Enhancement of primary production during drought in a temperate watershed is greater in larger rivers than headwater streams

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Abstract

Drought is common in rivers, yet how this disturbance regulates metabolic activity across network scales is largely unknown. Drought often lowers gross primary production (GPP) and ecosystem respiration (ER) in small headwaters but by contrast can enhance GPP and cause algal blooms in downstream estuaries. We estimated ecosystem metabolism across a nested network of 13 reaches from headwaters to the main stem of the Connecticut River from 2015 through 2017, which encompassed a pronounced drought. During drought, GPP and ER increased, but with greater enhancement in larger rivers. Responses of GPP and ER were partially due to warmer temperatures associated with drought, particularly in the larger rivers where temperatures during summer drought were > 10°C higher than typical summer baseflow. The larger rivers also had low canopy cover, which allowed primary producers to take advantage of lower turbidity and fewer cloudy days during drought. We conclude that GPP is enhanced by higher temperature, lower turbidity, and longer water residence times that are all a function of low discharge, but ecosystem response in temperate watersheds to these drivers depends on light availability regulated by riparian canopy cover. In larger rivers, GPP increased more than ER during drought, even leading to temporary autotrophy, an otherwise rare event in the typically light-limited heterotrophic Connecticut River main stem. With climate change, rivers and streams may become warmer and drought frequency and severity may increase. Such changes may increase autotrophy in rivers with broad implications for carbon cycling and water quality in aquatic ecosystems.

Droughts are a disturbance to river ecosystems with far-reaching effects on their structure and function. As freshwaters enter drought, the physical template (e.g., temperature, turbidity, conductivity, and pH) of stream and river ecosystems changes. These fundamental habitat alterations affect all components of the food web and the physicochemical environment (Stanley et al. 1997; Dahm et al. 2003). Many of the changes to river networks during drought are stressful to biota, for instance, low flows and network contraction can greatly reduce microbial metabolic rates (Amalfitano et al. 2008; Fazi et al. 2013; Timoner et al. 2014). Low water volumes and groundwater inputs with drought lead to increasing stream and river temperature extremes (Mundahl 1990; Lake 2003; Riis et al. 2017) and decreased flows reduce water oxygenation (Stanley et al. 1997; Pardo and García 2016; Woelfle-Erskine et al. 2017). Finally, fewer storms during drought means decreased inputs of terrestrial materials, including nutrients and allochthonous organic matter (Fazi et al. 2013). Reduced terrestrial resources can shift the base of aquatic food webs to more abundant autochthonous resources (Sabo et al. 2018).

Droughts are associated with harsh environmental conditions, but can also favor some processes. Low flows and high residence times increase internal recycling of nutrients (Paeil et al. 2006; Bruesewitz et al. 2013) and promote remobilization of nutrients if sediments become anoxic (Jordan et al. 2008).
Lower discharge increases water column residence times and decreases scouring of benthic communities, facilitating the production of large standing stocks of primary producers (Gilbert et al. 2014; Shi et al. 2014). Low flows also reduce water column turbidity, which can result in greater primary production if algae are light limited (Ochs et al. 2013; Hall et al. 2015; Mosley 2015). Ultimately, whether drought enhances or limits ecosystem processes in a stream or river may depend on the local environmental context.

Ecosystem metabolism—including gross primary production (GPP) and ecosystem respiration (ER)—integrates the response of riverine biota to drought from headwaters to major rivers. Yet, the underlying factors driving variation in ecosystem metabolism in fluvial ecosystems, particularly across network scales, are poorly understood (Bernhardt et al. 2018). The manner in which drought changes fluvial ecosystem metabolism may depend on stream size, here categorized by watershed area. There is some evidence that in headwater streams, drought lowers rates of ecosystem metabolism (Acuña et al. 2005; Crawford et al. 2017), but these studies are largely from temporary waters that cease to flow or dry completely due to network contraction during drought. Yet, there is reason to believe that even headwaters that do not dry out will have lower rates of GPP and ER. During drought, stressful environmental conditions such as extremely high temperatures, reduced inputs of nutrients and organic matter from upstream, and decreased water oxygenation are likely more severe in smaller streams than larger rivers (Timoner et al. 2014; Acuña et al. 2015; Sabater et al. 2016).

There is little information on the response of ecosystem metabolism in large rivers to drought, but studies from estuaries suggest that drought creates conditions that stimulate GPP in larger water bodies. Remobilization of nutrients due to sediment anoxia (Jordan et al. 2008) and enhanced nitrification (Paerl et al. 2006; Gilbert et al. 2014) and increased autotroph biomass production with increased residence time (Sin et al. 1999; Gilbert et al. 2014; Shi et al. 2014) are linked to warm season low flows in larger estuaries. However, other research has found that in estuaries, reduced upstream inputs of resources due to drought can both suppress (Wetz et al. 2011; Townsend et al. 2012) or not impact (Howarth et al. 2000) GPP and ER. Thus, understanding of the mechanisms controlling GPP and ER in large rivers and estuaries is still incomplete.

