Photosynthesis-light relationships are more variable in time than in space for a shallow eutrophic lake

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Running head: Variable PI curves

# Background

The data described here are from “light gradient incubations” conducted at Mývatn in in 2018 and 2019. Pelagic and benthic incubations were conducted at ST33 and Reykjahli in 2018 and at those two locations plus E5 in 2019. Here, I treat ST33 as reprsentative of the South Basin, Reykjahli as representative of the North Basin, and E5 as representative of the East Basin. In both years, there were substantial cyanobacteria blooms; it will probably be good to present data on spatiotemporal patterns in the blooms. In 2018, we collected data in June, July, and August; while in 2019 we only collected data in July and August. For a given year-month combination, sampling events across sites and zone (pelagic vs. benthic) were either conducted on the same day or within a few days. Note that some combinations of sample date, basin, and zone (benthic vs. pelagic) are missing.

Benthic incubations used intact sediment cores in the tall acrylic tubes, while pelagic incubations used water collected with the Schindler trap in the short tubes. Schinler tows were taken for the full water column depth at a given site to provided an integrated picture of the full water column. We wrapped tubes with varying layers of mosquito net or black plastic to create a gradient of light levels. For the benthci incubations, we also wrapped the bottom portion of each tube corresponding to the sediment layer with black plastic.

We conducted incubations using floating racks, with the tubes hanging at 0.5m following the routine incubations. After setting up the racks and shading, we allowed the tubes to acclimate for about 1h befor taking the initial DO readings. After the initial readings, the tubes were incubated for an average of either 6.24h (min = 3.48h; max 8.83h) for the pelagic or 1.99h (min = 1.05h; max 3.33h) for the benthic. I calculated the net metabolism in each tube as the change in DO concentration (converted to mg ), multiplied by the water column depth, and divided by the incubation duration. This resulted in areal flux rates, which can be interpreted as DO fluxes across either the sediment surface (for the benthic) or across an average water-column cross-section (for the pelagic). The benthic and pelagic data are comparable as aeral flux rates, although comparting total benthic vs. pelagic production would require integrating the pelagic fluxes across the full water column depth.

The ambient light environment during the incubations was quantified using combination of Li-COR readings taken multiple times during each incubation and HOBO loggers deployed on the racks (when available). The light available in the tubes was estimated based on the number of layers of mosquito net, for which we determined a fixed conversion using the Li-COR meter in empty acrylic tubes with the corresponding amount of shading and with the top stoppered.

Some additional data were taken, including midges (tube counts and larvaal form sieved sediment) and chlorophyll/phycocyanin from handheld probes and from filtration. However, these data have some gaps and there are some weird anamolies in the chlorophyll data (e.g., the hanheld and filtered measurements are not correlated, even though we have independent confirmation from other data that they should be). Therefore, I am not currently including those data in any analyses.

# Fitting the PI curves

I fit a single model to the data for all sites and sampling dates, done separately for the benthic and pelagic data. While I fit the two zones separately, I wanted to use a PI curve of the same form so that the parameter estimates would be comparable. The pelagic incubations showed clear signs of photoinhibition, while the benthic did not. Therefore, I fit the data with a two-parameter photoinhibition curve (plus a parameter for respiration):

where is the maximum GPP, is the optimum PAR, is respiration, and is a residual for observation . The function maps observations to date-site combination , such that a single PI curve is inferred for each.

The optimum PAR scales the rate at which the maximum GPP is reached (with higher corresopnding to a slower saturation). This can be illustrated by calcualating the initial slope of the PI curve (i.e., “” in the hyperbolic-tangent model):

where is base of the natural logarithm. An important corollary of this point is that is a meaningful parameter even if the observed PAR remains well below the optimum PAR. An alternative would be to parameterize the model in terms of and interpret the results in terms of this initial slope. However, the reparameterized version makes the overall form of the curve (and specifically as the max GPP) less clear. I also like that has units of PAR, which makes it easier to interpret its scale. Below I discuss how this can be related to the half-saturation constant to help compare my PI curve fits to Amanda’s *Inland Waters* paper.

