

Increased resource use efficiency amplifies positive response of aquatic primary production to experimental warming

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Abstract

Climate warming is affecting the structure and function of river ecosystems, including their role in transforming and transporting carbon (C), nitrogen (N), and phosphorus (P). Predicting how river ecosystems respond to warming has been hindered by a dearth of information about how otherwise well-studied physiological responses to temperature scale from organismal to ecosystem levels. We conducted an ecosystem-level temperature manipulation to quantify how coupling of stream ecosystem metabolism and nutrient uptake responded to a realistic warming scenario. A ~3.3°C increase in mean water temperature altered coupling of C, N, and P fluxes in ways inconsistent with single-species laboratory experiments. Net primary production tripled during the year of experimental warming, while whole-stream N and P uptake rates did not change, resulting in 289% and 281% increases in autotrophic dissolved inorganic N and P use efficiency (UE), respectively. Increased ecosystem production was a product of unexpectedly large increases in mass-specific net primary production and autotroph biomass, supported by (i) combined increases in resource availability (via N mineralization and N₂ fixation) and (ii) elevated resource use efficiency, the latter associated with changes in community structure. These large changes in C and nutrient cycling could not have been predicted from the physiological effects of temperature alone. Our experiment provides clear ecosystem-level evidence that warming can shift the balance between C and nutrient cycling in rivers, demonstrating that warming will alter the important role of in-stream processes in C, N, and P transformations. Moreover, our results reveal a key role for nutrient supply and use efficiency in mediating responses of primary producers to climate warming.

KEYWORDS

climate change, ecosystem respiration, gross primary production, headwater streams, nutrient cycling, nutrient use efficiency, stream metabolism, temperature

1 | INTRODUCTION

Climate warming is likely influencing the important role rivers play in processing and transporting carbon (C) and nutrients (Peterson et al.,

2001; Raymond et al., 2013; Woodward, Perkins, & Brown, 2010). Because of the dendritic and advective nature of river ecosystems, warming-induced changes in gross primary production (GPP) and ecosystem respiration (ER) could have far-reaching consequences for

the coupled uptake, storage, and delivery of nutrients to downstream habitats, including marine environments (Cole et al., 2007; Jarvie, Jickells, Skeffington, & Withers, 2012). It is thus imperative to understand how climate warming alters river metabolism and its coupling to the cycling of limiting elements such as nitrogen (N) and phosphorus (P).

The influence of warming on river ecosystems is shaped by direct effects of temperature on individual physiological rates and by indirect effects on species acclimation and adaptation, community composition, food web dynamics, and nutrient cycling (Padfield et al., 2017; Woodward, Perkins et al., 2010). Understanding and predicting these complex responses will benefit from leveraging recent frameworks rooted in first principles, including metabolic theory (MTE; Allen & Gillooly, 2009; Allen, Gillooly, & Brown, 2005; Anderson-Teixeira, Smith, & Morgan Ernest, 2012; Brown, Gillooly, Allen, Savage, & West, 2004) and ecological stoichiometry (Cross, Hood, Benstead, Huryn, & Nelson, 2015; Sterner & Elser, 2002). Although multiple studies have shown that MTE can help predict ecosystem metabolism across wide temperature gradients (López-Urrutia, San Martín, Harris, & Irigoien, 2006; Yvon-Durocher et al., 2012), considerable uncertainty remains concerning (i) how resource availability influences its predictions and (ii) how responses to warming might scale from individual organisms to whole ecosystems.

The bulk of our knowledge concerning ecological effects of warming comes from either correlative studies across large (and potentially confounded) spatial scales or small-scale, short-term laboratory or field studies (Woodward, Benstead et al., 2010). Ecosystem-level experiments provide a means for testing theoretical predictions while maintaining realistic levels of complexity (Carpenter, Chisholm, Krebs, Schindler, & Wright, 1995). Whole-stream warming experiments have rarely been attempted, however (but see: Ferreira & Canhoto, 2014; Hogg, Williams, Eadie, & Butt, 1995), and the effects of warming on stream ecosystem function have not yet been subject to comprehensive study. We used a before–after control–impact design (BACI) to evaluate the influence of a realistic climate-warming scenario on the structure and function of an Icelandic headwater stream. We collected background measurements in our experimental stream and a reference stream for 1 year and then used a novel gravity-fed geothermal heat-exchange system (Nelson et al., 2017; O’Gorman et al., 2014) to warm the experimental stream by ~3.3°C for a year. We develop a general framework for predicting the response of net primary production (NPP) to warming in lotic ecosystems (following: Anderson-Teixeira, Vitousek, & Brown, 2008; Cross et al., 2015; Davidson, Samanta, Caramori, & Savage, 2012) and use it, in combination with a C and N mass balance model, to disentangle the complex pathways through which warming influenced ecosystem production in our experimentally heated stream.

2 | THEORY

The metabolic theory of ecology (MTE) combines individual metabolic responses to temperature with changes in individual size and

community biomass structure to provide a powerful framework for understanding patterns of ecosystem production (Enquist et al., 2003; Enquist, Kerkhoff et al., 2007; Kerkhoff, Enquist, Elser, & Fagan, 2005; Michaletz, Cheng, Kerkhoff, & Enquist, 2014; Padfield et al., 2017; Yvon-Durocher et al., 2012). This framework begins with the prediction that, below optimal temperatures, mass-specific NPP (NPP_{ms}) increases exponentially with temperature following the Arrhenius–Boltzmann relationship:

$$NPP_{ms} = b_0 e^{-E_a/kT}, \quad (1)$$

where b_0 is a normalization constant, k is the Boltzmann constant (8.61×10^{-5} eV/K; $1 \text{ eV} = \sim 1.6 \times 10^{-19}$ J), T is temperature (Kelvin), and E_a is the activation energy (eV) for mass-specific primary production, which is predicted to be ~0.32 eV (Allen et al., 2005). It is common to scale from mass-specific to areal rates (NPP_A) by summing the product of mass-specific rates and biomass across all of the individuals or size-classes in an ecosystem (Allen et al., 2005; Enquist et al., 2003; Yvon-Durocher, Montoya, Trimmer, & Woodward, 2011); however, the applicability of this approach for benthic systems is limited, because the biomass of individual taxa is rarely enumerated. To bypass this limitation, we use total ecosystem autotroph biomass (B):

$$NPP_A = NPP_{ms}B. \quad (2)$$

This simplification assumes a constant relationship between NPP_{ms} and body size within the narrow size range exhibited by benthic algae and cyanobacteria (Cattaneo, 1987). MTE predicts that, with no change in resource availability, ecosystem biomass should decline with temperature (Brown et al., 2004) following an Arrhenius–Boltzmann relationship ($e^{E_b/kT}$, where E_b is the temperature dependence of autotroph biomass). This basic MTE formulation does not explicitly incorporate the influence of limiting resources on NPP_A . As resource limitation of aquatic NPP is common (Elser et al., 2007), it is critical to incorporate relative nutrient availability into Equation (2).

When considering limiting resources, we must account for the influence of warming on both resource availability and use efficiency (UE). Resource availability can be a strong mediator of metabolic responses to temperature (Jankowski, Schindler, & Lisi, 2014; López-Urrutia & Morán, 2007; Valett et al., 2008). Warming can also enhance both resource availability (Welter et al., 2015) and its use efficiency (De Senerpont Domis, Van de Waal, Helmsing, Van Donk, & Mooij, 2014; Woods et al., 2003). Anderson-Teixeira et al. (2008) developed a generalizable equation for NPP_A , which incorporates resources into Equation (2) as:

$$NPP_A = b_0 e^{-E_a/kT} B R^{\alpha_r}, \quad (3)$$

where R is the concentration of a limiting resource and α_r describes the conversion of resource r into NPP_A (i.e., resource use efficiencies). In some cases, R can vary exponentially with temperature following an Arrhenius–Boltzmann relationship ($e^{-E_r/kT}$, where E_r is the temperature dependence of resource r). This relationship is reasonable for the supply of nutrients from N_2 fixation or heterotrophic

mineralization, which have temperature dependences of approximately 2.2 eV (below 22°C) and 0.36 eV, respectively (Ceuterick, Peeters, Heremans, DeSmedt, & Olbrechts, 1978; Sinsabaugh & Follstad Shah, 2012); however, it is not reasonable for variables such as light. To account for warming-induced changes in resource UE, we can model resource UE as:

$$\alpha_r = n_r + \left(u_r * \frac{1}{kT} \right), \quad (4)$$

where n_r is the intercept and u_r is a coefficient describing how the UE of resource r changes with temperature (Davidson et al., 2012).

