Response of lake metabolism to catchment inputs inferred using high-frequency lake and stream data from across the northern hemisphere

Jessica R. Corman [1]*, Jacob A. Zwart [2]*, Jennifer Klug [3]*, Denise A. Bruesewitz [4]*, Elvira de Eyto [5],
Marcus Klaus [6], Lesley B. Knoll [7], James A. Rusak [8,9], Michael J. Vanni [7], María Belén Alfonso [10],
Rocio Luz Fernandez [11], Huaxia Yao [12], Kari Austnes [13], Raoul-Marie Couture [14],
Heleen A. de Wit [13], Jan Karlsson [15], Alo Laas [16]

[1]School of Natural Resources, University of Nebraska–Lincoln, Lincoln, Nebraska, USA
[2]Integrated Information Dissemination Division, U.S. Geological Survey, San Francisco, California, USA
[3]Biology Department, Fairfield University, Fairfield, Connecticut, USA
[4]Environmental Studies Department, Colby College, Waterville, Maine, USA
[5]Fisheries Ecosystems Advisory Service, Marine Institute, Newport, Co. Mayo, Ireland
[6]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden
[7]Department of Biology, Miami University, Oxford, Ohio, USA
[8]Dorset Environmental Science Centre, Ontario Ministry of the Environment, Conservation and Parks, Dorset, Ontario, Canada
[9]Biology Department, Queen's University, Kingston, Ontario, Canada
[10]Research Institute for Applied Mechanics, Kyushu University, Kasuga, Fukuoka Prefecture, Japan
[11]National Scientific and Technical Research Council (CONICET), Santa Fe, Argentina
[12]Inland Waters Unit, Ontario Ministry of the Environment, Conservation and Parks, Dorset, Ontario, Canada
[13]Section for Catchment Biogeochemistry, Norwegian Institute for Water Research, Oslo, Norway
[14]Department of Chemistry, Centre d'Études Nordiques, Université Laval, Quebec, Quebec, Canada
[15]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
[16]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia

Abstract

In lakes, the rates of gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP) are often controlled by resource availability. Herein, we explore how catchment vs. within lake predictors of metabolism compare using data from 16 lakes spanning 39°N to 64°N, a range of inflowing streams, and trophic status. For each lake, we combined stream loads of dissolved organic carbon (DOC), total nitrogen (TN), and total phosphorus (TP) with lake DOC, TN, and TP concentrations and high frequency *in situ* monitoring of dissolved oxygen. We found that stream load stoichiometry indicated lake stoichiometry for C : N and C : P ($r^2 = 0.74$ and $r^2 = 0.84$, respectively), but not for N : P ($r^2 = 0.04$). As we found a strong positive correlation between TN and TP, we only used TP in our statistical models. For the catchment model, GPP and R were best predicted by DOC load, TP load, and load N : P ($R^2 = 0.85$ and $R^2 = 0.82$, respectively). For the lake model, GPP and R were best predicted by TP concentrations ($R^2 = 0.86$ and $R^2 = 0.67$, respectively). The inclusion of N : P in the catchment model, but not the lake model, suggests that both N and P regulate metabolism

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*Correspondence: jcorman3@unl.edu; jzwart@usgs.gov; JKlug@Fairfield.edu; dabruese@colby.edu

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and that organisms may be responding more strongly to catchment inputs than lake resources. Our models predicted NEP poorly, though it is unclear why. Overall, our work stresses the importance of characterizing lake catchment loads to predict metabolic rates, a result that may be particularly important in catchments experiencing changing hydrologic regimes related to global environmental change.

Gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP = GPP − R) are key variables in lake ecosystems. These processes, known collectively as "lake metabolism," are closely related to trophic state (Cole et al. 2000; Staehr and Sand-Jensen 2007; Richardson et al. 2016) and influence food web structure, energy transfer, carbon (C) cycling, and greenhouse gas emissions (Cole et al. 2007; Hanson et al. 2014; Degerman et al. 2018). While scientists have long been interested in assessing metabolism in aquatic ecosystems (e.g., Odum 1957), it is only in the last few decades that advances and expansion of in situ high-frequency sensing technology have made the measurements tractable (e.g., Hanson et al. 2008; Solomon et al. 2013). The expansion of monitoring networks (such as the Global Lake Ecological Observatory Network [GLEON]) allows us to robustly observe and predict lake metabolic regimes.

Lake metabolic rates are often attributed to in lake parameters. For instance, GPP tends to relate positively to lake nutrient concentrations while R tends to relate positively to dissolved organic C (DOC) concentrations (Hanson et al. 2003; Sand-Jensen et al. 2007). Yet, lake nutrient and DOC concentrations often depend on catchment features (Jones et al. 2004; Solomon et al. 2015; Rodríguez et al. 2016). Therefore, catchment inputs should be important to modeling lake metabolic rates (Williamson et al. 2008; Oleksy et al. 2021).

Although the impacts of nutrient inputs on lake metabolism have long been recognized, studies have increasingly shown the importance of organic matter (OM, a source of carbon) inputs on metabolism, as well. For example, a study in 25 Danish lakes found heterotrophic conditions (R > GPP) mainly in forested areas with high OM inputs (Staehr et al. 2012). However, despite recent system-specific insights into the effects of external loads on lake metabolism (e.g., Sadro and Melack 2012; Rodríguez et al. 2016; Williamson et al. 2020), we still lack a general understanding of how the effect of catchment conditions vary within and across different lake types around the globe (Hanson et al. 2014; Solomon et al. 2015). Understanding these controls is crucial to predict how lake metabolism responds to future land use and climate changes.

Catchment export of nutrients and OM to lakes varies as a function of climate, hydrologic characteristics, and land cover (Raymond et al. 2016; Doyle et al. 2019), and this export to lakes can, in turn, be expected to result in substantial variation in lake metabolism (Sadro and Melack 2012; Alfonso et al. 2018; Williamson et al. 2020). While OM inputs generally fuel respiration (Cole et al. 2000; Hanson et al. 2003; Staehr et al. 2010), effects on GPP are more complex. Catchment loads of OM may lead to both increased OM-associated

nutrient inputs (e.g., Corman et al. 2018) and shading effects. GPP will therefore only increase if GPP-depressing shading effects from OM do not outweigh GPP stimulating effects from nutrient inputs (Hanson et al. 2003; Kelly et al. 2018).

The extent to which catchment inputs influence lake metabolism is likely dependent on several factors. First, stream load effects on lake metabolism are modified by lake morphometry. Larger stream loads relative to lake volumes are associated with higher metabolic responses to inflows (Shostell and Bukaveckas 2004; Russell et al. 2006), and a stronger decoupling of GPP and R (Richardson et al. 2016; Brighenti et al. 2018). This externally driven metabolic response to inflow tends to result in heterotrophic lakes (Sadro and Melack 2012; Vachon and Del Giorgio 2014). Second, as discussed above, the impacts of stream inputs on lake metabolism will depend on the relative impact of OM on respiration versus GPP-depressing shading. Finally, the effects depend on the degree to which stoichiometric ratios of nutrients in incoming stream water match with those in lake water, given the large importance of nutrient stoichiometry for nutrient limitation of primary producers and lake productivity (Bergström et al. 2008; Vanni et al. 2011).

