

# Dissolved organic carbon concentration controls benthic primary production: Results from in situ chambers in north-temperate lakes

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## Abstract

We evaluated several potential drivers of primary production by benthic algae (periphyton) in north-temperate lakes. We used continuous dissolved oxygen measurements from in situ benthic chambers to quantify primary production by periphyton at multiple depths across 11 lakes encompassing a broad range of dissolved organic carbon (DOC) and total phosphorous (TP) concentrations. Light-use efficiency (primary production per unit incident light) was inversely related to average light availability (% of surface light) in 7 of the 11 study lakes, indicating that benthic algal assemblages exhibit photoadaptation, likely through physiological or compositional changes. DOC alone explained 86% of the variability in log-transformed whole-lake benthic production rates. TP was not an important driver of benthic production via its effects on nutrient and light availability. This result is contrary to studies in other systems, but may be common in relatively pristine north-temperate lakes. Our simple empirical model may allow for the prediction of whole-lake benthic primary production from easily obtained measurements of DOC concentration.

Ecosystem primary production plays an important role in governing the production of higher trophic levels (Lindeman 1942; Blanchard et al. 2012). Lakes are often used as discrete ecosystems to provide insights into the dynamics of ecosystem production (e.g., Carpenter et al. 1985). Though lake primary production was historically viewed as mostly phytoplankton-based, benthic algae (periphyton) make sizeable contributions to whole-lake primary production, particularly in shallow and clearwater lakes where periphyton dominate whole-lake production (Vadeboncoeur et al. 2001, 2003; Ask et al. 2009b). Stable isotope analyses have shown that benthic energy sources are also crucial to benthic invertebrates and fish (Hecky and Hesslein 1995). Despite the importance of periphyton to whole-lake production and the reliance of higher trophic levels on benthic production, it is only recently that benthic metabolism has been considered in lake ecosystem models (Vadeboncoeur et al. 2008; Jones et al. 2012; Jäger and Diehl 2014).

Controls of benthic primary production are not universal across lakes. Where nutrient availability is naturally high or elevated due to anthropogenic inputs, phytoplankton biomass can regulate light availability and benthic primary production (Hansson 1992; Vadeboncoeur et al. 2003). Conversely, in cold, low-nutrient lakes where terrestrial organic matter often governs light availability, benthic production is driven by the concentration of chromophoric dissolved organic matter, which is often strongly correlated with, and measured as, dissolved organic carbon (DOC) concentration (Ask et al. 2009a). In the world's largest lakes, nutrient status may determine benthic production in nearshore waters, while steep

bathymetry reduces the relative contribution of periphyton to whole-lake production further offshore (Althouse et al. 2014). But these descriptions only represent the extreme ends of a lake type continuum and the controls of benthic production in intermediate lake types are unknown. Pristine north-temperate lakes constitute an ideal set of intermediate lake types because they encompass a wide range of DOC concentrations, have intermediate production, and experience cold winter and warm summer temperatures. We use the term 'pristine' here to describe lakes without significant human modifications of shoreline or the watershed.

Recent conceptual syntheses describe how light and nutrient availability regulate benthic contributions to whole-lake primary production. Vadeboncoeur et al. (2008) modeled the proportional contribution of benthic algae to whole-lake primary production across a wide range of lake types and established that maximum periphyton contribution was determined by light availability at depth and the ratio of mean depth to maximum depth. Expanding on these concepts, Jones et al. (2012) developed a model that quantified the potential reduction in periphyton production as dissolved organic carbon inputs increased. Recently, Jäger and Diehl (2014) modeled the competitive interactions between benthic and pelagic primary producers across habitat boundaries, and validated their model using whole-lake production data from 27 lakes. These conceptual advances highlight the mechanistic processes crucial to primary production in lakes and demonstrate the importance of benthic production in these systems. However, they do not allow for straightforward estimations of benthic production for individual lakes, nor do they provide empirical evidence for the effects of light attenuation determinants on benthic production.

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Table 1. Physical and chemical characteristics of the study lakes. Abb. is the lake name abbreviation,  $z_{\max}$  is the maximum depth of the lake,  $z_{\text{mean}}$  is the mean depth of the lake, DOC is dissolved organic carbon concentration, Color is the water color measured as absorption of light at 440 nm,  $K_D$  is the light extinction coefficient, Chl *a* is the chlorophyll *a* concentration, and TP is the total phosphorus concentration.

Lake	Abb.	Surface area (km <sup>2</sup> )	$z_{\max}$ (m)	$z_{\text{mean}}$ (m)	DOC (mg L <sup>-1</sup> )	Color (m <sup>-1</sup> )	$K_D$ (m <sup>-1</sup> )	Chl <i>a</i> ( $\mu\text{g L}^{-1}$ )	TP ( $\mu\text{g L}^{-1}$ )
Bay	BA	0.697	12.2	4.2	6.3	2.4	1.2	4.9	12.8
Bergner	BE	0.162	11.9	3.7	8.5	2.8	1.3	12.1	20.1
Brown	BR	0.296	4.9	2.7	5.4	1.8	1.4	7.4	69.0
Crampton	CR	0.259	18.5	5.0	4.7	1.6	0.9	2.2	6.4
East Long	EL	0.032	14.0	4.0	10.5	6.4	2.4	7.9	16.2
Hummingbird	HB	0.008	7.7	3.4	20.5	14.6	5.6	21.0	37.2
Inkpot	IN	0.067	5.2	2.9	8.2	2.3	1.2	11.0	27.9
Morris	MO	0.059	6.7	2.4	18.8	6.1	2.6	11.9	35.7
Raspberry	RB	0.042	6.1	3.0	7.4	2.7	1.6	6.6	23.0
Reddington	RE	0.046	16.0	2.5	22.2	15.1	4.8	11.4	38.3
West Long	WL	0.049	14.0	3.9	6.5	3.0	1.4	5.3	15.2