3 | PREDICTIONS

We can now formalize Equation (3) for our experimental and reference systems. As both streams are high-latitude ecosystems with low dissolved inorganic N (DIN) concentrations, we predict that, on an annual scale, light and N supply will influence NPP_A , yielding the predictive equation:

$$NPP_A = b_0 e^{-E_a/kT} e^{E_b/kT} L^{\alpha_L} (e^{-E_N/kT})^{\alpha_N}, \quad (5)$$

where L is light availability, α_L and α_N describe the conversion of light and nitrogen to NPP_A , and E_N is the temperature dependence of N supply. In the experimental and reference systems, total N supply is the sum of three N sources: DIN input to the reach, N

mineralization within the autotroph community, and N_2 fixation. DIN input is independent of the experimental manipulation; however, both N mineralization and N_2 fixation can increase exponentially with temperature (Ceuterick et al., 1978; Sinsabaugh & Follstad Shah, 2012). The temperature dependence of N supply, E_N , should equal the sum of the temperature dependence of inorganic N uptake ($E_{N,i}$), N mineralization ($E_{N,m}$), and N fixation ($E_{N,f}$; $E_N = E_{N,i} + E_{N,m} + E_{N,f}$; Anderson-Teixeira et al., 2008). We predict that E_N will be 2.56 eV ($E_{N,i} = 0$ eV, $E_{N,m} = 0.36$ eV, and $E_{N,f} = 2.2$ eV) when all three N sources are important, or 0.36 eV in the absence of N_2 fixation.

Equation (5) predicts responses in NPP_A to warming by combining the influence of temperature on NPP_{ms} , ecosystem biomass, resource supply, and resource UE (Figure 1). Several coefficients in Equation (5; e.g., E_b and α_N) must be empirically measured for specific taxa and systems (Cross et al., 2015). As a result, strict quantitative predictions about responses of NPP_A to warming cannot be made. We can, however, combine theory and empirical data to predict qualitative changes in these coefficients; NPP_{ms} , N supply, and N UE should increase with temperature (Allen et al., 2005; Sinsabaugh & Follstad Shah, 2012; Welter et al., 2015; Woods et al., 2003), while ecosystem biomass should decline with temperature when resource supply is held constant (Figure 1, Brown et al., 2004). When resource supply and UE are constant, declines in ecosystem biomass might balance increases in NPP_{ms} ($E_b = -E_a$), resulting in no change in NPP_A . Alternatively, the predicted increases in resource supply and UE might result in higher than expected ecosystem

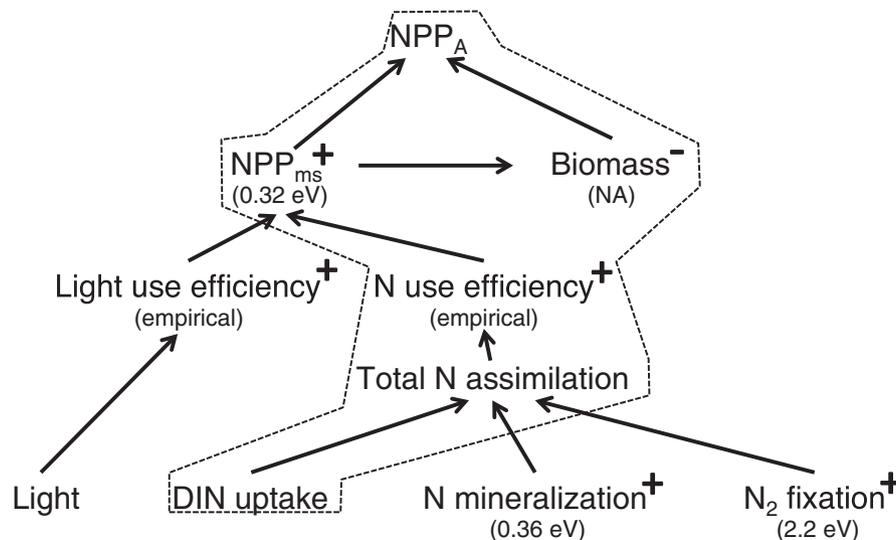


FIGURE 1 Conceptual diagram outlining the controls of areal NPP (NPP_A) and the pathways through which temperature mediates NPP_A . We predict that light and N limit autotrophic production. The influence of these resources on NPP_A will be mediated through species- or community-specific resource use efficiencies, as well as the effects of resources on autotrophic biomass and mass-specific production. As we lack information on these parameters for specific taxa, we used aggregate NPP_{ms} and biomass in our analyses (Equation 2). There are three likely N sources: uptake of dissolved inorganic N (DIN) derived from upstream, N mineralization within the reach, and N_2 fixation. We differentiate between DIN uptake and N mineralization because our DIN uptake estimate reflects biofilm net DIN uptake from the water column and likely does not incorporate N mineralization within benthic biofilms. We ignore the influence of temperature on net DIN uptake, since that parameter was directly measured. Parameters with positive (plus sign) and negative (minus sign) responses to temperature are highlighted and specific predictions are given when available. The dotted line encompasses the parameters incorporated into the DIN-UE metric, which is used in combination with mass balance approaches to infer the potential importance of N mineralization and N_2 fixation. This conceptual diagram does not incorporate feedbacks between these parameters or potential changes driven by acclimation or evolution

biomass or NPP_{ms} , which would combine to yield an increase in NPP_A with temperature. Consistent with this hypothesis, areal GPP increased exponentially with temperature in several aquatic studies, exhibiting apparent activation energies between 0.4 and 0.6 eV (Demars et al., 2016; Padfield et al., 2017; Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010). These positive apparent activation energies at the ecosystem scale suggest that changes in biomass, resource availability, and resource use efficiency may influence the scaling of metabolic rates from individuals to ecosystems.

While the relationship between aquatic ecosystem metabolism and temperature has been examined previously (Demars et al., 2011, 2016; Padfield et al., 2017; Yvon-Durocher et al., 2010, 2012), we lack information about how changes in biomass or resource supply shape metabolic rates at the ecosystem level. Here, we use the results of a whole-stream warming experiment to evaluate the mechanisms, via Equation (5), driving an unanticipated amplification of areal NPP with warming. Our results show that increased NPP_A during the warming manipulation was a function of increases in ecosystem biomass and NPP_{ms} , driven by increases in resource UE and N supply. We did not measure two potential N sources for autotrophs—N mineralization and N_2 fixation—so we use a C and N mass balance model to evaluate the potential importance of these sources. Together, these results highlight the potential importance of limiting resources in mediating responses to warming.

4 | MATERIALS AND METHODS

4.1 | Experimental design and application

Our experiment relied on a BACI design that involved monthly sampling of a suite of structural and functional characteristics in the experimental (IS7) and reference streams (OH2) for 1 year before and 1 year after warming. Both streams drain grassland catchments, and their primary production is strongly N-limited during the summer (Friberg et al., 2009). In October 2011, we began warming the experimental stream using a gravity-fed geothermal heat exchanger submerged in an adjacent geothermally warmed stream (IS8, annual mean temperature $\sim 24^\circ\text{C}$; Nelson et al., 2017). The input of warmed water from the heat exchanger into the experimental stream formed a 35 m warmed reach immediately upstream of its confluence with the Hengladalsá River.

4.2 | Organic matter pools

We collected benthic organic matter samples each month. Fine (250–1,000- μm) and coarse ($>1,000\text{-}\mu\text{m}$) material was collected with a Surber sampler (250- μm mesh, 0.0225- m^2 sampling area) at five randomly selected sites distributed throughout each reach. The captured material was placed in a bucket; cobble-sized material was scrubbed with a wire brush, rinsed, and then removed. The remaining material was sieved (250- μm) and preserved in 4% formaldehyde. In the laboratory, each sample was separated into identifiable categories (e.g., filamentous algae, leaf litter, *Ulva*, bryophytes), dried at

60°C , weighed, ashed at 500°C , and reweighed to obtain ash-free dry mass (AFDM).

Biofilms were sampled using a 35-mm slide mount (8 cm^2) as a template to sample the top of five rocks lacking bryophytes or large crops of filamentous algae. The area within the template was scrubbed with a wire brush and rinsed with stream water, and the resulting slurry was diluted to 125 ml. The slurry was returned to the laboratory in an opaque bottle, where subsamples (5 to ~ 100 ml depending upon particle density) were collected on two 25-mm GF/F filters for C:N and P analysis and a 47-mm GF/F filter for AFDM.

Filamentous algae were common in the experimental stream following warming and were not adequately characterized by the biofilm samples. We calculated total autotroph biomass as the sum of biofilm AFDM and the AFDM of autotrophs identified in the coarse particulate organic matter compartments. Our biofilm samples contained some heterotrophs and fine particulate organic matter, so this approach likely overestimates autotroph biomass.