In this study, we disentangle the influences of C, nitrogen (N), and phosphorus (P) catchment loads via stream inputs versus in situ C, N, and P concentrations on lake metabolism (Fig. 1). We combine lake in situ high temporal frequency
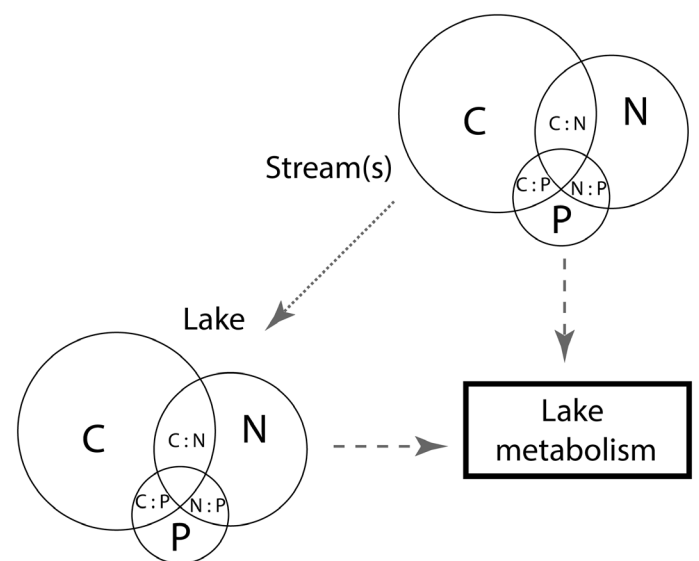

Fig. 1. The total and relative amounts of carbon (C), nitrogen (N), and phosphorus (P) in lakes and stream(s) are predicted to be related (dotted line) and these elements are predicted to impact lake metabolism (dashed lines).

data on dissolved oxygen (DO), meteorology, and water temperature with sampling of C, N, and P concentrations in lakes and stream inputs across 16 lakes spanning a wide range of stream loads, catchment conditions, and productivity. Our study objectives are to (1) explore the relationship between stream load and lake constituent concentration and stoichiometry across lakes, (2) identify how lake C, N, and P concentration and stoichiometry affect metabolism, and (3) identify how stream load C, N, and P concentration and stoichiometry affect metabolism. By separately considering the effects of in situ concentrations and loads of C, N, and P on lake metabolism, our study builds on a rich tradition of lake metabolism models (e.g., Hanson et al. 2003), but provides an explicit opportunity to explore different potential catchment inputs.

Methods

Dataset description

We solicited data about lakes and inflowing streams from members of GLEON. For each lake, we requested high-frequency (1–60 min) near-surface DO concentration, incident photosynthetically active radiation (PAR), wind speed, and water temperature measured at multiple depths including the depth of the DO sensor. For each inflowing stream, we requested daily estimates of discharge. For lakes and inflowing streams, we requested at least monthly, surface concentrations of C (as DOC), N (as total nitrogen, TN), and P (as total phosphorus, TP). While having the discharge and C, N, and P concentrations from all stream inputs was not a requirement for our data collection, we did require that inflow stream data represent a majority of stream inputs to the lake. The time series for each lake and inflowing stream ranged from a minimum of 90 d up to one year, centering around the ice-free season.

The lakes in our dataset varied widely in lake and catchment characteristics including lake area (8×10^3 to 2.7×10^8 m^2), mean depth (2.4–15.9 m), catchment area to lake area ratio (1.2–574), number of stream inflows (0–6 streams), lake water residence time (0.1–5.3 years), and catchment land cover (100% forest to 81% agriculture; Table 1). These catchment-lake systems were located in Northern Europe and North America with latitude ranging from 39.57°N to 64.25°N, and all but one lake fully stratified during summer.

Because these sampling efforts were not coordinated, researchers at each study lake had their own protocols for data collection, sample processing, types of sensors used, and quality assurance/quality control protocols. Depending on the study lake, high-frequency lake sampling ranged from sub-hourly to hourly, and lake and stream chemical constituents sampling ranged from sub-daily to monthly. When PAR was not available, it was estimated from shortwave radiation. Lake DOC concentration was not available for Lake Lillinonah and lake and stream DOC concentrations were estimated from measurements of total organic carbon (TOC) for Lake Langtjern (DOC

Table 1. Lake and catchment characteristics for the 16 lakes and reservoirs in our study.

Lake name	Year data collected	Latitude (decimal degrees)	Longitude (decimal degrees)	Country	# of inflows with data	Mean depth (m)	Lake area (km2)	Catchment/ surface ratio	Residence time (year)	Plot ID
Acton	2010	39.6	−84.8	United States	4	3.90	2.50	103.0	0.80	1
Crampton	2013	46.2	−89.5	United States	0	5.03	0.26	1.2	3.50	14
East Long	2013	46.2	−89.5	United States	1	4.04	0.03	2.6	1.23	8
Feeagh	2013	54	−9.6	Ireland	2	14.50	3.92	20.1	0.47	13
Harp	2013	45.4	−79.1	Canada	6	13.30	0.71	6.6	2.70	15
Langtjern	2013	60.4	9.7	Norway	2	2.00	0.23	20.9	0.15	12
Lillinonah	2014	41.5	−73.4	United States	2	13.00	6.26	574.0	0.10	3
Lillsjölidtjärnen	2012	63.9	18.6	Sweden	1	3.80	0.01	31.3	0.80	11
Mångstrettjärn	2013	64.3	18.8	Sweden	1	5.30	0.02	7.8	1.00	6
Mendota	2016	43.1	−89.4	United States	2	12.80	39.60	14.2	4.50	2
Morris	2013	46.3	−89.5	United States	3	2.42	0.06	19.1	0.10	4
Nästjärn	2013	64.2	18.8	Sweden	0	4.20	0.01	3.3	1.50	10
Övre Björntjärn	2012	64.1	18.8	Sweden	1	4.00	0.05	58.6	0.10	9
Struptjärn	2012	64	19.5	Sweden	1	3.80	0.03	25.4	1.70	7
Trout	2013	46	−89.7	United States	4	14.60	15.70	7.8	5.30	16
Võrtsjärv	2013	58.3	26	Estonia	5	2.80	270.00	12.5	1.00	5

was 95% of TOC for Lake Langtjern, $r^2 = 0.94$; de Wit et al. 2018) and from color for Lough Feeagh ($r^2 = 0.84$; Ryder 2015). All high- and low-frequency data were checked for outliers (i.e., implausible values) and removed if detected. Occasionally, some sites required gap-filling of missing data necessary for lake metabolism estimation, but only up to a maximum of 1-h gap fill using linear interpolation. More details on each study lake's sampling procedures along with raw data (e.g., high-frequency sensor data), derived data products (e.g., estimates of GPP, nutrient loads), and associated metadata can be found in the Data availability statement.

