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# Using stream dissolved oxygen and light relationships to estimate stream primary production on mountainous headwater stream ecosystems

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## Abstract

Headwater streams influence the carbon cycle, but their productivity estimation remains challenging. We propose the use of dissolved oxygen data (% saturation, DO<sub>sat</sub>) and on-site photosynthetically active radiation (PAR) data to develop DO<sub>sat</sub>~PAR curves as an analogy to the well-known photosynthesis-irradiance (P-E) curves. The premise of our research is that although these curves are simple, they provide detailed information of stream ecosystem productivity dynamics. We used data from two streams in the Oregon Coast Range to investigate daily gross primary productivity (GPP). We used properties of the light-limited portion of the DO<sub>sat</sub>~PAR regression curves to produce a model to estimate GPP. We found that the slope of the DO~PAR relation varied widely between  $1.6 \times 10^{-4}$  and 0.045 and had strong correlations ( $r^2 > 0.78$ ). The data from one of the two study sites (Oak Creek) was used for model development while the data from the other site (South Fork Mill Creek) was used for model validation. The model's ability to quantify the effects of a discrete storm event on stream productivity was tested by comparing GPP estimates calculated through a Bayesian framework (streamMetabolizer) and our raw data-driven estimates of GPP which were based on the variability of the DO<sub>sat</sub>~PAR regression curves. The proposed methodology was successful in estimating GPP in headwaters. We foresee that this method may be used to assess disturbances and construct a baseline understanding of productivity dynamics in other headwater ecosystems that is independent of the methodological challenges of the current stream metabolism models.

## KEYWORDS

gross primary productivity, high flows, linear model, mountainous stream

## 1 | INTRODUCTION

Gross primary productivity (GPP) is a key ecosystem function that influences stream nutrient cycling, stream food webs, and overall stream carbon dynamics (Hall & Hotchkiss, 2017). However, estimating stream productivity in small headwater ecosystems continues to be challenging due to low overall rates of primary production and a high degree of uncertainty in oxygen exchange rates with the atmosphere (reaeration) (Ulseth et al., 2019; Hall & Ulseth, 2020). Because

it is still difficult to accurately model stream primary production in these systems (Appling et al., 2018), we have a diminished capacity to quantify how primary production changes within and across seasons or how primary production responds to disturbance events.

Dissolved oxygen (DO) is a key metric in the modeling of stream primary production (Hall & Hotchkiss, 2017). In most cases, the concentration of DO increases through the day in conjunction with in-stream primary production because oxygen is a byproduct of photosynthesis. Dissolved oxygen then declines at night as it is consumed by respiration

of both autotrophs and heterotrophs. When primary production and respiration are the only processes influencing diurnal variability in DO, the range in DO between day and night can be used to estimate rates of primary production. However, DO levels in streams can be affected by air pressure, water salinity and temperature, and flow turbulence which affects the rate of atmospheric oxygen exchange. Dissolved oxygen, expressed as percent saturation (DO<sub>sat</sub>), is likely to be more closely associated to the productivity dynamics of the stream than DO concentration because the percent saturation value accounts for local water temperature (Diamond et al., 2021). Given the strong influence that primary production has on diurnal variations of DO<sub>sat</sub> levels, studies have suggested that the photoperiod daily ranges of DO<sub>sat</sub>, combined with other abiotic factors, can provide reliable proxy metrics for primary production that can be used to capture seasonal changes as well as to quantify the impacts of disturbance events such as high flows that disrupt benthic autotrophs—the main autochthonous primary producers in temperate mountain forested streams (Canadell et al., 2021; Diamond et al., 2021; Hill, 1996; Hornick et al., 1981; McCutchan & Lewis, 2002). For example, Bernhardt et al. (2018) used daily DO<sub>sat</sub> data to illustrate fundamental differences in stream metabolic regimes throughout the year, and Diamond et al. (2021) found that the daily range of DO combined with stream temperatures were strongly correlated with metabolism estimates in a fifth-order agricultural stream network in spring, summer, and fall. Because one of the most dominant factors influencing stream metabolism is light availability (Bernhardt et al., 2022; Blaszcak et al., 2023), we hypothesized that including data on light along with DO<sub>sat</sub> would yield a potentially strong proxy for stream primary production, in particular during the morning, given the increasing activity of primary producers as the system emerges from total darkness. We expected that coupling DO<sub>sat</sub> data with solar radiation data [photosynthetically active radiation (PAR)] at the same high-resolution time intervals, that is, DO<sub>sat</sub>-PAR curves, could provide a viable proxy metric for the relative amount of primary production.

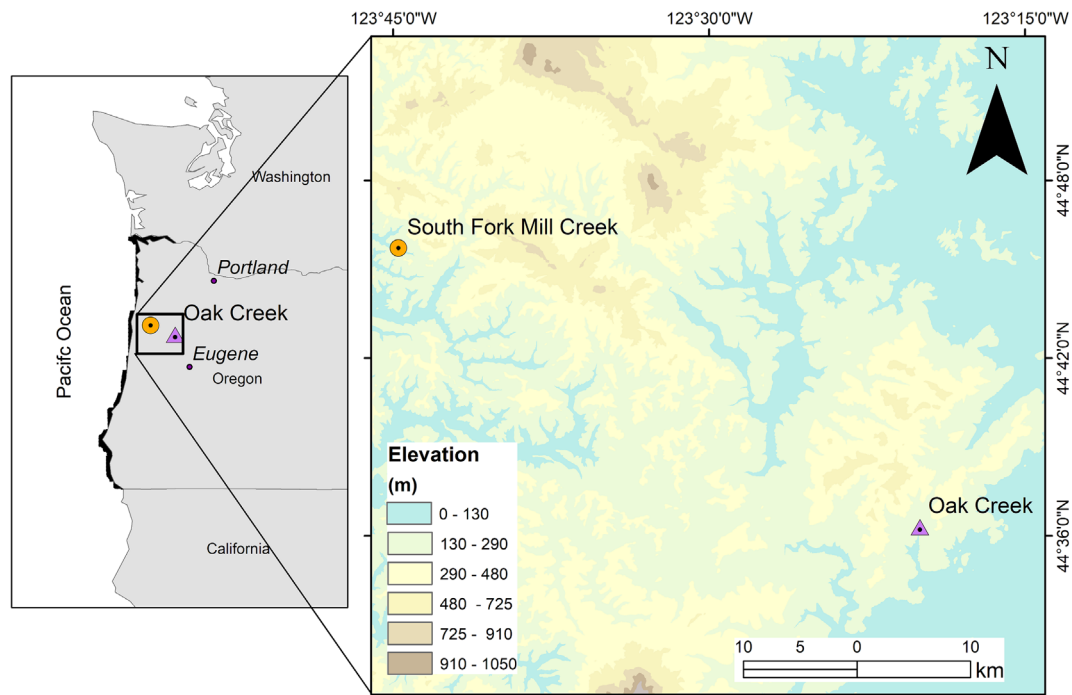
The use of proxy metrics is potentially powerful because they allow for a higher resolution understanding of stream processes over time and for an assessment of responses, even if an absolute measure of primary productivity is unattainable (Canadell et al., 2021; Diamond et al., 2021). Stream primary production estimates using open-channel metabolism methods depend on accurate estimates of reaeration. This is especially true in systems where primary production is low (Appling et al., 2018; Hall & Ulseth, 2020; Ulseth et al., 2019). If a model fails to accurately estimate reaeration in a stream (e.g., due to equifinality issues, see Appling et al. (2018)), we lose data and with it a “complete picture” of the site over time, which can be critical to understanding highly dynamic systems like small streams (Blaszcak et al., 2023; Munn et al., 2023). When data or synthetic ecosystem metrics are missing for multiple days, key information may be lost—especially regarding rapid changes during short storm events, which can cause notable declines in stream primary production estimates (Blaszcak et al., 2023; Roberts et al., 2007). For example, Beaulieu et al. (2013) found that they were unable to estimate ecosystem metabolism for c. 30% of the days in their 700-day monitoring effort due to the inability to adequately estimate gas exchange (87 days of missing

data). Similarly, working across a watershed and a range of stream sizes (43 stream sites), Diamond et al. (2021) found that only about 30% of their 8800 daily DO data had associated acceptable metabolism estimates with most failed estimates occurring in smaller streams. The inability to model air exchange rates can be addressed by direct empirical estimates from gas releases over the range of flow conditions to create a rating curve. While this process is possible (Beaulieu et al., 2013; Roberts et al., 2007), it is labor-intensive and often impractical, particularly in remote headwaters or under high flow conditions. Clearly, if an accurate estimate of GPP is required, true reaeration estimates must be produced; however, in many ecological studies, scientific questions can be answered based on comparisons of relative or proxy values, for example, when the focus is on whether and to what degree a system changes over time or in response to a disturbance (natural or anthropogenic).