In temperate regions, the interaction of temperature with drought is likely a key determinant of a system’s response. Droughts are driven by low precipitation and high evapotranspiration (McDonough et al. 2011). In temperate watersheds of the eastern United States, precipitation is largely aseasonal, but evapotranspiration is highest in the late summer and early fall when terrestrial productivity and evaporation are both high (Sadri et al. 2016). Thus, droughts in the northeastern United States most commonly occur when water temperatures are highest. This is important because both GPP and ER generally increase with temperature. Based on cellular biochemistry, temperature dependence should be greater for ER compared to GPP (Allen et al. 2005). Yet, temperature dependence of these functions at an ecosystem level is also controlled by environmental factors such as resource limitation (Kritzberg et al. 2010; Welter et al. 2015), hydrology (Demars et al. 2011a), carbon quality (Jane and Rose 2018), and light availability (Huryn et al. 2014). This likely explains why measurements of GPP and ER temperature dependence in streams do not always conform to estimates based on cellular biochemistry. Instead, temperature dependence of GPP in streams may be greater than, smaller than, or insignificantly different from ER (Demars et al. 2011b; Huryn et al. 2014; Song et al. 2018), depending on environmental conditions. Thus, how temperature dependence of GPP and ER changes as environmental conditions shift cannot be ignored.

In addition to temperature, drought also interacts with light availability. Decreased water column turbidity, often associated with reduced sediment transport during drought (Mosley 2015), increases light availability for primary producers and can stimulate GPP in stream and river ecosystems (Izagirre et al. 2008; Hall et al. 2015). Furthermore, droughts are generally most severe when solar insolation is high, which further increases light levels. Thus, higher aquatic light transmittance in streams and rivers during drought may stimulate GPP and increase its temperature dependence (Huryn et al. 2014).

The effect of light may vary with watershed size. Different responses of streams and rivers to drought (Bernhardt et al. 2018) may be caused by canopy cover, which controls how much sunlight actually reaches a channel (Julian et al. 2008). In temperate watersheds, riparian canopy cover decreases with increasing watershed size as widening channels expose river surface to more open sky (Vannote et al. 1980). Thus, although increased temperature and residence time and decreased turbidity during drought can occur across stream orders, it is possible that canopy cover will control drought response.

Here, we examined how changing environmental factors affected the rates and temperature dependence of GPP and ER. A network perspective is useful for making sense of ecosystem metabolism in flowing waters (Stanley et al. 2004). Thus, we leveraged an historic drought in the Connecticut River watershed to examine how changes occur to ecosystem metabolism at a network scale. We used continuous in situ measurements of ecosystem metabolism at 13 stream and river sites across the Connecticut River watershed to evaluate (1) how drought changed GPP and ER from headwaters to the main stem and (2) how temperature and light availability interact to influence GPP and ER with changing hydrologic conditions.

**Materials and methods**

**Method summary**

We used high-frequency in situ dissolved oxygen (DO) measurements to estimate ecosystem metabolism (GPP and ER) on an areal basis. Measurements were made in streams with
watershed areas ranging from 0.41 to 25,019 km² using 4329 d of ecosystem metabolism estimates. To isolate drought, we combined GPP and ER into three flow levels based on flow percentile—median baseflow (20th to 49th percentile), low flow (10th to 19th percentile), and drought (0th to 9th percentile). For ease of interpretation, flow percentiles are presented with the lowest numbers indicating lowest flow levels. Most days classified as drought flow occurred from June through December with drought days evenly split between summer and fall (Supporting Information Fig. S1).

Water temperatures were higher during drought than other seasons. To partition the influence of different mean temperatures on GPP and ER at the three categorical flow levels, we used linear models of the Boltzmann–Arrhenius equation. These models generated mean estimates of GPP and ER for each flow level (baseflow, low flow, and drought) at a set of standardized temperatures (5°C, 10°C, 15°C, and 20°C).

We report on GPP and ER in relation to turbidity, solar irradiance, and riparian canopy cover. To assess the impact of flow level on light obstruction, we measured turbidity in situ and compared these measurements to GPP and ER. To account for the impact of solar irradiance levels and cloud cover on primary production, incident shortwave solar radiation was estimated using data obtained from the North American Regional Reanalysis (NARR). Finally, stream reach percent canopy cover was estimated at each site using hemispherical photographs. Data used for analysis and the associated metadata are included with this publication as online Supporting Information.

Study sites

All stream and river sites (n = 13) were in the Connecticut River watershed, the largest watershed in the New England region of the United States (Fig. 1). Sites were primarily nested within two subwatersheds. Seven sites were in the Farmington River watershed in western Connecticut and five sites were in the Passumpsic River watershed in Northeastern Vermont (Table 1). One site was on the main stem of the Connecticut River near Thompsonville, Connecticut. Most of the Connecticut River watershed experienced drought for portions of 2015, 2016, and 2017 with seasonally adjusted flows along the main stem falling to levels not seen for 50 years. Flow conditions in some tributaries in Connecticut were even more extreme, dropping to 70-yr lows. Drought conditions were more severe in the Farmington River than the Passumpsic River, particularly in late 2016 and early 2017 (Supporting Information Fig. S2). All sites were at current or historic U.S. Geological Survey (USGS) gage sites.

Sonde data collection

Temperature, DO, and specific conductance were measured in situ at 15-min intervals using Eureka Manta 2 water quality sondes (Eureka Water Probes, Austin, Texas) from May 2015 through December 2017. Sensors were calibrated following manufacturer specifications and USGS protocols (Radtke et al. 2005; Rounds et al. 2013). A two-point DO calibration using nitrogen-sparged water and air-saturated water was applied. Calibrations were checked at least monthly year-round and biweekly during summer months. Specific conductance was checked with conductivity standards, and DO was checked by measuring air-saturated water. Performance of all sensors was evaluated with side-by-side deployments of a recently calibrated check sonde alongside the field sonde. If a sonde deviated 5% or more during either check, the unit was recalibrated. Once offloaded, all sonde data were checked and measurements impacted by biofouling or instrument malfunction were removed from the final dataset.