Load estimation

In most cases, stream TP, TN, and DOC concentrations were sampled at lower resolution than stream discharge. In these cases, we linearly interpolated stream TP, TN, and DOC concentration to the same time resolution as stream discharge. For example, if TP, TN, and DOC were sampled weekly but stream discharge was sampled daily, we linearly interpolated the weekly concentration values to obtain daily values. We chose linear interpolation because the correlations between stream discharge and stream constituent concentration were generally too low (e.g., Godsey et al. 2009) for appropriate use of the flow-proportionate interpolation method. Daily TP, TN, and DOC loads were calculated by multiplying stream concentration by stream discharge and summing across all inflowing streams for a given lake; we report loads in units of μg N or P (m^3 lake water)$^{-1}$ d^{-1} for TN or TP loads and mg C (m^3 lake water)$^{-1}$ d^{-1} for DOC loads.

Lake metabolism estimation

To estimate rates of GPP, R, and NEP, we fitted the maximum likelihood metabolism model, *metab.mle*, from the R package *LakeMetabolizer* (Winslow et al. 2016) to high-frequency DO data. This function estimates daily parameters for R and GPP that maximizes the likelihood of the model given the data for each day and uses high-frequency inputs of PAR and water temperature as model covariates for GPP and R, respectively. We accounted for oxygen exchange between the surface water and atmosphere using Fick's law of diffusion and the relationship between gas exchange velocity (k) and wind speed and lake area as described in Vachon and Prairie (2013). We slightly modified the *LakeMetabolizer* code to allow for estimates of uncertainty for each metabolism day using the maximum likelihood estimation. To estimate uncertainty in daily metabolism estimates, we used a bootstrapping routine as described by Solomon et al. (2013) and Zwart et al. (2017) where we created 1000 timeseries of pseudo-DO data for each metabolism day and refit the metabolism model to these data, generating a distribution of GPP, R, and NEP for each day. We report estimates of metabolism in mg O_2 (L lake water)$^{-1}$ d^{-1}.

We used our estimates of metabolism uncertainty to guide our decision to retain well-fitting or discard poorly fitting metabolism days. We calculated a coefficient of variation (CV; where CV = standard deviation/mean) for each metabolism day and retained days which had a CV of < 4 as this CV cutoff balanced the number of days retained for each lake and the interpretation of long-term metabolism for each lake. The handling of poorly fitting metabolism days remains an active area of research, and we are not aware of any consensus on a standardized approach across lake metabolism studies (*see* Winslow et al. 2016 for more discussion).

We observed an early morning rapid increase in DO in over half of the days in the Lake Mendota time series, which was a similar phenomenon to that reported by Richardson et al. (2016) in a different lake. On days when this
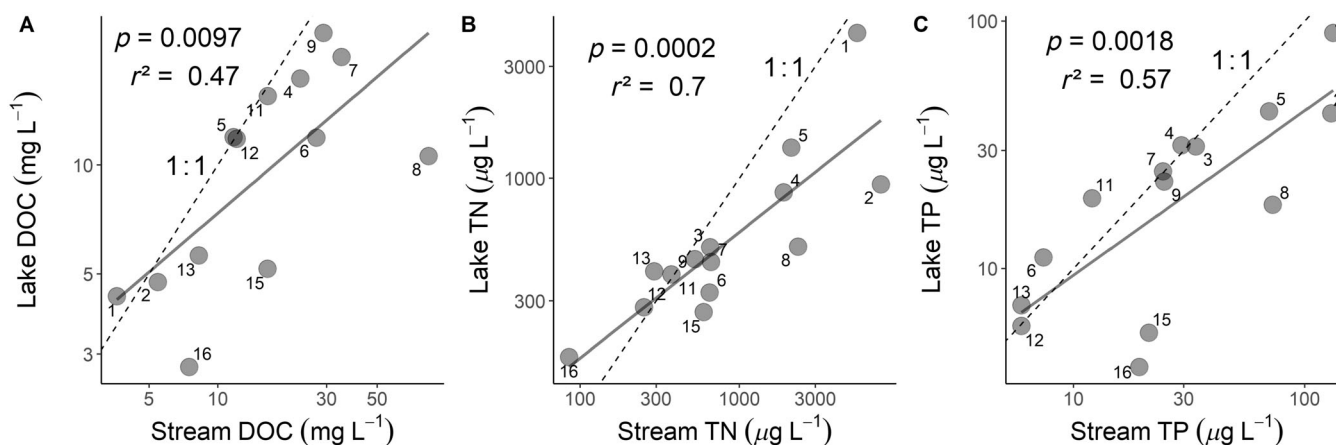