In this study, we assessed the use of proxy measures to estimate stream primary productivity and to identify and quantify dynamics of stream primary production over time. Our objective was to investigate the use of the DO<sub>sat</sub>-PAR relationships in forested headwater streams to develop relative estimates of stream productivity. Specifically, we evaluated whether parameters associated with the linear component of the relationship between DO<sub>sat</sub> and PAR and the observed DO<sub>sat</sub> range provided viable proxy measures of ecosystem productivity (GPP) that occur early in the day. These stream characterizations and the proxy metrics evaluated here, offer the ability to estimate the response of ecosystem processes to short- and long-term changes in headwater streams based on raw field observation data.

## 2 | STUDY AREA

This study was conducted in two third-order mountain streams in the Oregon Coastal Range, Oregon (USA) (Figure 1). Oak Creek was used to calibrate the GPP model, while South Fork Mill Creek was used for method validation. Oak Creek is a 6.7-km<sup>2</sup> watershed underlain primarily by Siletz River volcanics with basalt as its major lithologic constituent (Walker & MacLeod, 1991). Oak Creek drains within the McDonald-Dunn Research Forest of Oregon State University. The site has a Mediterranean climate with wet winters and mild summers, mean annual precipitation of 1620 mm (1997–2018), and mean annual temperature of 7.6 °C (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu/>, created 12 November 2021). The watershed has rugged topography with slopes ranging between 30% and 90% and a 140–650 m.a.s.l. elevation range. The main overstory consists of the conifer Douglas fir (*Pseudotsuga menziesii*) in the uplands of the watershed and deciduous big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) along the riparian corridors (Cargill, 2019). The study reach is 160 m long with a bankfull discharge of 3.4 m<sup>3</sup> s<sup>-1</sup>, average bankfull width of 6 m, a slope of 0.014 m m<sup>-1</sup>, and a median grain size (D<sub>50</sub>) of the channel bed of 47.6 mm (Katz et al., 2018). The mean daily flow between December 2017 and February 2019 was 0.13 m<sup>3</sup> s<sup>-1</sup>.



**FIGURE 1** Location of the two study streams, Oak Creek and South Fork Mill Creek. Both streams are in the Oregon Coast Range.

South Fork Mill Creek is a 4.3-km<sup>2</sup> catchment located near the center of the Oregon Coast Range. The stream drains west into the Siletz River and ultimately to the Pacific Ocean. The catchment is underlain primarily by sandstone and siltstone of the Tye Formation (Walker & MacLeod, 1991), and its climate is also Mediterranean with a mean annual precipitation of 2300 mm and mean annual temperature of 11 °C (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu/>, created 12 November 2021). The watershed is formed by steep forested mountain slopes (5–90%) with a 100–700-m elevation range. South Fork Mill Creek has a more open understory vegetation than Oak Creek, including ferns, grasses, stinging nettle, and salmonberry; the riparian vegetation is primarily deciduous including vine maple (*Acer circinatum*), red alder (*Alnus rubra*), and black cottonwood (*Papulus trichocarpa*). The study reach in South Fork Mill Creek is 160 m long with a bankfull discharge of 2.5 m<sup>3</sup> s<sup>-1</sup>, average bankfull width of 7 m, a slope of 0.008 m m<sup>-1</sup>, and a D<sub>50</sub> of the channel bed of 29.7 mm (Bair et al., 2019). Mean annual discharge between December 2017 and 2019 was 0.19 m<sup>3</sup> s<sup>-1</sup>.

### 3 | METHODS

#### 3.1 | Field observations

We used 10-min data collected between December 2017 and May 2019. Each site was instrumented with a MiniDOT optical sensor (Precision Measurement Engineering; Vista, CA, USA) to measure DO (mg L<sup>-1</sup>) and temperature (°C) within the water column. Three cosine-corrected Odyssey Photosynthetic Irradiance Loggers

(Dataflow Systems Ltd; Christchurch, New Zealand), calibrated with a LI-COR quantum sensor (Campbell Scientific; Logan, UT, USA), measured PAR (μmol m<sup>-2</sup> s<sup>-1</sup>) along the reach. PAR loggers were placed immediately above the stream to capture an average of the available radiation reaching the stream surface. Although measurements of PAR at the stream benthos can yield better estimates of GPP in a full metabolic model (Kirk et al., 2020), we focused on PAR measurements just above the stream surface because (1) most studies have and can access surface data more practically than benthic data and (2) many temperate headwaters are relatively shallow and clear, and therefore, we assume that light attenuation has a limited effect relative to deeper and/or darker streams (Kirk et al., 2020). A Levellogger Edge water level and a Barologger (Solinst; Georgetown, Ontario, Canada) provided barometric-compensated water depth (m) that was transformed into discharge (m<sup>3</sup> s<sup>-1</sup>) based on a depth-discharge rating curve previously developed for each system (Bair et al., 2019; Katz et al., 2018). There were sampling interruptions due to sensor malfunction and operative decisions at both sites resulting in semicontinuous time series rendering 367 days of effective data between December 14, 2017 and February 14, 2019, at the Oak Creek site, and 285 days of effective data between March 20, 2018 and May 10, 2019, at the South Fork Mill Creek site.

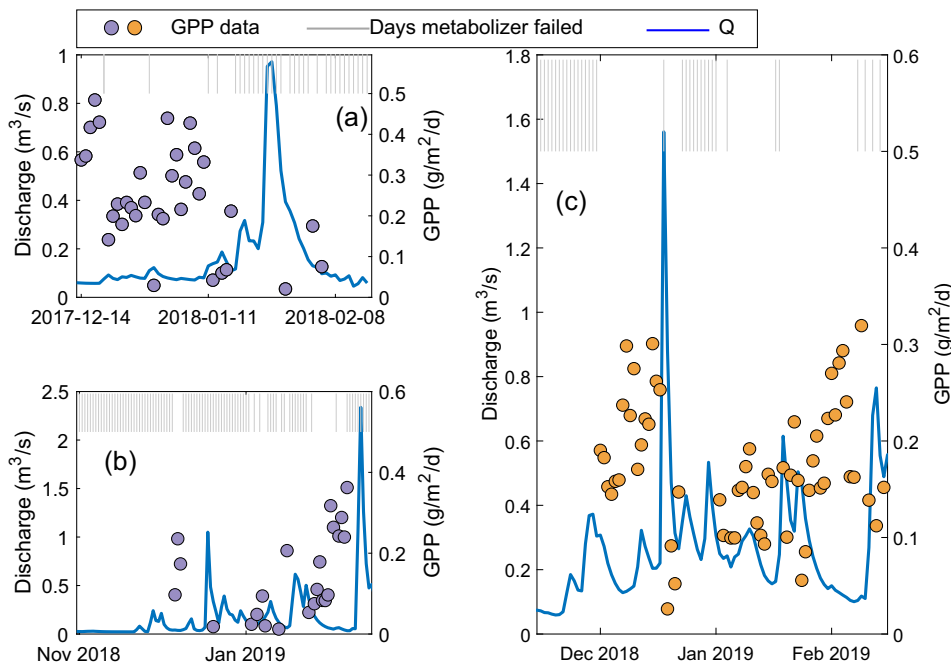
#### 3.2 | Gross primary productivity modelling data

In a previous investigation, we modeled winter season daily GPP (g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) during the 2017–2019 period at the two study sites

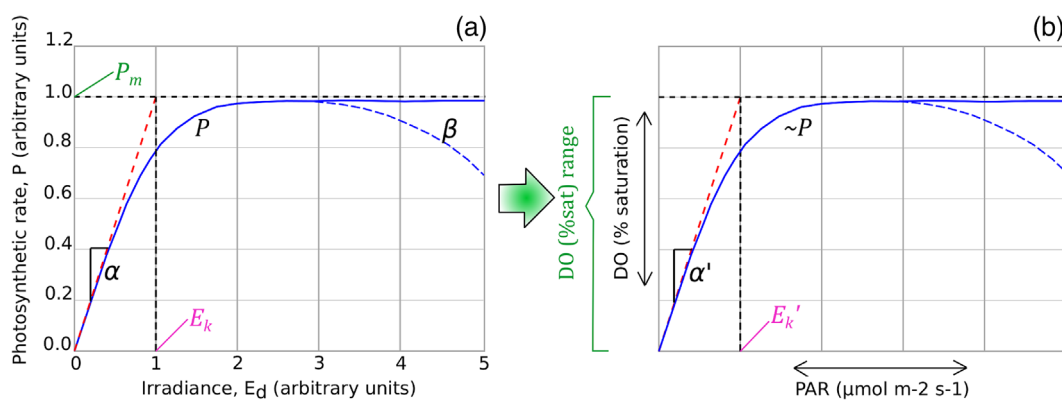
(Cargill et al., 2021). The estimated GPP values varied between  $2 \times 10^{-3}$  and  $8.2 \times 10^{-1}$  g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for Oak Creek and  $2 \times 10^{-2}$  and  $6.9 \times 10^{-1}$  g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for South Fork Mill Creek. All GPP estimates were obtained using a single-station open-channel method through the streamMetabolizer R package (Appling et al., 2018). Although in Cargill et al. (2021) we aimed to model GPP over a wet season in which we had 190 days in Oak and 82 days in South Fork, the model only provided a reliable result for 76 days in Oak Creek (40% of all days with available data) and 68 days in South Fork Mill Creek (83% of all days with available data) (Figure 2). Metabolizer failed in all these instances due to negative GPP values or failure to converge. We used the GPP estimates of Cargill et al. (2021) for the winter season (December 1–February 15) for model calibration.