Hydrology

Discharge and channel morphology data were obtained for the 11 sites with active gages from the National Water Information System (United States Geological Survey 2016). During
the period of this study, USGS gages at Nepaug River and Phelps Brook were not actively maintained by USGS. At these sites, stage was measured using pressure transducers. Existing USGS rating curves were updated using a combination of salt injections, velocity-area methods, and stage-discharge measurements. Relationships between discharge and mean channel depth \((z)\) at each site were developed using channel data obtained from NWIS. At Bunnell Brook, Nepaug River, Phelps Brook, Pope Brook, Sleepers River, Still River, and Tributary W9 sites, additional channel transects were measured to develop more accurate discharge–channel depth relationships. In larger rivers, such surveys were not feasible.

Daily flow percentiles were calculated from flow duration curves developed for each site from the previous 10 water years of discharge data (2008–2017) using the hydroTSM package in R 3.4.2 (R Core Team 2016). For the Nepaug River and Phelps Brook sites, 10 yr of discharge data were not available. For these sites, flow percentiles were derived from the nearby Bunnell Brook USGS gage site. The validity of using Bunnell Brook flow percentiles at the Nepaug River and Phelps Brook sites was tested by computing Spearman’s correlation coefficients for the period of discharge record shared between each study gage site and the Bunnell Brook gage site. Spearman correlations for shared periods of daily discharge records were greater than 0.9 for both the Nepaug River and Phelps Brook sites compared to Bunnell Brook.

### Ecosystem metabolism modeling

In aquatic environments, aerobic ecosystem metabolism is measured by observing changes in DO concentrations over time. Photosynthesis increases DO concentrations during daylight hours, while respiration is assumed to consume oxygen at a constant rate regardless of light level. Thus, aquatic productivity and respiration can be estimated by observing daily changes in DO. We used single-station open channel diec DO models to estimate ecosystem metabolism (Odum 1956). In rivers and streams, estimates of ecosystem metabolism must account for atmospheric gas exchange, which varies greatly over time and space. Here, we report gas exchange rate normalized to a Schmidt number of 600 \((K_{600}, \text{d}^{-1})\).

We estimated ecosystem metabolism as free parameters in models describing DO concentrations in rivers (Holtgrieve et al. 2010; Appling et al. 2018). We modeled ecosystem metabolism using the R package streamMetabolizer 0.10.1 (Appling et al. 2017). To estimate GPP, ER, and K600, we fit ecosystem metabolism models to DO data using the following model structure:

\[
\Delta m_O_{i,d} = \left( \frac{GPP_{i,d}}{z_{i,d}} \times \frac{PPFD_{i,d}}{PPFD_d} \right) \times \left[ \frac{ER_{i,d}}{z_{i,d}} + \frac{f_i,d(K600_d)(O_{sat,i,d} - mO_{i,d})}{\Delta t} \right] 
\]

(1)

Here, \(mO_{i,d}\) is modeled DO concentration for timestep \(i\) on day \(d\); \(O_{sat,i,d}\) is DO saturation for timestep \(i\) on day \(d\) estimated following established methods (Garcia and Gordon 2003); \(\Delta t\) represents the length of each timestep (15 min in this study); \(GPP_{i,d}\) and \(ER_{i,d}\) are average GPP and ER (both in g O\(_2\) m\(^{-2}\) d\(^{-1}\)) on day \(d\), respectively; \(z_{i,d}\) is average cross-sectional depth of each upstream reach as described above; \(K600_d\) is estimated standardized gas exchange rate (d\(^{-1}\)) scaled to a Schmidt number of 600 on day \(d\); \(PPFD_{i,d}\) is photosynthetic photon flux density at timestep \(i\) on day \(d\); and \(PPFD_d\) represents the sum of solar insolation for day \(d\).

Ecosystem metabolism parameters GPP, ER, and K600 were fit with Bayesian Markov chain Monte Carlo (MCMC) estimation. We did not have a priori information regarding ecosystem metabolism parameters for our study sites, thus priors were derived from literature values (Appling et al. 2017, 2018). Priors were defined as 3.1 (SD 6.0) g O\(_2\) m\(^{-2}\) d\(^{-1}\) for GPP and -7.1 (SD 7.1) g O\(_2\) m\(^{-2}\) d\(^{-1}\) for ER.
When \( K600 \) is fit alongside GPP and ER, it is possible for multiple solutions that generate equivalent fits for \( mO_{ij} \)—a problem known as equifinality (Appling et al. 2018). To address this problem, daily estimates of \( K600 \) for each site were partially pooled in a hierarchical model. At a stream or river site, gas exchange rates are strongly related to flow (Raymond et al. 2012). Thus, \( K600 \) values were binned by discharge (\( Q \)), and a piecewise relationship was developed. For each site, \( Q \) bins were set at 0.2 natural log units spanning the range of \( Q \) values observed at each site throughout the study. The prior for daily standard deviation of \( K600 \) was set at 2% of the median daily \( K600 \) value for each site obtained from an initial model run wherein estimates of \( K600 \) were not pooled. Estimates of prior probability for mean \( K600 \) were drawn from the distributions derived from unpooled predictions of \( K600 \). Modeling settings are described by the model variant “b_Kb_oipi_tr_plrckm.stan.” Each Bayesian metabolism model was run on four MCMC chains with 1000 burn-in steps and 2000 saved steps using the MCMC program Stan (Stan Development Team 2017). Convergence was estimated as the Gelman–Rubin \( R < 1.1 \). The output of the model is posterior probability distributions of daily estimates of GPP, ER, and \( K600 \).