4.3 | Ecosystem metabolism

We used the two-station open-channel method to measure GPP, ER, and net ecosystem production (NEP) in the experimental and reference streams (Hall & Tank, 2005; Hall, Tank, Baker, Rosi-Marshall, & Hotchkiss, 2016; Marzolf, Mulholland, & Steinman, 1994; Young & Huryn, 1998). Detailed methods for ecosystem metabolism as well as other ancillary time-series data (e.g., water temperature, light, discharge) are described in the SI text. The two-station method calculates metabolism as the difference in dissolved oxygen (DO) between the top and the bottom of the reach, after accounting for sources of DO gains and losses such as reaeration and groundwater exchange. We deployed optical dissolved oxygen (DO) probes at the top and bottom of the experimental and reference reach each month for at least 24 hr. Reaeration was measured using a modification of the method of Tobias, Bohlke, Harvey, and Busenberg (2009) that has been described in detail by Huryn, Benstead, and Parker (2014; see Appendix S1). We used salt dilution gauging to measure groundwater exchange (see Appendix S1). A Bayesian framework was used to solve for several parameters in the metabolism model, which included terms for ER, a light-saturation model for GPP (Jassby & Platt, 1976), reaeration, and groundwater DO exchange (Hall et al., 2016; Holtgrieve, Schindler, Branch, & A'mar, 2010). The model accounts for the effects of groundwater dilution following Hall and Tank (2005). During some months, we were able to collect >24 consecutive hours of DO data. For these months, we analyzed each day separately and report the mean of the daily parameter estimates. Values for ER and GPP were converted from units of DO to units of C using a photosynthetic quotient of 1.2 and a respiratory quotient of 0.8 (Bott, 2006). Finally, we estimated daily and annual GPP with a statistical model combining photosynthesis-irradiance coefficients estimated from DO-profiles with hourly travel time and light data, using a bootstrapping approach (see Appendix S1).

4.4 | Nutrient uptake

We used the TASCC method (Covino, McGlynn, & McNamara, 2010) to separately measure NH_4^+ -N, NO_3^- -N, and SRP uptake rates in both streams each month. The TASCC method allows for a well-constrained estimate of uptake rates at ambient concentrations, although all non-isotopic addition methods overestimate these rates to some degree (Trentman et al., 2015). In summary, a slug containing dissolved nutrients (NH_4Cl , NaNO_3 , or Na_2HPO_4) and Cl^- (NaCl) was added far enough above the upstream metabolism station to allow for adequate mixing (~5–10 m). Then, at the downstream end of the reach, we collected 20 water samples (in 250-ml Nalgene® bottles) distributed throughout the Cl^- breakthrough curve. Following the release, each water sample was filtered (PES, 0.45 μm 25-mm syringe filters; Environmental Express, Charleston, South Carolina, USA) using a 50-ml polyethylene syringe and transferred to a new sample-rinsed 50-ml polyethylene Falcon tube (Fisher Scientific, Pittsburgh, Pennsylvania, USA), which was frozen upon return to the laboratory. We conducted the three uptake measurements successively (NH_4^+ , PO_4^{3-} , and then NO_3^-). Uptake measurements for the three species were conducted on the same day, except for rare exceptions, to maintain consistency between the three releases. Ammonium concentrations were measured using the orthophthalaldehyde fluorometric method (Holmes, Aminot, Kerouel, Hooker, & Peterson, 1999), as modified by Taylor et al. (2007). Nitrate and chloride concentrations were measured using ion chromatography (Dionex ICS 2000; Dionex Corp., Sunnydale, CA, USA), while SRP concentrations were measured using the ascorbic acid method (Murphy & Riley, 1962). These data were combined with other ancillary data (ambient nutrient concentrations, width, discharge, and travel time from the predicted time series; see SI text) to estimate ambient nutrient uptake rates ($\text{mg m}^{-2} \text{hr}^{-1}$), following Covino et al. (eq. 12; 2010).

4.5 | Resource use efficiency and demand

To assess how the warming experiment influenced the use and coupling of energy and elements, we calculated autotroph light, N, and P UE. Resource UE is net C production per net resource assimilated; however, various measures characterize UE over different temporal scales and hierarchical levels (e.g., communities vs. ecosystems; Sterner & Elser, 2002). Thus, we present two measures of autotroph N and P UE. First, we present ecosystem DIN and SRP UE, which is calculated from C, N, and P fluxes. Ecosystem DIN and SRP UE are the quotients of net primary production (NPP; $\text{mol C m}^{-2} \text{day}^{-1}$) and nutrient uptake ($\text{mol nutrient m}^{-2} \text{day}^{-1}$). NPP is the difference between GPP and autotrophic respiration, which we assumed to be 50% of GPP (Hall & Tank, 2003). This also makes the assumption that warming does not influence the balance of autotrophic respiration and production, based on studies indicating that acclimation, adaptation, and shifts in community assemblage balance these processes (Enquist, Kerkhoff, Huxman, & Economo, 2007; Gifford, 2003; Padfield, Yvon-Durocher, Buckling, Jennings, & Yvon-Durocher, 2015). Our calculation of ecosystem nutrient UE also makes

several additional assumptions concerning benthic C and nutrient cycling that we evaluate in the Section 6. Second, we present autotroph community N and P UE, which is autotroph C:N or C:P. Autotroph C:N and C:P were calculated as a weighted average of the stoichiometries of components of total autotroph biomass (e.g., biofilm, filamentous algae, and bryophytes). Light-UE is the quotient of daily GPP ($\text{mol C m}^{-2} \text{day}^{-1}$) and daily integrated photosynthetically active radiation ($\text{mol PAR m}^{-2} \text{day}^{-1}$).

4.6 | Statistical analysis

We used randomized intervention analysis (RIA; Carpenter, Frost, Heisey, & Kratz, 1989) to test for changes in ecosystem response to the warming manipulation. The RIA test statistic is the difference between the mean differences of the experimental (E) and reference (R) observations before and during the warming manipulation:

$$(\overline{E_B - R_B}) - (\overline{E_D - R_D}), \quad (6)$$

where the subscripts B and D refer to before and during the warming manipulation, respectively. We estimated the sample distribution using randomization to create 10,000 new time series of differences sampled without regard to position. The *p*-value is the proportion of randomized time series with greater mean differences than the RIA test statistic. All observations were $\log_{10}(x + 1)$ -transformed. Months with missing data were removed from the analysis. As the RIA test statistic evaluates relative differences, there is no requirement that the experimental and reference systems be similar prior to the intervention. RIA is best at identifying treatment effects when the intervention has consistent directional effects throughout the measurement period (e.g., warming increases primary production). This may not be the case over an annual cycle because of seasonality, resulting in decreased power to identify trends. We used the mean estimates of whole-stream metabolism fluxes from each month in our analysis. Analyses were performed in R version 3.2.4 (R Core Team, 2016). Figures were created using the "ggplot2" package (Wickham, 2009).

4.7 | NPP model development and evaluation

Here, we adapt our framework for predicting how warming influences NPP_A (Equation 5) to better understand responses in the experimental and reference streams. For both streams, we centered temperature at 6°C, approximating the pretreatment mean. Next, we log-transformed Equation (5) to yield the following multiple linear regression model:

$$\ln \text{NPP}_A = \ln b_0 + E_{A,\text{app}} \left(\frac{1}{kT_c} - \frac{1}{kT} \right) + \alpha_L \ln L + \alpha_N \ln N, \quad (7)$$

where $E_{A,\text{app}}$ is the apparent activation energy of NPP_A ($E_{A,\text{app}} = -E_a + E_b + E_{N,m} + E_{N,f}$) and N is DIN uptake. We used DIN uptake to characterize DIN availability, instead of DIN concentration or yield, because this flux best reflects N availability to autotrophs. We factored out the influence of ecosystem biomass by evaluating a similar model for NPP_{ms} :

$$\ln \text{NPP}_{\text{ms}} = \ln b_0 + E_{\text{ms,app}} \left(\frac{1}{kT_c} - \frac{1}{kT} \right) + \alpha_L \ln L + \alpha_N \ln N \quad (8)$$

where $E_{\text{ms,app}}$ is the apparent activation energy of NPP_{ms} ($E_{\text{ms,app}} = -E_a + E_{\text{N,m}} + E_{\text{N,f}}$). The difference between $E_{\text{A,app}}$ and $E_{\text{ms,app}}$ is an estimate of E_b ; however, temperature coefficients cannot be interpreted in isolation for models with a temperature \times N interaction (i.e., when α_N increases with temperature). In equations (7) and (8), α_N is the DIN-UE, because any contribution of N mineralization and N_2 fixation will be represented in the apparent activation energy terms.