### 3.3 | DOsat–PAR relationship and abiotic stream metrics

Key proxy metrics in this analysis are based on the DOsat–PAR relationship, which is analogous to the structure of the photosynthesis–irradiance (P–E) curves (Figure 3). The P–E curves describe the response of a given community of primary producers to the available solar irradiance (Ryther, 1956). These curves have been applied to both terrestrial and aquatic systems to understand underlying ecosystem processes (Bouman et al., 2018; Forget et al., 2007; Sand-Jensen, 1997; Staehr et al., 2016). A P–E curve has an initial linear slope ( $\alpha$ ) related to light-limited conditions (i.e., the capacity of photosynthetic pigments to capture photons) and a maximum productivity value ( $P_m$ ) that is reached under light-saturated conditions either



**FIGURE 2** GPP estimates for winter (December–February 15) obtained through StreamMetabolizer (Cargill et al., 2021) between 2017 and 2019 in Oak Creek (A, B) and between 2018 and 2019 in South Fork Mill Creek (C). Filled markers indicated GPP estimates with metabolizer (56 for Oak Creek and 59 for South Fork Mill Creek) that were used in this study. Metabolizer failed 117 days in Oak Creek and 35 days in South Fork Mill Creek due to negative GPP values or failure to converge. These days are indicated with the gray lines.



**FIGURE 3** (A) The photosynthesis–irradiance (P–E) curve illustrating an initial linear phase ( $\alpha$ ), and asymptote ( $P_m$ ) and potential photosaturation ( $\beta$ ). (B) Analogous conceptual model for the relationships between photosynthetically active radiation (PAR) and dissolved oxygen saturation (DOsat) in stream water.

asymptotically or as a peak. In the latter case, photoinhibition occurs and productivity decreases at the highest observed irradiances (Figure 3A) (Kirk, 1994b). The photosynthetic response of benthic algae is typically modeled with a two-parameter (the initial linear slope  $\alpha$  and the specific photosynthetic rate at optimal illumination  $P_m$ ) hyperbolic tangent equation (Boston & Hill, 1991; Jassby & Platt, 1976) with an additional parameter ( $\beta$ ) when photoinhibition occurs (Platt et al., 1980). For either case, it is possible to determine the onset of photosaturation ( $E_k$ ), an irradiance value corresponding to the point at which the maximum photosynthetic rate ( $P_m$ ) would be reached if the system was exclusively under light-limited conditions (i.e., the intersection point between  $P_m$  and the line with slope  $\alpha$ ). Analogous to this P-E dynamic, the relationship between irradiance values (PAR) and the DOsat content can be used to construct a DOsat-PAR curve during the photoperiod of each day (Figure 3B). When changes in DOsat are attributed to changes in GPP, the daylight response of DOsat as a function of PAR may then be used as an approximation of the whole system's primary productivity (Canadell et al., 2021).

For our analysis, we focus on three key metrics associated with the linear component of the daily relationship between DOsat and PAR: (1) the slope which is similar to the slope ( $\alpha$ ) in the P-E relationship (Figure 3); (2) the coefficient of determination ( $R^2$ ) of the fit between DOsat-PAR, which provides an indication of the strength of the assumption that changes in DOsat result from changes in GPP; and (3) the range of DOsat (DO.range, % saturation) similar to  $P_m$  within the linear portion of the DOsat-PAR relationship, which is analogous (although clearly not identical) to the peak photosynthetic rate ( $P_m$ ) in the P-E curve. The total daily range in DO saturation through the full photoperiod (DO.range.photo, % saturation) has been found to be a valuable proxy metric in other studies (Diamond et al., 2021), and it is included in a larger model comparison analysis discussed below. In exploring the linear component of the daily relationship between DOsat and PAR, we only used data from the early portion of the day when the system is transitioning from a period of no light (with no GPP and 0 PAR) to a period of elevated light. By focusing on this part of the day, we avoid issues with potential hysteresis in the relationship between PAR and DOsat over the course of the day. Because daylight hours, sun angle, and the timing of peak PAR vary throughout the year, it is inappropriate to pick a set period or a set time of day in identifying the "first part of the day." We therefore focused on selecting a set maximum PAR value as a cutoff for the DOsat-PAR relationships that could be applied to the proxy data analysis. We selected the PAR range by testing how daily values of each of the three focal metrics related to "known" daily GPP estimates (Cargill et al., 2021) in our model training stream across PAR values that ranged from 0–50 to 0–200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure S1). We chose to use the 0–100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  range because this range had high consistent linearity with our three focal predictors, and this range could be transferrable to systems where light saturation occurs at lower PAR ranges than our exploratory site.

Given the analogous nature of the DOsat-PAR relationship to P-E curves, we expect a clear positive linear relationship between PAR

and DOsat during the day from 0 to 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . On days with high GPP, the resulting linear regression should have a strong  $R^2$ , a positive and significant slope ( $\alpha'$ ), and a large DO.range. In contrast, on days with less GPP or on days when other processes (e.g., turbidity or channel bed mobility) are disrupting GPP, we would expect a weak  $R^2$ , a shallower and less significant slope ( $\alpha'$ ), and a low DO.range.

### 3.4 | Developing models to estimate stream GPP from the DOsat-PAR relationships and abiotic stream metrics

Beyond the three metrics derived from the DOsat and PAR relationship (slope,  $R^2$ , DO.range), we also consider as covariates mean water temperature ( $^{\circ}\text{C}$ ), mean daily water depth (m), total photoperiod hours (hours.photo), the full photoperiod range of DOsat (DO.range, %), and two metrics proposed by Diamond et al. (2021): the daily range of DO ( $\text{g m}^{-3}$ ) and the daily DO range multiplied by the average water depth ( $\text{g m}^{-2}$ ). A correlation matrix was used to identify the independent variables to include in a set of linear models to estimate daily GPP (Figure S2 and Table S1). Ultimately, we selected eight potential

**TABLE 1** Potential predictors for gross primary productivity (GPP) in Oak Creek.

Predictor	Code	Description
Dissolved oxygen range (% saturation)*	DOrange	DO.range
	<b>DOrange.norm</b>	DO.range normalized to the maximum observed value.
$R^2$ *	<b><math>R^2</math></b>	Coefficient of determination
Slope*	<b>slope</b>	Slope
Water temperature ( $^{\circ}\text{C}$ )	<b>temp</b>	Mean water temperature for data points used in the DOsat-PAR plot (0–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
	Depth.norm	Mean water depth, normalized to the maximum observed value
Water depth (m)	<b>Depth.norm.in</b>	Natural log-transformed mean water depth, normalized to the maximum observed value
	hours.photo	Daily number of light hours
Full photoperiod range of DOsat (% Sat)	<b>DO.range.photo</b>	Total daily DO range during the photoperiod
	PAR.total.photo	Total PAR observed during the photoperiod
Daily range of DO ( $\text{g m}^{-3}$ )	D24h.DORange	Parameters in Diamond et al. (2021)
Daily DO range times average water depth ( $\text{g m}^{-2}$ ).	<b>D24h.DORange.depth</b>	

Eight variables in bold were used in linear models (Table S2).

\*Parameters of the fit between DOsat-PAR in the range of 0–100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

\*\*Variables discarded based on correlation matrix (Figure S2).

predictors of GPP at Oak Creek (Table 1); given our goal of creating a model with transferability and to compare more directly between our two focal streams, we normalized two of the predictors (DO.range and Depth) with respect to their maximum observed value at the site. We considered 89 models with 1–5 covariates (Table S2).

We conducted an AIC analysis (Symonds & Moussalli, 2011; Wagenmakers & Farrell, 2004) to determine the best linear models considering different combinations of covariates (Table 1) to predict the GPP at Oak Creek using the *aictab* function within the R “AICcmodavg” package (Mazerolle, 2023) supplemented by AIC weights (Burnham & Anderson, 2002). The variance inflation factor (VIF) (*vif* function within the R “car” package) (Fox & Weisberg, 2019) was used to inform model selection. As such, we discarded models with VIF above 4. Finally, we used a cross-validation (fourfolds) to evaluate the predictive power of the top models to predict GPP at Oak Creek using the *train* function within the R “caret” package (Kuhn, 2008). Covariate pairs with absolute correlation coefficient greater than 0.6 were not included in the same model. The top candidate models to predict GPP at Oak Creek were used to estimate GPP in South Fork Mill Creek. We compared these predictions of GPP to the GPP estimates calculated with stream-Metabolizer (Cargill et al., 2021).