Fig. 2. Average lake vs. stream concentrations of (**A**) DOC, (**B**) TN, and (**C**) TP. The 1 : 1 relationship is plotted as a dashed line (for reference) and the linear model best fit as a solid line indicating with *p*-values and r^2 included in each panel. The slope and intercept for the best fit lines for each panel (in parenthesis) are (**A**) 0.54 and 0.33, (**B**) 0.54 and 1.16, and (**C**) 0.66 and 0.31. Point labels indicate rank order of mean annual lake GPP where 1 is the highest mean annual GPP (Table 1). Note that all variables are plotted on a log-scale.
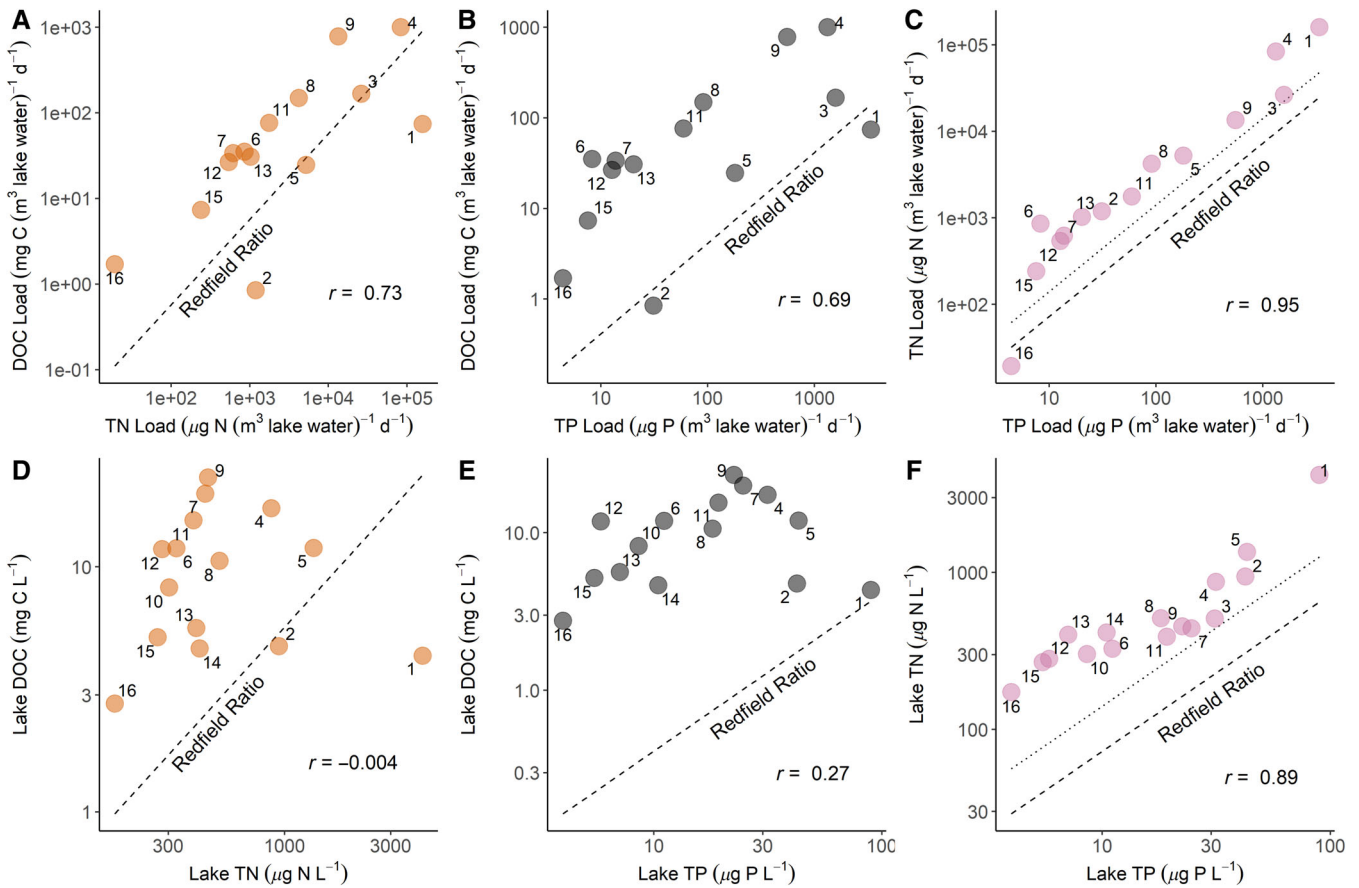
Fig. 3. Annual average DOC, TN, and TP loads (**A–C**) to each lake given in units of elemental flux per lake water volume per day and annual average lake DOC, TN, and TP concentrations (**D–F**) plotted against common nutrient stoichiometric ratios (C : N, C : P, and N : P). Pearson correlation between each plotted variable is included in each panel, and the Redfield ratio for each elemental ratio is shown as the short dashed black line in each panel. For (**C**) and (**F**), a short, dotted black line indicates N : P = 31 : 1. Point labels indicate rank order of mean annual lake GPP where 1 is the highest mean annual GPP (Table 1). Note that all variables are plotted on a log-scale.
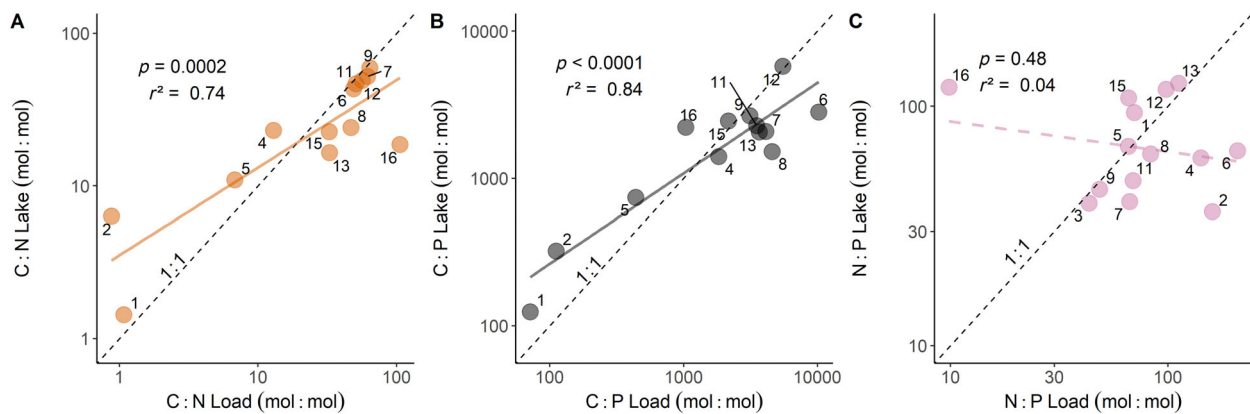
Fig. 4. Average loads vs. lake stoichiometry for C : P, C : N, and N : P. Solid lines show significant linear regressions, the dashed line for N : P is not significant, and black dashed lines show the 1 : 1 relationship for reference. *p*-values and r^2 are included in each panel. The slope and intercept for the best fit lines are 0.57 and 1.25 for (**A**), 0.61 and 2.74 for (**B**), and −0.13 and 4.75 for (**C**), respectively. Point labels indicate rank order of mean annual lake GPP where 1 is the highest mean annual GPP. Note that all variables are plotted on a log-scale.
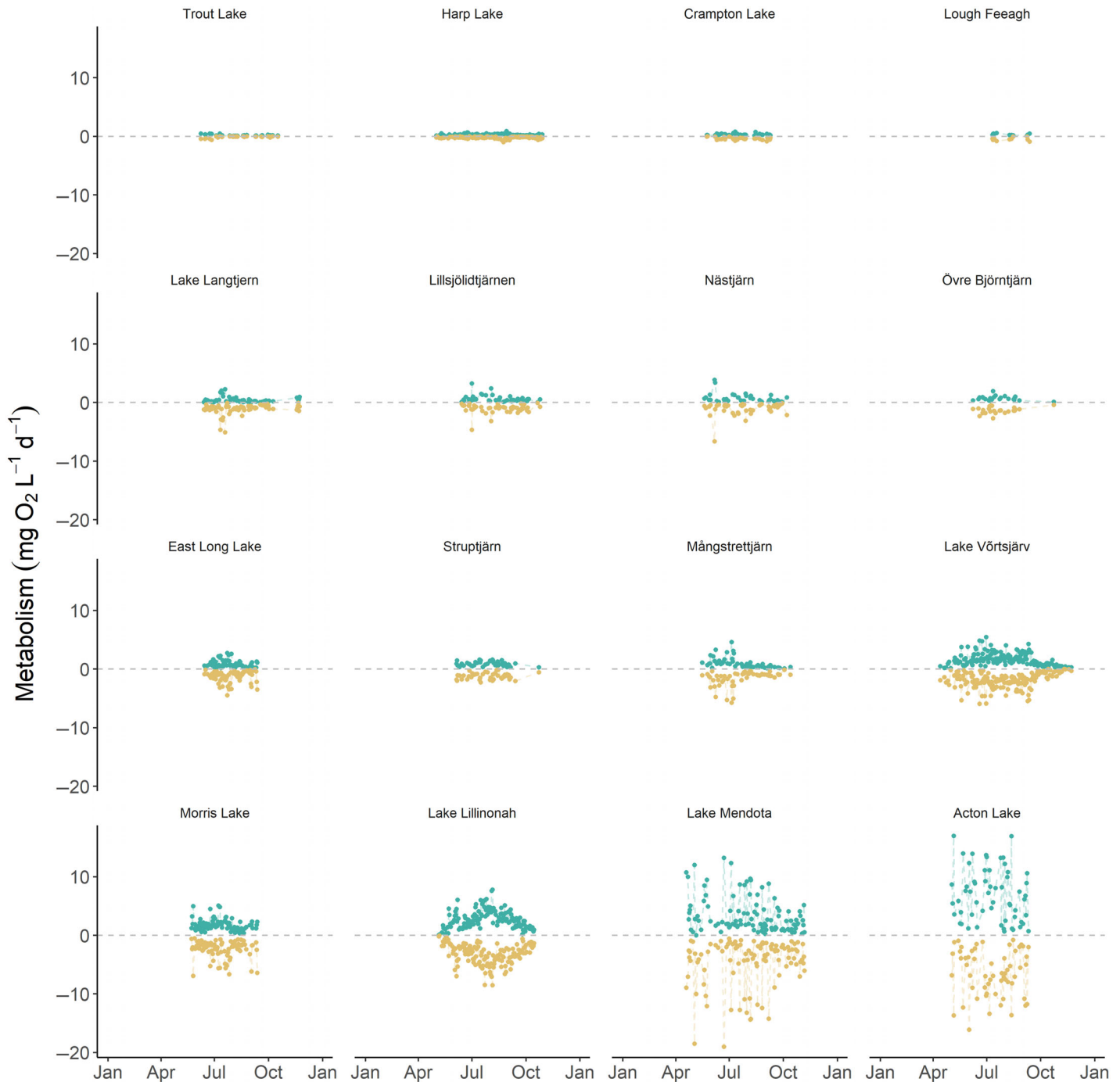
Fig. 5. Daily lake metabolism estimates for each lake in the dataset where GPP estimates are positive and R estimates are negative. Each point is a well-fitting metabolism estimate while poorly fitting days (above coefficient of variation cutoff of 4; *see* "Methods" section for more details) are excluded from the plot. The lines are to help show subannual patterns in metabolism and daily variation. Plot panels are ordered from lowest to highest mean annual lake gross primary production.