We assessed all parameters for normality and homogeneity of variance. Light was square-root-transformed to meet these assumptions, while other parameters were $\log(x + 0.001)$ -transformed. To test predictions concerning the influence of temperature on biomass, resource UE, and the apparent activation energies of NPP_A and NPP_{ms} , we fit equations (7) and (8) using the function lm in R (R Core Team, 2016). Preliminary analysis indicated no temporal autocorrelation in model residuals, so we did not utilize a more complex autoregressive model. We used AIC_C to determine the most likely model based on the data (Burnham & Anderson, 2002).

4.8 | Ecosystem C and N mass balance model

To determine the potential contribution of autotroph community N-UE, as well as unmeasured N sources (N_2 fixation and N mineralization) and C sinks (organic C exudates), to changes in NPP_A following warming (Figure 1), we used a simple stoichiometric mass balance model of ecosystem N demand (Hall & Tank, 2003):

$$\text{Ecosystem N demand} = (\text{NPP} \times \text{autotroph N:C}) + (\text{HP} \times \text{heterotroph N:C}), \quad (9)$$

where HP is heterotrophic production. Following Hall and Tank (2003), we calculated HP as

$$\text{HP} = \frac{(\text{HGE} \times \text{HR})}{(1 - \text{HGE})}, \quad (10)$$

where HGE is heterotrophic growth efficiency and HR is heterotrophic respiration ($\text{ER} - 0.5 \times \text{GPP}$). As we did not measure heterotroph parameter values, which vary widely across aquatic ecosystems, we used both moderate and low growth efficiency estimates (0.2 and 0.05; del Giorgio, Cole, & Cimleris, 1997), as well as low and high heterotroph C:N estimates (5 and 20; Danger, Gessner, & Bärlocher, 2016) to place conservative bounds on estimates of ecosystem N demand. The difference between ecosystem DIN uptake and N demand is a measure of the balance between DIN supply and demand; a N imbalance (i.e., negative values) would be indicative of an unmeasured N source or C sink.

5 | RESULTS

5.1 | Warming manipulation

The warming manipulation increased average water temperature in the experimental stream by 3.3°C (Figure 2a), while mean water

temperature in the reference stream increased by 0.8°C (Fig. S1a). The mean water temperature anomaly was 2.6°C (Fig. S1b). Stream water inorganic N and P concentrations were not affected by the warming manipulation (Table S3).

5.2 | Organic matter pools

Contrary to our prediction, mean autotroph biomass increased by 35% during the warming manipulation, although the difference in annual averages was only marginally significant (Table 1, Figure 2b). Mean biomass of the green filamentous algae *Ulva* sp. was 645% higher during the warming manipulation due to a large bloom in June and July. While this mean increase was not statistically significant (Figure 2b, Table 1), *Ulva* sp. dominated the autotroph community during the bloom. Coarse particulate organic matter was 46% higher after the warming manipulation, likely due to the increase in the filamentous alga *Ulva*, the only component of this pool to change significantly (Table 1). The warming manipulation did not affect biomass of biofilm, the bryophyte *Jungermannia* sp., or fine particulate organic matter (Table 1).

5.3 | Ecosystem metabolism

Both mean GPP and ER increased by 0.7 g C m⁻² day⁻¹ in the experimental stream during the warming manipulation (Figure 3, Table 1); however, only the increase in GPP was significant. During warming, average GPP nearly tripled in the experimental stream relative to the prewarming year (Figure 3a, Table 1), with peaks in production in March–April and June–July. Only the June–July peak in production was associated with the *Ulva* bloom (Figure 2b). When the *Ulva* bloom months were removed, the increase in GPP remained significant ($p = .04$). Annual GPP was 2× higher during the warming manipulation (Fig. S3). In contrast, average and annual GPP in the reference stream were similar between years (Table 1, Figs S3 and S4). NEP did not differ between years in either the experimental or reference stream (Figure 3b, Table 1, Fig. S4b), since the absolute increases in GPP and ER in the experimental stream were balanced.

5.4 | Nutrient uptake

The warming manipulation did not affect mean DIN or SRP uptake rates (Table 1, Figure 4); however, uptake rates were seasonally variable. DIN and SRP uptake rates were strongly related to common physical, chemical, and biological drivers of nutrient uptake rates (Appendix S1: Table S4, Fig. S5). For example, DIN uptake rates in the experimental stream were best predicted by a multiple regression model containing DIN concentration, GPP, and total organic matter AFDM (Table S4, $R^2 = 0.78$).

5.5 | Statistical models of NPP

The most likely model of areal and mass-specific NPP for the reference stream contained only a term for temperature (Tables S5 and

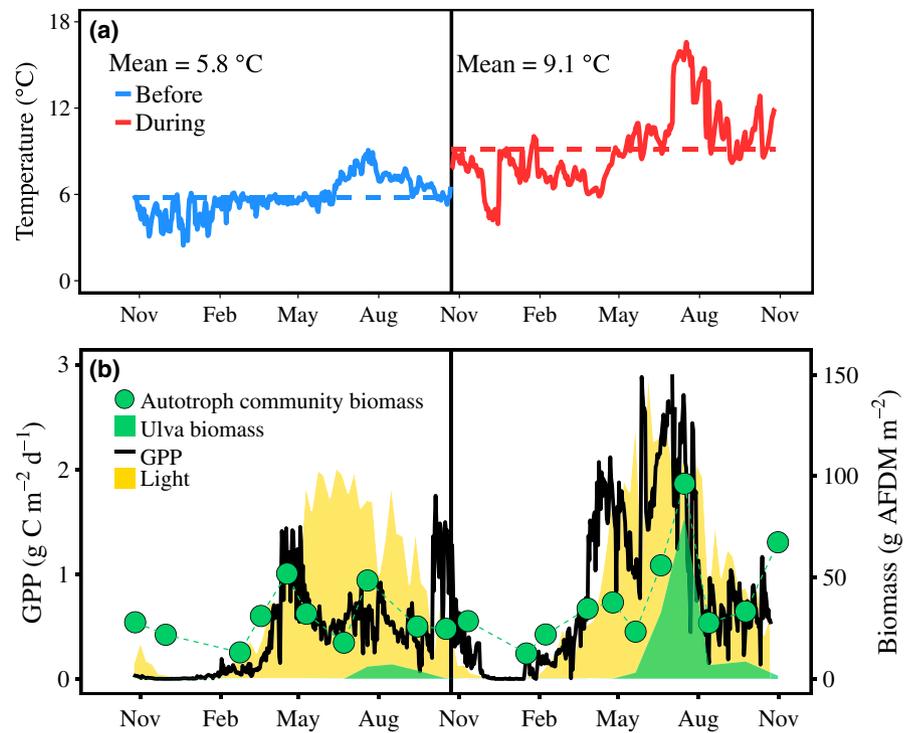


FIGURE 2 Water temperatures were higher during the warming manipulation, but retained the same seasonality (a). Gross primary production was higher during the warming manipulation (b), and there was a shift in the autotroph community toward dominance of *Ulva* during June and July (b). Weekly integrated photosynthetically active radiation (b) is shown on an arbitrary scale as a measure of the growing season. During the warming manipulation, gross primary production peaked in April–May and June–July. The second peak in production was associated with an *Ulva* bloom as shown in the photographs of the experimental stream in July before (c, 2011) and during (d, 2013) the warming manipulation. Photographs of the experimental stream before and after the warming manipulation were adapted from O’Gorman et al. (2014, box 2). Temperature and autotroph biomass time series from the reference stream are shown in Figs S1 and S2, respectively



S6). In the reference stream, the apparent activation energy of NPP_{ms} ($E_{ms,app}$) was 2.2 eV, over three times higher than predicted for primary production ($E_a = 0.32$ eV; Allen et al., 2005), but similar to the activation energy of N_2 fixation ($E_{N,f} = \sim 2.2$ eV; Ceuterick et al., 1978). Not surprisingly, NPP_{ms} in this system was strongly correlated with the total biomass of two N_2 -fixing cyanobacteria species ($R^2 = 0.49$, $p < .001$).

In the experimental stream, mean NPP_A tripled during the warming manipulation (Table 1). The amplification of NPP_A in the experimental stream during warming resulted from increased ecosystem DIN-UE and a greater than expected increase in autotroph biomass

and NPP_{ms} . The best model for both NPP_A and NPP_{ms} contained light and a DIN uptake \times temperature interaction (Tables 2 and 3, Figure 5). NPP_A increased with temperature when DIN uptake rates were low and decreased with temperature when DIN uptake rates were high. As a result, ecosystem DIN-UE ($NPP_A \times N \text{ uptake}^{-1}$) also increased with temperature at low DIN uptake rates and declined with temperature at high DIN uptake rates (Figure 5). Increased DIN-UE at high temperatures could reflect increased autotroph community N-UE, N mineralization ($E_{N,m}$), or N_2 fixation ($E_{N,f}$).