Understanding the responses of lake processes to environmental changes is important given global shifts in nutrient availability (Bennett et al. 2001), DOC concentration (Monteith et al. 2007), and other factors. Benthic organisms in lakes may stand to be particularly affected by such shifts because they are often sedentary and highly influenced by the environmental conditions of the water column above them. Photosynthetic benthic organisms, in particular, have the potential to respond to shifts in light availability caused by algal shading or DOC concentration. Many algal assemblages, from those associated with corals in the Red Sea (Porter et al. 1984) to those underneath sea ice in the Antarctic (Palmisano et al. 1986), exhibit photoadaptation through physiological or compositional changes that influence their light-use efficiency at different levels of light availability. To our knowledge, no evidence has been presented supporting or disproving photoadaptation of lake periphyton.

Here, we evaluated several potential drivers of benthic primary production in a set of pristine north-temperate lakes, and assessed the evidence for photoadaptation of benthic algal assemblages within these lakes. We used a novel benthic chamber method for efficiently collecting large amounts of in situ periphyton production data. We hypothesized that DOC would be the best predictor of benthic production because it is the primary driver of light climate in this lake region. We also hypothesized that the efficiency with which benthic algae use incident light would increase with depth, because deeper algal assemblages would differ compositionally or physiologically from those in shallower waters.

## Methods

*Study site and timing*—The 11 study lakes are located at the University of Notre Dame Environmental Research Center on the Michigan–Wisconsin border, USA (46°13'N, 89°32'W). The morphometry and limnology of the lakes are highly varied. Surface area ranges from 0.008 km<sup>2</sup> to 0.697 km<sup>2</sup> and maximum depth from 4.9 m to 18.5 m. DOC varies between 4.7 mg L<sup>-1</sup> and 22.2 mg L<sup>-1</sup> and total

phosphorous (TP) between 6.4  $\mu\text{g L}^{-1}$  and 69.0  $\mu\text{g L}^{-1}$ . The substrate in all of these lakes is dominated by unconsolidated organic matter, sometimes as a thin layer over sand but more often as thick deposits, especially at deeper sites. A few of our deployment sites contained gravel and fine woody debris, but none had sizeable rocks or large woody debris. See Table 1 for more detailed lake descriptions.

Data collection occurred in seven of the lakes between June and August in 2012, and in four of the lakes between May and July in 2013. Each lake was sampled three times in 2012, with each sampling period occurring 2–4 weeks after the previous one. The four lakes visited in 2013 were each sampled twice, again 2–4 weeks apart.

*Data collection*—We used benthic chambers to estimate in situ rates of benthic primary production. We constructed the chambers using half-ellipsoid clear acrylic skylights (EZ Tops World Wide) weighted with steel chains (Fig. 1). The acrylic domes were adhered to 0.75 m  $\times$  0.75 m sheets of polyvinyl chloride shower pan liner of 1 mm thickness, each with a 0.38 m diameter circular section excised from the center. The domes absorbed < 3% of incident light in the photosynthetically active portion of the spectrum, and did not detectably focus the light. Dissolved oxygen (DO) concentration and temperature were measured and logged using small, self-contained optical sensors (miniDOT; Precision Measurement Engineering). These sensors have specified accuracies of  $\pm 0.3$  mg O<sub>2</sub> L<sup>-1</sup> and  $\pm 0.1$ °C. The sensors were attached to the interiors of the chambers using Velcro® and were programmed to record data every 5 min (2012) or 10 min (2013). Immediately before and after deployments, loggers were placed in vapor-saturated air for 0.75–1.25 h at a stable temperature. In each case, the DO signal stabilized after 10–15 min. These data were used to correct for drift of the logger, which we assumed occurred linearly between calibration periods.

We placed benthic chambers at 5%, 25%, and 60% of surface light when possible. To calculate these light levels, we measured the photosynthetically active radiation (PAR) every 0.5 m in depth until the sensor reached the sediment

