ECOSYSTEMS

Spatial and Temporal Variability of Nutrient Dynamics and Ecosystem Metabolism in a Hyper-eutrophic Reservoir Differ Between a Wet and Dry Year

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ABSTRACT

Climate change alters hydrologic regimes, including their variability. Effects will be pronounced in aquatic ecosystems, where resource subsidies (e.g., nutrients, carbon) drive key ecosystem processes. However, we know little about how changing hydrologic regimes will modulate the spatiotemporal dynamics of lake biogeochemistry and ecosystem metabolism. To address this, we quantified ecosystem metabolism and nutrient dynamicsat high spatial resolution in Acton Lake, a hyper-eutrophic reservoir in the Midwestern US. We captured two consecutive growing seasons with markedly different watershed discharge and nutrient loading. Temporal variability often exceeded spatial variability in both wet and dry years. However, relative spatial variability was higher in the dry year, suggesting that internal processes are more important in structuring spatial dynamics in dry years. Strikingly, marked differences in watershed discharge and nutrient loading between years produced relatively small differences in many lake metrics, suggesting resilience to hydrologic variability. We found little difference in gross primary productivity between wet and dry years, but ecosystem respiration was higher in the wet year, shifting net ecosystem production below zero. Discrete storm events produced strong, yet ephemeral and spatially explicit effects, reflective of the balance of stream input and discharge over the dam. Increases in limiting nutrients were restricted to near stream inlets and returned to pre-storm baseline within days. Ecosystem metabolism was suppressed during storm events, likely due to biomass flushing. Understanding how changing hydrologic regimes will mediate spatiotemporal dynamics of ecosystem metrics is paramount to preserving the ecological integrity and ecosystem services of lakes under future climates.

Key words: Environmental variability; Storm; Ecosystem metabolism; Carbon; Nitrogen; Phosphorus.

Author contributions TJW and MJV conceived and designed the study with advice by WHR. TJW performed the research and data analysis. TJW wrote the manuscript with feedback from MJV and WHR.

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HIGHLIGHTS

- Temporal variability usually exceeds spatial, but spatial increases in dry years.
- Storms produce large, yet sometimes ephemeral and spatially explicit, effects.
- Wet years may shift the lake from net carbon sink to a net carbon source.

INTRODUCTION

Climate change is expected to increase the variability, frequency, and severity of both drought and precipitation events in the upcoming century (US National Climate Assessment 2013), and such changes appear to be already underway (Karl and Knight 1998; Knapp and others 2015; Naz and others 2018). Effects of these changes will have broad consequences across many terrestrial and aquatic ecosystems (Wilcox and others 2016; Grossiord and others 2017; Sinha and others 2017). Aquatic ecosystems, which are heavily subsidized by the surrounding landscape, are particularly sensitive to variations in the hydrological cycle (Marcarelli and others 2011; Larsen and others 2016). In lakes, externally supplied resources from the terrestrial landscape, e.g., carbon (C), nitrogen (N) and phosphorus (P) drive key ecosystem processes (Carpenter and others 2005; Kaushal and others 2010). N and P support primary production, and organic C stimulates bacterial production and respiration, shaping community structure and trophic energy flow.

Terrestrial subsidies to aquatic ecosystems are often highly variable and positively correlated with stream discharge, which is in turn influenced by precipitation. Increases in the frequency and intensity of precipitation events are expected to dramatically alter the magnitude and duration of subsidy pulses to lakes (Adrian and others 2009). Though much is known about the importance of terrestrial subsidies to lakes, we still know little about how changing precipitation and hydrologic regimes will influence nutrient cycling and ecosystem metabolism during discrete storm events, in between events, and during relatively longer (months–years) wet and dry periods (Sadro and Melack 2012; Vachon and del Giorgio 2014; Gilling and others 2017). This is surprising, given the wide recognition that aquatic ecosystems contribute significantly to global biogeochemical cycles and greenhouse gas emissions (Cole and others 2007; Deemer and others 2016), and that these ecosystem functions are likely to be sensitive to variability in subsidies. Given that hydrologic variability is likely to increase in frequency and severity, it is critical that we understand how it impacts spatiotemporal patterns of lake metabolism and biogeochemistry.

Variability in tributary discharge can influence lakes through a number of potential mechanisms (Stockwell and others 2020). High discharge events deliver pulses of essential limiting nutrients (e.g., N and P), and organic and inorganic C (Sadro and Melack 2012; Vachon and del Giorgio 2014). Nutrient pulses likely enhance both primary production and ecosystem respiration, with organic C pulses further enhancing ecosystem respiration (Vachon and del Giorgio 2014; Gilling and others 2017). However, in some watersheds high discharge events also deliver simultaneous pulses of sediments, which can create light-limiting conditions that inhibit primary production (Vanni and others 2006; Kelly and others 2018a). Additionally, high discharge events can promote thermocline deepening and mixing, bringing nutrients up into surface or near-surface water where they can be utilized by autotrophs for primary production (Gilling and others 2017). Further, abrupt changes in water level during high discharge events can also alter mixing dynamics (Zohary and Ostrovsky 2011). Lastly, high discharge can physically flush autotrophic and heterotopic biomass from lakes, potentially reducing primary production and respiration (Roelke and others 2010; Havens and others 2017; but see Rennella and Quirós 2006). We can predict how these mechanisms (inputs of nutrients, organic C, and sediments, and hydrological flushing) might operate in isolation, but predicting their combined effects remains a significant challenge because of opposing and potentially interactive effects. As such, understanding how these mechanisms modulate metabolism and nutrient cycling in lakes is paramount to predicting future climate change effects and managing system responses to those changes.

The effects of both discrete discharge events and sustained periods of relatively high or low discharge may not be homogenously distributed within a lake, and are likely tobe reflective of discharge event magnitude, distance from inlet tributaries, discharge from lake outflows and lake size relative to watershed area (Kimmel and others 1990; Ford 1990; da Silva and others 2005; Vachon and del Giorgio 2014; Havens and others 2017). For instance, periods of little to no discharge may promote a high degree of spatial heterogeneity due to limited vertical and horizontal mixing that can

enhanceor suppress patchy ecosystem processes (Kratz and others 2006; Abell and Hamilton 2014). Periods of moderate discharge may also result in high spatial heterogeneity, if strong gradients form along the inflow to outflow continuum. In contrast, high discharge may create a homogenizing effect if lake residence time becomes short (e.g., days), which is not uncommon in reservoirs (Thornton 1990). In addition to these physical drivers, spatial heterogeneity will be mediated by biological processes such as nutrient uptake, ecosystem metabolism, and secondary production (Van de Bogert and others 2012; Sadro and others 2011), e.g., phytoplankton biomass recovers quickly after storms flush their biomass, owing to high nutrient concentrations (Walz and Welker 1998; Rennella and Quirós 2006; Vanni and others 2006).

In this study, we examined how hydrologic variability affected biogeochemical metrics and metabolicprocesses in Acton Lake, a hyper-eutrophic reservoir in southwestern Ohio. Indeed, much of the Midwestern US has already experienced changes in the timing and magnitude of streamflow, with mean annual precipitation expected to increase further with future climate change (US National Climate Assessment 2013; Demaria and others 2016). Specifically, we examined temporal and spatial variability in several metrics, during a relatively wet versus dry year, and during discrete storm events. We asked the following general questions: (a) Do the spatial and temporal dynamics of biogeochemical and ecosystem metabolism metrics differ between relatively wet and dry years? (b) How do discrete high discharge events mediate biogeochemical spatial dynamics and whole-lake metabolism? (c) Which of three mechanisms (alleviation of nutrient limitation, increased light limitation, and flushing) are likely most important in mediating whole lake metabolism? We explored these questions using a spatially explicit sampling program combined with higher frequency storm-based sampling in a hyper-eutrophic reservoir in two consecutive years with markedly different watershed nutrient loading and discharge.

METHODS

Study Site

Acton Lake was constructed for recreational use in 1957 in southwestern OH (39.582°N, − 84.757°W) by damming Four Mile Creek, its main tributary. Acton Lake has a surface-release dam that did not release hypolimnetic water during our study period. Therefore, there was no outflow over the dam during relatively dry periods when lake level dropped below the spillway (late summer and autumn), but high discharge events can flush large amounts of water out of the lake (Vanni and others 2006). Acton is a relatively shallow lake (mean depth 3.9 m, surface area 232 ha) and has a relatively large ratio of watershed area to lake surface area (∼ 111). Watershed land use is predominantly row crop agriculture (> 80%) with minimal urban areas; forested areas are mostly restricted to Hueston Woods State Park, where the lake resides, and some riparian areas outside the park (Vanni and others 2001). The lake is hypereutrophic, and during our study period (May–September 2015–2016) mean chlorophyll *a* concentration was 58 ± 29 µg L^{-1} and Secchi depth was 0.51 ± 0.17 m ($\pm$ SD). We established 6 sampling locations at about 500 m intervals along the long axis of Acton Lake from the inflow area near the inlet streams (∼ 1.5 m deep) to the outflow area near the dam (∼ 8.0 m deep; Figure 1).
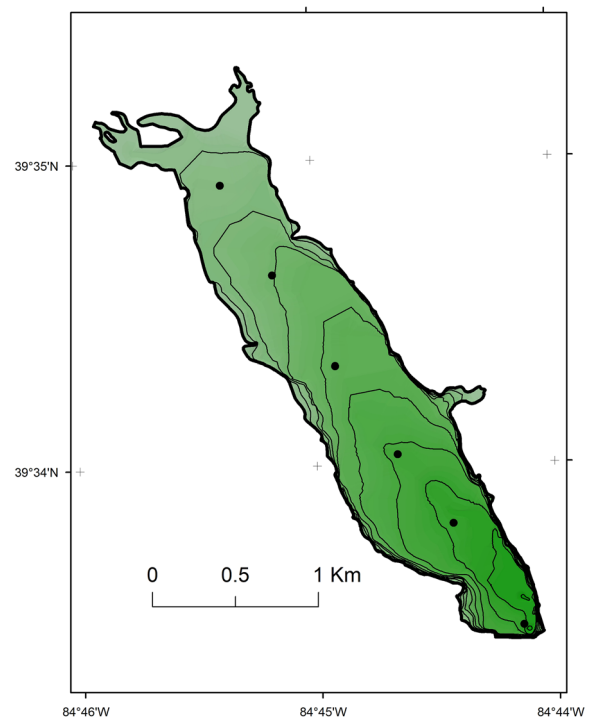
Figure 1. Sampling sites (black dots) in Acton Lake during the 2015 and 2016 study period. Depth contour intervals are 1 m.