For each site, DO concentration, DO saturation concentration, channel mean depth, water temperature, modeled incident photosynthetically active radiation (PAR), and \( Q \) at 15-min timesteps were entered into the model. Water temperature, conductivity, and DO concentration were measured by the Manta sondes. Atmospheric pressure to determine DO saturation point was measured by HOBO pressure transducers (Onset, Bourne, Massachusetts) deployed in both the Farmington and Passumpsic subwatersheds. Incident PAR (\( \mu \)mol photons \( m^{-2} \cdot s^{-1} \)) was modeled following Yard et al. (2005). Small gaps in the dataset were filled by linear interpolation, and days with more than three missing hours of measurements were excluded from the model input.

Temperature dependence

As is generally true in the northeastern United States (Hodgkins and Dudley 2011), drought conditions were most severe during late summer—August and September 2016. Thus, streamflow and temperature were generally negatively correlated in this study with the highest temperatures observed during drought conditions (Fig. 2a). Considering that both ER and GPP increase with temperature (Yvon-Durocher et al. 2012; Padfield et al. 2017), it was important to account for the fact that mean temperatures during drought conditions were higher than baseflow. To do this, we calculated mean rates of GPP and ER at standardized temperatures (5°C, 10°C, 15°C, and 20°C) for both median baseflow and drought conditions. The relationship between temperature and GPP and ER, respectively, was tested using linear models of the Boltzmann–Arrhenius equation (Arrhenius 1889; Yvon-Durocher et al. 2012):

\[
\ln G(T) = E_G \times (1/kT_C - 1/kT) + \ln G(T_C) \times Q + E_i \times (T \times Q) 
\]

Fig. 2. Plots of mean daily (a) water temperature, (b) water temperature range, (c) specific conductance (\( \mu S \ cm^{-1} \)), (d) turbidity in FNU, (e) mean daily GPP, and (f) mean daily ER for sites in the Farmington River and Passumpsic River watersheds and the site on the main stem of the Connecticut River. Physicochemical variables were compared across flow levels—baseflow (20th to 49th percentile discharge), low flow (10th to 19th percentile discharge), and drought (0th to 9th percentile discharge). Each point represents the mean of estimates for headwaters (stream orders 1–3), mid-order (orders 4–6), and main stem (order 7) reaches during baseflow, low flow, and drought conditions, respectively. Error bars represent the standard error of the mean with sites as experimental units (\( n = 13 \)). Data presented are from May 2015 through December 2017.
where $G(T)$ is the GPP rate at a site at temperature $T$ in Kelvin ($K$), $E_C$ is the apparent activation energy of GPP in electron volts (eV), $k$ is the Boltzmann constant, and $T_C$ is the temperature around which temperature data were centered (i.e., 288.15 K). For ecosystem-level measurements modeled by the Boltzmann–Arrhenius equation, apparent activation energy of GPP ($E_C$) is interpreted as representing the temperature dependence of GPP. The intercept, $lnG(T_C)$, is the log-transformed mean rate of GPP at temperature $T_C$. These same parameters were also calculated for ER. Apparent activation energy ($E_R$) and the mean rate of ER at standard temperature, $T_C$ – $lnER(T_C)$, were calculating by replacing the terms in Eq. 2 related to GPP with the equivalent ER terms.

For each site, $E_G$, $E_R$, $G(T_C)$, and $ER(T_C)$ were estimated using linear models that included flow level as a categorical variable with a $Q \times T$ interaction term included. To assign discharge level ($Q$), observations for each site were grouped according to three discharge levels: baseflow (20th to 49th percentile $Q$), low flow (10th to 19th percentile $Q$), and drought (0th to 9th percentile $Q$). When a significant flow vs. temperature ($Q \times T$) interaction was found, three estimates for $E_G$ and $E_R$ were produced based on the three flow levels—baseflow, low flow, and drought. The three levels for the $Q$ variable were selected on the basis of a sensitivity analysis: initially data were grouped in $Q$ bins that spanned five percentile units (0th to 4th, 5th to 9th, ..., 45th to 49th), and $E_G$ and $G(T_C)$ were estimated for each flow percentile bin. We observed that values above 20th percentile generally grouped together, whereas low flow (10th to 19th) and drought (0th to 9th) flow levels also grouped distinctively on the basis of similar values for $E_G$ and $G(T_C)$. Selection of these flow percentiles was supported by existing definitions of drought. The United States Drought Monitor uses 10th percentile (10th to 49th) and drought (0th to 9th) levels as a categorical variable with a $Q \times T$ interaction term included. The United States Drought Monitor uses 10th percentile flows at USGS gages to mark the threshold between moderate and severe drought (NDMC 2018).