### 3.5 | Capacity of proxies and models to capture event and seasonal GPP dynamics

We explored the use of the developed model of GPP to capture external controls of GPP. We used one of the top candidate models to estimate GPP over the winter period with available data at Oak Creek and South Fork Mill Creek and to investigate the effects of a relatively large flood on GPP. In doing this, we isolated a single storm event per site to evaluate how the predicted GPP using our model structure responded to these high flow events; we aimed to investigate pre-, during, and post-event conditions in the daily resolution that our model structures were able to provide. The single focal storm at Oak

Creek was  $1 \text{ m}^3 \text{ s}^{-1}$  (30% of bankfull flow) (Katz et al., 2018) while the single focal storm at South Fork Mill Creek was  $1.6 \text{ m}^3 \text{ s}^{-1}$  (64% of bankfull flow) (Bair et al., 2019).

## 4 | RESULTS

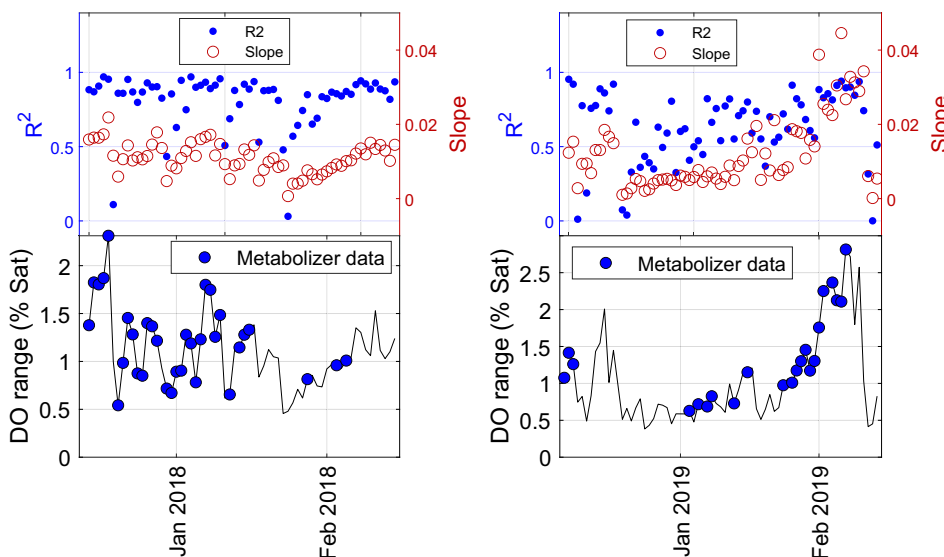
### 4.1 | Dissolved oxygen–DO–PAR relationship

We estimated daily values of slope,  $R^2$ , and DO.range of the DOsat–PAR relationship in the 0–100  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  range for 132 days in Oak Creek and 69 days in South Fork Mill Creek between 2018 and 2019 (Figures 4 and 5). The slope varied between  $1.6 \times 10^{-4}$  and  $4.5 \times 10^{-2}$  in Oak Creek and between  $4.2 \times 10^{-3}$  and  $3.51 \times 10^{-2}$  in South Fork Mill Creek. As expected,  $R^2$  was strong for both Oak Creek (mean = 0.72) and South Fork Mill Creek (mean = 0.79) (Figures 4 and 5). The DO.range was similar between sites and varied between 0.38 and 2.81 in Oak Creek and between 0.55 and 2.60 for South Fork Mill Creek (Figures 4 and 5).

Pearson correlations indicated strong positive relationships between GPP and all the three parameters of the DO–PAR relationship ( $r > 0.49$ ) and with DO.range.photo, the total daily DO.range during the photoperiod ( $r = 0.74$ ). Strong negative relationships were found between GPP and depth ( $r < -0.58$ ) and the daily depth-scaled DO range ( $r = -0.37$ ). Weaker relationships were found between GPP and the daily DO range ( $r = 0.28$ ), the daily number of light hours ( $r = -0.16$ ), and water temperature ( $r = -0.30$ ) (Table S1 and Figure S2).

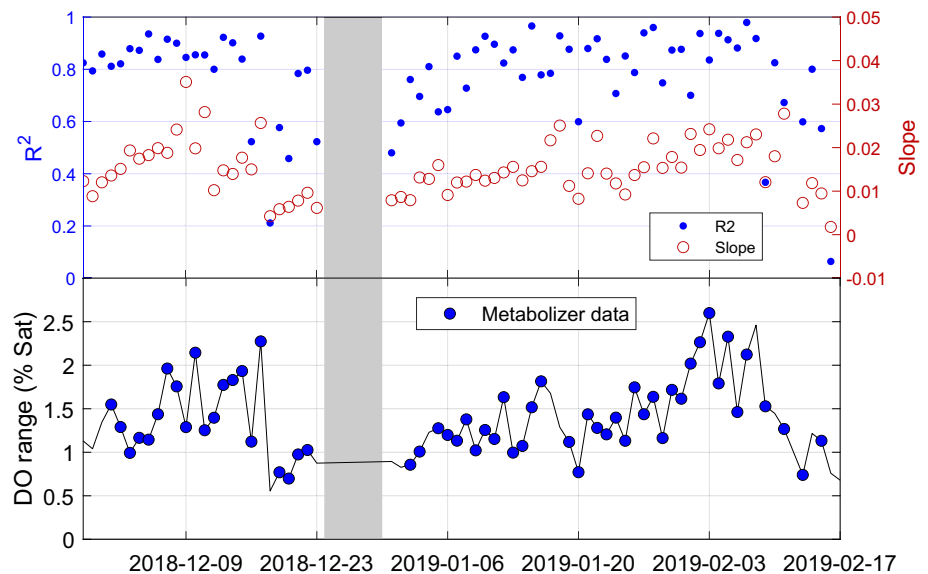
### 4.2 | Model development to estimate gross primary productivity

The total weight for each of the potential predictors across the considered models varied between  $3.03 \times 10^{-5}$  for depth-scaled DO diel range (D24h.DORange.depth) and 0.46 for total photoperiod hours



**FIGURE 4** Temporal variability of the parameters of the relationship between DOsat and PAR: slope, coefficient of determination ( $R^2$ ), and range of DOsat (DO.range) for winter periods of 2017–2018 and 2018–2019 at Oak Creek. The markers indicate the days for which GPP estimates from Metabolizer are available.

**FIGURE 5** Temporal variability of the parameters of the relationship between DOsat and PAR: slope, coefficient of determination ( $R^2$ ), and range of DOsat (DO.Range) for the winter period of 2018–2019 at South Fork Mill Creek. The markers indicate the days for which GPP estimates from Metabolizer are available, and the gray area indicates a period over which no data was available.



(hours.photo) (Table S3). The AIC analysis indicated four candidate models with similar statistical power (Table S4) as indicated by the Delta AIC < 2 (Burnham & Anderson, 2002). All top model structures included as covariates the coefficient of determination of the fit between DOsat and PAR ( $R^2$ ), total photoperiod hours (hours.photo), and photoperiod range of DOsat (DO.range.photo) (Table 2). Three of the top four models included mean water temperature (temp), one model included natural log-transformed mean water depth, normalized to the maximum observed value (Depth.norm.ln), and one model included depth-scaled DO diel range (D24h.DORange.depth) (Table 2). Cross-validation on the four top models to predict GPP at Oak Creek yielded strong model performance with cross-validation  $r^2$  between 0.72 and 0.80 (Table 2 and Figure 6). However, the model yields a negative GPP value for 1 day. The VIC for the covariates in the four best-supported models was below 3.0 (Table S5).

### 4.3 | Testing the Oak Creek GPP model at the South Fork Mill Creek site

We used data for 59 days over the winter season (Figure 2) that had available GPP data (Cargill et al., 2021) and complete daily DO–PAR data to derive model parameters. The performance of three of the top 4 models was strong with  $r^2$  between 0.64 and 0.72 (Figure 7). These three models (Figure 7A,B,D) accurately depicted the temporal patterns of GPP (Figure S3, S4, S6) yielding one to three negative values. One of the top four models, m.five.4, underestimates GPP yielding 46 negative GPP estimates (Figures 7C and S5). The three models that best predicted GPP at South Fork Mill Creek, m.five.3, m.three.23, and m.four.8, shared as covariates the coefficient of determination of the DOsat–PAR relationship ( $R^2$ ), the daily number of light hours (hours.photo), and the full photoperiod range of DOsat (DO.range.photo). Two of these models, m.five.3 and m.four.8, included water temperature. The worst model to predict GPP at South Fork Mill

Creek, m.five.4, was the only model that included the daily DO range times the average water depth (D24h.DORange.depth) as a covariate.

### 4.4 | Capacity of the site-specific models to capture event and seasonal GPP dynamics

We selected the most parsimonious model to predict GPP (model m.five.3, Table 2), to analyze changes in GPP during the winter period for both Oak Creek and South Fork Mill Creek (Figure 8). We used the model not only for the days in which we had GPP estimates from metabolizer but also for days in which metabolizer failed to produce values (Figure 2). That is, we solved for GPP for 161 days in Oak Creek and 81 days in South Mill Creek. This encompasses a potential strength of the proxy metrics because we were able to increase the number of winter days with GPP estimates from 55 to 161 days in Oak Creek and from 59 to 81 days in South Fork Mill Creek.