Watershed Discharge and Nutrient Loading

Detailed methods for obtaining discharge and nutrient loading from the Acton Lake tributary streams can be found in Vanni and others (2001), Renwick and others (2008, 2018), and Kelly and others (2018b). Briefly, three tributaries encompassing 86% of the Acton Lake drainage basin are equipped with pressure transducers that log stream stage at 10 min intervals, which is converted to discharge using rating curves. In addition, automated water samplers (ISCO, Teledyne, Lincoln, NE) collect water samples from each inlet tributary every 7 h. All samples are processed during high flow events, while during baseflow conditions 3–7 samples per week are processed for concentrations of dissolved inorganic N (NO_3-N and NH_4-N) and P (soluble reactive P; SRP).

Lake Physical and Chemical Metrics

During baseflow conditions, we conducted weekly sampling at the 6 sites for concentrations of dissolved nutrients (NO_3-N, NH_4-N, SRP), total nutrients (total P; TP, and total N; TN), seston nutrients (carbon; C, N, P), non-volatile (inorganic) suspended solids (NVSS; fraction remaining after 4 h at 550 °C), and chl$a$ as a proxy for phytoplankton biomass. Dissolved nutrient samples were 1.0 μm filtered (Type A/E glass fiber, Pall Corp., New York, NY), acidified below 2 pH, and stored at 4°C until analysis. Total nutrient samples were not filtered, but similarly acidified, stored at 4°C, and persulfate digested prior to analysis. Seston P samples were collected on Type A/E filters and digested with HCl prior to analysis. Dissolved and total nutrients and seston P concentrations were quantified with a Lachat QC 8000 autoanalyzer (Lachat Instruments, Loveland, CO). Seston C and N samples were collected on Type A/E filters and analyzed on a CE Elantech Flash 2000 CHN analyzer (CE Elantech, Lakewood, NJ). Additionally, we measured secchi depth, light attenuation (quantum sensor, LI-COR, Lincoln, NE), and temperature and dissolved oxygen (DO) vertical profiles (ProODO, YSI, Yellow Springs, OH). During periods of high discharge, we conducted opportunistic sampling of these parameters at daily frequencies.

Ecosystem Metabolism

We measured ecosystem metabolism metrics, specifically gross primary production (GPP), net ecosystem production (NEP), and ecosystem respiration (ER) by deploying dissolved oxygen (DO; HOBO) loggers that took measurements at 15 min intervals at the 6 sampling sites. For 5 of 6 sites the probes were suspended at 1.5 m depth, but the probe at the site closest to tributaries was suspended at 1.0 m due toits shallowness. Mixing depth was considered to be where DO was greater than 1.0 mg L^{-1}, determined from vertical DO profiles. Ecosystem metabolism metrics (GPP, NEP, ER) were calculated using the ''mle'' model within the ''metab'' function in the R package ''Lake Metabolizer'' (Winslow and others 2016; R Core Team 2018).

Data Analysis

Spatial interpolations within each sampling date were created using inverse distanced weighted interpolation between the 6 sampling locations in Acton Lake. These were generated using the ''idw'' function in the R package ''gstat''(Pebesma 2004; Gräler and others 2016; R Core Team 2018). We then generated daily estimates using linear interpolation through time for days between sampling dates with the ''zoo'' function in the R package ''zoo'' (Zeileis and Grothendieck 2005).

We used the coefficient of variation (CV; standard deviation/mean) to estimate both spatial and temporal variability on non-interpolated data. On each sampling date, spatial variability (S) was calculated as the CV across all six sample sites. Temporal variability (T) was calculated as the CV across all dates within a year (separate for 2015 and 2016) at each site. Then, we estimated the ratio of spatial to temporal variability (S:T) by dividing spatial CV on a given date by the temporal CV for each of the six samples sites, generating six ratio estimates which were then averaged. Confidence intervals for S:T were generated using blocked bootstrapping with the ''tsboot'' function in the R package ''boot'' (Davison and Hinkley 1997; Canty and Ripley 2017). Block length was set at data length$^{1/3}$ with 10,000 iterations. Metrics with non-overlapping 95% confidence intervals were considered to be significantly different.

RESULTS

Watershed Discharge and Nutrient Loading

Our study captured a relatively wet year (2015) and a relatively dry year (2016). Cumulative tributary discharge during the study period was 46 versus 14×10^6 m^3 in the wet and dry years, respectively (Figure 2A). These 2 years represent
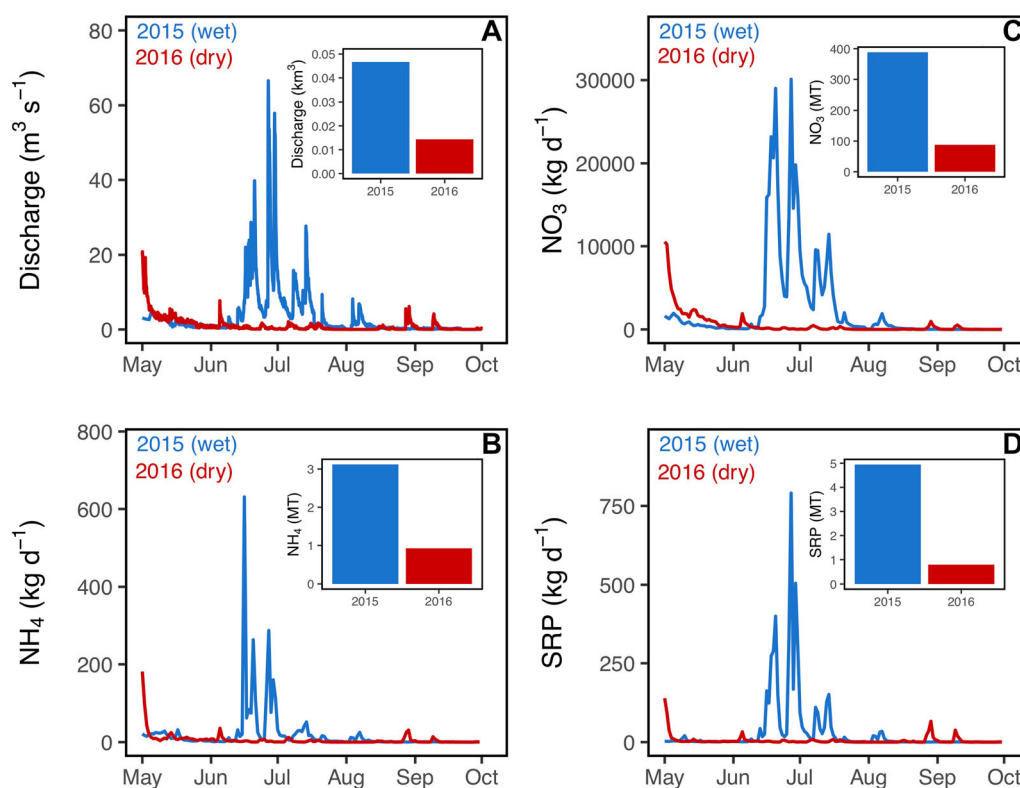
Figure 2. Daily discharge (**A**) and nutrient loading (NH4-N **B**; NO3-N **C**; soluble reactive phosphorus; SRP; **D** from the tributaries that feed Acton Lake with inset panels showing cumulative discharge and nutrient loading for the study period in a relatively wet (2015) and a relatively dry (2016) year.

the 7th and 20th ranks for cumulative May–September discharge, over a 24-year period (1994–2017; Supplemental Information Figure 1). In 2015, May–June precipitation was 253 mm, while in 2016 precipitation for these two months totaled 156 mm (Supplemental Information Figure 1). In addition, January–April precipitation was lower in 2015 than 2016, and so presumably groundwater levels and soil moisture were lower also. More rain fell in late summer in 2016 than 2015, but did not generate large inflow events. As a result, in 2015 the average inflow for the May–September period was 3.53 m^3 s^{-1}; in 2016 it was 1.08 m^3 s^{-1}. The largest discrete storm event during the study period attained peak discharge on June 27, 2015, and was bracketed by an approximately 3–4 week period or relatively high discharge from mid-June through mid-July. Peak discharge, on June 27, 2015, was in the 99th discharge percentile for daily mean discharge (3672 days, from 1994–2017) with a maximum hydraulic flushing rate of 0.36 d^{-1}, and a residence time of 2.7 d. Mean residence times for 2015 and 2016 study period were 420 and 1210 days, respectively. During storms, residence time was as short as 2.7 d, and 2015 and 2016 had

16 and 2 days out of 153 with residence time < 10 days, respectively (Supplemental Information Figure 3).

Nitrate loading during the study period was 3.88 versus 0.87 × 10^5 kg in 2015 and 2016, respectively (Figure 2B). Ammonium loading during the study period was 3.12 and 0.92 × 10^3 kg in 2015 and 2016, respectively (Figure 2C), and SRP loading was 49.4 and 8.03 × 10^2 kg in 2015 and 2016, respectively (Figure 2D). Thus, discharge, NO3-N, NH4-N and SRP loadings were 3.3, 4.6, 3.4, and 6.2 times higher in the wet year than in the dry year, respectively. These nutrient loadings represent the 7th and 20th rank years for nitrate, the 14th and 22nd rank years for ammonium, and the 8th and 19th rank years for SRP during the study period in 2015 and 2016, respectively.