Equation 2 was fit using the R function lm with an alpha level of 0.05 selected a priori for all comparisons. If the interaction term ($Q \times T$) was not significant, it was removed from the model. Using the models produced here, estimates of GPP and ER at 5°C, 10°C, 15°C, and 20°C—and associated 95% confidence intervals—were produced.

**Autotrophic respiration fraction**

Autotrophic respiration ($AR_a$), the fraction of GPP that is subsequently respired by autotrophs and closely associated heterotrophs can be calculated by modeling how ER changes with GPP (Hall and Beaulieu 2013). As GPP increases, respiration by autotrophs also increases. Thus, as GPP increases, the minimum possible value of ER increases. The $AR_a$ for a given site can be calculated by conducting quantile regression with GPP as the independent variable and the 90th percentile of ER as the dependent variable. The result quantifies the relationship between GPP and the minimum value of ER, with $AR_a$ equaling the slope of the regression. Quantile regressions were conducted using the quantreg package in R 3.4.2 following Hall and Beaulieu (2013).

**Canopy cover estimation**

Triplicate full-frame hemispherical canopy photos were taken with a Kodak SP360 camera at each site during leaf-on conditions between June and August, 2017. Canopy photos were processed using Sidetlook 1.1.01 (Nobis and Hunziker 2005; Cescaatti 2007). Images were subsequently processed using standard protocols for CIMES canopy cover analysis software (Gonsamo et al. 2011). For the Passumpsic River main stem, Farmington River at Unionville, Connecticut, and the Connecticut River at Thompsonville, channel depth prevented us from collecting canopy cover data. Following (Detenbeck et al. 2016), we found a significant relationship between channel bankfull width and logit-transformed proportion canopy cover. We then used this relationship to estimate canopy cover at those sites where it could not be directly measured.

**Geospatial data**

Incident shortwave radiation (W m$^{-2}$) at each site was estimated from NARR (Mesinger et al. 2006) data provided by the National Center for Atmospheric Research. Data were corrected following (Zhao et al. 2013). At each site, for each timestep available, incident shortwave radiation was extracted from the cell containing the study site, as well as the surrounding eight cells, and the mean of these nine cells was taken. Daily mean incident shortwave radiation was compared to net ecosystem production (NEP = GPP + ER) and GPP using linear models in R 3.4.2. Incident shortwave radiation was log-transformed to meet the assumption of normality for linear models.

**Statistical analysis**

For all statistical tests, an alpha level of 0.05 was selected a priori. For linear models, compound symmetry covariance was assumed, and $p$ values were reported with Satterthwaite approximation. Model residuals were evaluated for normality and homoscedasticity and, if violated, variables were log-transformed to meet model assumptions. Statistics are presented with F-statistics as follows: $F_{n(df,df)} = F_{stat}$, where $n(df)$ is the numerator degrees of freedom, and $F_{stat}$ is the F-statistic. If a significant difference was detected, differences between factor levels were tested by Tukey multiple mean comparisons conducted using R package lsmeans (Lenth 2016). Comparisons across sites for major variables (e.g., temperature, turbidity, specific conductivity, GPP, and ER; Fig. 2) were made using mixed effects models with sites ($n = 13$) used as experimental units and flow (baseflow, low flow, and drought) and stream size (headwaters, mid order, and main stem) as categorical variables. An interaction term was included. If this term was not significant, it was removed from the final model. We used R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2016) for
mixed models. We used models with Newey–West covariance matrices to estimate standard error for each site to account for temporal autocorrelation of data (Newey and West 1987; Shultz et al. 2018). Newey–West covariance matrices were generated with automated bandwidth selection (Newey and West 1994) to eliminate subjective parameter selection. Standard errors for each group of sites (headwater, mid order, and main stem) were pooled using standard methods (Cohen 1988).

**Results**

Drought-enhanced GPP and ER in larger watersheds

Water temperatures were generally highest when drought conditions were greatest and differed significantly across flow regimes ($F_{2,26} = 87.0, p < 0.0001$). Tukey tests confirmed that temperatures were significantly higher during low flow ($p < 0.0001$, df = 26) and drought ($p < 0.0001$, df = 26) than baseflow (Fig. 2a), but no significant temperature difference was found between low flow and drought conditions. In addition to flow level, temperature was also significantly related ($F_{2,13} = 7.14, p = 0.0081$) to stream size grouped as headwaters (stream orders 1–3), mid order (orders 4–6), and main stem (order 7). The largest temperature change from baseflow to drought conditions was detected in the main stem of the Connecticut River (stream order 7), increasing by $\Delta$°C compared to $\Delta$°C for lower stream order sites (Fig. 2a). Ultimately, temperatures were significantly greater in the main stem ($p = 0.015$, df = 13) and mid-order channels ($p = 0.030$, df = 13) than headwaters across all flow conditions according to Tukey tests. Daily temperature variability—measured as the mean daily temperature range in °C—significantly increased ($F_{2,26} = 7.52, p = 0.0027$) at all sites from baseflow to drought conditions ($p = 0.0005$, df = 26), with the greatest increase found in the main stem of Connecticut where the mean daily temperature range increased from $0.90^\circ$C to $1.65^\circ$C (Fig. 2b).