occurred, it was difficult to fit metabolism models to the DO time series. Thus, we followed methods from Richardson et al. (2016) and removed the portion of the DO time series when this was occurring (6 h immediately after

sunrise) and fit the metabolism model to the remaining DO data. This resulted in 22 more metabolism days that were below our CV cutoff for acceptable metabolism fits in Lake Mendota.
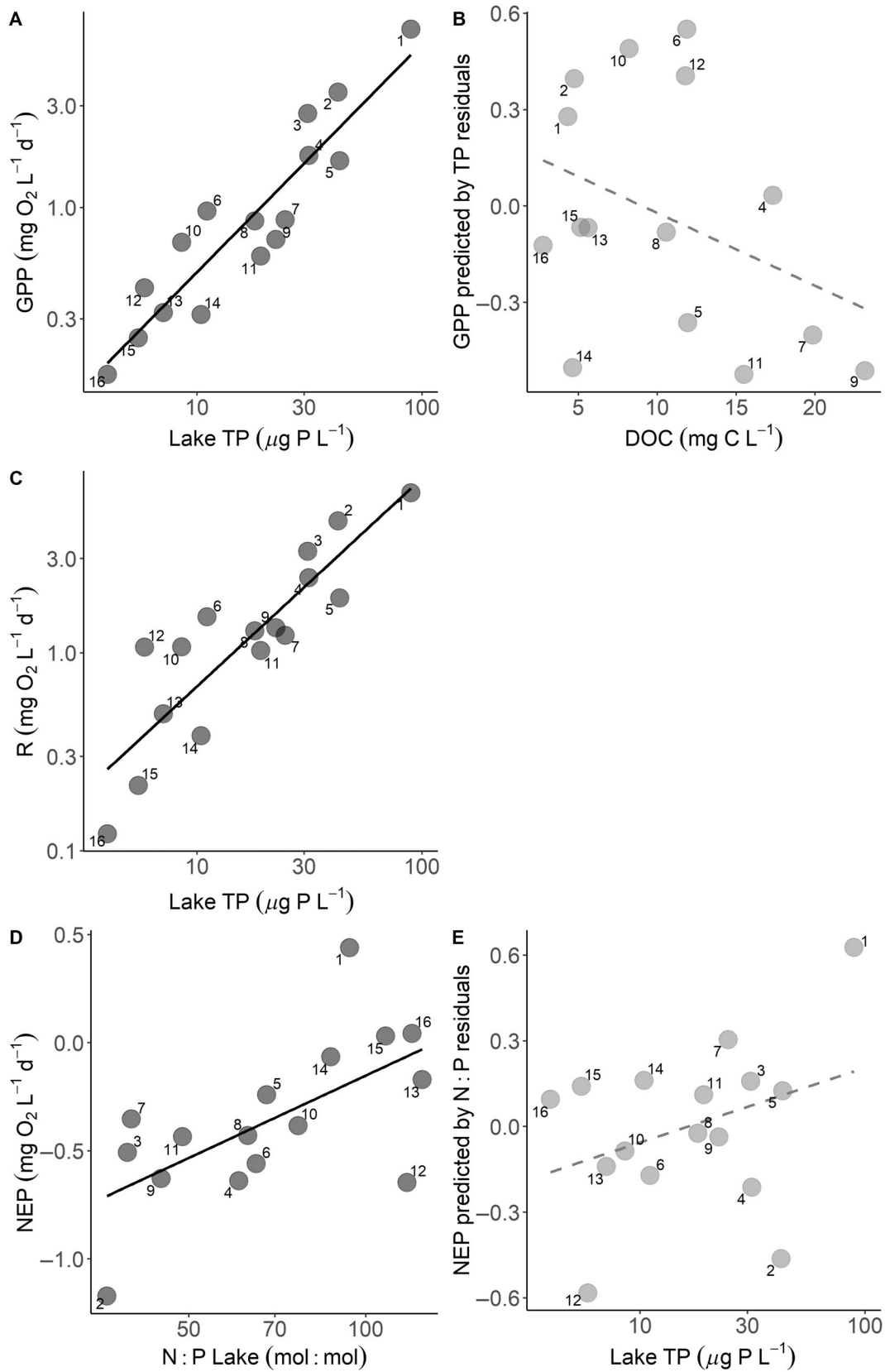
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Statistical analyses

To explore relationships among stream load and lake stoichiometry, we used correlation analysis and linear regression. First, we explored relationships between calculated average daily stream loads and average lake chemical composition across all lakes. Next, we explored within lake relationships between daily loads and lake chemical composition. We use the Redfield ratio (106 C : 16 N : 1 P) and the benchmark N : P ratio of 31 : 1 (Downing and McCauley 1992) as indicators of potential nutrient enrichment or deficiency in stream and lake stoichiometric values. Finally, we explored whether stream load stoichiometry was related to lake stoichiometry across lakes. When we report the ratios of our data, we use the C : N, C : P, or N : P denotations for simplicity, even though these values are describing the ratio of DOC to TN, DOC to TP, and TN to TP, respectively.

To identify how chemical composition and stoichiometry affect lake metabolism, we used linear regression models based on our conceptual figure (Fig. 1). We used these models to determine (1) how lake chemical concentration and stoichiometry is related with lake metabolism and (2) how stream load chemical concentration and stoichiometry is related with lake metabolism. Variables were log-transformed to meet assumptions of normality in the model, if necessary. Because several lake and stream chemical concentrations were highly correlated with each other, we removed variables as potential covariates of a linear regression model until the variance inflation factor for each covariate was below 2.5, which indicated a low level of multicollinearity. We calculated the variance inflation factor using the *vif()* function from the *car* R package (Fox and Weisburg 2019). The resulting set of potential covariates for the stream load and lake models included DOC, log-transformed TP, and log-transformed N:P as load or concentration, respectively. We fit all possible combinations of these covariates to annual estimates of GPP, R, and NEP.