Lake Nutrients

We found low spatial variability but high temporal variability in TN and NO$_3$-N, (the most abundant N form in the lake) in both wet and dry years (Figure 3A, B, F, G). In contrast, NH$_4$-N (the least abundant and more biologically available dissolved N form) showed more spatial variability than the
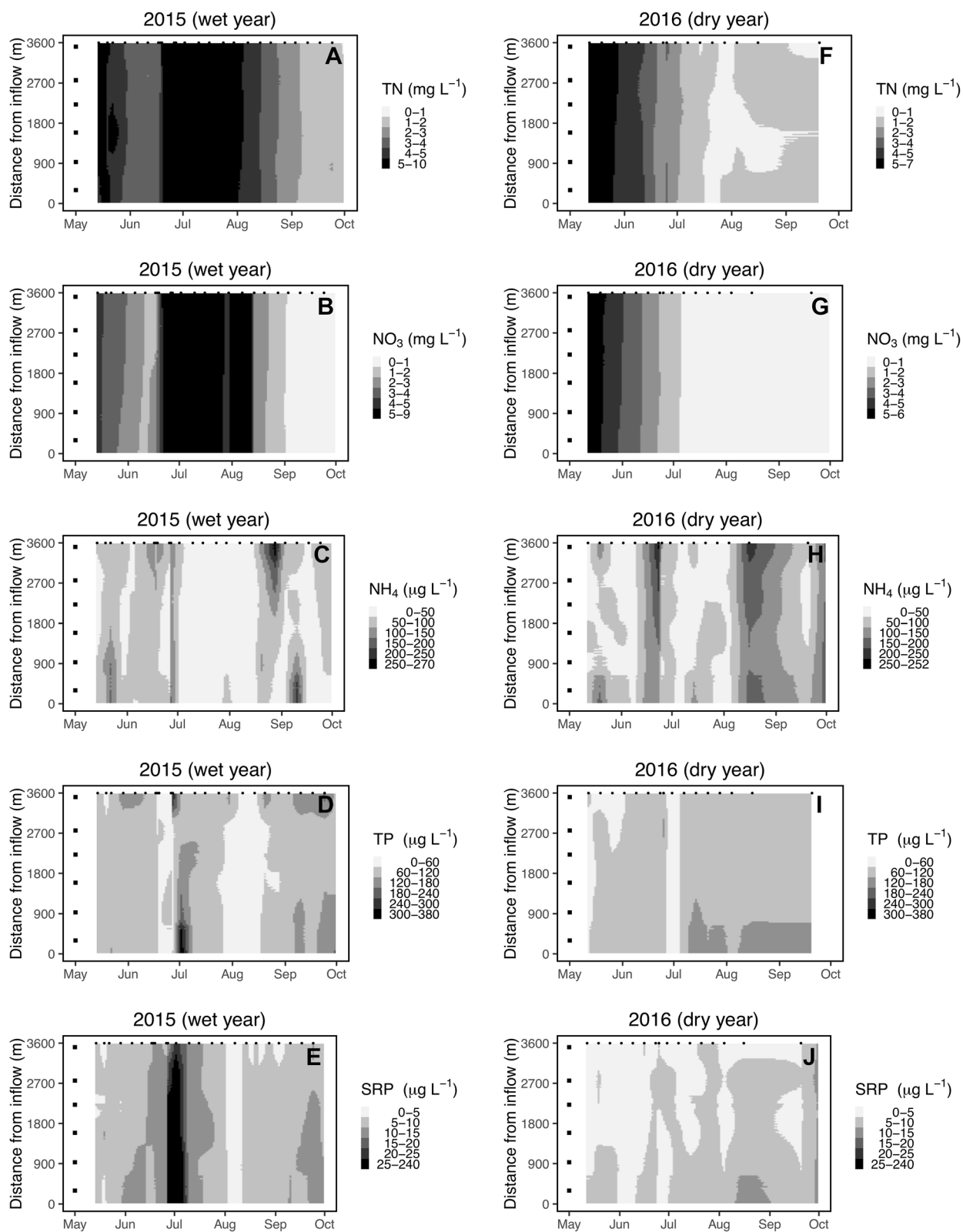
◄Figure 3. Total and dissolved nutrients in Acton Lake during a relatively wet (2015) and a relatively dry (2016) year. Total nitrogen (TN; **A, F**), NO3-N (**B, G**), NH4-N (**C, H**), total phosphorus (TP; **D, I**), and soluble reactive phosphorus (SRP; **E, J**). *Y*-axis values represent longitudinal distance along a continuum from inlet streams (0 m) to the outflow over the dam (3600 m), with black squares representing sampling sites. Values along *y*-axis were generated using inverse-distanced weighted interpolation from 6 sampling locations. Linear interpolation was used to generate daily values between sampling dates (represented by black dots). Note: bin sizes not always consistent between years.

other N forms, with concentrations often highest near the shallow inflow area and/or the deeper outflow area (Figure 3C, H), but generally not in mid-lake. We found similar spatial patterns in TP, which was often highest at the inflow and outflow areas (Figure 3D, I). In contrast, SRP concentrations were higher near the inflow area and often declined towards the outflow area, especially in the dry year (Figure 3E, J).

Mean TN concentrations were higher in the wet year (4.6 ± 2.1 vs. 2.7 ± 1.8 mg L^{-1} in 2015 and 2016, respectively; Figure 4A). The inter-annual pattern was similar for NO_3-N, as much of the TN is NO_3-N; thus, NO_3-N concentrations were 3.5 ± 2.4 versus 1.9 ± 1.9 mg N L^{-1} in 2015 (wet) and 2016 (dry), respectively (Figure 4B). There was little difference in mean NH_4-N concentrations in the wet and dry years, at 62.9 ± 30.7 versus 71.4 ± 44.9 µg L^{-1} in 2015 and 2016, respectively (Figure 4C). During the large storm event in 2015, mean whole-lake NO_3-N declined by about half but then increased substantially thereafter, whereas NH_4-N increased threefold during the event but quickly returned to pre-storm levels. Furthermore, NH_4-N sometimes increased markedly during dry periods (Figure 4B, C). We also found little difference in mean TP concentration in the wet versus dry years (85 ± 28 vs. 90 ± 17 µg L^{-1} in 2015 and 2016, respectively; Figure 4D). In contrast, mean SRP concentrations were higher in the wet year: 13.6 ± 17.6 versus 5.03 ± 0.80 µg L^{-1} in 2015 and 2016, respectively (Figure 4E). This was largely due to the large storm event that occurred during late June and early July, when SRP concentrations spiked to 90.4 µg L^{-1}, a 9.0-fold increase, but only for a brief period (Figure 4E).

Total N and dissolved N forms (NO_3-N, NH_4-N) generally had relatively low spatial variability compared to temporal variability, i.e., S:T < 1 (Figure 4F–H). However, for both TN and NH_4-N,

S:T was significantly higher in the dry year compared to the wet year, but there was no significant interannual difference in S:T for NO_3-N (Figure 4F–H). S:T was 0.13 and 0.29 for TN, 0.10 and 0.58 for NH_4-N, and 0.12 and 0.15 for NO_3-N in 2015 (wet) and 2016 (dry), respectively (Figure 6). The S:T for TP was generally below 1 for the wet and dry year, but was significantly higher in the wet year (Figure 4I). S:T for SRP was mostly below 1 in the wet year, but often was not significantly different from (had overlapping confidence intervals with) 1 in the dry year (Figure 4J). Further, SRP S:T was significantly higher in the dry year than in the wet year (Figure 4J).

Lake Physical and Biological Metrics

Concentrations of non-volatile suspended solids (NVSS) were generally higher in the shallow inflow area of the lake, likely reflective of tributary inputs and wind driven sediment resuspension in this shallow unstratified region (Figure 5A, D). In contrast, chl*a* and Secchi depth did not display consistent spatial patterns, in either the wet or dry year (Figure 5B, C, E, F). Despite substantially higher overall discharge and higher peak storm events in 2015, mean NVSS concentrations for the entire study period were not markedly higher at 7.6 ± 5.5 versus 7.15 ± 2.6 mg L^{-1} (mean ± SD, using all sites and dates) in 2015 and 2016, respectively (Figure 6A). Mean chl*a* concentration for the entire season was somewhat higher in the wet year, at 62 ± 26 versus 52 ± 21 µg L^{-1} in 2015 and 2016, respectively (mean ± SD; Figure 6B). With slightly higher NVSS and chl*a* concentrations, mean secchi depth was corresponding lower in the wet year at 0.49 ± 0.14 and 0.53 ± 0.13 m in 2015 and 2016, respectively (mean ± SD; Figure 6C). The large storm even in 2015 resulted in a dramatic, yet ephemeral, increase in NVSS concentration (4.7-fold), and corresponding declines in chl*a* concentration (2.2-fold) and Secchi depth (2.0-fold; Figure 6A–C).

The S:T (ratio of spatial to temporal variability) for NVSS was significantly higher in the dry year (2.49) than in the wet year (0.72; bias corrected mean; Figure 6D). Spatial variability was much higher than temporal variability (ratio > 1) in the dry year, whereas the opposite was true in the wet year. In contrast, we found little difference in the chl*a* S:T in the wet and dry year and this ratio was much lower than 1 in both years (0.591 and 0.596 in 2015 and 2016, respectively; Figure 6E). We found that the dry year had a significantly higher S:T for Secchi depth in the dry year, although it was
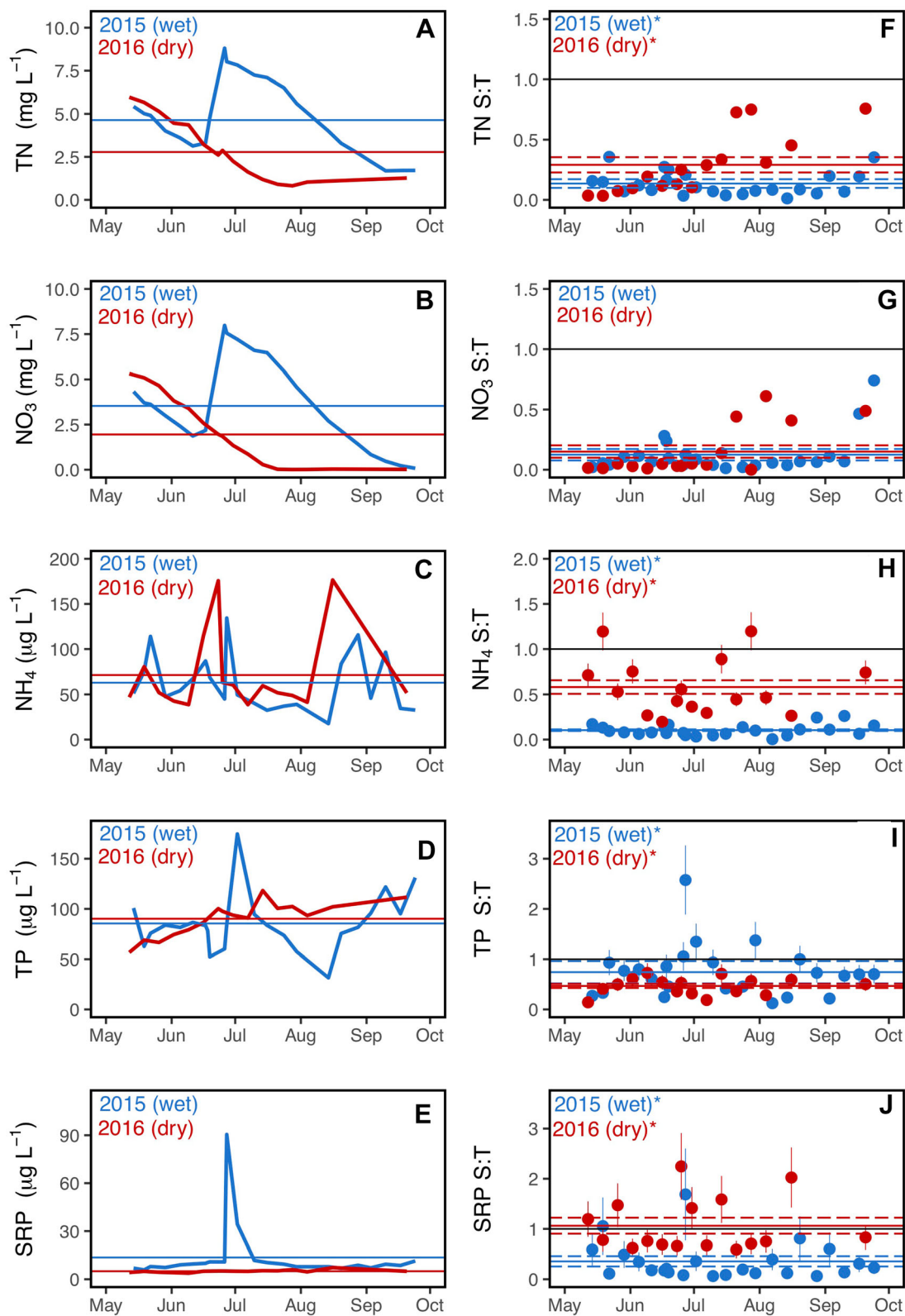
◄**Figure 4.** Total and dissolved nutrients in Acton Lake during a relatively wet (2015) and a relatively dry (2016) year. Values are the lake wide means generated from the 6 sampling sites. Total nitrogen (TN; **A**), NO3-N (**B**), NH4-N (**C**), total phosphorus (TP; **D**), and soluble reactive phosphorus (SRP; **E**). The ratio of the coefficient of variation in space (S) and the coefficient of variation through time (T) for TN (**F**), NO3-N (**G**), NH4-N (**H**), TP (**I**), and SRP (**J**). Solid lines represent study period means and dashed lines represent 95% CIs generated through time series bootstrapping.