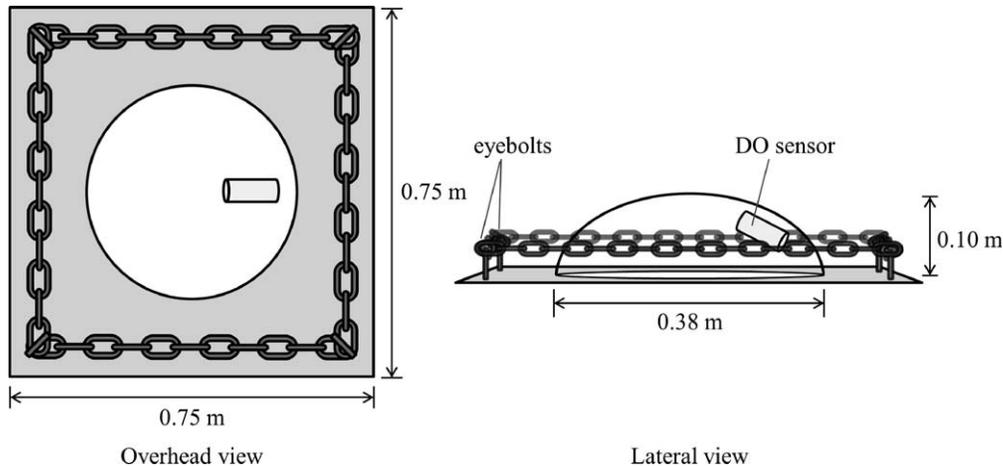


Fig. 1. Diagram of benthic chamber used to collect DO data for periphyton production calculations. The optical DO sensor logged the DO data and was adhered to the inside of the dome using Velcro<sup>®</sup>. The entire apparatus was weighted with steel chains attached to eyebolts in the corners of the apparatus. Benthic chambers were deployed by descent through the water column using a rope attached to the eyebolts.

or until light readings fell below 1% of the surface PAR. PAR measurements were taken using an underwater quantum PAR sensor (LI-192SA; LI-COR Biosciences) and light meter (LI-250A) lowered through the water column on a frame designed to keep the sensor facing the water surface. Light profiles were attained approximately once per month throughout the summer for each of the study lakes. The light attenuation coefficient ( $K_D$ ) for each profile was calculated using the standard method (Kirk 1994) and used to determine the deployment depths for specific light levels. When the lake bathymetry did not allow for deployment at 60% average light availability, chambers were deployed at the highest light level possible. When chamber deployments were not possible at either the 60% or 25% light levels, only two chambers were deployed and the remaining one was used to provide an additional data point in a lake with a broader depth–light gradient. Chambers were deployed for 3–7 d in each sampling period. No DO data were used from partial deployment days. We lowered the chambers very slowly to their deployment locations, using ropes attached to eyebolts, in order to minimize disturbance of the surface sediments.

We characterized lake-water chemistry from integrated samples of the upper mixed layer of each lake. We measured DOC using a total organic carbon analyzer (TOC-V; Shimadzu Scientific Instruments), TP by colorimetric assay after persulfate digestion (Menzel 1965), and chlorophyll *a* (Chl *a*) by methanol extraction and fluorometric analysis (Welschmeyer 1994). All water chemistry samples ( $n = 2$ –12 per lake-year) were taken within the range of deployment dates for a given lake.

**Daily estimates**—Daily benthic production rates were calculated by assessing the rate of change in DO using the method developed by Cole et al. (2000), modified for benthic metabolism by eliminating the term for diffusion exchange with the atmosphere (Fellows et al. 2006). We summarize these data with a standard Michaelis–Menten photosynthesis–irradiance ( $P$ – $I$ ) relationship fit by maxi-

mum likelihood (Turner et al. 1983). Traditionally, these relationships are constructed by incubating a single algal community in the lab at a series of controlled light levels. In contrast, in our in situ approach we embrace additional sources of variability such as spatial heterogeneity in algal communities and day-to-day variation in the light climate experienced by a given algal community. Consequently, the photosynthesis at a given light level is more variable in our data than in traditional assays, and the  $P$ – $I$  parameters are not always well-constrained. We calculated light-use efficiencies by dividing the daily benthic primary production estimates by the cumulative daily incident PAR; note that this quantity is the assemblage-level efficiency,  $\iota$ , described in Solomon et al. (2013), not the biomass-specific efficiency,  $\alpha$ , commonly estimated in lab-based culture experiments. Simple linear regression analyses were used to compare the light-use efficiencies to average light availability and DOC concentration, and the log-transformed  $P$ – $I$  parameters ( $p$ Max, and the half-saturation constant,  $K$ ) to DOC concentration and each other. We also assessed light-use efficiencies for strong positive or negative trends over the course of each deployment to determine whether our chamber method of measuring benthic production was imparting any strong container effects. Light-use efficiencies were used for this analysis rather than production estimates to eliminate confounding cloud cover effects.

The final data set included 28–40 daily benthic production estimates for each of the 11 study lakes. Every estimate represents a single day of primary production by periphyton at a particular site. Light received at a site over a day of deployment was estimated from the percentage of surface light reaching the benthic chambers based on calculations of light attenuation in each lake at chamber deployment, and measured surface light at a meteorological station within 5 km of all lakes. The actual incident light varied depending on daily and seasonal weather patterns.

**Whole-lake estimates**—We estimated whole-lake production rates for each of our 11 study lakes. For every set of

deployments in a single lake, production estimates were linearly interpolated at 0.5 m depth intervals from the mean daily rates at a given deployment depth. Benthic production  $\leq 1\%$  of surface light availability was assumed to be zero and production at a depth of 0 m was assumed to occur at the same rate as production at the minimum deployment depth. The product of the benthic production estimates for each 0.5 m depth interval and the sediment area within that interval were summed across all depths. The resulting cumulative production estimate was divided by the sediment area of the entire lake to give whole-lake benthic primary production per unit area.