The values of GPP we estimated using the top model m.five.3 (Table 2) varied between 0 and  $0.64 \text{ g m}^{-2} \text{ d}^{-1}$  for both Oak Creek and South Fork Mill Creek. A high streamflow event in January 2018 illustrates the impact of high flows in both systems (Figure 9). Oak Creek responds quickly to flow disturbances with GPP declining to almost zero (Figure 9A,B). The system did not return to pre-storm GPP levels 29 days after the storm. The same storm at South Fork Mill Creek also reduced GPP but the reduction was modest, and the system returned to pre-storm conditions between 21 and 24 days after the end of the storm event.

## 5 | DISCUSSION

Primary production is a fundamental ecosystem process that has implications for biogeochemical cycling and food web dynamics in both aquatic and terrestrial ecosystems. In streams, advances in DO

**TABLE 2** Parameter estimates and summary statistics for the best-supported models to predict GPP at Oak Creek.

Model code name	Covariate	b (SE) <sup>a</sup>	XCr <sup>2</sup>	AIC	AICw	Δi	RMSE
m.five.3	Intercept	0.638 (0.287)	0.77	– 139.6	0.3	0	0.065
	R <sup>2</sup>	0.262 (0.08)					
	Depth.norm.ln	– 0.092 (0.048)					
	temp	0.005 (0.009)					
	hours.photo	– 0.101 (0.026)					
m.three.23	Intercept	0.907 (0.253)	0.80	– 138.9	0.2	0.65	0.066
	R <sup>2</sup>	0.227 (0.08)					
	hours.photo	– 0.12 (0.025)					
	DO.range.photo	0.191 (0.025)					
m.five.4	Intercept	0.819 (0.257)	0.74	– 138.5	0.2	1.04	0.064
	R <sup>2</sup>	0.24 (0.08)					
	temp	– 0.003 (0.007)					
	hours.photo	– 0.103 (0.026)					
	DO.range.photo	0.176 (0.026)					
	D24h.DORange.depth	– 2.313 (1.412)					
m.four.8	Intercept	0.918 (0.254)	0.72	– 137.6	0.1	1.98	0.066
	R <sup>2</sup>	0.236 (0.081)					
	temp	– 0.006 (0.007)					
	hours.photo	– 0.117 (0.025)					
	DO.range.photo	0.184 (0.027)					

These models were selected based on the Akaike information criteria (AIC), the change in the AIC relative to the best-supported model (Δi), and AIC weights (AICw) for the best supported (i.e., with Δi < 2).

Abbreviations: XCr<sup>2</sup>, mean cross-validation r<sup>2</sup>; RMSE, root-mean-square prediction error (fourfolds).

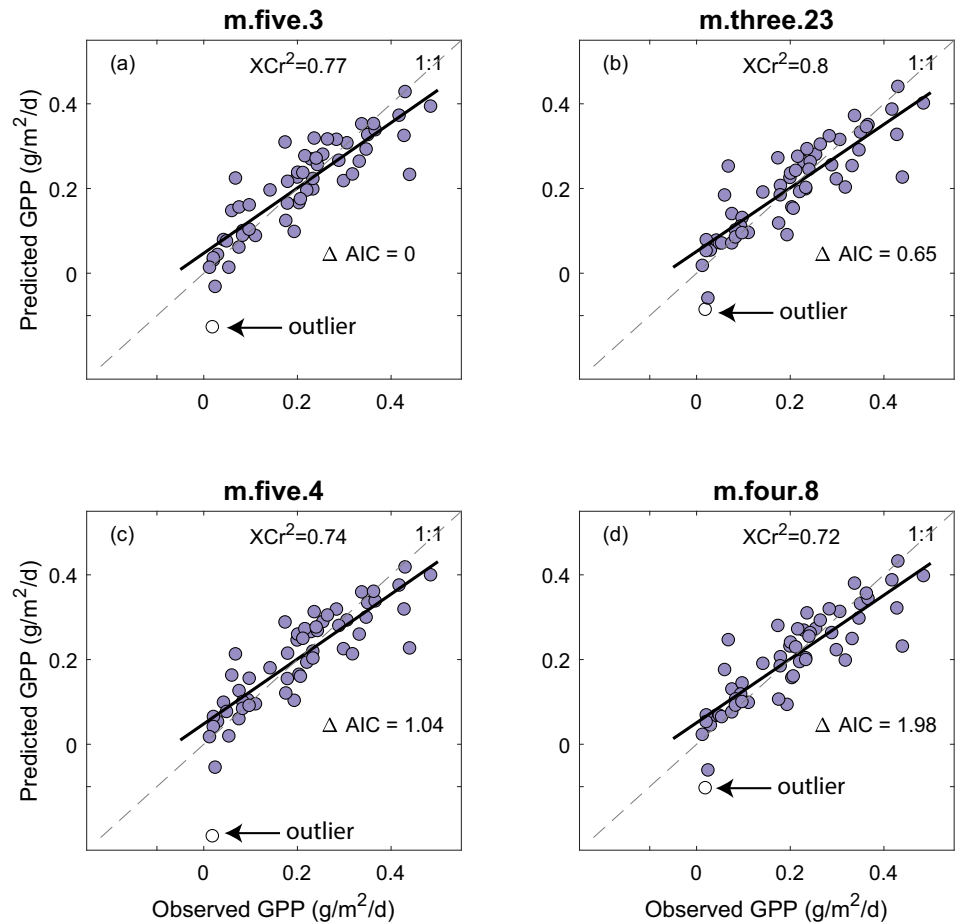
<sup>a</sup>Coefficient value and standard error in parenthesis.

logging capabilities and in the models for open-channel metabolism have greatly expanded the range of systems in which aquatic ecologists can estimate rates of primary production (Bernhardt et al., 2018). Headwater streams however remain areas where highly complex reach hydraulics create conditions that may prevent modeling of reaeration and substantially limit our ability to obtain consistent estimates of GPP (Appling et al., 2018; Ulseth et al., 2019). When data for synthetic ecosystem metrics are missing for multiple days, key information may be lost—especially in capturing ecosystem responses to short-term events. Having incomplete information prevents researchers from understanding the “complete picture” of the site. We found that the raw, high-resolution time series of DO and PAR may be used to construct DOsat–PAR curves, in a similar manner as the P–E curves, and that the parameters of these DOsat–PAR curves may be used to estimate GPP in forested headwater streams. The GPP estimates from multiple linear models aligned well with observed GPP in a headwater stream, and the estimates effectively captured ecosystem dynamics during an acute disturbance event. The use of these high-resolution raw data does not replace the value of accurate estimates of GPP when specific carbon fixation data is needed, but the strong relationship that we found suggests that these proxy estimates are valid in assessing relative rates of GPP. Further, the clear

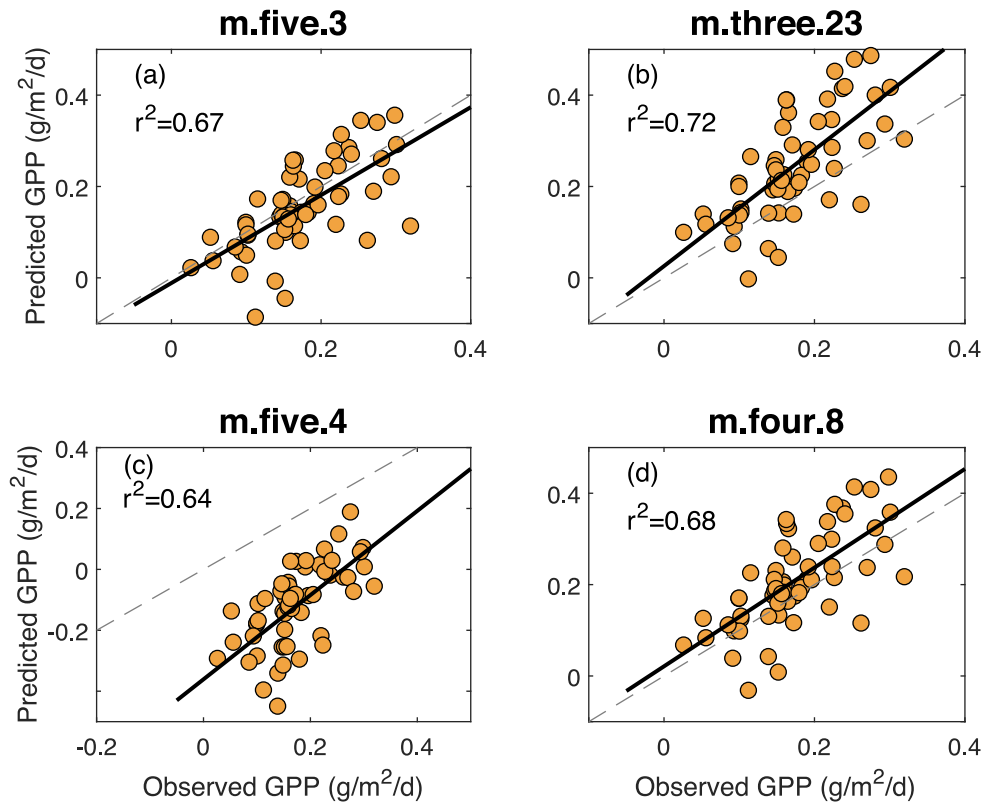
responses in our proxy metric estimates to a streambed disturbance indicate that these proxy-derived estimates are valid in stream studies where one is interested in quantifying the response of GPP to changes imposed upon streams and stream riparian areas (naturally or in an experimental context).