less than 1 in both years (0.57 and 0.78 in 2015 and 2016, respectively; Figure 6F).

Lake Seston Nutrients

We found that lake seston nutrients were occasionally higher near the inflow and declined towards the outflow; however, the strength of this spatial pattern varied markedly among constituents and between years (Figure 7). Seston C did not show a consistent pattern in the wet year, whereas it was frequently higher in the inflow and declined
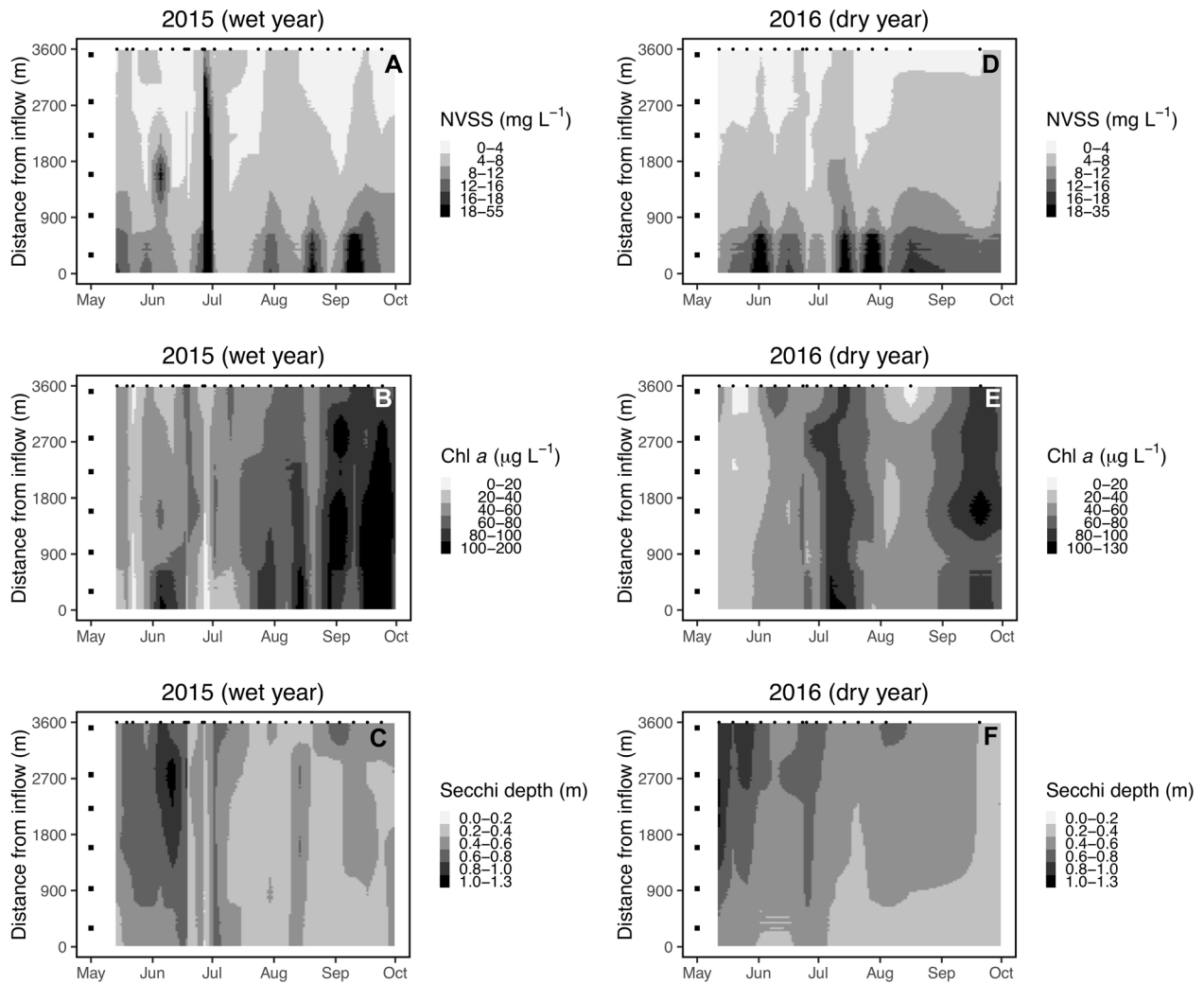
Figure 5. Non-volatile suspended solids (NVSS; **A, D**), chlorophyll a (**B, E**), and Secchi depth (**C, F**) in Acton Lake during a relatively wet (2015) and relativity dry year (2016). *Y*-axis values represent longitudinal distance along a continuum from inlet streams (0 m) to the outflow over the dam (3600 m), with black squares representing sampling sites. Values along *y*-axis were generated using inverse-distanced weighted interpolation from 6 sampling locations. Linear interpolation was used to generate daily values between sampling dates (represented by black dots). Note: bin sizes not always consistent between years.
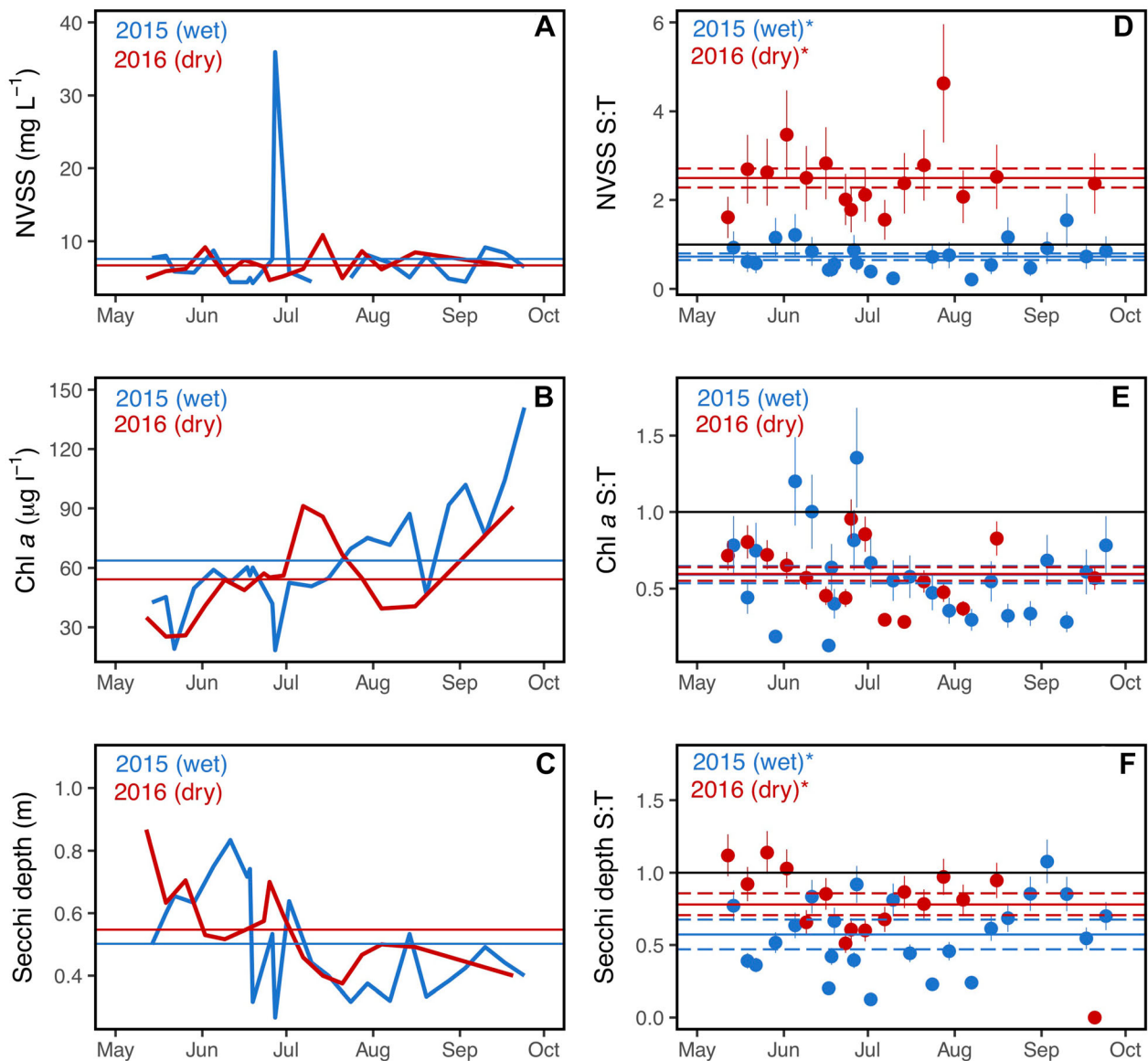
Figure 6. Non-volatile suspended solids (NVSS; **A**), chlorophyll a (**B**), and Secchi depth (**C**) in Acton Lake during a relatively wet (2015) and relativity dry year (2016). Values are the lake wide means generated from the 6 sampling sites. The ratio of the coefficient of variation in space (S) and the coefficient of variation through time (T) for NVSS (**D**), Chl a (**E**), and Secchi depth (**F**). Solid lines represent study period means and dashed lines represent 95% CIs generated through time series bootstrapping.

towards the outflow in the dry year (Figure 7A, D). Seston N showed a slight tendency to be higher in the inflow area, and this did not vary markedly between years (Figure 7B, E). Finally, seston P showed a slight tendency to be higher in the inflow area during the wet year, but did not have any consistent spatial pattern during the dry year (Figure 7c, F).