We used model selection to determine which combination of four lake characteristics best predicted our whole-lake production estimates. The lake characteristics considered are commonly measured in limnological surveys and describe the light climate of lakes (DOC and Chl *a*), nutrient availability (TP), and periphyton habitat availability (depth ratio, as a descriptor of lake bathymetry). We fit linear models to the log-transformed whole-lake production estimates using all 16 additive combinations of these parameters. We performed model selection using Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ; Hurvich and Tsai 1989). The relative importance of the four explanatory variables was calculated by summing the Akaike weights over all the models containing the variable in question (Burnham and Anderson 2002). All analyses were performed in R version 3.0.1 (R Foundation for Statistical Computing 2013) and model selection was done using the MuMIn package.

## Results

Diel oxygen curves exhibited the expected patterns of net oxygen production during daylight hours and net oxygen consumption at night (Fig. 2). The amplitude of the curves was related to light availability; the largest DO excursions occurred on sunny days and at shallow depths. There was no evidence that enclosing the sediment altered conditions in such a way as to directionally change production over the course of deployments; light-use efficiency declined significantly across the deployment period only once in 94 deployments and increased significantly in four deployments.

Rates of benthic primary production varied within and among lakes (Fig. 3). Minimum rates ranged from 0 mg C m<sup>-2</sup> d<sup>-1</sup> to 156 mg C m<sup>-2</sup> d<sup>-1</sup> across the 11 study lakes, and maximum rates ranged from 350 mg C m<sup>-2</sup> d<sup>-1</sup> to 2270 mg C m<sup>-2</sup> d<sup>-1</sup>. Despite the fact that we measured primary production under field conditions, our results generally followed expected *P-I* relationships as measured in controlled laboratory settings; photosynthesis increased rapidly with light at low light levels, and saturated at higher light levels. The variability in the measured rates meant that *P-I* parameter estimates were uncertain (average of  $\pm 280\%$  for *pMax* and  $\pm 1160\%$  for *K*). Although our *P-I* parameter estimates should therefore be interpreted with caution, we noted a positive relationship between the log-transformed *pMax* and *K* estimates ( $p < 0.001$ ) and a negative relationship between log-transformed *pMax* and

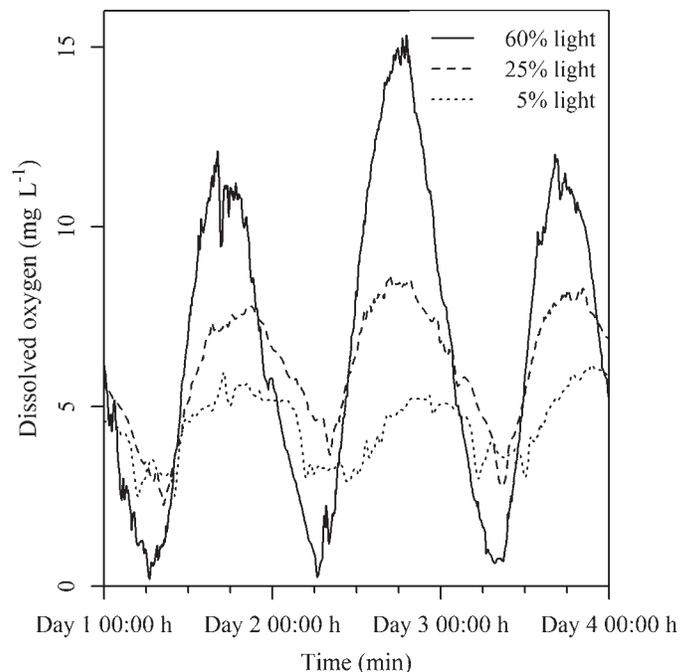


Fig. 2. Typical diel oxygen curves obtained from DO loggers in three benthic chambers. These data were measured in chambers deployed concurrently for three complete days at different average light availabilities within a single lake.

DOC ( $p = 0.006$ ), consistent with the idea that photosynthetic capacity of benthic algal assemblages is limited by background light attenuation.

The light-use efficiencies of benthic algal assemblages were negatively related to average light availability in 7 of the 11 lakes (Fig. 4). The slopes of this relationship varied from  $-50$  mg C mol<sup>-1</sup> to  $-485$  mg C mol<sup>-1</sup> (mol = one mole of photons); in other words, the light-use efficiency in these lakes increased by 50–485 mg C mol<sup>-1</sup> for every percentage point reduction in average light climate.