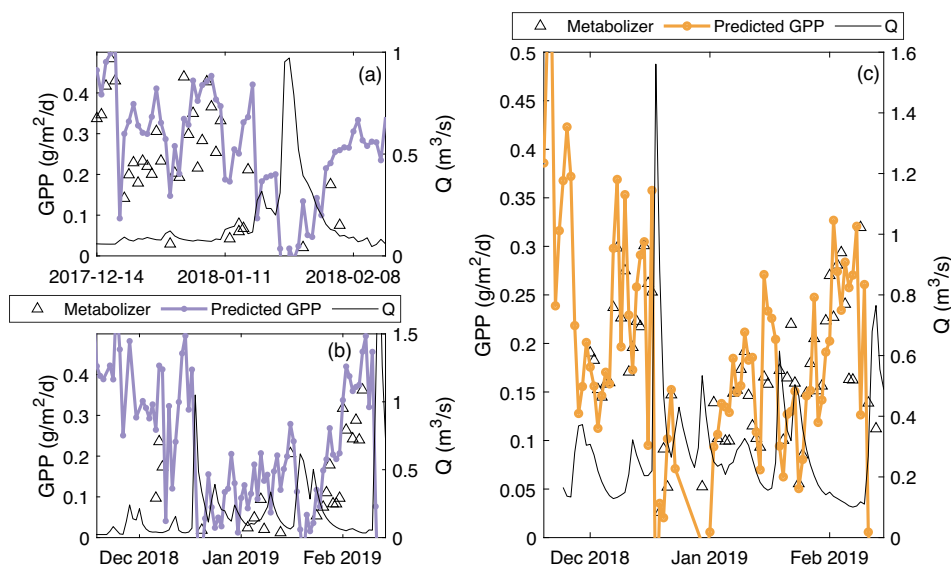
Other recent studies have shown that proxy metrics can be used to estimate GPP and identify spatial patterns in GPP in agricultural and glacial stream systems (Canadell et al., 2021; Diamond et al., 2021; Mulholland et al., 2005), but few proxy metric assessments have been made in forested headwaters, which are often highly shaded and have small daily fluctuations in DO saturation, making them difficult systems in which to estimate GPP. Studies assessing proxy metrics for stream GPP have found the daily range in DO through the day (Canadell et al., 2021; Diamond et al., 2021; Mulholland et al., 2005) and stream depth (Diamond et al., 2021) to be effective metrics with more detailed aspects of daily light fluxes having been included less frequently (general measures of daily PAR or canopy cover have been more widely used) (e.g., Blaszczyk et al., 2023; Kirk et al., 2020; Munn et al., 2023). In our study, stream depth was a factor in some of our models, but it was not a consistently important metric across all top models. Diamond et al. (2021) suggested that the importance of depth in their proxy estimate

**FIGURE 6** Observed (Metabolizer) versus predicted GPP at Oak Creek using the best-supported models (Tables 2 and S4): (A) best model ( $\Delta AIC = 0$ ) with five explanatory variables:  $R^2$ , Depth, norm.ln, temp, hours.photo, and DO.range.photo; (B) second model ( $\Delta AIC = 0.64$ ) with three explanatory variables  $R^2$ , hours.photo, and DO.range.photo; (C) third-best model ( $\Delta AIC = 1.04$ ) with five explanatory variables:  $R^2$ , temp, hours.photo, DO.range.photo, D24h.DORange.depth; and (D) fourth-best model ( $\Delta AIC = 1.98$ ) with four explanatory variables:  $R^2$ , temp, hours.photo, and DO.range.photo. The cross-validation  $r^2$  ( $XCr^2$ ) is indicated. Solid line indicates the relationship between observed and predicted GPP, and the dashed line is a 1:1 relationship.

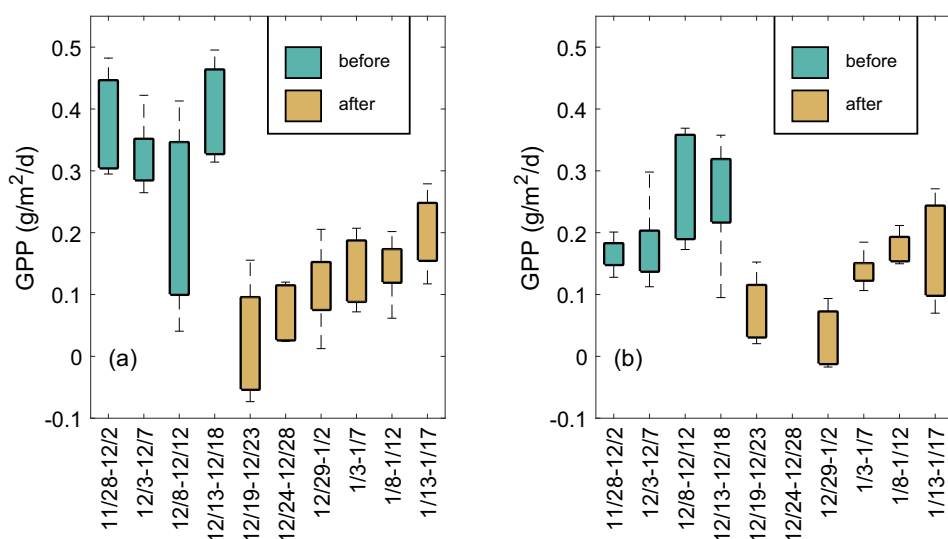


**FIGURE 7** Observed versus predicted GPP at South Fork Mill Creek using the best-supported models derived from the Oak Creek model selection (Figure 4, Table 2). (A) Best model with five explanatory variables:  $R^2$ , Depth, norm.ln, temp, hours.photo, and DO.range.photo; (B) second model with three explanatory variables:  $R^2$ , hours.photo, and DO.range.photo; (C) third-best model with five explanatory variables:  $R^2$ , temp, hours.photo, DO.range.photo, and D24h.DORange.depth; and (D) fourth-best model with four explanatory variables:  $R^2$ , temp, hours.photo, and DO.range.photo. Solid line indicates the relationship between observed and predicted GPP, and the dashed line is a 1:1 relationship.





**FIGURE 8** Estimates of GPP for Oak Creek (A,B) and South Fork Mill Creek (C) using stream metabolizer (open markers) and best linear model m.five.3 with covariates  $R^2$ , Depth, norm.ln, temp, hours.photo, and DO.range.photo (Table 1). GPP was predicted for 161 days in Oak Creek and for 81 days in South Fork Mill Creek.



**FIGURE 9** Pre- and post-storm GPP response at the Oak Creek (A) and South Fork Mill Creek (B) using model m.five.3 with covariates  $R^2$ , Depth, norm.ln, temp, hours.photo, and DO.range.photo (Table 1). Panels depict 5-day boxplots of median and interquartile GPP range.

models was likely due to the wide range of stream sizes included in their study, thereby increasing the range of depths and the relative influence of depth on GPP across their study streams. We focus on only two streams of comparable size, but during our focal period (winter), these sites had substantial fluctuations in stream flow, and we therefore attribute the inclusion of depth in one of our top models to the effects of high flow events on GPP (Cargill et al., 2021; Cronin et al., 2007; Katz et al., 2018; Segura et al., 2011) rather than as a result of a wide range of stream sizes and depths. Daily DOsat range was included within all four of our top AIC models in our study, but DO metrics and depth alone did not produce strong models to predict GPP. The AIC analysis indicated that the  $R^2$  of the fit between PAR and DOsat in the first part of the day was also an important predictor, more important in fact than stream temperature or water depth. Overall, we found that the collective use of DOsat-PAR curve metrics (slope, coefficient of determination, and DOrange) substantially improved the proxy GPP estimates in this system. Our findings

support the value and viability of using daily DO range and depth as a proxy for GPP as suggested by others; however, we found that light metrics were also important additional factors to include with daily DOsat range to improve GPP estimates in our forested headwater ecosystems.

Stream PAR data for this study was derived from a single measurement of light above the stream, which we acknowledge may not reflect reach-scale PAR or the amount of light reaching the stream benthos (Kirk et al., 2020). In forested streams, light may be spatially variable along a stream (Kaylor et al., 2017; Warren et al., 2013) and temporally variable over seasons (Hill & Dimick, 2002) or within a day (Heaston et al., 2017). The water column attenuates light exponentially due to scattering and absorbing of photons by water, water-soluble humic substances, tripton and phytoplankton (Kirk, 1994a), and although the depth of the water column is not large in headwater mountain streams, moderate and large floods may suspend silts and clays which can significantly reduce light penetration through the

water column (Davies-Colley et al., 1992; Davies-Colley & Smith, 2001; Kirk et al., 2020). Kirk et al. (2020) found that measurements of benthic light yield better estimates of GPP than those from the stream surface. Although our light measurement was from only one location and above the stream, it still clearly captured key seasonal light dynamics and the potential attenuation of light during and after storms manifested in a poor fit between PAR and DOsat and so was accounted for to some degree in our analysis (although it does not determine whether a poor fit was a result of light attenuation or loss of benthic biofilms). Although it is not a perfect reflection of light flux to the system, based on the AIC model results here, we suggest that a single measurement of PAR above the stream is a valuable raw data metric that should be logged along with stream depth and DO if researchers plan to conduct proxy estimates of GPP.

