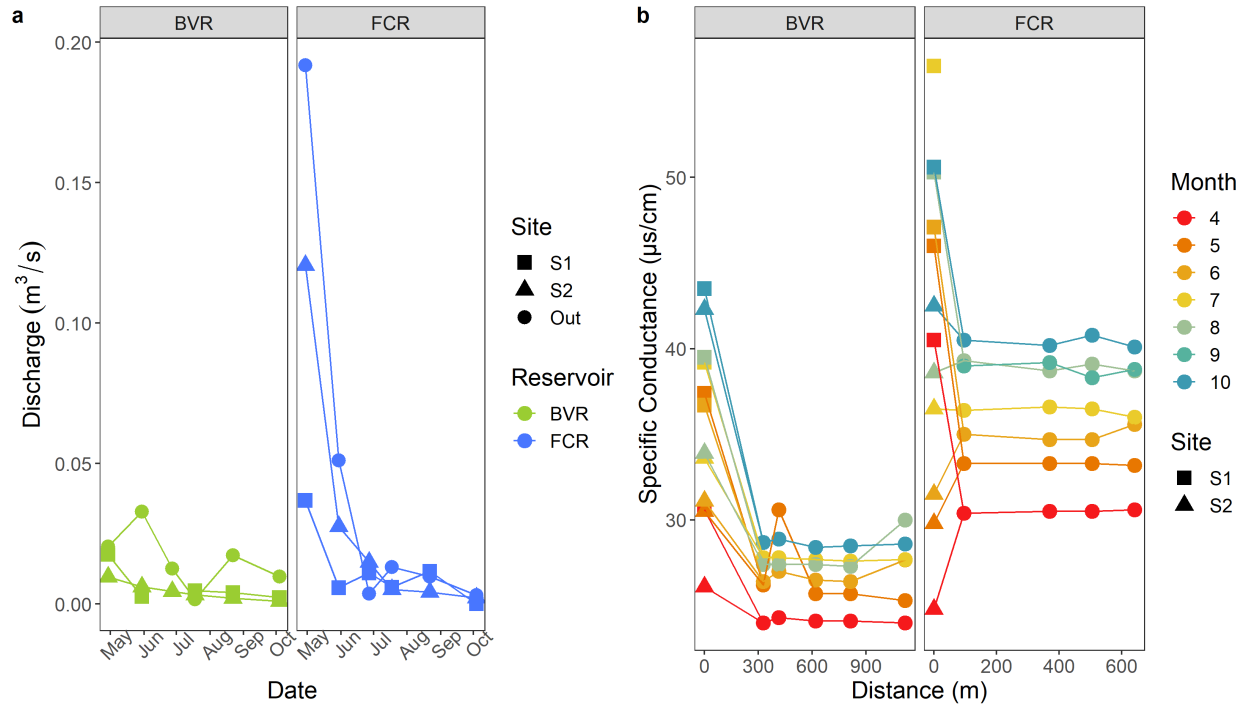
28

Fig. 4 a) Discharge at all stream (inflow and outflow) sites on all sampling dates, with Falling Creek Reservoir (FCR) sites represented in blue and Beaverdam Reservoir (BVR) sites in green. Site S1 refers to sites FS1 or BS1, while Site S2 refers to sites FS2 or BS2, with reservoir designated by color and panel. Sites designated as 'Out' represent the outflow dynamics for each reservoir and were estimated at FS3 at FCR and B4 in BVR. b) Specific conductance at all sites and for all sampling dates, with colors representing the month of sampling, from 4 (April) to 10 (October). Stream sites are represented by triangles or squares, while sites within the reservoir are represented by circles. Specific conductance was not collected at BVR sites in September
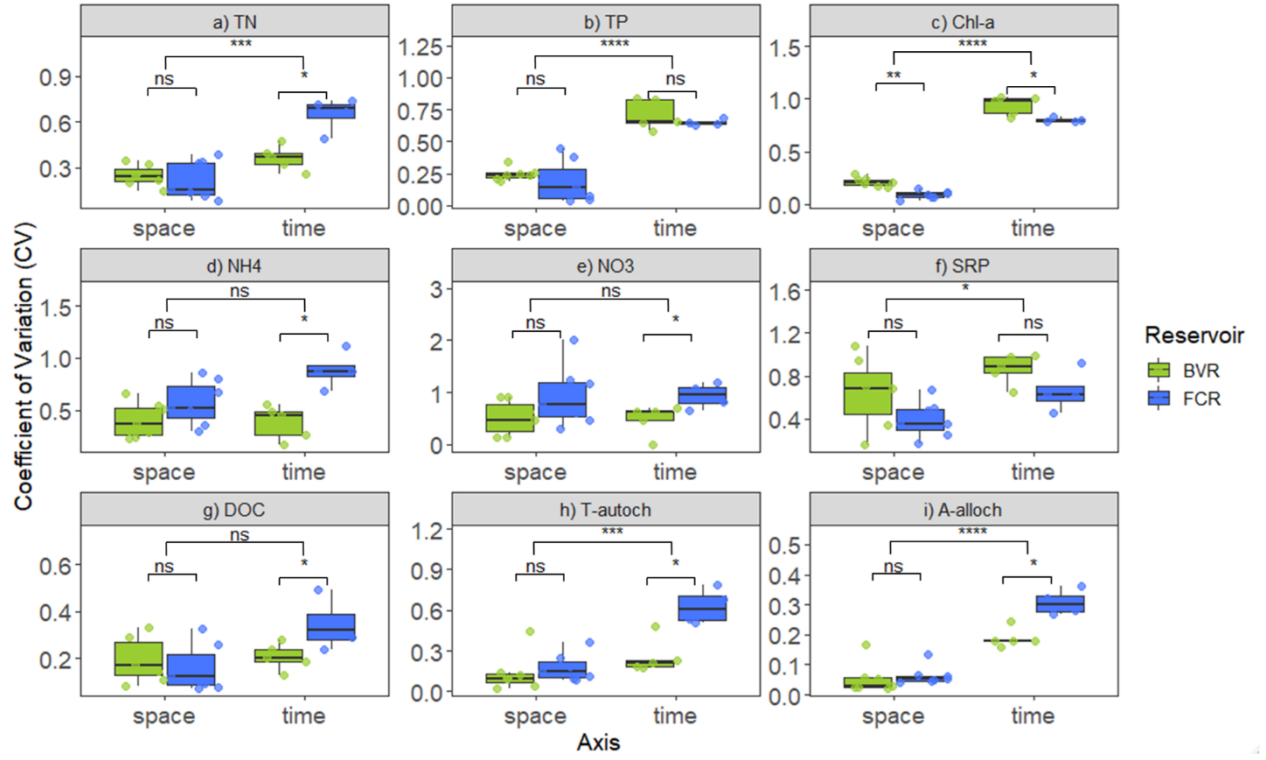
Fig. 5 Heterogeneity, as measured by coefficient of variation, over space (CV_{space}) and time (CV_{time}) for BVR and FCR for total nutrients (TN and TP), chl-a, dissolved nutrients (NH_4, NO_3, SRP), dissolved organic carbon quantity (DOC), and dissolved organic carbon quality (Peak T, autochthonous, and Peak A, allochthonous). Bars above pairing represent the pairing of groups for significance testing. 