Whole-lake benthic primary production was controlled primarily by the effect of DOC on light availability (Fig. 5). DOC was highly correlated with water color ( $R^2 = 0.84$ ,  $p < 0.001$ ), and therefore dictated lake-light climate as summarized by the light extinction coefficient  $K_D$  ( $R^2 = 0.85$ ,  $p < 0.001$ ); algal biomass, as measured by Chl *a* concentration, did not explain any additional variation in lake light climate ( $p > 0.100$ ; see Table 1). Whole-lake production estimates varied between 9.3 mg C m<sup>-2</sup> d<sup>-1</sup> and 286.4 mg C m<sup>-2</sup> d<sup>-1</sup>. DOC alone explained 86% of the variability in the log-transformed whole-lake production rates. Other models with moderate support included a DOC term together with depth ratio ( $\Delta AIC_c = 2.44$ ), Chl *a* ( $\Delta AIC_c = 4.72$ ), or TP ( $\Delta AIC_c = 5.18$ ), although the additional variability explained was small and did not justify the inclusion of additional parameters in the model (Table 2). DOC was the most important predictor of benthic production with a relative importance of 99.8%, followed by depth ratio (21.2%). Chl *a* and TP were the least important explanatory variables (7.3% and 6.1%). The signs of the additional parameters indicate that benthic production rates are higher when lakes have

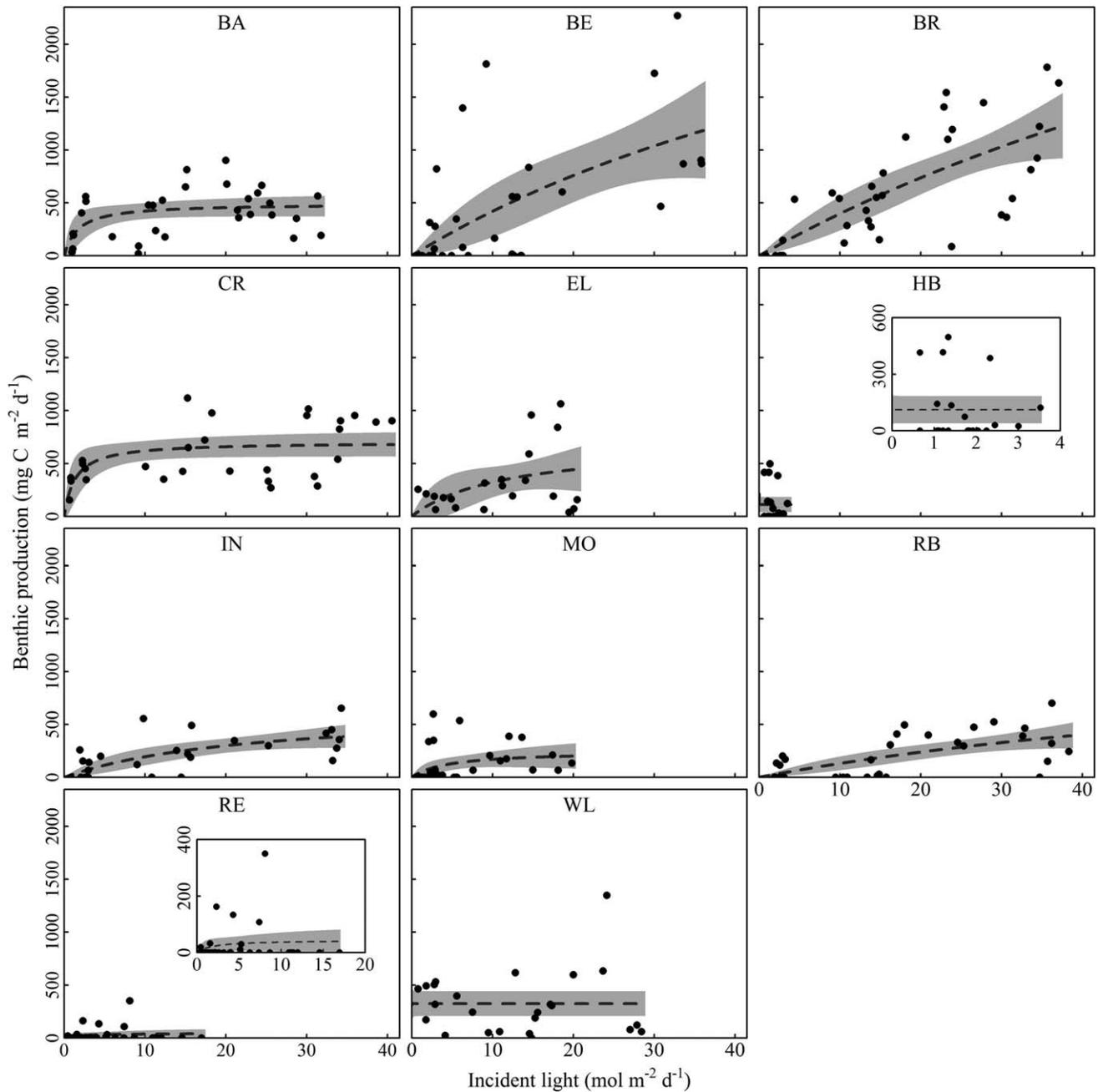


Fig. 3. Benthic primary production data fit with  $P-I$  curves. Each panel shows data for a single lake and each point represents periphyton production for a single day of deployment. Panel titles correspond to the lake name abbreviations listed in Table 1. Incident light refers to the light reaching the sediment surface. Insets display data at a higher resolution for the two darkest lakes, where the range of incident light and benthic production was smallest. Ninety-five percent prediction intervals were constructed for the  $P-I$  curves using the delta method. Benthic chambers were deployed at intervals throughout the summer and experienced daily variation in cloud cover.

larger shallow areas or when nutrient availability and phytoplankton biomass are lower.