Despite large differences in nutrient loading during the wet and dry years, we found little difference in mean seston C, N, and P concentrations

(Figure 8A–C). Mean seston C was 4.3 ± 1.2 and 4.4 ± 0.9 mg L^{-1}, mean seston N was 0.76 ± 0.23 and 0.80 ± 0.15 mg L^{-1}, and mean seston P was 84 ± 19 and 85 ± 8 µg L^{-1} in 2015 and 2016, respectively (Figure 8A–C). The large storm event in 2015 precipitated a sharp decrease in seston C and N (1.3 and 1.6-fold decline, respectively), but increased seston P concentrations about 1.5-fold (Figure 8A–C). Seston C and N generally had low spatial variability relative to temporal variability, with mean S:T well below 1 (Figure 8D, E). Fur-
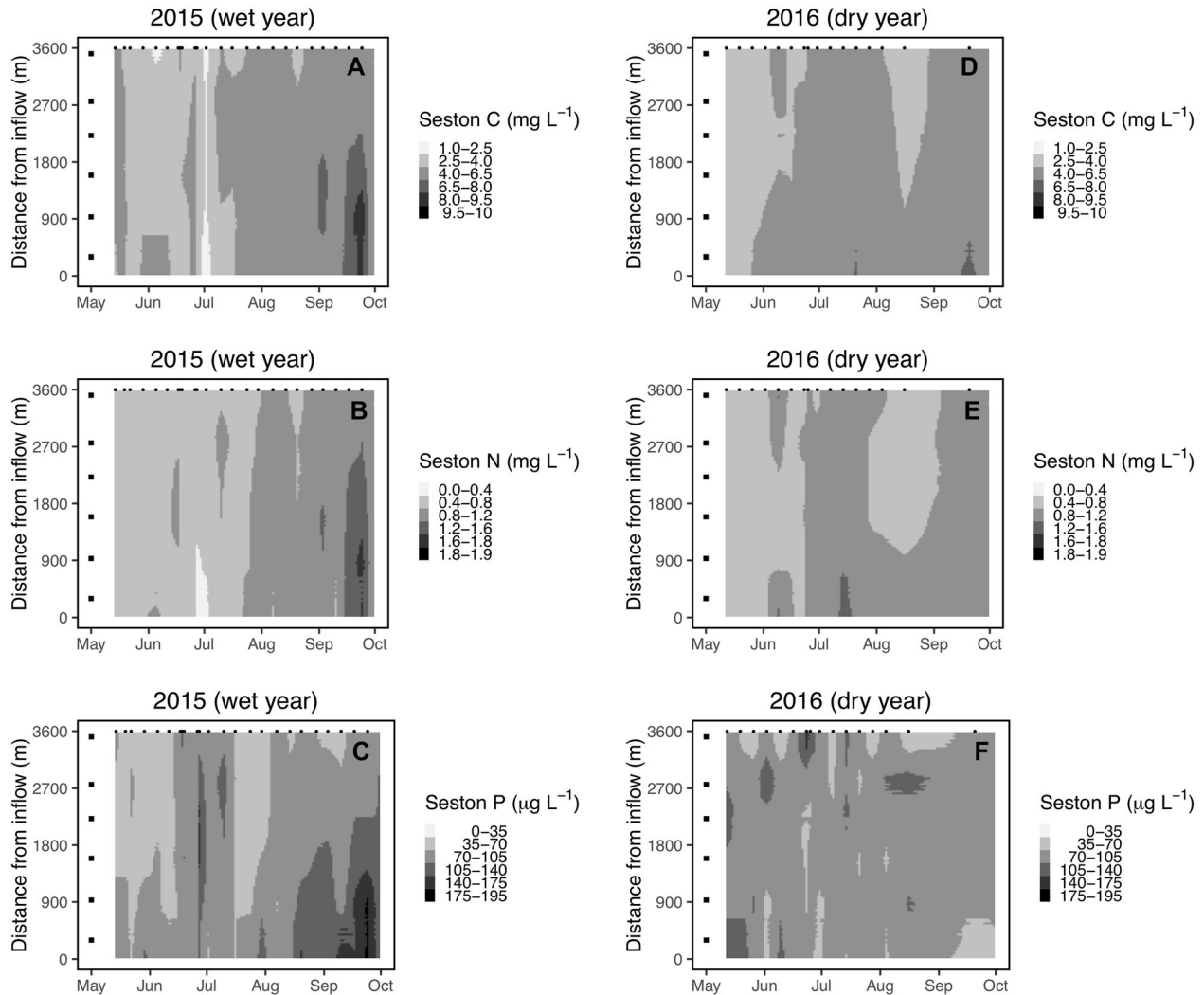
Figure 7. Seston carbon (C; **A, D**), seston nitrogen (N; **B, E**), and seston phosphorus (P; **C, F**) in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). *Y*-axis values represent longitudinal distance along a continuum from inlet streams (0 m) to the outflow over the dam (3600 m), with black squares representing sampling sites. Values along *y*-axis were generated using inverse-distanced weighted interpolation from 6 sampling locations. Linear interpolation was used to generate daily values between sampling dates (represented by black dots). Note: bin sizes not always consistent between years.

ther, there was no significant difference in mean seston P and N S:T in the wet and dry year (Figure 8D, E). In contrast, mean S:T for seston P was significantly higher in the dry year (1.01) versus the wet year (0.66), and the 95% confidence overlapped 1 in the dry year (Figure 8F).

Seston Stoichiometry

We found no consistent spatial pattern in seston C:N in either the wet or dry year (Figure 9A, D). In the wet year, seston C:P was more frequently higher in the outflow area, than in the inflow area (Figure 9B). However, in the dry year C:P was more spatially variable and occasionally high in both the inflow and outflow areas (Figure 9E). Seston N:P behaved similarly with higher values occurring more frequently in the outflow area during the wet year, whereas in the dry year N:P was occasionally high in both the inflow and outflow areas (Figure 9C, D).

Overall mean C:N for the study period differed little between years, and was 6.7 ± 0.7 and 6.5 ± 0.5 (molar) in 2015 and 2016, respectively (Figure 10A). In contrast, mean C:P was slightly higher in the dry year (147 ± 35), than in wet year (135 ± 43) (Figure 10B). Similarly, N:P was also higher in the dry year, with mean N:P 22.6 ± 5.2
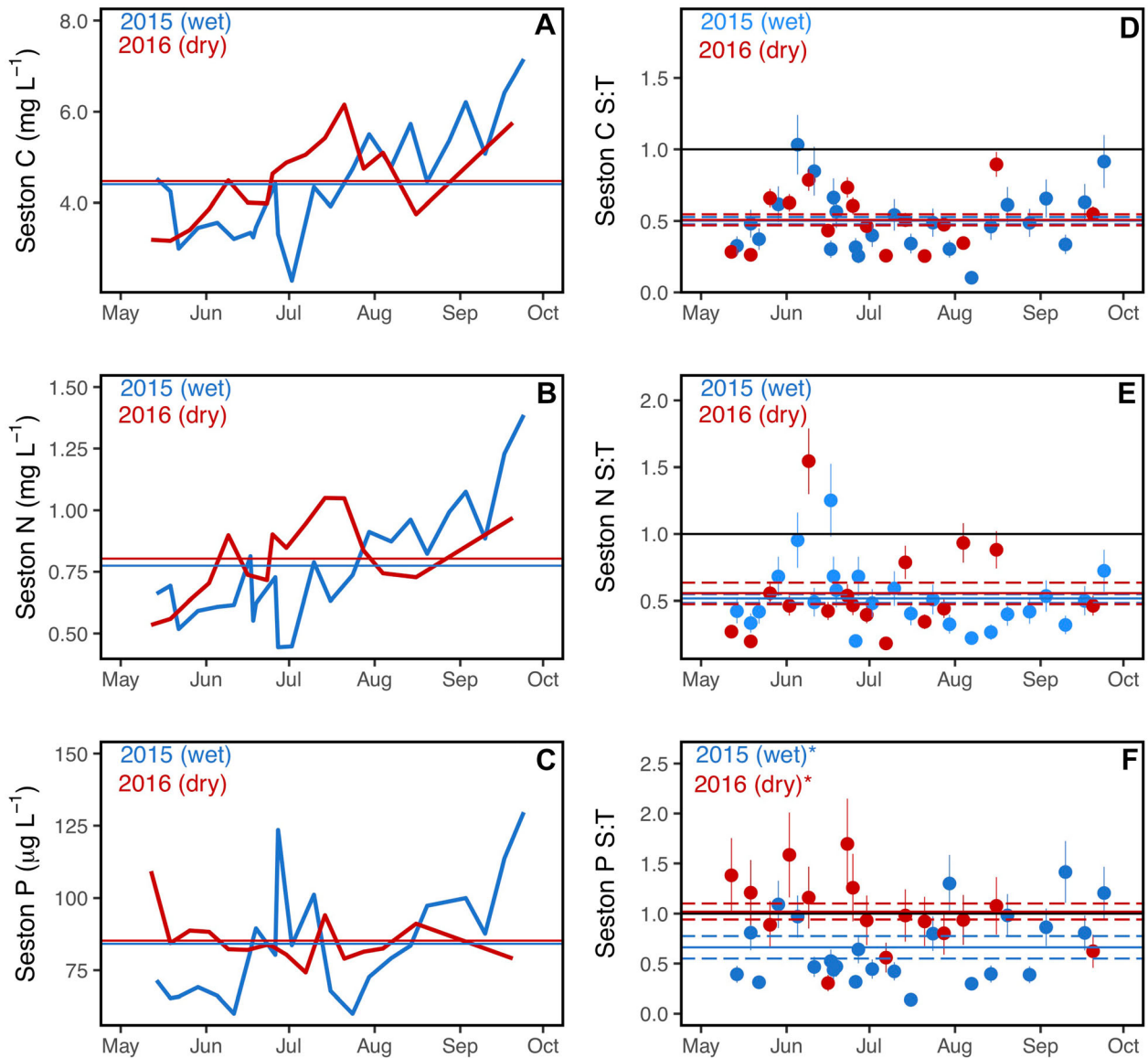
Figure 8. Seston carbon (C; **A**), seston nitrogen (N; **B**), and seston phosphorus (P; **C**) in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). Values are the lake wide means generated from the 6 sampling sites. The ratio of the coefficient of variation in space (S) and the coefficient of variation through time (T) for C (**D**), N (**E**), and P (**F**). Solid lines represent study period means and dashed lines represent 95% CIs generated through time series bootstrapping.

versus 20.3 ± 6.1 in the wet year (Figure 10C). During the large storm event in 2015 we observed a marked increase in mean C:N (1.28-fold increase), and declines in both C:P and N:P (2.01 and 2.24-fold decreases, respectively; Figure 10A–C).