GPP increased from baseflow to drought in most systems, but the increase was particularly pronounced in the main stem of the Connecticut River (Fig. 2e). In the main stem, mean daily GPP significantly increased by almost $18$ g O$_2$ m$^{-2}$ d$^{-1}$ ($p < 0.0001$; df = 26) and ER by $13$ g O$_2$ m$^{-2}$ d$^{-1}$ ($p = 0.019$; df = 26) from baseflow to drought (Fig. 2e,f). This trend of a greater GPP response in the main stem contributed to a significant interaction between stream size and flow level for log-transformed GPP ($F_{4,26} = 7.14; p = 0.0005$). As a result, GPP in the Connecticut River main stem was significantly greater than GPP in mid-order ($p = 0.045$; df = 14.1) and headwater streams ($p = 0.0077$; df = 14.1) during drought conditions.

Both GPP and ER increased in the main stem of the Connecticut River during all three summers of the study (Fig. 3d,e). Even so, GPP and ER were highest in the drought summer of 2016. GPP and ER generally increased with temperature but were highest during drought at a given temperature. Approximately 50% of the increase in GPP and ER during drought could be attributed to higher temperatures that occurred during drought conditions (Fig. 4; Supporting Information Figs. S3, S4 and Tables S1–S3).

Although part of the drought response in metabolism was due to higher temperature, a similarly large proportion of the response was temperature independent. Comparisons of mean GPP and ER at standard temperatures ($5^\circ$C, $10^\circ$C, $15^\circ$C, and $20^\circ$C) showed that, when controlling for temperature, both GPP and ER were still higher during drought compared to baseflow conditions (Figs. 4, 5). For most sites, there was also a

![Fig. 3. Plots of mean daily (a) temperature, (b) turbidity, (c) discharge, (d) GPP, and (e) ER by month for the Connecticut River at Thompsonville. Data from May through October of 2015, 2016, and 2017 are presented. Error bars represent the standard error of the mean of each variable averaged over the month.](image-url)
significant interaction between discharge level and temperature when explaining both GPP (11 out of 13 sites) and ER (7 out of 13; Supporting Information Table S1). Thus, the influence of temperature varied with discharge.

How much GPP changed during drought varied with watershed size. For GPP, the increase during drought was positively correlated to watershed area at all temperatures (Fig. 5; Supporting Information Table S4). A correlation between watershed area and GPP enhancement during drought was detectable at all temperatures, but strongest at the 20°C level ($F_{1,11} = 347; p < 0.0001$). By contrast, the increase to ER under drought was only significantly correlated to log-transformed watershed area at $\sim 20°C$ (Fig. 5h; $F_{1,9} = 15.3, p = 0.0045$). In the Connecticut River main stem during drought conditions, GPP increased by almost 11 g O$_2$ m$^{-2}$ d$^{-1}$ from 3.4 to 14.0 g O$_2$ m$^{-2}$ d$^{-1}$ at a standardized temperature of 20°C (Fig. 5d; Supporting Information Table S2). By comparison, ER increased by only $\sim 4$ g O$_2$ m$^{-2}$ d$^{-1}$ at 20°C (Fig. 5h; Supporting Information Table S3).

Increase in GPP during drought linked to canopy cover

Potential light exposure was greatest in larger rivers because stream canopy cover openness was positively correlated with watershed area, leading to a correlation between light transmittance and GPP increase with drought (Fig. 6). At the highest temperatures, the strong response in the main stem of the Connecticut River was responsible for driving this relationship (Fig. 6).

Light exposure during drought

Drought was associated with fewer cloudy days and months when sunlight is most intense. Mean daily incident shortwave radiation increased from $\sim 175$ W m$^{-2}$ during baseflow conditions to almost 250 W m$^{-2}$ during drought (Supporting Information Fig. S5). In the main stem of the Connecticut River where enhancement of GPP was strongest, increased incident solar radiation was significantly positively related to GPP at all discharge levels. Further, the GPP (g O$_2$ m$^{-2}$ d$^{-1}$) per watt of incident shortwave radiation was
greater under drought conditions than either baseflow or low flow (Fig. 7).

**Decreased turbidity during drought**

Water column light transmittance increased during drought. Turbidity decreased significantly across scales from baseflow to drought conditions (Fig. 2d; $F_{2,26} = 8.12$, $p = 0.0018$). Mean daily turbidity was negatively related to GPP at 8 of the 13 sites studied here (Supporting Information Table S5). Changes to GPP occurred even though the magnitude of the change in turbidity was rather small. The largest change to turbidity was in the Connecticut River main stem where mean daily turbidity decreased by only about 3.5 Formazin Nephelometric Units (FNU)—from $6.29 \pm 0.31$ to $2.81 \pm 0.23$ FNU from baseflow to drought conditions (Fig. 2d). Despite these small changes, turbidity was significantly related to primary production (Fig. 8). This negative relationship between turbidity and GPP was strongest in the main stem of the Connecticut River (Fig. 8; $F_{1,742} = 278$, $p < 0.0001$, $r^2 = 0.27$).

**Productivity : respiration increases in larger rivers during drought**

When $P : R$ (GPP : ER) ratios were compared for baseflow vs. drought conditions at standardized temperatures, only the
largest rivers—along the main stems of the Connecticut, Farmington, and Passumpsic Rivers—showed a substantial change in response to drought (Supporting Information Fig. S6). Most smaller stream reaches were highly heterotrophic (P : R << 1) under baseflow conditions and changed little under drought conditions. Although almost all sites were heterotrophic (P : R < 1) on almost all days, the main stem of the Connecticut River and some sites in the Farmington River watershed did become autotrophic (P : R > 1) when temperatures were high under drought conditions (Fig. 7).