After accounting for variation in resource supply (DIN and light), autotroph biomass and NPP_{ms} increased more than expected in the

TABLE 1 Randomized intervention analysis (p_{RIA}) of changes in monthly mean organic matter pools, ecosystem fluxes, and autotroph biomass stoichiometry between the year before and during the warming manipulation (mean, SD)

	Reference stream		Experimental stream		p_{RIA}
	Before	During	Before	During	
Organic matter pools					
Biofilm (g AFDM m^{-2})	24.5 (9.7)	18.1 (7.9)	27.5 (11.0)	24.5 (12.8)	.353
FPOM (250–1,000- μm , g AFDM m^{-2})	26.8 (10.7)	21.7 (14.8)	23.0 (13.6)	16.5 (12.0)	.992
CPOM (>1,000- μm , g AFDM m^{-2})	18.6 (7.0)	13.7 (8.9)	17.2 (10.0)	25.1 (26.2)	.014*
<i>Ulva</i> sp. (g AFDM m^{-2})	0 (0)	0 (0)	1.6 (2.8)	12.1 (24.4)	.162
<i>Jungermannia</i> sp. (g AFDM m^{-2})	0.0 (0.0)	0.1 (0.1)	1.7 (1.8)	2.6 (2.3)	.352
Autotrophs (g AFDM m^{-2})	25.1 (9.8)	18.7 (8.0)	29.5 (12.4)	40.0 (24.3)	.052 [†]
Ecosystem fluxes					
GPP (g C $m^{-2} day^{-1}$)	0.6 (0.8)	0.6 (0.8)	0.4 (0.4)	1.1 (0.9)	.049*
ER (g C $m^{-2} day^{-1}$)	-1.8 (0.9)	-2.0 (1.6)	-0.9 (0.7)	-1.6 (0.9)	.263
NEP (g C $m^{-2} day^{-1}$)	-1.2 (0.9)	-1.4 (1.4)	-0.5 (0.7)	-0.5 (1.0)	.413
NPP _A (g C $m^{-2} day^{-1}$)	0.3 (0.4)	0.3 (0.4)	0.2 (0.2)	0.6 (0.4)	.007*
NPP _{ms} (g C g AFDM ⁻¹ day^{-1})	0.012 (0.020)	0.015 (0.020)	0.007 (0.006)	0.013 (0.008)	.359
DIN uptake rate (mg N $m^{-2} hr^{-1}$)	2.7 (2.6)	1.9 (1.3)	3.3 (3.1)	3.3 (1.7)	.660
SRP uptake rate (mg P $m^{-2} hr^{-1}$)	9.9 (7.8)	12.0 (5.2)	10.1 (10.1)	7.8 (5.2)	.382
Light use efficiency (g C mol PAR ⁻¹)	0.1 (0.1)	0.1 (0.1)	0.1 (0.2)	0.3 (0.2)	.025*
DIN use efficiency (C:N molar)	7.0 (6.1)	8.4 (11.4)	3.4 (2.8)	13.4 (15.7)	.011*
SRP use efficiency (C:P molar)	4.3 (5.6)	2.6 (3.2)	4.6 (6.0)	18.6 (19.1)	.001**
Autotroph biomass stoichiometry					
C:N (molar)	15.1 (4.9)	10.3 (1.6)	13.5 (3.5)	15.1 (4.3)	.009**
C:P (molar)	119.8 (50.7)	92.7 (29.8)	160.3 (57.3)	146.9 (39.7)	.241
N:P (molar)	0.5 (0.8)	0.4 (0.4)	1.7 (1.7)	1.8 (1.1)	.859

[†] $p < .1$, * $p < .05$, ** $p < .01$, *** $p < .001$. p_{RIA} 's < 0.05 are considered significant and are highlighted in bold text.

experimental stream during warming. While the temperature \times DIN uptake interaction confounds direct interpretation of apparent activation energies, we can infer these from model predictions at low (first quartile) and high (third quartile) DIN uptake rates. Apparent activation energies for areal and mass-specific NPP declined with increasing DIN uptake ($E_{A,app}$: 1st quartile DIN uptake = 4.89 eV, 3rd quartile DIN uptake = 0.99 eV; $E_{ms,app}$: 1st quartile DIN uptake = 4.40 eV, 3rd quartile DIN uptake = 0.32 eV). The apparent activation energy of autotroph biomass ($E_b = E_{A,app} - E_{ms,app}$) was -0.49 – 0.67 eV, greater than the negative value predicted by MTE in the absence of changes in resource supply (Brown et al., 2004). $E_{ms,app}$ was consistent with MTE predictions at high DIN uptake, but was $\sim 13\times$ higher than expected when DIN uptake was low, suggesting a role for increased N supply and UE under these conditions.

5.6 | Ecosystem resource use efficiency

Consistent with the NPP multiple regression models, mean annual ecosystem resource UE increased significantly during the warming manipulation. In the experimental stream, autotroph light-UE (g C GPP mol PAR⁻¹) increased by 93% during the experiment (Table 1). Similarly, autotrophic DIN- and SRP-UE (as measured by ecosystem flux ratios) increased by an average of 289% and 281%, respectively

(Table 1, Figure 6). During experimental warming, values of DIN and SRP UE were high throughout the growing season and peaked in April and June.

5.7 | Autotroph community nutrient use efficiency

Autotroph community N-UE (i.e., C:N) was higher during the warming manipulation, particularly between June and August (Table 1, Figure 6). The increase in autotroph community N-UE corresponds with the dominance of *Ulva*, which had higher C:N ratios than biofilm (*Ulva* C:N = 23.1 ± 7.3 ; biofilm C:N = 12.0 ± 3.0 ; mean ± 1 SD). The warming manipulation did not influence autotroph community C:P or N:P (Table 1, Figure 6).

5.8 | Ecosystem C and N mass balance model

We used the C and N mass balance model to evaluate whether changes in autotroph community N-UE could support the increase in NPP_A observed during the warming manipulation. When the difference between DIN uptake and ecosystem N demand (NPP_A \times autotroph N:C) is negative, mass balance predicts an unmeasured N source (N mineralization or fixation) or C sink (organic C exudates). In the experimental stream, changes in autotroph community N-UE

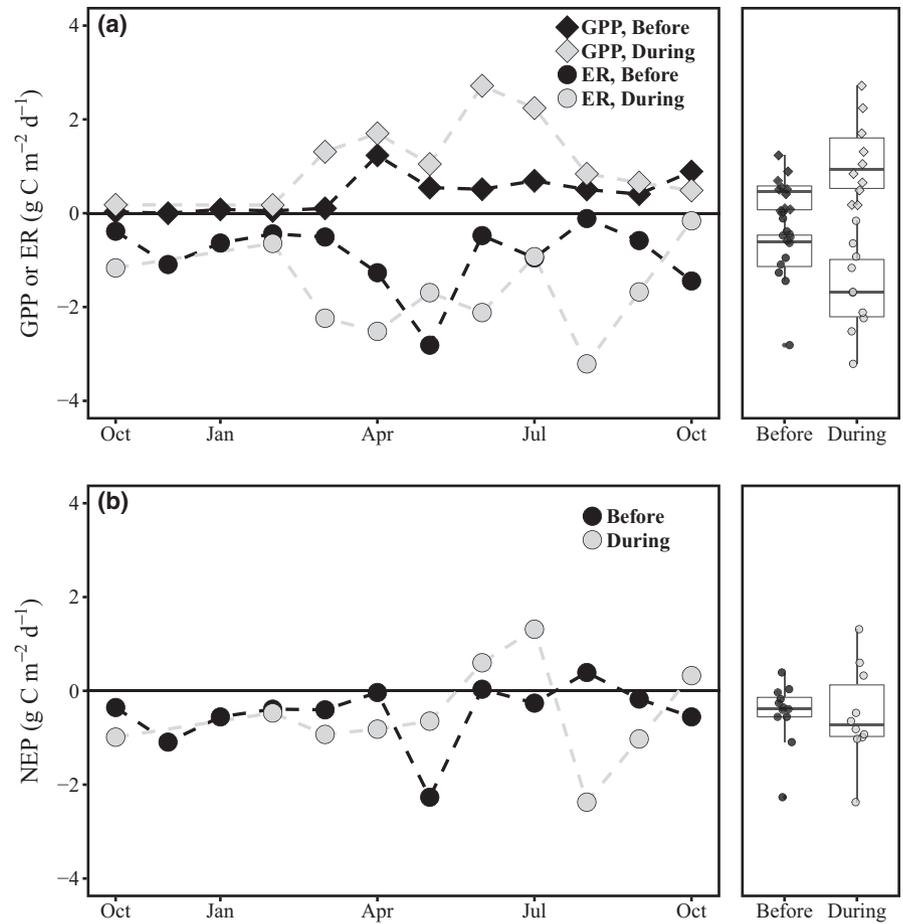


FIGURE 3 Time series and box plots of stream metabolism in the experimental stream before and during the warming manipulation. Warming was associated with a 170% increase in gross primary production on average (a, positive values). Ecosystem respiration increased by a similar magnitude, but was not statistically significant (a, negative values). Net ecosystem production did not differ between years (b). Daily and annual metabolic rates for both streams are shown in Fig. S3. Monthly metabolic rates for the reference stream are shown in Fig. S4