Mean S:T for C:N, C:P and N:P was less than 1 for both wet and dry years (Figure 10D–F). There was no significant difference in C:N S:T in the wet versus dry year (Figure 10D). However, C:P and N:P were both significantly higher in the dry year (Figure 10E, F). Mean C:P for S:Twas 0.36 versus

0.82 in 2015 and 2016, respectively, whereas mean S:T for N:P was 0.47 versus 0.84 in 2015 and 2016, respectively (Figure 10F).

Ecosystem Metabolism

We did not observe markedly different spatial patterns of ecosystem metabolism between the wet and dry years, except during the high discharge period from late June through early July 2015 (Figure 11). This several week period of high dis-
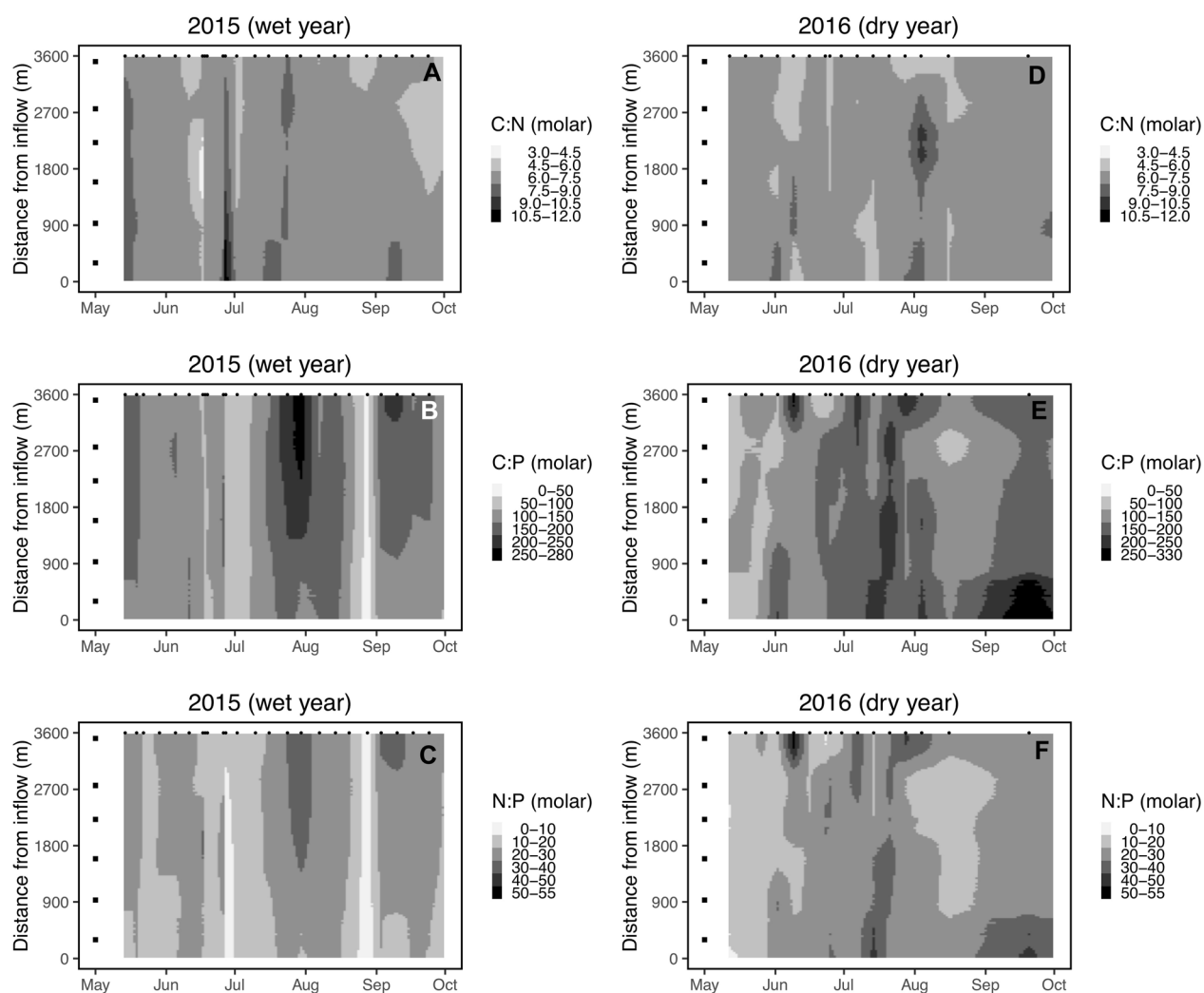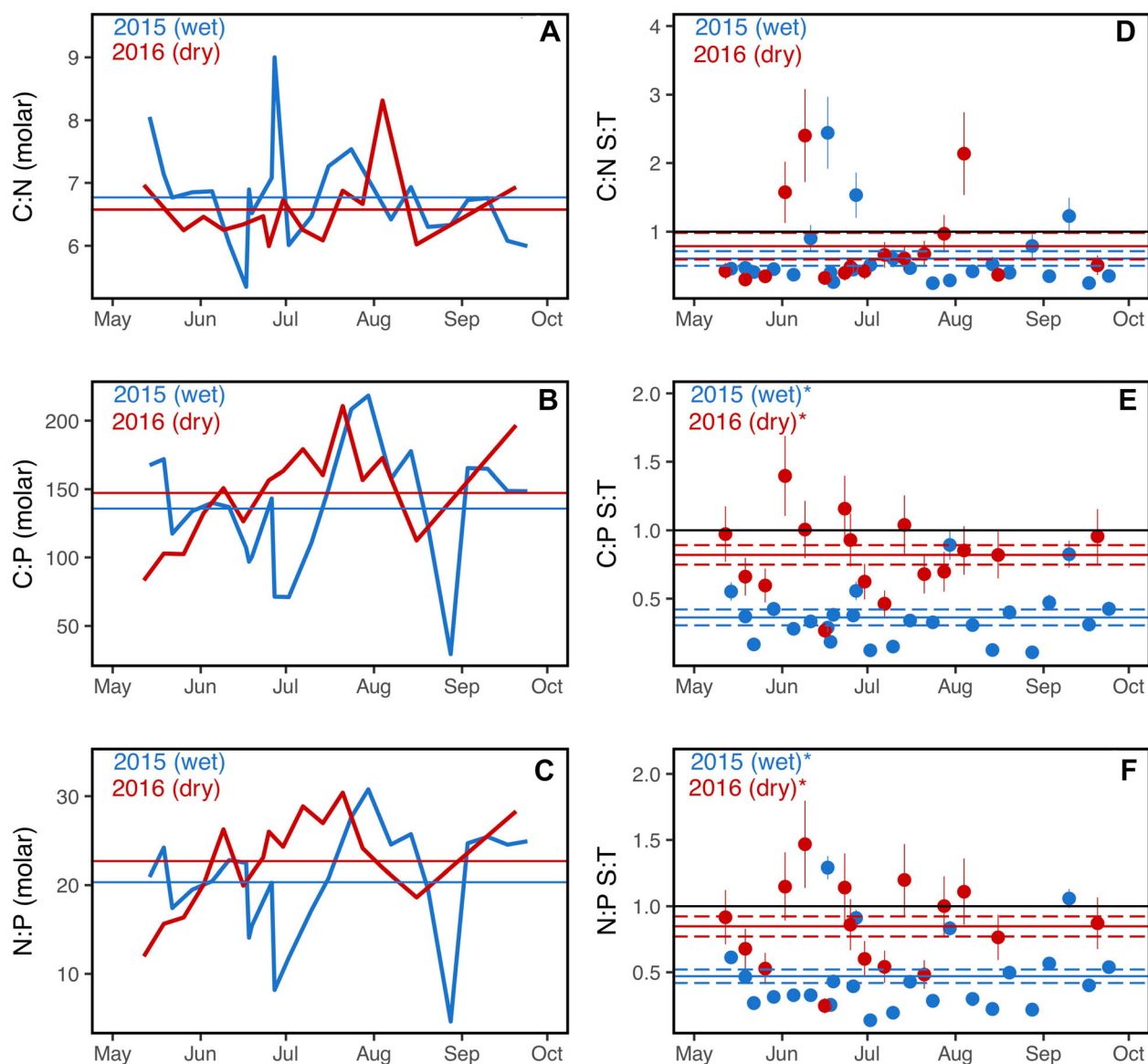
Figure 9. Molar carbon to nitrogen (C:N; **A, D**), carbon to phosphorus (C:P; **B, E**), and nitrogen to phosphorus (N:P; **C, F**) ratios in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). *Y*-axis values represent longitudinal distance along a continuum from inlet streams (0 m) to the outflow over the dam (3600 m), with black squares representing sampling sites. Values along *y*-axis were generated using inverse-distanced weighted interpolation from 6 sampling locations. Linear interpolation was used to generate daily values between sampling dates (represented by black dots). Note: bin sizes not always consistent between years.

charge, centered around the large storm event on June 27, 2015, resulted in a clear suppression of GPP and ER, but lesser changes in NEP (Figure 11). The suppression effect persisted longer in the inflow areas, and diminished with increasing distance from inlet tributaries (Figure 11).

Despite large differences in overall nutrient loading we found only a small difference in mean GPP between the wet and dry years (Figure 12A). Whole lake mean GPP was 4.2 versus 4.9 mg DO L^{-1} d^{-1} in 2015 (wet) and 2016 (dry), respectively (Figure 12A). However, NEP was substantially lower in the wet year, at − 0.1 versus 1.9 mg DO

L^{-1} d^{-1} in 2015 and 2016, respectively (Figure 12B). This was largely due to higher ER in the wet year, at 4.3 and 2.9 mg DO L^{-1} d^{-1} in 2015 and 2016, respectively (Figure 12C). Ecosystem metabolism was dampened or suppressed during and following the 2015 storm event likely due to biomass removal via flushing (Figure 12A–C). During that storm, mean whole lake GPP was 2.5-fold lower for the week following the peak discharge day, compared to the week preceding (Figure 12A). For the same time periods, mean ER declined 2.9-fold, and NEP increased slightly (1.5-fold; Figure 12B, C).