Temperature dependence greater for GPP than ER

We calculated activation energies for GPP ($E_G$) and ER ($E_R$) to estimate temperature dependence. There was no significant difference for $E_G$ or $E_R$ among the three flow levels (Supporting Information Fig. S7 and Table S6). Activation energies for $E_G$ (mean: 0.442 eV; SE: 0.032) were consistently higher than for $E_R$ (mean: 0.168 eV; SE: 0.032). Temperature dependence of both GPP and ER were substantially higher in the main stem of the Connecticut River than other sites. Mean $E_G$ was 0.733 in the main stem, 0.440 in mid-order rivers, and 0.373 in headwaters. Similarly, mean $E_R$ was 0.534 in the main stem, 0.123 in mid-order rivers, and 0.159 in headwaters.

**Fig. 7.** GPP and NEP at the Connecticut River at Thompsonville. Plotted against daily mean incident shortwave radiation ($W m^{-2}$) as estimated from NARR data. Data were divided into three groups based on discharge percentile as described in the methods: (a and d) baseflow, (b and e) low flow, and (c and f) drought. Lines in panels a–c indicate significant linear relationships between log-transformed daily mean incident shortwave radiation and log-transformed daily GPP. Red dashed lines in panels d–f indicate NEP of 0. Data presented are from May 2015 through December 2017.

**Fig. 8.** Daily mean turbidity measured in FNU compared to daily GPP in the main stem of the Connecticut River at Thompsonville, Connecticut. To avoid log-transforming zero values, 0.5 was added to daily mean turbidity. A significant regression ($p < 0.001$) was obtained when comparing daily mean turbidity (plus 0.5) to primary production: $\log_{10}(GPP) = -1.262 \times \log_{10}(Turb + 0.5) + 0.984$. Data presented are from May 2015 through December 2017.
Discussion

Drought in the Connecticut River watershed enhanced riverine GPP, though this effect was dependent on watershed size. A recent review has stressed the importance of using datasets from a broad range of sites in order to understand the metabolic regimes of flowing waters (Bernhardt et al. 2018). Here, we investigated the variability in metabolism within a nested set of watersheds that varied over 5 orders of magnitude in watershed size over 3 yr. In general, GPP was low across all conditions (\(< 1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}\)) in the small (\(< 100 \text{ km}^2\)) watersheds due to light limitation from forest canopy but was enhanced significantly during drought in larger rivers. Light limitation of GPP by forest canopy in temperate systems is often discussed (Vannote et al. 1980; Bernhardt et al. 2018), although not widely demonstrated through a systematic set of measurements across nested watersheds. More research is needed to increase our knowledge base and ability to model the combined impact of canopy cover, temperature, and water clarity on primary production across watersheds.

The highest rates of metabolism occurred during low flows associated with drought conditions (Fig. 2). During this period, GPP levels in the main stem of the Connecticut River averaged more than 20 g O$_2$ m$^{-2}$ d$^{-1}$, rivaling GPP rates of highly productive, semiarid, reservoir-dominated systems, where GPP has been reported as high as 36 g O$_2$ m$^{-2}$ d$^{-1}$ (Davis et al. 2012). Periods of extended low flows led to a change in the hydraulics of rivers which can favor high rates of GPP (Julian et al. 2013; Morling et al. 2017). Longer residence times with low velocity also favors the build-up of autotroph biomass (Sin et al. 1999; Glibert et al. 2014; Shi et al. 2014), while prolonged periods of low velocity will decrease biomass loss due to the disturbance associated with scour and advection (Bernhardt et al. 2018). Greater producer biomass increases the probability that light reaching the riverine environment will be intercepted by an autotroph. Finally, a decrease in river depth with drought can lead to increased sunlight for benthic primary producers (Julian et al. 2008) and a decrease in the depth of mixing for water column primary producers (Cole et al. 1992), creating conditions more favorable for positive growth.

The amount of light reaching the water surface also increased during drought conditions affecting metabolism across the network (Figs. 5–7). Higher solar radiation levels due to decreased cloud cover and season during drought led to more radiation reaching streams and rivers. During drought, daily mean incident shortwave radiation was \( \sim 40\% \) greater than baseflow conditions. How much of this additional shortwave radiation reaches the stream or river, however, was scale dependent due to a lack of forest canopy in large systems compared to heavily shaded headwaters streams (Fig. 6). The lower water velocities associated with drought conditions also led to lower turbidity (Fig. 2d), which was linked to higher GPP in the Connecticut main stem (Fig. 8). This finding adds to the mounting evidence that water clarity, particularly turbidity, is a central factor controlling GPP in inland and coastal waters (Izagirre et al. 2008; Hall et al. 2015; Shen et al. 2015). Turbid waters may still support high GPP if depths are low (Bunn et al. 2003), and aromatic DOM may inhibit autochthonous production even during low flows (Mehring et al. 2013). Interestingly, here we report a significant change to GPP in response to small changes in turbidity when FNU is below 10 (Fig. 8), suggesting sensitivity even at these low turbidities.