The specific models and model parameters developed for the current study are likely applicable for winter-season GPP estimates in forested low- and mid-order streams in western Oregon, Washington, and northern California because those areas have similar winter climate regimes and similar lithologies (Segura et al., 2020; Wissler et al., 2022). In other regions, we suggest that the GPP estimates derived from models in this study are likely to correctly reflect *relative* GPP rates, but they may produce inaccurate actual GPP estimates due to differences in temperature, light, and nutrient levels. Both temperature (Demars et al., 2011) and nutrient levels (Bernhardt et al., 2018) affect stream GPP and likely the slope of the DOsat–PAR relationship and the magnitude of the DO increase during the period of increasing morning light. However, even if the parameter values differ, we expect that the fundamental relationships will hold. Therefore, even if the use of metrics from this study may systematically overestimate or underestimate GPP, the use of these metrics to estimate a proxy GPP value can be used in pre- and post-analysis to quantify changes in processes following a disturbance or stream modification. An additional consideration in broader extrapolation of these metrics is changes in streamflow that substantially reduce water volume and can therefore affect water surface area to volume ratios. Depth is accordingly also an important consideration. While depth is included in two of our top models, at much lower summer flow, changes in surface area to volume in streams may more substantially influence the exchange of oxygen with the atmosphere and therefore the degree of DO saturation (Mulholland et al., 2001). This may in turn affect the slope of the DOsat–PAR relationship and the maximum DO saturation level. Although different temperatures, lithologies, and depths may affect the slope or max DO saturation levels, we expect the parameter for the fit of the relationship between DOsat and PAR at the start of the day ( $R^2$  value of the relationship between DOsat and PAR with PAR values from 0 to  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) to remain relatively robust. Finally, even though we demonstrated that three of the top four models were able to provide substantially more daily estimates of GPP than stream metabolizer, the models still yield one negative GPP estimate in Oak Creek and one to three negative GPP estimates in South Fork Mill Creek, all of which are impossible and would therefore need to be excluded. However, these numbers of negative (excluded) values are far lower than the number of days stream metabolizer

failed to provide an estimate (117 days in Oak Creek and 35 days in South Fork Mill Creek).

Overall, although specific values derived from this study's model parameter values may not be as directly applicable to all other systems, we suggest that the metrics themselves are valid in developing proxies, even if regional parameterization is required for more accurate estimates. This is because the metrics here not only are founded on strong empirical relationship between proxy estimates and those derived from stream metabolizer but also because the development of these metrics are grounded in a fundamental and well-established relationship between light and primary production. By focusing on light dynamics at the start of the day—beginning when there is no light—and running to a light exposure level restricted to the linear part of the PAR–DOsat curve, this framework should apply to both forested and shaded or more open systems. This is because all systems are light limited at the start of the day, and thus, GPP will increase with light. However, a new set of regional or seasonal parameters may need to be developed in order to generate accurate GPP estimates for other regions or at other times of year.

## 6 | CONCLUSION

We found that high-frequency measurements of DO saturation and light availability in streams together can yield strong proxy estimates for stream primary production and that the proxy estimates from these metrics can clearly identify ecosystem-level impacts to stream GPP. The AIC analysis identified four models to predict GPP in Oak Creek with similar statistical power. Three of these models performed well to predict GPP in South Fork Mill Creek. These models included coefficient of determination of the DOsat–PAR relationship ( $R^2$ ), the daily number of light hours (hours.photo), the full photoperiod range of DOsat (DO.range.photo), and two of the models included water temperature. The proxy metrics here did a good job of capturing the disruptive effects of storm events on GPP in these systems. The proxy metrics clearly identified impacts of a storm event on GPP with results that were comparable with the full GPP estimates from stream metabolizer (Cargill et al., 2021). For both sites, flow pulses generated a negative response in GPP, but the effect was stronger at Oak Creek. Even though the flow pulses appear to imprint a weaker signal on the GPP estimates at South Fork Mill Creek, the site-specific model is able to produce a time series of GPP that responds to both flow events. The proxy metrics also provided an advantage over the metabolizer GPP estimates because we were able to obtain data for every day. The proxy data provided continuous estimates that allowed for a clearer picture of GPP recovery following storm events. Overall, the ability to estimate total or relative GPP in forested headwater ecosystems opens opportunities to use simple instrumentation to assess seasonal and annual GPP trends as well as responses of forested headwater systems to disturbances such as floods, forest management, wind-throw events, ice storms, wildfire, urban/suburban development and flooding, as well as stream restoration efforts.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

Datasets of environmental variables used to model stream metabolism and the modeled stream metabolism results for two streams are available at the ScholarsArchive@OSU at <https://doi.org/10.7267/1v53k431f>.