Models were compared using Akaike Information Criterion (AIC) and any model within two AIC units of the best fit model was reported.

Results

Lake constituent and stream loading variation

The range in lake and catchment physical characteristics resulted in varied loading rates of DOC, TN, and TP and variable lake constituent concentrations. Stream constituent concentrations were on average higher than and positively related to lake concentrations (Fig. 2; Table 1). Both lake and stream concentrations spanned a wide range, representing a diverse set of lentic and lotic conditions (Fig. 2).

The C, N, and P loading rates on a lake volume basis varied widely across the catchment-lake systems and throughout the time series for each lake (Supporting Information Figs. S1–S3). Daily loading rates ranged from 0 to 6.72 g C (m^3 lake water)$^{-1}$ d^{-1} for DOC, 0 to 933 mg N (m^3 lake water)$^{-1}$ d^{-1} for TN, and 0 to 46 mg P (m^3 lake water)$^{-1}$ d^{-1} for TP across all catchment-lake systems (Supporting Information Table S1). Morris Lake and Övre Björntjärn exhibited subannual ranges in daily DOC loading nearly as large as the range across all catchment-lake systems (range of 6.12 and 6.70 g C (m^3 lake water)$^{-1}$ d^{-1}, respectively), while Acton Lake exhibited by far the largest subannual range in daily TN and TP loading (range of 930 mg N (m^3 lake water)$^{-1}$ d^{-1} for TN and range of 46 mg P (m^3 lake water)$^{-1}$ d^{-1} for TP).

Average annual load stoichiometry varied greatly across the catchment-lake systems as load C : P ranged from 74 to > 11,500, load C : N ranged from 0.90 to 108, and load N : P ranged from 10 to 234 (Fig. 3). The subannual range in daily load stoichiometry within a given catchment-lake system was nearly as large or larger than the range in average load stoichiometry across catchment-lake systems (Supporting

Table 2. Linear multiple regression models of annual average lake variables to predict annual average GPP, R, and NEP. Only models within two AIC units of the best fit model for each response variable are shown and all models in the table had significant *p*-values at the 0.05 level.

Response variable	Intercept	DOC	ln (TP)	ln (TN : TP)	AIC	R^2
ln (GPP)	7.65		1.04		20.80	0.86
ln (GPP)	8.24	−0.28	1.09		22.40	0.88
ln (−R)	7.86		1.03		30.10	0.76
NEP	−2.87			0.59	13.10	0.40
NEP	−2.49		0.19	0.83	13.50	0.52

(Figure legend continued from previous page.)
Fig. 6. Lake variables which best predict (**A**, **B**) GPP, (**C**) R, and (**D**, **E**) NEP. The *y*-axis in the second panel in each row plots the residuals of the regression plotted in the first panel. Solid lines indicate a significant best fit line and dashed lines are not significant (*p* ≥ 0.05). Point labels indicate rank order of mean annual lake GPP where 1 is the highest mean annual GPP. Parameter estimates are listed in Table 2. Note that Lake TP, Lake N : P, R, and GPP are plotted on a log-scale.

Information Fig. S4). Load N : P stoichiometry was almost always above the benchmark ratios (Fig. 3; Supporting Information Fig. S4).

Lake C : P ratios were almost always a magnitude of order higher than the Redfield C : P ratio (106 : 1), except in Lake Mendota and Acton Lake. Lake C : N ratios showed a similar trend as C : P ratios, with Lake Mendota and Acton Lake also exhibiting nutrient enrichment relative to organic C. Across all the lakes, N : P ratios were almost always higher than 16:1 or 31 : 1, suggesting the potential for P limitation of metabolism in these lakes (Fig. 3; Supporting Information Fig. S4). Load stoichiometry was indicative of lake nutrient stoichiometry for
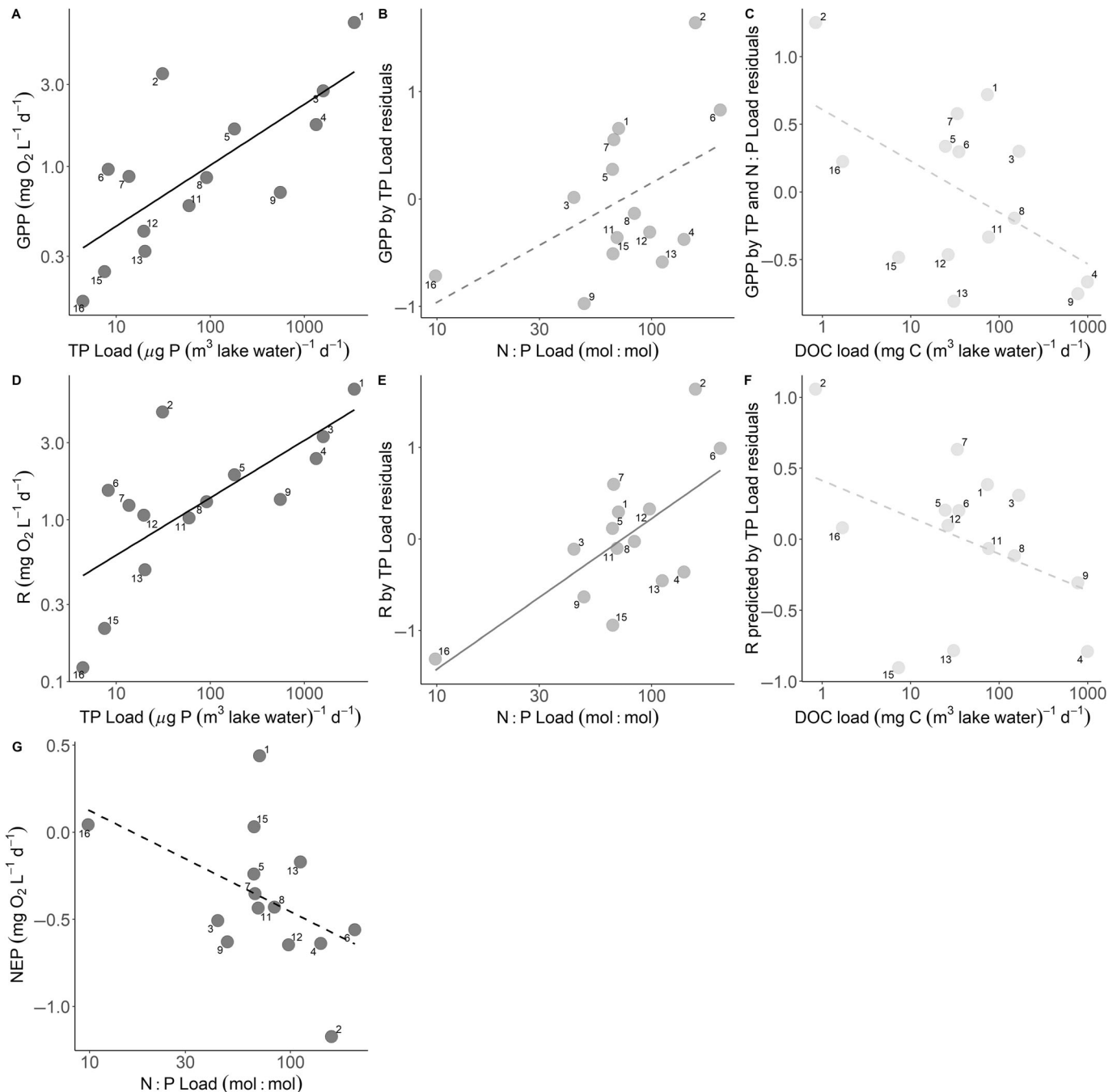
Fig. 7. Load variables which best predict (**A–C**) GPP, (**D–F**) R, and (**G**) NEP. The *y*-axis in the 2nd and 3rd panels in each row plots the residuals of the regression plotted in the panel to the left. Solid lines indicate a significant best fit line and dashed lines are not significant ($p > 0.05$). Point labels indicate rank order of mean annual lake GPP where 1 is the highest mean annual GPP. Parameter estimates are listed in Table 3. Note that Load TP, Load DOC, Load N : P, R, and GPP are plotted on a log-scale.