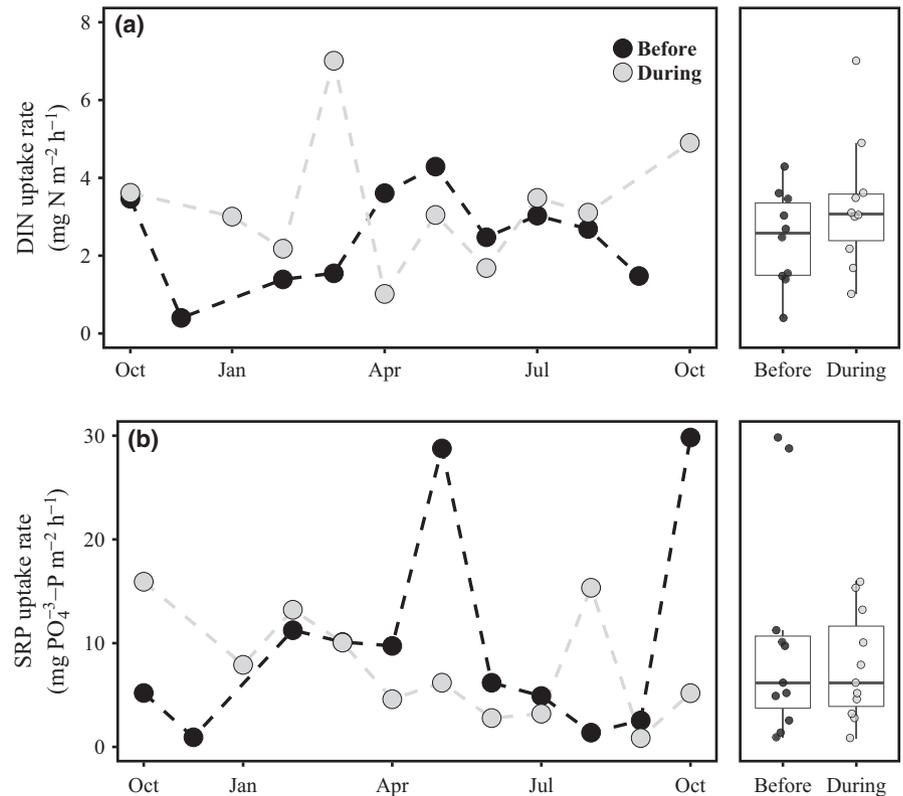


FIGURE 4 Time series and box plots of whole-stream dissolved inorganic N (DIN) and P uptake rates in the experimental stream before and after the warming manipulation. Warming did not alter mean whole-stream DIN ($\text{NH}_4^+ + \text{NO}_3^-$, (a) or SRP (b) uptake rates. Nutrient uptake rates for the reference reach are shown in Fig. S6

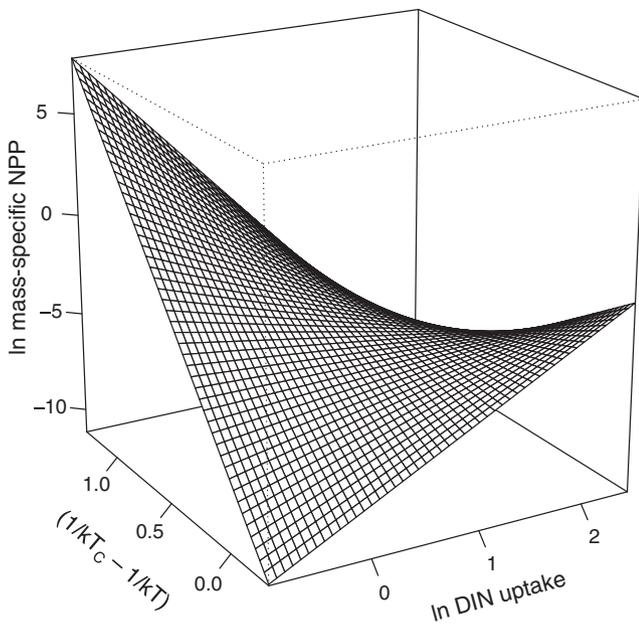


FIGURE 5 Prediction surface of the most likely model (Table 2, Model 4) for mass-specific net primary production in the experimental stream. This model contained terms for light, dissolved inorganic N uptake, and centered inverse temperature ($1/kT_c - 1/kT$)

and DIN uptake were sufficient to support autotrophic and heterotrophic production during all but 2 months (Figure 7). During April and June of the warming manipulation, there was an ecologically significant N deficit that corresponded with peaks in autotrophic production (Figure 7) and periods of low DIN concentrations (N deficit $\sim 105.5 + 43.0 \times \log \mu\text{g DIN L}^{-1}$; $R^2 = 0.27$, p -value = .028; Fig. S8), implying that these were periods of severe N limitation. There were also periods of N deficit in the reference stream that were positively correlated with the biomass of N_2 fixing cyanobacteria (N deficit $\sim -8.6 + -65.6 \times \text{mg AFDM m}^{-2}$; $R^2 = 0.44$, $p < .001$). Thus, peak autotroph production in both streams was associated with high N demand, which was not fully supported by variation in DIN uptake and community N-UE, suggesting a role for N mineralization and fixation within the biofilm.

6 | DISCUSSION

Results of our whole-stream warming manipulation indicate that climate warming could lead to large and difficult-to-predict changes in river metabolism and its coupling to nutrient cycles. During the warming manipulation, ecosystem productivity in the experimental stream tripled. Our results suggest that ecosystem responses to warming were driven by greater than expected increases in biomass and mass-specific NPP supported by increases in resource UE and N availability. Indeed, ecosystem DIN and SRP UE, which reflect both autotroph nutrient UE and internal nutrient cycling within benthic autotroph communities, increased nearly fourfold, indicating that a 3.3°C temperature increase altered the coupling of C, N, and P within this ecosystem. Our results further indicate that responses to warming emerge from interactions between population-, community-, and ecosystem-scale properties that presently cannot be predicted from theory. Climate warming may thus cause unexpected changes in the coupling of C and nutrient transformations within river ecosystems, altering their future roles in transforming, and delivering elements across landscapes.

Increased ecosystem production during the warming manipulation was a function of unexpectedly large increases in both autotroph biomass and mass-specific NPP. During the warming manipulation, the contribution of autotroph biomass to the temperature dependence of ecosystem production increased with DIN uptake rate. From the first to the third quartile of DIN uptake, the apparent activation energy of biomass (E_b) increased from 10% to 68% of the apparent activation energy of NPP_A ($E_{A, \text{app}} = -E_a + E_b + -E_{N,m} + -E_{N,p}$), indicating that when DIN uptake rates were low, NPP_A increased with temperature because mass-specific production increased; whereas, when DIN uptake rates were high, NPP_A increased with temperature because biomass increased.