Higher temperatures associated with summer droughts in this temperate watershed were also partly responsible for the increased GPP and ER. Water temperatures during drought conditions were higher than baseflow, which enhanced both photosynthesis and respiration. High-temperature excursions during drought are due to decreased thermal buffering by groundwater and lower thermal capacity from reduced water volumes (Hodgkins and Dudley 2011). As air temperatures rose during the summer at the height of the drought, so did the mean daily water temperature and temperature range (Figs. 2a,b, 3a). Interestingly, the temperature difference was greatest in the largest stream order, where temperatures were \( \sim 10^\circ\text{C} \) higher in drought than baseflow conditions compared to 2–5°C for smaller systems (Fig. 2a), contributing to the watershed size effect of drought response. Thus, increased temperatures and light availability synergistically increased GPP during drought particularly in larger rivers leading to high levels of productivity.

The impact of temperature on stream metabolism reported here adds to a growing body of literature. We found that temperature stimulated GPP more than ER in all sites across all flow levels (Supporting Information Fig. S7). The relatively high values of $E_G$ reported here are consistent with a recent global synthesis (Demars et al. 2016). Based on cellular biochemistry, however, ER should be more responsive to temperature than GPP (Allen et al. 2005). Furthermore, in contrast to our study, a recent study of stream apparent activation energies of GPP and ER in streams reported that increased temperatures will result in a convergence of GPP and ER temperature sensitivity (Song et al. 2018). We argue that in temperate ecosystems, temperature response is determined by a complex interplay between temperature and other variables that may covary. That is, environmental factors such as light levels, turbidity, nutrient levels, and water residence time can covary with temperature, particularly in temperate watersheds, and either suppress or enhance the apparent temperature sensitivity at the ecosystem level.

Here, GPP temperature dependence increased with light availability (Huryn et al. 2014). This change to GPP likely influenced ER both directly and indirectly. Throughout this study, $A_R$ was responsible for approximately 50% of ER (Supporting Information Table S7). High levels of GPP increase the release of highly labile autochthonous DOM by algae (Bertilsson and Jones Jr 2002), which likely stimulated ER during drought. If supplies of labile autochthonous DOM are consistent across temperature levels, apparent $E_R$ should decrease (Jane and Rose 2018). Here, apparent $E_R$ was consistently lower than apparent $E_G$, because respiration was fueled by highly variable GPP that was greatest when temperatures
were highest. In fact, Song et al. (2018) report that $E_C$ exceeded $E_R$ in $\sim80\%$ of measurements in boreal ecosystems, which is consistent with our study of temperate streams and rivers of the northeastern United States and may indicate that covariation of discharge, water temperature, and water clarity is common in temperate and boreal humid forests. Further work is needed to determine why apparent $E_R$ and $E_C$ conform to theoretical expectations in some studies (Perkins et al. 2012; Huryn et al. 2014) but not others (Welter et al. 2015; Demars et al. 2016; Song et al. 2018; this study).

Our findings are consistent with theory on the interaction between the physical template and biogeochemistry of watersheds. The RCC hypothesized that GPP would be regulated by canopy cover in small streams and by turbidity, sunlight levels, and residence time in larger systems (Vannote et al. 1980). Furthermore, a recent conceptual paper on the metabolism of rivers underscored the importance of the interaction of incident light, disturbance, and canopy cover (Bernhardt et al. 2018). Interestingly, in this study, we were only able to demonstrate these drivers by controlling for flow and focusing on the lowest flow periods, which for this watershed also coincides with large changes in light and temperature. By doing so, we conclude that drought acts to stimulate GPP through higher temperature, reduced turbidity, and increased sunlight exposure, but only when light is not first intercepted by riparian canopy cover. We believe that the interactions between flow and the physical template of watersheds found here may lead to similar responses in other temperate forested watersheds. Future work across nested watersheds with a varying physical template and climate will be important to testing the consistency of this relationship. For instance, in river networks where canopy cover in headwaters is lower, we expect that a drought response will occur further upstream than in the Connecticut River watershed.

The overall carbon and oxygen budget of these ecosystems, or their net ecosystem productivity (NEP), is determined by the balance between GPP and ER. Consistent with other’s work (Dodds et al. 1996; Ulseth et al. 2018), we found that a strong response of GPP to light was the driving factor behind NEP and P : R increases in the larger Connecticut, Farmington, and Pasumpsc Rivers (Fig. 7). GPP increased enough at high light availability to drive NEP positive on a few days (Fig. 7). Thus, these periods of low flow and high sunlight might be critical for autochthonous carbon production. More autochthonous carbon will affect the broader food web (Wagner et al. 2017; Sabo et al. 2018) and transform heterotrophic microbial community structure and function (Sabater et al. 2011; Hosen et al. 2017).

These findings are significant to global change research. Climate change is predicted to increase stream water temperatures (Nelson and Palmer 2007; Demaria et al. 2016). The frequency, length, and severity of droughts are projected to increase as well (Dai 2013), though it is uncertain whether these changes will substantially affect streamflow in the Northeastern United States (Demaria et al. 2016). Increased water temperature, decreased baseflow, or longer low flow periods with climate change will likely stimulate riverine GPP. Land management significantly alters the riparian zone and suspended sediment content and therefore the light regime of streams and rivers, which will modulate the response of ecosystem metabolism to climate change. Here, we demonstrate that the response of metabolism is highly modified by a predictable interaction among temperature, light availability, and discharge. More nested watershed studies are needed across watersheds with different land cover, nutrient loads, and hydrologic regimes to more broadly assess the response of stream metabolism to global change.

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None declared