## Discussion

*Methodological considerations and comparisons to previous benthic production estimates*—The rates of benthic primary production that we measured in situ were similar to those reported by previous authors who used much more

labor-intensive core incubation methods. For depths between 1 m and 2 m, our rates ranged between 0 mg C m<sup>-2</sup> d<sup>-1</sup> and 1120 mg C m<sup>-2</sup> d<sup>-1</sup>. In comparison, Vadeboncoeur et al. (2001) reported rates between 36 mg C m<sup>-2</sup> d<sup>-1</sup> and 2640 mg C m<sup>-2</sup> d<sup>-1</sup> at 1.5 m in depth for four lakes in the same region as our study lakes, three of which were artificially fertilized and all of which had a DOC concentration < 15.0 mg L<sup>-1</sup>. At the whole-lake level, our rates ranged from 9.3 C m<sup>-2</sup> d<sup>-1</sup> to 286.4 C

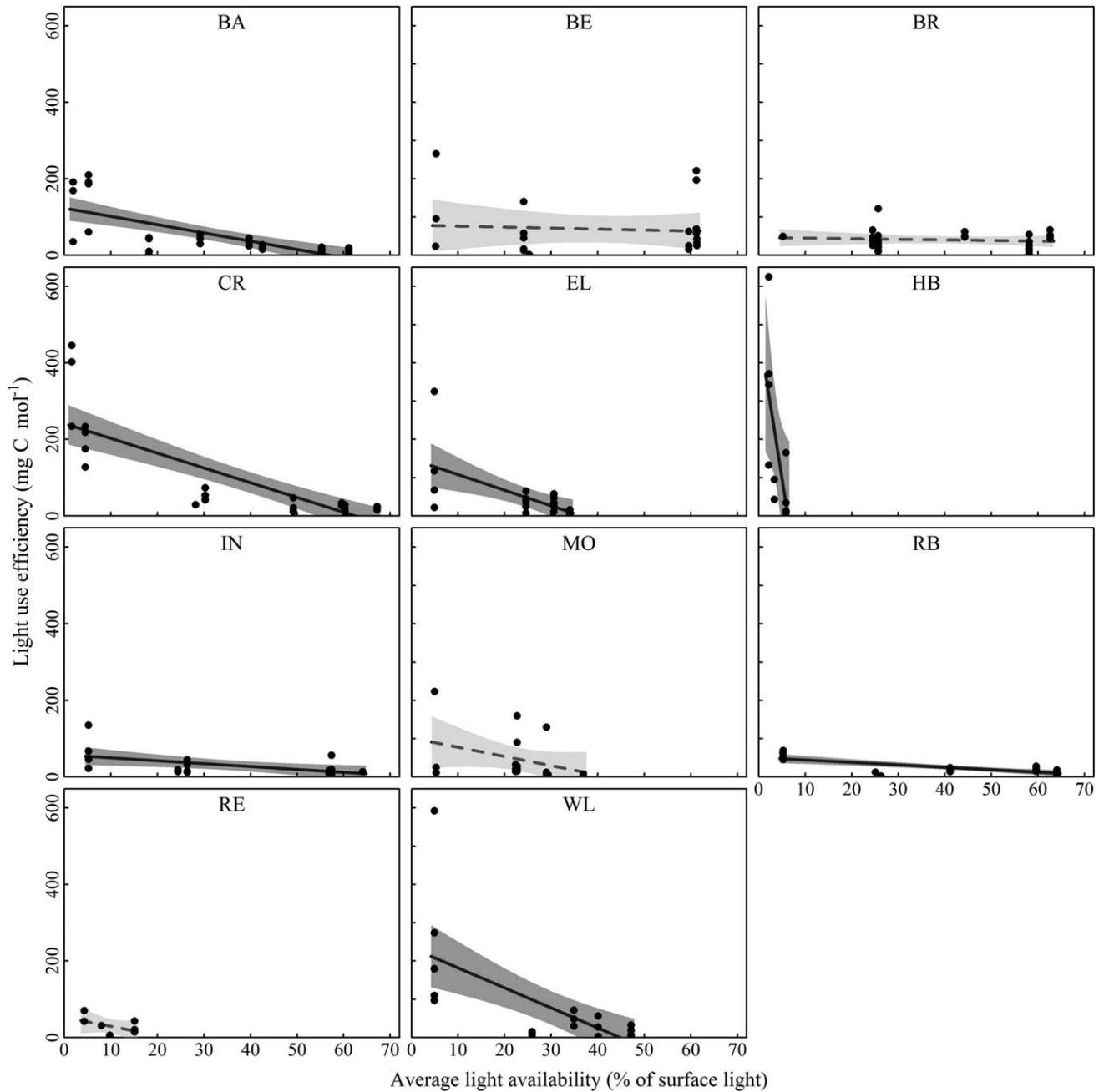


Fig. 4. Photoadaptation of benthic algal assemblages. Each panel shows data for a single lake and the panel titles correspond to the lake name abbreviations listed in Table 1. Lakes where periphyton assemblage-level (not biomass-specific) light-use efficiency declines significantly with average light availability have solid regression lines and dark grey 95% prediction intervals. Those with non-significant declines have dashed regression lines and light grey prediction intervals.