Figure 10. Molar carbon to nitrogen (C:N; **A**), carbon to phosphorus (C:P; **B**), and nitrogen to phosphorus (N:P; **C**) ratios in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). Values are the lake wide means generated from the 6 sampling sites. The ratio of the coefficient of variation in space (S) and the coefficient of variation through time (T) for C:N (**D**), C:P (**E**), and N:P (**F**). Solid lines represent study period means and dashed lines represent 95% CIs generated through time series bootstrapping.

S:T for ecosystem metabolism metrics was highly variable with means generally slightly less than one, except for NEP in 2015 (Figure 12D–F). We found no significant difference in the S:T for GPP, NEP, and ER in the wet versus dry year (Figure 12D–F). Mean GPP S:T was 0.81 and 0.82 in 2015 and 2016, respectively (Figure 12D). Mean NEP S:T was 1.25 and 0.86 in 2015 and 2016, respectively (Figure 12E). Mean ER S:T was 0.77 and 0.82 in 2015 and 2016, respectively (Figure 12F).

DISCUSSION

We successfully captured the spatial and temporal patterns of nutrient dynamics and ecosystem metabolism in a eutrophic reservoir, over two consecutive years that varied markedly in watershed discharge and nutrient loading. These seemingly profound differences in watershed discharge and nutrient loading did not always result in comparably large changes in many of the lake metrics we examined. Indeed, even the dramatic effects produced by large discharge events were relatively
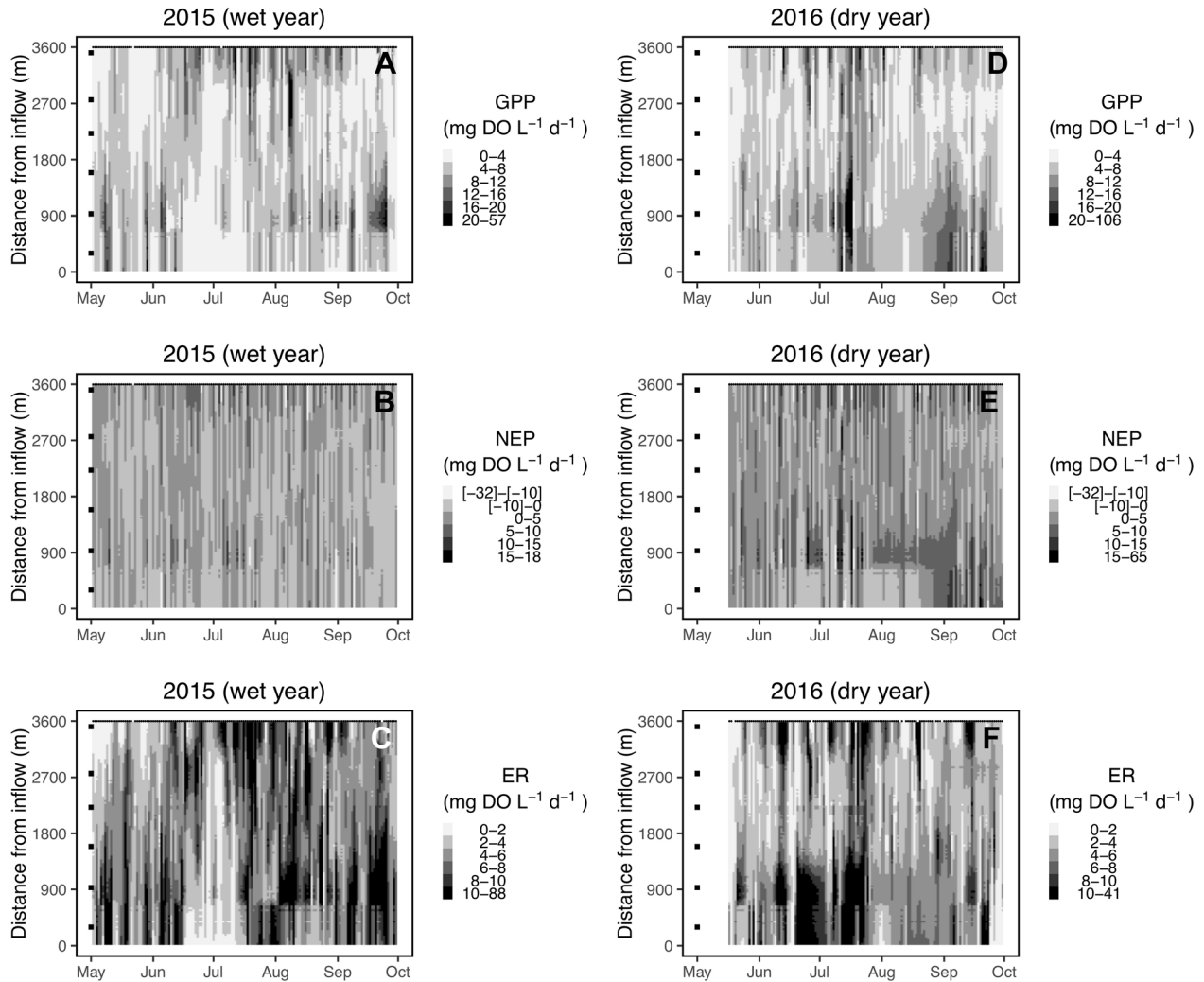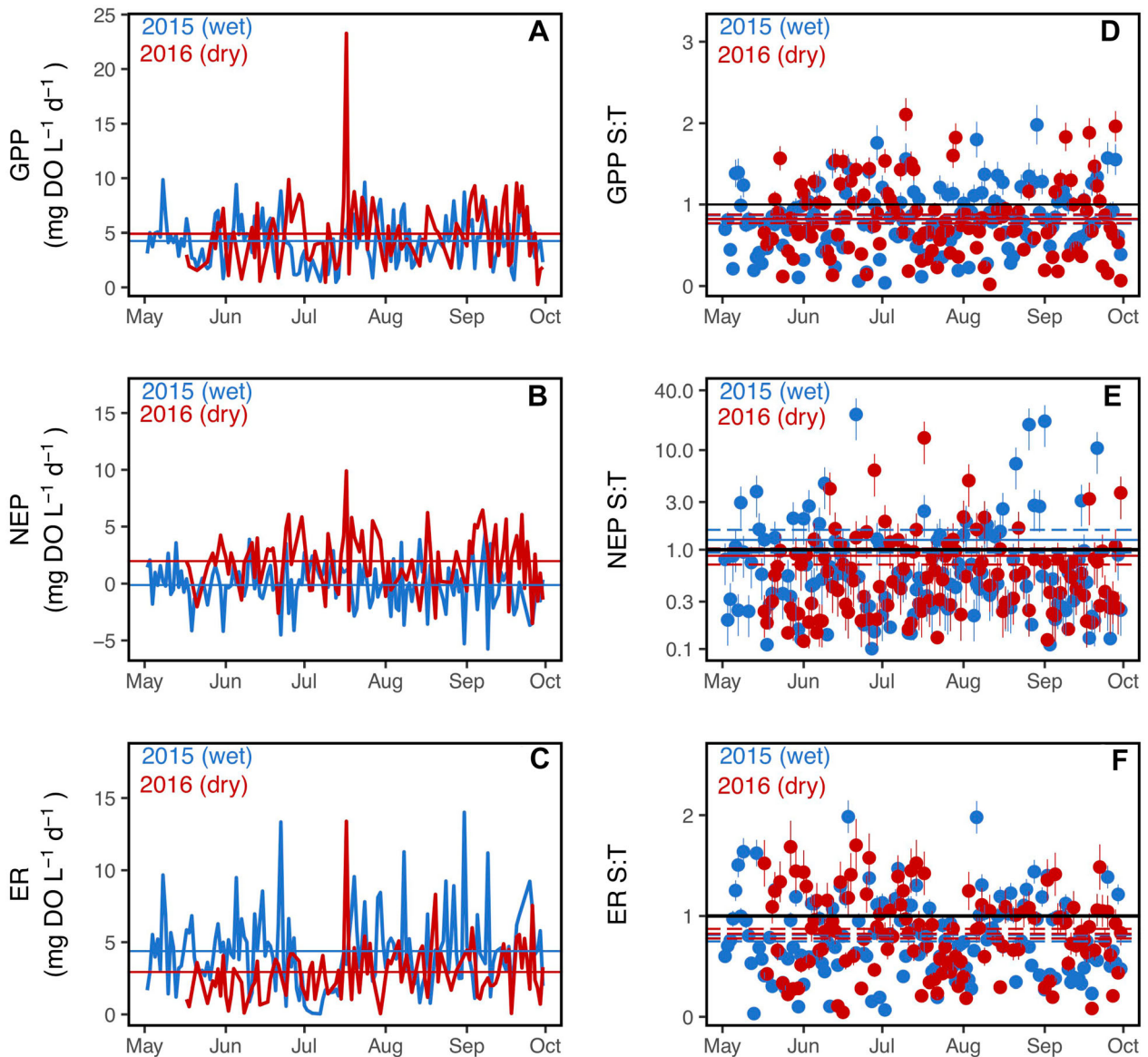
Figure 11. Ecosystem metabolism in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). Gross primary production (GPP; **A, D**), net ecosystem production (NEP; **B, E**) and ecosystem respiration (ER; **D, F**). *Y*-axis values represent longitudinal distance along a continuum from inlet streams (0 m) to the outflow over the dam (3600 m), with black squares representing sampling sites. Values along *y*-axis were generated using inverse-distanced weighted interpolation from 6 sampling locations. Linear interpolation was used to generate daily values between sampling dates (represented by black dots). Note: bin sizes not always consistent between years and ER expressed as a positive value.

short-lived. However, despite the lack of comparable scaling and the ephemeral nature of discrete storm events, we nevertheless observed many important differences between the wet and dry years.