The large role that mass-specific production played in driving responses in ecosystem production during warming contrasts with terrestrial research indicating that changes in ecosystem biomass across temperature gradients are the primary driver of patterns in net ecosystem production (Michaletz et al., 2014). This contrast may be due to differences in biomass dynamics; stream ecosystems typically contain

TABLE 2 Multiple regression models for areal net primary production (NPP) in the experimental stream as a function of light, dissolved inorganic N (DIN) uptake, and centered inverse temperature ($1/kT_c - 1/kT$)

	Model 1	Model 2	Model 3	Model 4
Intercept	-2.5 (-3.6 to -1.4)***	-5.0 (-6.8 to -3.1)***	-6.1 (7.6 to -4.5)***	-4.6 (-5.9 to -3.4)***
$(1/kT_c - 1/kT)$	2.8 (0.5-5.1)*	1.6 (-0.4 to 3.6)	1.0 (-0.6 to -2.6)	7.4 (4.2-10.5)***
Light ($\times 10^{-4}$)		6.7 (2.2-11.2)**	6.4 (2.9-9.8)**	3.1 (0.3-5.8)*
DIN uptake			1.4 (0.6-2.3)**	1.3 (0.7-1.8)***
DIN $\times (1/kT_c - 1/kT)$				-5.0 (-7.3 to -2.7)***
F-statistic	6.45 _{1,18}	9.81 _{2,17}	15.21 _{3,16}	31.11 _{4,15}
R^2	0.26	0.54	0.74	0.89
AICc	88.9	82.8	74.8	61.3

Model one contains only temperature as a predictor variable; additional predictor variables are added sequentially to models two through four. Model four, the most likely model based on AICc, is the global model, containing all predictor variables and an interaction between temperature and DIN uptake.

* $p < .05$, ** $p < .01$, *** $p < .001$.

TABLE 3 Multiple regression models for mass-specific net primary production (NPP) in the experimental stream as a function of light, dissolved inorganic N (DIN) uptake, and centered inverse temperature ($1/kT_c - 1/kT$)

	Model 1	Model 2	Model 3	Model 4
Intercept	-5.8 (-7.0 to -4.7)***	-8.2 (-1.0 to -6.3)***	-9.3 (-0.1 to -7.6)***	-7.7 (-9.0 to -6.4)***
$(1/kT_c - 1/kT)$	2.1 (-0.3 to 4.4) [†]	0.9 (-1.2 to 3.0)	0.3 (-1.4 to 2.0)	7.0 (3.9–10.2)***
Light ($\times 10^{-4}$)		6.7 (2.0–11.5)**	6.4 (2.6–10.2)**	2.7 (-0.1 to 5.6) [†]
DIN uptake			1.4 (0.5–2.3)**	1.2 (0.6–1.8)***
DIN $\times (1/kT_c - 1/kT)$				-5.2 (-7.5 to 2.9)***
F-statistic	3.52 _{1,17}	7.05 _{2,16}	11.09 _{3,15}	26.81 _{4,14}
R ²	0.17	0.47	0.69	0.89
AICc	84.9	79.74	73.29	58.9

Model one contains only temperature as a predictor variable; additional predictor variables are added sequentially to models two through four. Model four, the most likely model based on AIC_c, is the global model, containing all predictor variables and an interaction between temperature and DIN uptake.

* $p < .05$, ** $p < .01$, *** $p < .001$, [†] $p < .10$.

short-lived species with biomass that is frequently recovering from disturbances, while terrestrial ecosystems have relatively longer-lived species and biomass that is more commonly at steady state.

Multiple top-down and bottom-up mechanisms contributed to increased NPP_{ms} and biomass with warming; however, much of the increase can be linked to increases in resource supply and use efficiency. Changes in herbivory likely made only a trivial contribution to the increase in NPP_A; estimated herbivory declined by approximately 2.7 g C m⁻² year⁻¹ (Nelson, 2016), while net primary production increased by 82.5 g C m⁻² year⁻¹. There was also no change in the availability or uptake of dissolved nutrients during the warming manipulation, although it is likely that unmeasured N sources increased during some months. Resource UE increased greatly during the warming manipulation. In particular, ecosystem DIN-UE in the N-limited

experimental stream increased by 289% on average. These patterns suggest that the amplified response of ecosystem production to warming was associated with an increase in resource UE at the ecosystem level—higher rates of C-fixation per unit resource (i.e., light and dissolved inorganic nitrogen)—influenced, at least in part, by shifts in autotroph community structure and stoichiometry.

What mechanisms were responsible for the greater than expected increase in ecosystem DIN-UE? This metric reflects autotroph N-UE when the majority of DIN uptake is utilized by autotrophs and other N sources are trivial. We can use the ecosystem C and N mass balance model to evaluate when these assumptions might be violated and determine the processes that contributed to the amplified response of NPP_A to warming. The ecosystem C and N mass balance model indicates that changes in autotroph community N-UE were sufficient to

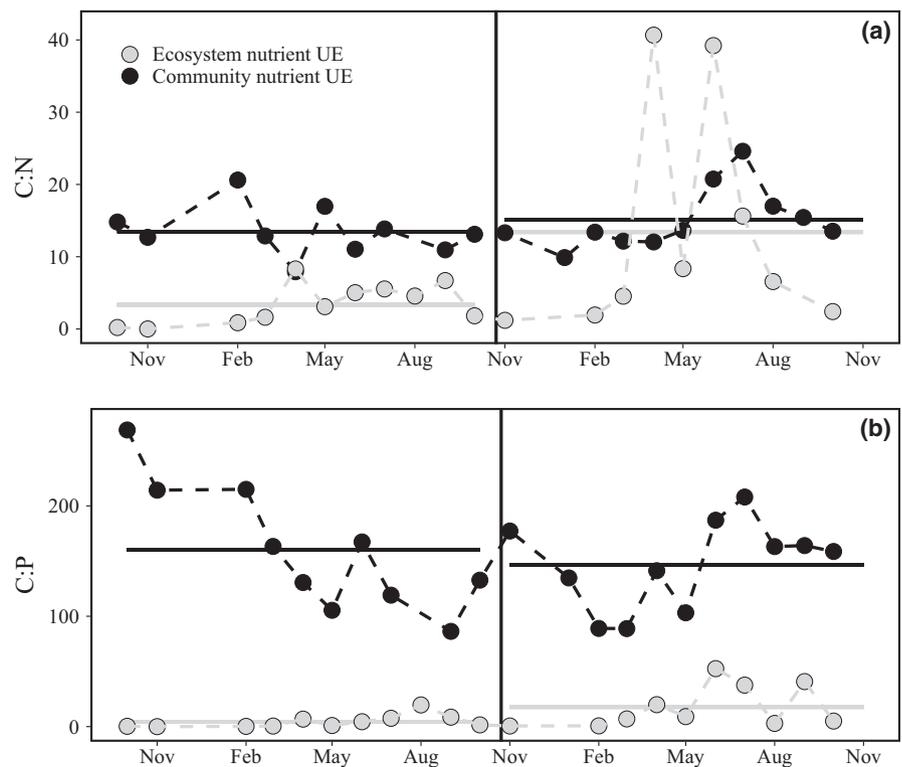


FIGURE 6 Ecosystem (NPP DIN uptake⁻¹) and autotroph community (biomass C:nutrient stoichiometry) measures of nitrogen (a) and phosphorus (b) use efficiency in the experimental stream. Note: the x-axis represents the time from October 2010 to October 2012. The vertical bar indicates the beginning of the warming manipulation, and the horizontal bars are the mean response before or during the warming manipulation. Ecosystem and community measures of N- and P-use efficiency in the reference stream are shown in Fig. S7

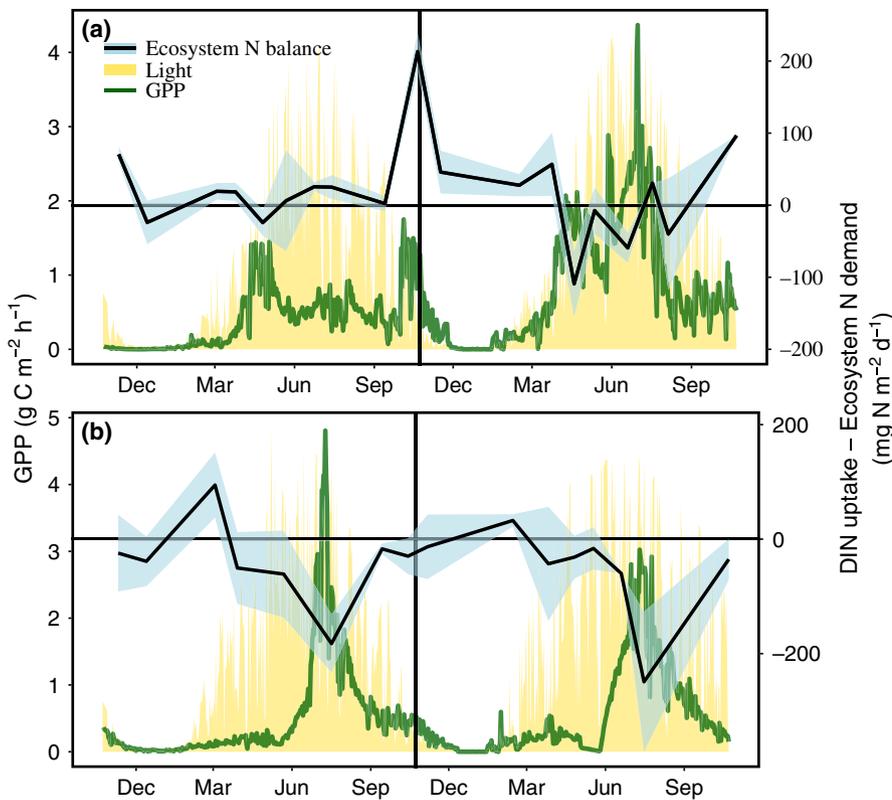


FIGURE 7 The ecosystem C and N mass balance model predicts an imbalance between ecosystem N demand and dissolved inorganic N (DIN) uptake (blue ribbon, $\text{mg N m}^{-2} \text{day}^{-1}$) during some months in the experimental (a) and reference (b) streams. Negative values indicate that estimated ecosystem N demand is greater than measured DIN uptake. The blue ribbons encompass estimates using medium and high heterotrophic growth efficiencies and low and high values of heterotroph C:N (see text). Gross primary production (GPP) (green line) and light (yellow ribbon) are displayed for context. Light has been scaled to match GPP. The vertical bar indicates the beginning of the warming manipulation