$\text{m}^{-2} \text{d}^{-1}$ , which is similar to the range of  $0.7 \text{ C m}^{-2} \text{d}^{-1}$  to  $195.8 \text{ C m}^{-2} \text{d}^{-1}$  reported in 15 small, unproductive Swedish lakes (Ask et al. 2009a). Our rates are also comparable with the range of 13–878  $\text{mg C m}^{-2} \text{d}^{-1}$  compiled from published estimates for 23 lakes of diverse morphometry, nutrient states, and disturbance regimes (Vadeboncoeur et al. 2002). Though dark lakes were not well-represented in these 23 lakes and the values overestimate periphyton production because they incorporate macrophyte production, our whole-lake production esti-

mates fall within this range for all but our darkest study lake ( $9.3 \text{ mg C m}^{-2} \text{d}^{-1}$ ).

Given the similarity between our rates and other published values, our chamber-based method may be attractive because of its ability to generate many estimates with comparatively little effort and cost. Benthic chambers have long been used to measure metabolic processes of benthic organisms in aquatic environments, but these are usually complex and expensive structures. Much of the complexity required for such designs results from the need

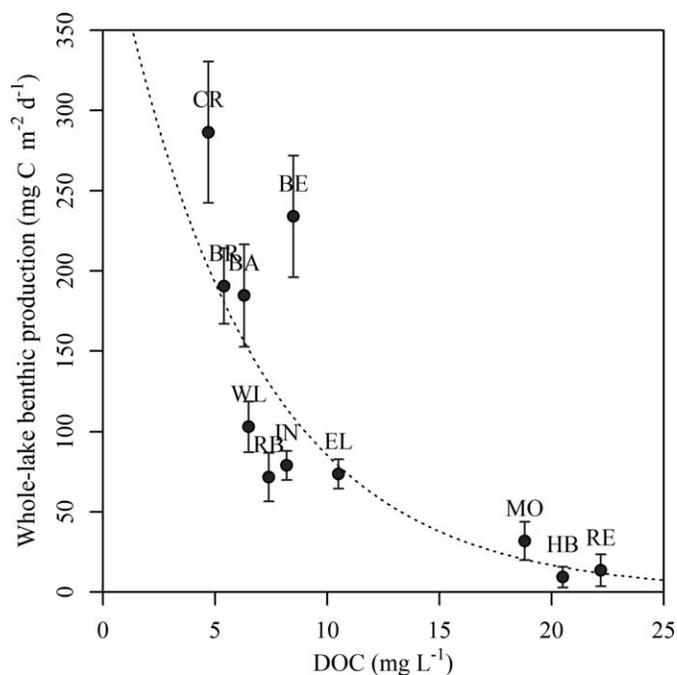


Fig. 5. Whole-lake benthic primary production as a function of lake DOC concentration. The fitted line uses the parameter coefficients from the top log-linear model (Model 1 in Table 2). Whole-lake production estimates were averaged across all deployment dates; error bars show the standard errors for the mean values.

to overcome heavy flow, simulate tidal currents, prevent vertical stratification in the enclosed water, or eliminate bubbles formed from excessive photosynthesis by macrophytes. All of these considerations are less critical when dealing with lake periphyton than with other photosynthetic organisms in river or marine benthic communities. In our study, we chose a very simple benthic chamber design in order to facilitate a relatively large number of easily deployed experimental units that could be installed in remote lakes. The simplicity and low-cost elements of our design come with potential trade-offs in performance, and would likely not be suitable for measuring benthic metabolism in flowing waters or where metabolic rates are extremely high.

One noteworthy feature lacking from our chambers but common in those used in marine environments is a stirring mechanism. The importance of intra-chamber stirring

during deployment was historically debated (Cahoon 1988 and citations therein), and more recently the influence of site sediment characteristics, stirrer design, and stirring rate on the diffusive boundary layer and therefore sediment exchange has been explored in great depth (e.g., Broström and Nilsson 1999). Combined, this work suggests that, when carefully tailored to local current velocities, sediment characteristics, and other conditions, stirring can provide a more accurate picture of instantaneous sediment–water exchange. These practices have been adopted by a number of groups working in the marine environment (Tengberg et al. 1995). On the other hand, intense site-specific calibration would preclude even moderate cross-site comparative studies, particularly with the financial and personnel resources typically available to freshwater ecologists working on these questions.

Fortunately, we have four reasons to believe that a lack of stirring did not strongly bias our estimates of benthic primary production. (1) Most importantly, our benthic production estimates were similar to those measured by previous authors using sediment core incubations in similar lakes, as described at the beginning of this section. (2) Our calculation of benthic primary production depends on the change in the DO concentration over 24 h rather than on the DO concentration itself. Although a lack of stirring likely generated a DO concentration gradient extending from the sediment to the sensor, we expect that this gradient slows the response time of the sensor (just as the gas-permeable coating on the sensor detector does) but not the temporal pattern of change in DO. (3) We found no evidence of directional changes in biological activity across our deployments, and therefore infer that a lack of stirring did not fundamentally alter the biological activities of benthic communities at the scales we measured. (4) Sadro et al. (2011) reported minimal effects of stirring on metabolism estimates in similar benthic chambers in lakes.