Discrete Storm Events

We found that discrete storm events can produce strong, but short-lived, spatially explicit effects. That storm events can have strong effects on lakes is not particularly surprising, but the short-lived nature of the effects we observed is striking. It is generally hypothesized, and somewhat supported, that storms have profound and prolonged effects

(Sadro and Melack 2012; Vachon and del Giorgio 2014; Gilling and others 2017; but see Gallardo and others 2012). For instance, Gilling and others (2017) found that experimentally simulating storm-induced mixing in a clear-water lake enhanced GPP for over 4 weeks, even though the simulated ''storm event'' lasted less than 1 day. They attributed this persistence to alleviation of light and nutrient limitation that resulted from the mixing of hypolimnetic water with surface waters. However, in Acton Lake we saw an immediate suppressive effect of high discharge events on GPP and ER. N and P alternate as the primary limiting element in Acton Lake, depending on conditions

Figure 12. Ecosystem metabolism in Acton Lake during a relatively wet (2015) and a relatively dry (2016 year). Gross primary production (GPP; **A**), net ecosystem production (NEP; **B**) and ecosystem respiration (ER; **D**). Values are the lake wide means generated from the 6 sampling sites. The ratio of the coefficient of variation in space (S) and the coefficient of variation through time (T) for GPP (**D**), NEP (**E**), and ER (**F**). Solid lines represent study period means and dashed lines represent 95% CIs generated through time series bootstrapping. Note: ER expressed as a positive value.

and season (Hayes and others 2015; Andersen and others 2019), and an addition of N and P this large, if applied in isolation, should enhance metabolic rates. Instead, both GPP and ER were suppressed. This suggests autotrophic biomass removal via hydraulic flushing (perhaps in conjunction with sediment-induced light limitation) more than compensated for increased nutrient availability, resulting in a net suppression of both primary production and respiration. This contrasts with previous work in a pristine alpine lake that found a

large storm event reduced GPP, but enhanced ER (Sadro and Melack 2012). Sadro and Melack (2012) attributed reduced GPP to phytoplankton biomass flushing, and enhanced ecosystem respiration tomicrobial activity fueled by large allochthonous organic carbon matter inputs. Gallardo and others (2012) found similar, though short-term, reduced primary production and enhanced respiration in shallow oligotrophic oxbow lakes following pulsed discharge events. This suggests that response to discrete discharge events may also be dependent

upon tropic status and the degree of net hetero- versus autotrophy in addition to hydrology and lake morphology.

Wet Versus Dry Years

DIN and SRP loading rates to the lake were 4.4-fold and 6.1-fold higher, respectively, during the wet year compared to the dry year. This did not promote a correspondingly large increase in primary producer biomass (as measured by chl*a*), which was only 1.1-fold higher in the wet year, or photosynthetic rate (GPP), which was actually lower in the wet year. This suggests that increased nutrient loading at this timescale does not always cause higher primary producer biomass or primary production (Weyhenmeyer and others 2004; Rennella and Quirós 2006). Kelly and others (2018a) also found that Acton Lake chlorophyll in a given-month is not correlated with nutrient loading during that same period. Rather, chl*a* is negatively related to NVSS concentration (because suspended sediments attenuate light) and positively related to nutrient cycling by sediment-feeding fish (Kelly and others 2018a). Increased watershed nutrient loading obviously results in higher phytoplankton biomass and production in the long term, but our results and those of Kelly and others (2018a) suggest that over shorter time scales factors other than external loading regulate phytoplankton. The watershed delivers nutrients that may become available later via internal cycling, which has been shown to be important in this system (Williamson and others 2018). Indeed, excretion by gizzard shad (an abundant benthivorous fish) was higher in 2016 which may have buffered the system against lower external nutrient loading (Vanni unpublished data). In addition, as mentioned above, decreased light and more rapid flushing can offset the effects of increased nutrients during storm events. Finally, a large fraction of watershed nutrient loading may be unavailable to primary producers because dissolved nutrients are exported over the dam during high discharge periods when residence time is short, before phytoplankton can utilize them. In contrast, long residence times would reduce biomass flushing, creating conditions that may allow for phytoplankton blooms to develop. However, sustained periods of long residence time may induce nutrient limitation, reducing phytoplankton biomass and suppressing primary productivity, though we did not observe that in this study.

Despite small differences in mean chl*a* concentrations and GPP in both years, we found higher ER in the wet year, which reduced mean NEP to slightly less than 0. This is likely due to the increased respiration of allochthonous subsidies from watershed tributaries, and it suggests that increasing precipitation frequency and severity may alter the net C balance of reservoirs, shifting them from net sinks to net sources of C (Tranvik and others 2009; Einola and others 2011). Knoll and others (2013) also found that Acton Lake was a net CO_2 sink during a dry summer (2007) but a net CO_2 source during a wet summer (2008), using data on CO_2 flux between water and the atmosphere as well as C mass balance. This was likely due to the higher organic and inorganic C loading observed in wetter year (Knoll and others 2013).

Spatial and Temporal Dynamics

The classic model of reservoir physical structure envisions three zones: the riverine, transition, and lacustrine, along the axis from inlet tributaries to the dam (Kimmel and others 1990). This model predicts that nutrient and sediment concentrations will be highest in the riverine zone and decline steadily towards the lacustrine zone in response to stream inputs of nutrients and sediments, nutrient uptake, and sediment settling. In response, this model predicts that phytoplankton biomass and primary production will be highest in the center or transitional zone of the reservoir, as this area balances nutrient and light limitatio, i.e., sediment settling alleviates light limitation allowing for enhanced nutrient uptake and primary production. In contrast with this model, we did not observe a mid-lake peak in either primary producer biomass (as measured with chl*a*) or primary production (GPP). This may be attributable to the relatively shallow depth in the inflow site. Knoll and others (2003) found that in many Ohio reservoirs (including Acton) light attenuation was higher in the inflow compared to the outflow regions, likely due to watershed inputs and sediment resuspension, as the Kimmel and others (1990) model predicts. However, because the inflow regions of many Ohio reservoirs are shallow (1–2 m), mean light intensity in the mixed layer is often similar to mean light in the deeper, but clearer, mixed layer of the outflow (Knoll and others 2003). Further, lake morphology (especially length to width ratios, residence time, and dendricity) likely influences the applicability of the Kimmel and others (1990) model. Longer, narrower, and/or more dendritic reservoirs with longer residence times may separate into more clearly defined zones as per the Kimmel and others (1990) model. This may manifest as

Table 1. Physical, Chemical, Biological and Integrative Metrics Measured in Acton Lake During a Relatively Wet (2015) and a Relatively Dry (2016) Year

Parameter	2015 (wet) S:T	2016 (dry) S:T	S:T wet vs. S:T dry
Physical	---	---	---
Non-volatile suspected solids	*	*	
Secchi depth	*	*	
Chemical	---	---	---
Total nitrogen	*	*	
Seston nitrogen	*	*	
NO$_3$	*	*	
NH$_4$	*	*	
Total phosphorus	*	*	
Seston phosphorus	*		
Soluble reactive phosphorus	*		
Seston carbon	*	*	
Carbon : nitrogen (molar)	*	*	
Carbon : phosphorus (molar)	*	*	
Nitrogen : phosphorus (molar)	*	*	
Biological	---	---	---
Chlorophyll *a*	*	*	
Gross primary production	*	*	
Net ecosystem production			
Ecosystem respiration	*	*	

The ratio of the coefficient of variation in space (S) to the coefficient of variation through time (T) is used to assess the relative strength of temporal and spatial variability within and between years. Green indicates higher mean spatial variability (S:T > 1), and grey indicates higher mean temporal variability (S:T < 1) within the wet (2015) and dry (2016) years. An *occasions where the 95% confidence intervals did not overlap 1, that is S:T was significantly different from 1. Orange cells indicate a higher S:T in the dry year relative to the wet year, blue cells indicate the converse, and no color indicates no difference in relative S:T between the wet and dry years.

increased spatial heterogeneity and dampen the effect of changing hydrologic regimes. Understanding how these patterns emerge across a broad gradient of reservoir size and morphology will likely be an active and fruitful avenue for future research. We realize that our results derive from just one lake; we view our study as a first step that provides a foundation for additional studies in more lakes.

We found that mean temporal variability usually exceeded spatial variability. In the wet year, this was the case for all metrics (Table 1). Spatial variability relative to temporal variability increased during the dry year, but even in this year temporal variability was higher for most metrics (Table 1). This suggests that internal processes (e.g., nutrient uptake, recycling, sedimentation) rather than external drivers (e.g., watershed discharge) may

become more important in driving spatiotemporal variability in dry years which have fewer flood events (Kratz and others 2006). For instance, excretion by gizzard shad, a high biomass benthivorous fish, has been shown to be an important nutrient source in Acton, particularly during periods of low watershed discharge (Kelly and others 2018a; Williamson and others 2018). Gizzard shad are unlikely to be homogeneously distributed, with fish density responding to resource availability and physical structure (e.g., hypolimnetic hypoxia/anoxia). This may partially explain why relative spatial variability was higher for NH$_4$-N and SRP in the dry year, as they are the primary nutrients excreted by gizzard shad. As gizzard shad are important nutrient sources, spatial heterogeneity in their distribution may enhance spatial variability in

other lake metrics, e.g., phytoplankton nutrient limitation (Andersen and others 2019).

We recognize that our study includes only one wet and one dry year, raising the question of whether these patterns would hold when comparing several years. Indeed, an examination of long-term trends (> 1 decade) in Acton Lake from lower frequency ($\sim$ weekly) and lower spatial resolution (2 sites corresponding with our study sites closest to the lake inflow and the outflow; Figure 1) revealed similar patterns to those presented by this study (Supplemental Information Figure 4), i.e., the ratio of spatial to temporal variability declined with increasing cumulative watershed discharge for some metrics, suggesting that the findings of this study are generalizable across longer timescales (Supplemental Information Figure 4), e.g., long-term records show that S:T was significantly negatively correlated with cumulative discharge for Secchi depth and NVSS ($p < 0.05$), marginally significant for total P ($p = 0.06$) and not significant for chl$a$ ($p > 0.10$; Supplemental Information Figure 4).

There is growing recognition that long-term studies conducted at high temporal and spatial resolution are needed to better understand ecosystems, and however studies that capture both spatial and temporal variability are less common (Kratz and others 2003; Sadro and others 2011; Natchimuthu and others 2016). In the coming century climate change will continue to increase the variability, frequency, and severity of both drought and precipitation events (US National Climate Assessment 2013; Knapp and others 2015; Naz and others 2018). In addition, we anticipate that climate change will influence the seasonal timing of rainfall and stream discharge (Dai and others 2015; Pathak and others 2016; Byun and others 2019). Understanding how these changing hydrologic cycles will impact aquatic ecosystems is of paramount concern, as they contribute significantly to global biogeochemical cycling and provide vital ecosystem goods and services (Tranvik and others 2009; Aufdenkampe and others 2011; Green and others 2015). Understanding the mechanisms and drivers of spatiotemporal variability will be essential to managing and preserving aquatic ecosystems in a period of global change.

ACKNOWLEDGEMENTS

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