Table 3. Linear multiple regression models of annual average load variables to predict annual average GPP, R, and NEP. Only models within two AIC units of the best fit model for each response variable are shown and all models in the table had significant p-values at the 0.05 level except for the non-intercept model used to predict NEP.

Response variable	Intercept	ln (DOC Load)	ln (TP Load)	ln (TN:TP Load)	AIC	R^2
ln (GPP)	4.05	−0.33	0.55	0.61	31.40	0.85
ln (−R)	3.44	−0.22	0.48	0.8	34.40	0.82
ln (−R)	3.86		0.34	0.72	34.70	0.74
NEP	0.7			−0.25	17.10	0.22
NEP	−0.38				17.30	0.00

C : N and C : P, but not for N : P (Fig. 4). For most of the catchment-lake systems, load C : N and load C : P was higher than lake C : N and lake C : P, while there was no clear trend in N : P between streams and lakes.

How does lake concentration and stoichiometry influence lake metabolism?

Lakes included in our dataset spanned a range of productivity, and hence metabolism. Oligotrophic lakes like Trout Lake, Harp Lake, Crampton Lake, and Lough Feeagh had very low levels of GPP or R (< 0.5 mg O_2 L^{-1} d^{-1}) (Fig. 5; Supporting Information Table S1) whereas metabolism rates in the more productive lakes like Lake Mendota and Acton Lake reached 10 mg O_2 L^{-1} d^{-1} for GPP and R. Average annual GPP and R was tightly correlated across lakes ($r = 0.96$, $p < 0.001$).

Lake nutrient concentration and stoichiometry predicted annual lake GPP and R ($R^2 = 0.86$, $R^2 = 0.76$, respectively) and, to a lesser extent, NEP ($R^2 = 0.40$; Fig. 6; Table 2; Supporting Information Fig. S4). Lake TP concentrations positively influenced GPP and R, though the GPP model improved slightly with the inclusion of DOC, which was negatively related to GPP (Table 2). N : P was the best predictor of NEP with NEP increasing with higher N : P ratios. The NEP model fit improved with the inclusion of TP.

How does load magnitude and stoichiometry influence lake metabolism?

Lake-volume weighted stream load and stoichiometry were also stronger predicters of GPP and R ($R^2 = 0.85$ and $R^2 = 0.82$, respectively), then NEP ($R^2 = 0.22$; Fig. 7; Table 3; Supporting Information Fig. S5). The best models for GPP and R included load DOC, TP, and load N : P (Table 3). The best model for NEP included load N : P. In contrast to the lake NEP model, the N : P coefficient in the load NEP model was negative.

Discussion

Despite the relatively narrow latitudinal range of our study, the overall and relative amount of C, N, and P inputs and metabolic rates showed tremendous variability within and across lakes (Fig. 3; Supporting Information Figs. S1–S4). Our analyses illustrate that the stoichiometry of stream load is positively related with lake stoichiometry for C : N and C : P

(Fig. 4) and these ratios (as well as N : P) are generally above the Redfield ratio (Fig. 3). Both absolute constituent load, concentration, and ratios were important in predicting GPP and R, though different conclusions about drivers of lake metabolism vary somewhat depending on whether we considered load or lake concentration and stoichiometry. Interestingly, in our diverse lake set, GPP and R were well-predicted by our models, but NEP was not (Tables 1, 2).

In our study, we quantified catchment inputs based on available information about C, N, and P inputs from inlet streams. Our approach necessarily ignored other potential inputs of these elements (e.g., atmospheric deposition or groundwater flux) which may be important to some lake ecosystems (e.g., Caraco et al. 1992). However, these additional inputs likely account for only a minor amount of the mass balance in most of our study lakes (i.e., Pall et al. 2011; Knoll et al. 2013; Zwart et al. 2017; Klaus et al. 2018). Our approach may also have underestimated the impact of storm events on material inputs (Carpenter et al. 2015; Kelly et al. 2018), as the stream chemical data was not on a daily scale. Yet, for our study objectives, which consider the patterns at an annual scale, we consider our approach robust.

To calculate lake metabolism, we relied on a model fitting procedure which can be influenced by internal and external factors not captured in the model. These factors include lake turbulence and sensor placement. We used daily metabolic uncertainty estimates to guide our decision on which metabolism days to keep in our analysis and which days to exclude. We chose a CV threshold of four for well-fitting metabolism days as this CV cutoff balanced the number of days retained for each lake and the interpretation of long-term metabolism for each lake. A low CV cutoff has the potential to bias metabolism estimates toward calm, sunny days, which could lead to a high bias in GPP (Rose et al. 2014). Indeed, lower CV cutoffs (e.g., ½ to 2) resulted in higher mean annual GPP for most lakes, but the CV cutoff of four seemed to limit bias towards higher GPP and high PAR days while also providing reasonably confident metabolism model fits. We are confident that these well-fitting days and aggregation to annual scale captures meaningful cross-lake variation in metabolism estimates to be used to examine impacts of watershed loads and lake nutrient concentrations on lake metabolism.

Relationships between stream and lake constituents

There is an increasing focus on understanding the amount and transformation of chemical constituents as they move from catchments into lakes and downstream (Cole et al. 2007; Vanni et al. 2011; Maranger et al. 2018). Our results offer an opportunity to look more closely at stoichiometric shifts at the catchment scale (Figs. 2, 4; Schade et al. 2005). Compared with the findings of Maranger et al. (2018), who concluded that the ratios of C : N, C : P, and N : P are generally lower in streams than in lakes and reservoirs, we found a pattern of convergence in stoichiometric ratios moving from stream to lake ecosystems (Fig. 4). In our study, the catchment/lake systems with lower stoichiometry of loads than the mean reported by Maranger et al. (2018; C : N = 7, C : P = 166, N : P = 25) increased in C : N, C : P, and N : P, while systems with higher stoichiometry of loads decreased when going from streams to lakes (Fig. 4). The correlation between load and lake ratios (e.g., C : N and C : P in this study, Fig. 4, and N : P in a similar, but smaller scale study by Vanni et al. 2011) suggests similar biogeochemical processing may be occurring across all of the study lakes, but what biogeochemical processing is occurring is dependent on load stoichiometry. Processes that may shift C : N : P stoichiometry include (1) lake processes that differentially impact elements (e.g., denitrification, sedimentation, mixing; Maranger et al. 2018); (2) nutrient regeneration by zooplankton (Bergström et al. 2015); and (3) the balance of autotrophic and heterotrophic respiration to ecosystem-level R (Knoll et al. 2018). Longer studies that better constrain C, N, and P inputs and processing rates will help tease apart these potential mechanisms within and across catchment/lake systems.