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## REFERENCES

- Appling, A. P., Hall, R. O. Jr., Yackulic, C. B., & Arroita, M. (2018). Overcoming equifinality: Leveraging long time series for stream metabolism estimation. *Journal of Geophysical Research: Biogeosciences*, 123, 624–645. <https://doi.org/10.1002/2017jg004140>
- Bair, R. T., Segura, C., & Lorion, C. M. (2019). Quantifying restoration success of wood introductions to increase Coho Salmon Winter Habitat. *Earth Surface Dynamics Discuss.*, 2019, 1–19. <https://doi.org/10.5194/esurf-2019-10>
- Beaulieu, J. J., Arango, C. P., Balz, D. A., & Shuster, W. D. (2013). Continuous monitoring reveals multiple controls on ecosystem metabolism in a suburban stream. *Freshwater Biology*, 58, 918–937. <https://doi.org/10.1111/fwb.12097>
- Bernhardt, E. S., Heffernan, J. B., Grimm, N. B., Stanley, E. H., Harvey, J. W., Arroita, M., Appling, A. P., Cohen, M. J., McDowell, W. H., Hall, R. O. Jr., Read, J. S., Roberts, B. J., Stets, E. G., & Yackulic, C. B. (2018). The metabolic regimes of flowing waters. *Limnology and Oceanography*, 63, S99–S118. <https://doi.org/10.1002/lno.10726>
- Bernhardt, E. S., Savoy, P., Vlah, M. J., Appling, A. P., Koenig, L. E., Hall, R. O., Arroita, M., Blaszcak, J. R., Carter, A. M., Cohen, M., Harvey, J. W., Heffernan, J. B., Helton, A. M., Hosen, J. D., Kirk, L., McDowell, W. H., Stanley, E. H., Yackulic, C. B., & Grimm, N. B. (2022). Light and flow regimes regulate the metabolism of rivers. *Proceedings of the National Academy of Sciences*, 119, e2121976119. <https://doi.org/10.1073/pnas.2121976119>
- Blaszcak, J. R., Yackulic, C. B., Shriver, R. K., & Hall, R. O. Jr. (2023). Models of underlying autotrophic biomass dynamics fit to daily river ecosystem productivity estimates improve understanding of ecosystem disturbance and resilience. *Ecology Letters*, 26, 1510–1522. <https://doi.org/10.1111/ele.14269>
- Boston, H. L., & Hill, W. R. (1991). Photosynthesis–light relations of stream periphyton communities. *Limnology and Oceanography*, 36, 644–656. <https://doi.org/10.4319/lo.1991.36.4.0644>
- Bouman, H. A., Platt, T., Doblin, M., Figueiras, F. G., Gudmundsson, K., Gudfinnsson, H. G., Huang, B., Hickman, A., Hiscock, M., Jackson, T., Lutz, V. A., Mélin, F., Rey, F., Pepin, P., Segura, V., Tilstone, G. H., van Dongen-Vogels, V., & Sathyendranath, S. (2018). Photosynthesis–irradiance parameters of marine phytoplankton: Synthesis of a global data set. *Earth System Science Data*, 10, 251–266. <https://doi.org/10.5194/essd-10-251-2018>
- Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference*. Springer-Verlag.
- Canadell, M. B., Gómez-Gener, L., Cléménçon, M., Lane, S. N., & Battin, T. J. (2021). Daily entropy of dissolved oxygen reveals different energetic regimes and drivers among high-mountain stream types. *Limnology and Oceanography*, 66, 1594–1610. <https://doi.org/10.1002/lno.11670>
- Cargill, S. (2019). *The influence of lithology on stream metabolism in mountain systems*. Oregon State University.
- Cargill, S. K., Segura, C., Villamizar, S. R., & Warren, D. R. (2021). The influence of lithology on stream metabolism in headwater systems. *Ecology*, n/a, e2284. <https://doi.org/10.1002/eco.2284>
- Cronin, G., McCutchan, J. H. Jr., Pitlick, J., & Lewis, W. M. (2007). Use of shields stress to reconstruct and forecast changes in river metabolism. *Freshwater Biology*, 52, 1587–1601. <https://doi.org/10.1111/j.1365-2427.2007.01790.x>
- Davies-Colley, R. J., Hickey, C. W., Quinn, J. M., & Ryan, P. A. (1992). Effects of clay discharges on streams. *Hydrobiologia*, 248, 215–234. <https://doi.org/10.1007/BF00006149>
- Davies-Colley, R. J., & Smith, D. G. (2001). Turbidity suspended sediment, and water clarity: A Review1. *JAWRA Journal of the American Water Resources Association*, 37, 1085–1101. <https://doi.org/10.1111/j.1752-1688.2001.tb03624.x>
- Demars, B. L., Russell Manson, J., Ólafsson, J. S., Gíslason, G. M., Gudmundsdóttir, R., Woodward, G., Reiss, J., Pichler, D. E., Rasmussen, J. J., & Friberg, N. (2011). Temperature and the metabolic balance of streams. *Freshwater Biology*, 56, 1106–1121. <https://doi.org/10.1111/j.1365-2427.2010.02554.x>
- Diamond, J. S., Bernal, S., Boukra, A., Cohen, M. J., Lewis, D., Masson, M., Moatar, F., & Pinay, G. (2021). Stream network variation in dissolved oxygen: Metabolism proxies and biogeochemical controls. *Ecological Indicators*, 131, 108233. <https://doi.org/10.1016/j.ecolind.2021.108233>
- Forget, M.-H., Sathyendranath, S., Platt, T., Pommier, J., Vis, C., Kyewalyanga, M. S., & Hudon, C. (2007). Extraction of photosynthesis–irradiance parameters from phytoplankton production data: demonstration in various aquatic systems. *Journal of Plankton Research*, 29, 249–262. <https://doi.org/10.1093/plankt/fbm012>
- Fox, J., & Weisberg, S. (2019). *An {R} Companion to Applied Regression*. Thousand Oaks {CA}.
- Hall, R. O., & Hotchkiss, E. R. (2017). Chapter 34 – Stream metabolism. In G. A. Lamberti & F. R. Hauer (Eds.), *Methods in stream ecology* (pp. 219–233). Academic Press. <https://doi.org/10.1016/B978-0-12-813047-6.00012-7>
- Hall, R. O. Jr., & Ulseth, A. J. (2020). Gas exchange in streams and rivers. *WIREs Water*, 7, e1391. <https://doi.org/10.1002/wat2.1391>
- Heaston, E. D., Kaylor, M. J., & Warren, D. R. (2017). Characterizing short-term light dynamics in forested headwater streams. *Freshwater Science*, 36, 259–271. <https://doi.org/10.1086/691540>
- Hill, W. (1996). 5 - Effects of Light. In R. J. Stevenson, M. L. Bothwell, & R. L. Lowe (Eds.), *Algal Ecology* (pp. 121–148). Academic Press. <https://doi.org/10.1016/B978-012668450-6/50034-5>
- Hill, W. R., & Dimick, S. M. (2002). Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. *Freshwater Biology*, 47, 1245–1256. <https://doi.org/10.1046/j.1365-2427.2002.00837.x>
- Hornick, L. E., Webster, J. R., & Benfield, E. F. (1981). Periphyton production in an Appalachian Mountain Trout Stream. *The American Midland Naturalist*, 106, 22–36. <https://doi.org/10.2307/2425132>
- Jassby, A. D., & Platt, T. (1976). Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography*, 21, 540–547. <https://doi.org/10.4319/lo.1976.21.4.0540>
- Katz, S. B., Segura, C., & Warren, D. R. (2018). The influence of channel bed disturbance on benthic chlorophyll a: A high resolution

- perspective. *Geomorphology*, 305, 141–153. <https://doi.org/10.1016/j.geomorph.2017.11.010>
- Kaylor, M. J., Warren, D. R., & Kiffney, P. M. (2017). Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams. *Freshwater Science*, 36, 1–13. <https://doi.org/10.1086/690624>
- Kirk, J. T. O. (1994a). *Light and Photosynthesis in Aquatic Ecosystems* (2nd ed.). Cambridge University Press.
- Kirk, J. T. O. (1994b). Photosynthesis as a function of the incident light. In J. T. O. Kirk (Ed.), *Light and Photosynthesis in Aquatic Ecosystems* (pp. 271–313). Cambridge University Press. <https://doi.org/10.1017/CBO9780511623370.012>
- Kirk, L., Hensley, R. T., Savoy, P., Heffernan, J. B., & Cohen, M. J. (2020). Estimating benthic light regimes improves predictions of primary production and constrains light-use efficiency in streams and rivers. *Ecosystems*, 24, 825–839. <https://doi.org/10.1007/s10021-020-00552-1>
- Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of Statistical Software*, 28, 1–26. <https://doi.org/10.18637/jss.v028.i05>
- Mazerolle, M. J. (2023). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.2. doi: <https://cran.r-project.org/package=AICcmodavg>
- McCutchan, J. H. J., & Lewis, W. M. J. (2002). Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*, 47, 742–752. <https://doi.org/10.4319/lo.2002.47.3.0742>
- Mulholland, P. J., Fellows, C. S., Tank, J. L., Grimm, N. B., Webster, J. R., Hamilton, S. K., Martí, E., Ashkenas, L., Bowden, W. B., Dodds, W. K., McDowell, W. H., Paul, M. J., & Peterson, B. J. (2001). Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology*, 46, 1503–1517. <https://doi.org/10.1046/j.1365-2427.2001.00773.x>
- Mulholland, P. J., Houser, J. N., & Maloney, K. O. (2005). Stream diurnal dissolved oxygen profiles as indicators of in-stream metabolism and disturbance effects: Fort Benning as a case study. *Ecological Indicators*, 5, 243–252. <https://doi.org/10.1016/j.ecolind.2005.03.004>
- Munn, M. D., Konrad, C. P., Miller, M. P., & Jaeger, K. (2023). A comparison of spatial and temporal drivers of stream metabolism. *Freshwater Biology*, 68, 1751–1764. <https://doi.org/10.1111/fwb.14163>
- Platt, T., Gallegos, C. L., & Harrison, W. G. (1980). Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research*, 38(4), 1159–1170. [https://doi.org/10.1016/0198-0149\(82\)90087-5](https://doi.org/10.1016/0198-0149(82)90087-5)
- Roberts, B. J., Mulholland, P. J., & Hill, W. R. (2007). Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems*, 10, 588–606. <https://doi.org/10.1007/s10021-007-9059-2>
- Ryther, J. H. (1956). Photosynthesis in the ocean as a function of light intensity. *Limnology and Oceanography*, 1, 61–70. <https://doi.org/10.4319/lo.1956.1.1.0061>
- Sand-Jensen, K. (1997). Broad-scale comparison of photosynthesis in terrestrial and aquatic plant communities. *Oikos*, 80, 203–208. <https://doi.org/10.2307/3546536>
- Segura, C., Bladon, K. D., Hatten, J. A., Jones, J. A., Hale, V. C., & Ice, G. G. (2020). Long-term effects of forest harvesting on summer low flow deficits in the Coast Range of Oregon. *Journal of Hydrology*, 585, 124749. <https://doi.org/10.1016/j.jhydrol.2020.124749>
- Segura, C., McCutchan, J. H., Lewis, W. M., & Pitlick, J. (2011). The influence of channel bed disturbance on algal biomass in a Colorado mountain stream. *Ecohydrology*, 4, 411–421. <https://doi.org/10.1002/eco.142>
- Staeher, P. A., Brighenti, L. S., Honti, M., Christensen, J., & Rose, K. C. (2016). Global patterns of light saturation and photoinhibition of lake primary production. *Inland Waters*, 6, 593–607. <https://doi.org/10.1080/IW-6.4.888>
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Ulseth, A. J., Hall, R. O., Boix Canadell, M., Madinger, H. L., Niayifar, A., & Battin, T. J. (2019). Distinct air–water gas exchange regimes in low- and high-energy streams. *Nature Geoscience*, 12, 259–263. <https://doi.org/10.1038/s41561-019-0324-8>
- Wagenmakers, E.-J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11, 192–196. <https://doi.org/10.3758/BF03206482>
- Walker, G. W., & MacLeod, N. S. (1991). Geologic map of Oregon: U. S. Geological Survey, scale 1:500,000, 2 sheets. U. S. Geological Survey.
- Warren, D. R., Keeton, W. S., Bechtold, H. A., & Rosi-Marshall, E. J. (2013). Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. *Aquatic Sciences*, 75, 547–558. <https://doi.org/10.1007/s00027-013-0299-2>
- Wissler, A. D., Segura, C., & Bladon, K. D. (2022). Comparing headwater stream thermal sensitivity across two distinct regions in Northern California. *Hydrological Processes*, 36, e14517. <https://doi.org/10.1002/hyp.14517>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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