*Photoadaptation*—We found evidence for photoadaptation of benthic assemblages (Fig. 4). The negative relationship observed between light-use efficiency and average light climate indicates that deeper periphyton are better adapted for photosynthesizing in low-light environments within these systems. We cannot attribute this result to any particular mechanism without further inquiry, though depth-specific compositional and physiological differences between algal assemblages (e.g., chlorophyll concentration) are two plausible explanations. It is interesting to note that

Table 2. Coefficient values and model selection statistics for linear models fit to the log-transformed whole-lake production data. Terms used were chlorophyll *a* (Chl *a*) concentration, depth ratio (DR), dissolved organic carbon (DOC), and total phosphorous (TP). Statistics shown are the differences from the top model  $\Delta AIC_c$  ( $\Delta AIC_c$ ), Akaike model weights ( $w_i$ ), and  $R^2$ . Models are ordered by  $\Delta AIC_c$ . Only models within 8  $AIC_c$  units of the top model are reported here; the unreported 12 models cumulatively accounted for < 2% of model support. For the top model, the standard errors of the parameters were 0.28 for the intercept and 0.022 for the DOC main effect, and the residual standard error was 0.45.

Rank	Intercept	Chl <i>a</i>	DR	DOC	TP	$\Delta AIC_c$	$w_i$	$R^2$
1	6.07	—	—	−0.163	—	0.00	0.671	0.86
2	6.79	—	−1.67	−0.172	—	2.44	0.198	0.89
3	6.15	−0.028	—	−0.146	—	4.72	0.063	0.86
4	6.11	—	—	−0.161	−0.002	5.18	0.050	0.86

the biomass-specific light-use efficiency probably decreases even more steeply with light climate than does the assemblage-level light-use efficiency,  $\iota$ , because the high-light sites with low  $\iota$  also probably have higher periphyton biomass (Hansson 1992). We also observed a significant positive relationship among lakes between the photosynthetic capacity ( $p\text{Max}$ ) and the half-saturation constant ( $K$ ). Although the estimates of  $p\text{Max}$  and  $K$  were uncertain and the relationship between them should be interpreted with caution, it suggests that lakes in which benthic algae can sustain high primary production at high light levels also have a smaller range of light levels at which high production rates can be sustained.

*DOC controls benthic primary production*—The importance of DOC concentration to benthic primary production was confirmed by model selection. DOC alone was a strong predictor of periphyton production, explaining 86% of the variability in the log-transformed production data. The DOC-only model was the top model when performing model selection using  $AIC_c$ . DOC was by far the most important predictor of benthic production, with a relative variable importance 4.7 times higher than the next best predictor (depth ratio) and 16.4 times higher than TP. This result is intuitive because DOC is the primary driver of light climate in these systems, accounting for 66–86% of light attenuation in all but one of the study lakes (calculated using the equation from Jones et al. (2012) for the light attenuation coefficient,  $K_D$ ). It is unsurprising, therefore, that we observed a negative relationship between the log-transformed  $p\text{Max}$  estimates and DOC, indicating that lakes with higher DOC concentrations had lower photosynthetic capacities. The second-best model included a depth-ratio term with a highly negative coefficient, reflecting the fact that the availability of shallow, well-lit habitats can also limit whole-lake benthic primary production (Vadeboncoeur et al. 2008).

Our results suggest that in relatively pristine north-temperate lakes, as in arctic lakes (Ask et al. 2009a), DOC and not TP may be the primary control on benthic primary production rates due to its effect on light availability. Both TP and Chl  $a$  slightly reduced benthic production in other considered models, but these had considerably less empirical support than the top model, which contained neither of these parameters. Although the signs of these parameters are consistent with the idea that phytoplankton biomass can limit periphyton production, these processes do not seem to be very important in regulating benthic production in these lakes. The lack of a TP effect on benthic production is likely a result of its relatively low effect on light availability; algal shading only accounts for 12–30% of light attenuation in all but one of our study lakes. This result is contrary to studies in lakes where nutrient availability is high and phytoplankton biomass determines periphyton production; therefore, this raises the question of how representative the nutrient compositions of our study lakes are in comparison with the many thousands of other north-temperate lakes (Hansson 1992; Vadeboncoeur et al. 2003). To determine how similar the phosphorus concentrations of our lakes were to other lakes in this region, we compared our TP range with that of the random set of 168

lakes sampled by Hanson et al. (2007) in the Northern Highlands Lake District of Wisconsin, which included lakes with and without anthropogenic P inputs. The TP range from our pristine lakes encompassed 75% of that range.

DOC appears to be the main driver of benthic primary production in these pristine north-temperate systems. This result has broad consequences given the importance of benthic production to lake food webs and the variability of DOC across the landscape and through time. We found evidence for photoadaptation of benthic algal assemblages within our study lakes, which is particularly relevant in the context of global shifts in lake characteristics that influence light availability and the need to understand the ways in which lake processes respond to these shifts. Our in situ method for estimating benthic primary production may be a useful new tool for rapidly increasing understanding of the controls on this important ecosystem process. Furthermore, our simple regression model may allow for fairly accurate prediction of whole-lake benthic primary production from easily obtained measurements of DOC concentration.

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