Predictors of metabolism

By using data from this diverse range of catchment/lake systems, we documented a large range in constituent loading rates (Supporting Information Figs. S1–S3) and captured a range of GPP and R from very low-productivity Trout Lake to highly eutrophic Acton Lake (Fig. 5). Despite the inclusion of lakes with characteristics that may decouple metabolic processes (e.g., highly productive lakes, Solomon et al. 2013, or lakes with high DOC, Hanson et al. 2003), we found tight coupling of average annual GPP and R across lakes in our study, similar to previous work (e.g., Cole et al. 2000; Oleksy et al. 2021; Klaus et al. 2022).

Our approach considers both the importance of C : N : P stoichiometry and the relative role of lake vs. stream loading concentrations on lake metabolism. As in previous studies (Solomon et al. 2013; Oleksy et al. 2021), we saw strong correlations between N and P parameters. This relationship led to our decision to include only P, and not N, concentrations in our model. Furthermore, to avoid our models being overfit or confounded by multicollinearity, we used variance inflation factor to determine which variables to include. N : P was generally positively related to metabolism parameters (Figs. 6, 7).

The inclusion of N : P suggests that the relative amount of N may be more important than the overall concentration or load. This result coupled with the strong relationships between N and P suggest that both nutrients are important for regulating lake metabolism. Indeed, other lakes with high N : P have shown increases in GPP with high N loading (e.g., Bogard et al. 2017; Kelly et al. 2021).

The fits for our GPP and R models were relatively similar for the models using lake predictor variables (Table 2) and the models using load predictor variables (Table 3), but there were some interesting differences. Load N : P was an important predictor of GPP and R but lake N : P was not. As discussed above, we saw no correlation between N : P load and lake N : P so lakes with high load N : P were not the same as those with high lake N : P. It is possible that the forms of N and P were different between the stream input vs lake and that load N : P is a better predictor of what is available for metabolism, while lake N : P reflect what is "left" after metabolism (or other biogeochemical processes).

Allochthonous organic material inputs can regulate algal biomass and lake metabolism via positive and negative stimulation of algal growth and production (i.e., Kelly et al. 2018; Isles et al. 2021), yet much of this previous work has relied on using lake DOC as a proxy for DOC load. Importantly, we were able to incorporate load DOC, rather than just lake DOC, in our analysis. Both lake and load DOC explained some of the residual variation in metabolism once the effects of P and/or N:P were removed. For both GPP and R, the coefficient was negative, suggesting that there was a shading effect of DOC on GPP in our lakes. Furthermore, it is likely that the negative effect of DOC on R is driven through its influence on GPP as R is heavily influenced by GPP (both respiration by algae and by bacteria using algal-derived carbon). Interestingly, we did not find a unimodal relationship between load DOC and metabolism in our study (Supporting Information Fig. S7). Instead, we observed a wedge-shaped pattern of lake GPP as predicted by lake DOC. This pattern is consistent with predictions by Kelly et al. (2018) when loads of DOC and nutrients are not tightly coupled across space or time.

Our models do a better job of predicting annual GPP and R than NEP (Tables 1, 2). The lake and stream load models identified a relationship between lake or load N : P and NEP, but the fits were poor. NEP may be more difficult to fit because it exhibits much lower average annual variation relative to GPP and R (also *see* Hanson et al. 2003). Other variables which influence metabolism and could contribute to the lack of fit include lake morphometry (Staehr et al. 2012), residence time (Oleksy et al. 2021), and phytoplankton community composition (Zwart et al. 2015); however, including these variables was beyond the scope of our study.

Ongoing anthropogenic factors affecting stream inputs and implications for lake metabolism

We showed that loading of chemical constituents from catchments was highly variable across space and time and

had strong connections with lake chemistry and metabolism. Due to these connections, ongoing landscape changes (e.g., brownification, altered hydrology, changes in atmospheric deposition, and catchment management practices) may result in altered lake metabolic regimes. For example, the close correlation between constituent loading C : P and C : N and lake C : P and C : N suggests that future changes in the stoichiometry of OM loading, potentially related to brownification, could affect lake processes (Creed et al. 2018). These shifts will likely vary across regions and with catchment/lake characteristics such as land use and morphometry (Seekell et al. 2018).

While not a focus of this study, our results highlight the within-year variability in the amount and stoichiometry of C, N, and P loading to lakes (Supporting Information Fig. S4), variability that has been reported elsewhere to impact lake metabolism (Zwart et al. 2017; Williamson et al. 2021). Because constituent loading rates are generally related to the volume of water entering a lake from the catchment (Carpenter et al. 2015; Williamson et al. 2021), changes in hydrology have potential to affect metabolism in lakes (Hrycik et al. 2021). A more detailed analysis of seasonal patterns in load vs. lake nutrients will further improve understanding and prediction of lake metabolism under future environmental changes that are expected to change the timing and magnitude of hydrologic loading events (Raymond et al. 2016; Wu and Yao 2022).

Conclusions

Lake metabolism is recognized as a fundamental property of lake ecosystems. Metabolic rates drive food webs, affect downstream export, contribute to global carbon cycling, and enhance or impair recreational opportunities. Our results highlight the importance of considering both total and relative N, P, and C impacts on lake metabolism, and that the relative importance of these predictors of lake metabolism can vary when considering stream load versus lake metrics. Hence, catchment-lake management may be more successful when the models used to make predictions about lake conditions include stream load information. Future field and modeling studies related to how changes in catchment loading, hydrology, or other factors not considered here (i.e., temperature) affect metabolism at multiple timescales, as well as studies on lakes outside of the north-temperate zone (e.g., Brighenti et al. 2018; Poikane et al. 2022), will help us better predict changes in lake metabolism related to global change. Furthermore, as much as stream C, N, and P loadings can affect lake metabolism, lake metabolism can also imprint in downstream exports of C, N, and P. Therefore, understanding how metabolism is influenced by multiple catchment forcings will not only lead to better predictions of how lake metabolism may change in the future, but also how this affects landscape-scale carbon and nutrient cycling along the aquatic continuum.

Data availability statement

The data that support the findings of this study are openly available in the Environmental Data Initiative (EDI) Data Portal at https://doi.org/10.6073/pasta/ba8861853e02b19c9693cb100f722a02. The code that supports the findings of this study are openly available at https://zenodo.org/record/8408298.

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Conflict of Interest Statement

The authors have no conflict of interest to declare.