'ns' denotes a non-significant relationship ($p > 0.05$), a single asterisk '*' represents $p < 0.05$, three asterisks '***' represents $p < 0.0001$, and four asterisks '****' represents $p < 0.00001$
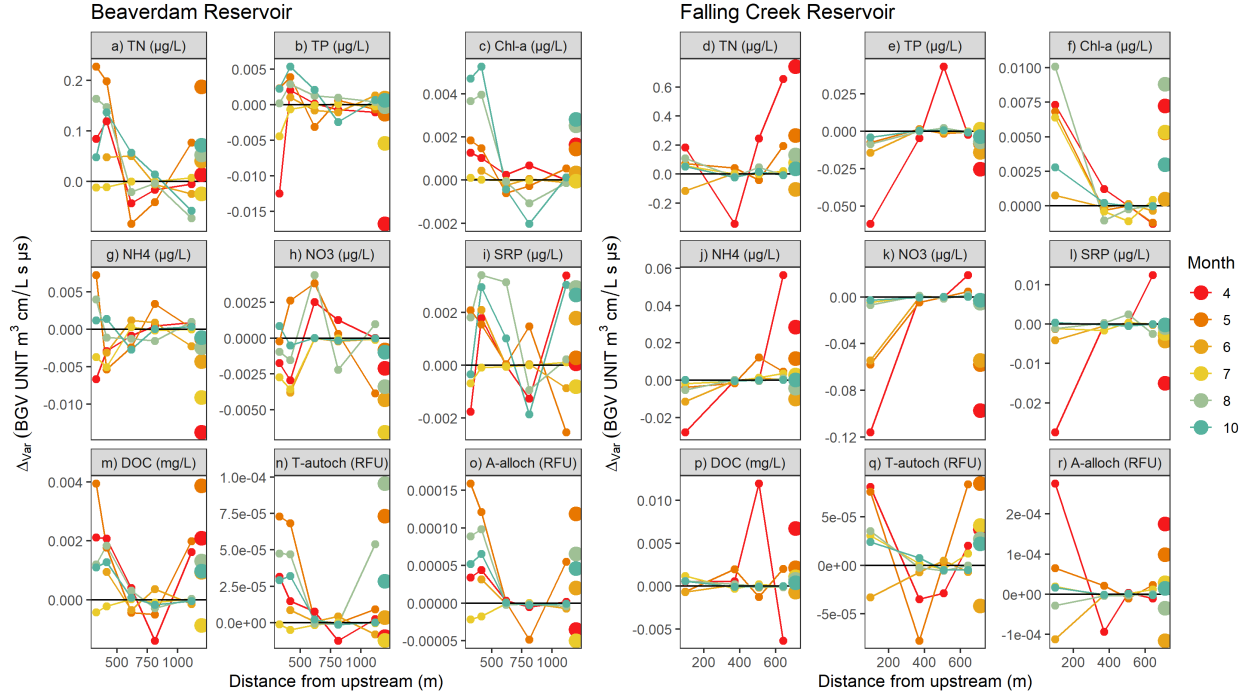
Fig. 6 $_{var}$, or the change in biogeochemical variables, along the reservoir continuum corrected by specific conductance with each variable represented in individual panels. $_{var}$Site, which represents the change between sites, is shown at each sampling site along the reservoir continuum and $_{var}$WR, which represents the change from inflow stream sites and the furthest downstream site, is shown in large points at the further downstream site on the x-axis. See *Methods: Spatially explicit processing of biogeochemical variables* for a full description of $_{var}$Site and $_{var}$WR (Eq. 1). Color represents the month in which the sample was collected, from 4 (April) to 10 (October). 'BGV UNIT' stands for the individual units of each biogeochemical variable, which are listed in each panel label. Samples were not collected at stream sites in September and are excluded from this analysis