support elevated NPP_A during all but 2 months of the warming manipulation. During April and June, there was an ecologically significant N imbalance ($\text{DIN uptake} - \text{ecosystem N demand} < 0$), implying that one or more N sources were missing from our mass balance model. Increased N mineralization and N_2 fixation likely filled this N deficit, although the relative contribution of these N sources would vary seasonally. N_2 fixers are commonly late colonists during stream seasonal succession (Grimm & Petrone, 1997; Power, Holomuzki, & Lowe, 2013) and diatoms with N_2 -fixing symbionts were observed in the experimental stream in July but not in April of the warming manipulation (I. Hansen & P. Furey, personal communication). Nitrogen mineralization within the biofilm community, which would not be captured in whole-stream uptake measurements, was likely an important N source throughout the growing season. Imbalances between DIN uptake and ecosystem N demand could also be interpreted as autotroph or heterotroph C losses (e.g., dissolved organic C exudates), which were not adequately characterized by the model. While C losses may have contributed to model imbalances, the correlation between N deficit and DIN availability indicates that these were periods of N limitation. During these periods, nitrogen mineralization and N_2 fixation likely contributed to increased ecosystem production. For example, the N deficit in the reference stream was positively correlated with the biomass of N_2 -fixing cyanobacteria and presumably higher N supply via fixation. Taken together, our results indicate that the increase in ecosystem production during the warming manipulation was a function of increased biomass and mass-specific production, supported by combined increases in resource availability (N mineralization and N_2 fixation) and UE, the latter associated with changes in community structure.

Responses to warming in many ecosystems may involve increased community and ecosystem nutrient UE. A meta-analysis by Woods et al. (2003) indicated that a common measure of organismal N and P UE (C:N and C:P, respectively) increased with temperature in algae, plant, and invertebrate populations. Further, increases in community-level P UE have been observed in lake microcosm experiments (De Senerpont Domis et al., 2014) and in latitudinal analyses (Yvon-Durocher, Dossena, Trimmer, Woodward, & Allen, 2015). In terrestrial ecosystems, there are also examples of increased N-UE with warming due to community shifts and increases in N cycling (An et al., 2005). We are not aware of an example of increased ecosystem nutrient UE with warming in aquatic ecosystems. Yet, this type of response may be common because many biogeochemical N transformations have much higher temperature dependences than primary production, suggesting that more nutrients could become available at higher temperatures (Bouletreau, Salvo, Lyautey, Mastroiello, & Garabetian, 2012; Ceuterick et al., 1978; Sinsabaugh & Follstad Shah, 2012; Vanni & McIntyre, 2016). These results suggest that predicting responses of net production to warming will require a better understanding of how temperature influences community structure and nutrient cycling.

The *Ulva* bloom during July and August of the warming manipulation was initially surprising. *Ulva* was present at low biomass in the experimental stream prior to the warming manipulation, but does not dominate autotroph communities in nearby geothermal streams with temperature regimes similar to the experimental stream during warming (Gudmundsdottir et al., 2011). Yet, the bloom community had traits that may be characteristic of responses to warming in N-limited ecosystems. *Ulva* has a high potential growth rate (Rosenberg

& Ramus, 1982; Xiao et al., 2016) and also has high population and “ecosystem” N-UE. First, the C:N of the *Ulva* community was nearly double that of the biofilm community, indicating higher N-UE at the population level. Second, as a filamentous alga, *Ulva* increases hydrologic retention, allowing for both high retention of dissolved nutrients and greater nutrient cycling within the algal mat. Third, diatoms with N₂-fixing symbionts were observed within the bloom, suggesting that newly fixed N may also be made available to these communities (Power et al., 2008). Communities with similar functional traits—filamentous algae with high C:N and N₂-fixing diatoms—are observed in nearby geothermal streams (Gudmundsdottir et al., 2011). This comparison suggests that, although it may be difficult to predict exactly which taxa will respond to higher temperatures, warming may predictably lead to autotroph communities that exhibit higher resource use efficiency and nutrient cycling.

Metabolic theory and ecological stoichiometry provide useful frameworks for understanding how ecosystem fluxes vary with temperature (Cross et al., 2015; Padfield et al., 2017; Yvon-Durocher et al., 2012), potentially offering a powerful tool for predicting responses to climate warming. Yet, our study illustrates how difficult it can be to predict metabolic responses to warming at the ecosystem level. We observed a large increase in ecosystem production driven by an increase in biomass and NPP_{ms} that resulted from changes in resource UE and N cycling. Similar patterns have been observed in terrestrial ecosystem warming experiments, in which the direct effects of warming on net production appear less important than indirect effects on resource availability and UE (Elmendorf et al., 2012; Wu, Dijkstra, Koch, & Hungate, 2012). While the model we developed from previous studies explained much of the variation in metabolic responses to warming ($R^2 = 0.89$), it cannot be used to make predictions a priori because model coefficients related to the influence of temperature on biomass and resource use efficiencies must, at present, be empirically determined (Cross et al., 2015). Developing a generalizable framework for understanding how ecosystem metabolism responds to warming will require a better understanding of how temperature influences unknown parameter values (i.e., autotroph biomass, resource use efficiency and nutrient cycling), the coupling of metabolism and resources, and adaptation to warmer environments (Padfield et al., 2015, 2017).

Our results are also consistent with recent studies of terrestrial ecosystems demonstrating that short-term responses to warming may differ from those in the long term (Elmendorf et al., 2012; Wu et al., 2012). For instance, the responses to 1 year of experimental warming we document here diverge from patterns observed in a survey of nearby geothermally warmed streams that presumably have had stable temperature regimes for decades. The increase in areal and mass-specific GPP in the experimental stream was higher than expected based on temperature dependencies measured along a temperature gradient in these geothermal streams, where nutrient uptake also increased with temperature (Demars et al., 2011; Hannesdóttir, Gíslason, Ólafsson, Ólafsson, & O’Gorman, 2013; Padfield et al., 2017). These comparisons and previous work in terrestrial ecosystems (Elmendorf et al., 2012; Wu et al., 2012) highlight the

importance of understanding decadal-scale responses to climate warming, and the associated need for controlled, ecosystem-scale warming experiments that are conducted over the long term.

Our whole-stream warming experiment indicates that a reasonable warming scenario can—at least initially—lead to a substantial increase in autotrophic production and a change in its coupling with dissolved inorganic nutrient supply. These responses have implications at both stream reach and regional scales. At the reach scale, our results suggest that warming leads to autotroph communities that use dissolved nutrients more efficiently, a scenario that could have implications for herbivore growth and the flux of nutrients through food webs. At the regional scale, headwater streams will continue to play an important role in nutrient cycling, but will likely export higher quantities of lower-quality organic matter downstream, potentially leading to higher rates of ER and hypoxia, as well as increased organic matter storage in recipient ecosystems. Thus, warming will likely change the way rivers couple and transform carbon and nutrients. These changes could alter the role of rivers in global biogeochemical cycles (Peterson et al., 2001; Raymond et al., 2013) in ways that are difficult to predict using single-species physiological predictions and existing theoretical frameworks.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

JPB, WFC, ADH, and PWJ conceived and designed the experiment; JMH, JPB, WFC, and ADH conceived and designed the measurements; JMH, JPB, WFC, GMG, ADH, JRJ, DN, and JSO conducted the experiment; JMH, DN, and CT analyzed the samples; JMH analyzed the data; JMH wrote the first draft; JMH, JPB, WFC, GMG, ADH, JRJ, DN, JSO, and CT commented on the manuscript.

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SUPPORTING INFORMATION

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