Variation in was modeled as

where is a standard-normal deviate for site-date combination . This is the same as modeling variation in as following a lognormal distribution, with log-scale mean and . This parameterization makes clear that can be interpreted as scaling proportional deviations with respect to a reference scale . For example, implies that a 1-standard deviation change on the log scale would result in an increase of 65% or decrease of 60% on the natural scale. Variation in and was modeled analagously, with parameters and for the former; and $\mu\_{\rho\right}$ and for the latter. Because the standard deviations characterize proportional deviations with respect to some reference scale, they are directly comparable to each other, despite the fact that has different units than and .

I z-scored the aeral DO flux data and divided PAR by its mean across the full data set for each zone prior to fitting the model. I then back-scaled the parameters accordingly. I fit the models using Bayesian approach in Stan 2.19, run in R 4.0.3 usin the rstan package. The model was fit with 4 chains, 3000 iterations (1500 of warm-up and 150 of sampling), tree depth of 11, and “adapt delta” of 0.975. Convergence was assessed by the number of divergent transitions and the potential scale reduction factor (R̂), which quantifies the relative variance within and between chains. We used posterior medians as point estimates and quantile-based uncertainty intervals with coverage analogous to standard errors (16% and 84% quantiles for 68% coverage). The model used standard-normal priors for the means of the lognormal distributions and Gamma priors with 1.5 and scale parameter 0.75 for all standard deviations.

# Results

The photoinhibition model fit both the pelagic and benthic data well (Figures [1](#fig:nep-pel) and [2](#fig:nep-ben)). Benthic GPP was clearly detected for all date-site combintions, while for several dates in both the North and South basins GPP was very low across all light levels. For those date-site combinations that did have substantial pelagic GPP, there was evidence of modest photoinhibition. In contrast, benthic GPP did not appear to be photoinhibited on any sample dates.

For the pelagic PI curves, maximum GPP varied substantially through time in both the North and South basins (Figures [3](#fig:par) and [4](#fig:sd)) broadly corresponding to increases in water-column cyanobactera [data not shown, but it would be good to do so I think]. However, pelagic optimum PAR and respiration were very similar between basins and remained quite stable through time.

Optimum PAR and respiration remained largely

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In contrast, there were other dates in both basins where

The pelagic PI curves appear to show much variation in the maximum GPP, with some sample dates in both the North and South basins having negligible GPP across all light levels. Other sample dates have substantial GPP peaking at a level well below the observed maximum, and therefore have indications of photoinhibition. The benthic PI curves appear to have less variation in overall net metabolism and there seems to be little evidence of photoinhibition.

These general impressions are supported by the parameter esimtates. Optimum PAR remains fairly consistent through time and among locations for both the pelagic and benthic incubations, with the main exception being benthic production in August 2019 in the East Basin. Max GPP is more variable, especially for the pelagic incubations. The large changes in pelagic GPP correspond pretty clearly with the presence of cyanobacterial blooms (as mentioned above, it would be good to back this up with observational data of the bloom). Max GPP for the benthic incubations was relatively stable by comparison. In contrast, respiration was fairly consistent for the pelagic incubations, while for the benthic incubations it was much higher in August of 2019 (which is driven by low observed NEPs, as seen in Figure [2](#fig:nep-ben)). I don’t have an easy explanation for this; the most obvious explanation would be temperature, but there really isn’t a clear association in the data.

The relative variation implied by the standard deviations (Figure [4](#fig:sd)) supports the interpretations described above. Variation in pptimum PAR was similar for benthic and pelagic production.

To quantify the relative variation among sites and among sampling dates (i.e., within sites), I used ANOVA to calculate F ratios of between vs. within site variation in , , and on a log scale. Moreoever, I report the log F ratio, which is symmetrical about 0 with 0 indicating equal variance within and between sites. I performed this calculation across the full posterior distirbutions for the parameters, resulting in a posterior distribution of log F ratios. For all but one parameter, the log F ratios were less than zero, indicating greater variation among sampling dates (i.e., within sites) than among sites (Figure [5](#fig:var)). The two F ratios most clearly below zero, pelagic max GPP and benthic respiration, correspond to the two parameters with the greatest overall level of variability (Figure [4](#fig:sd)). Together, these results indicate that variation in parameters of the pelagic and benthic PI curves was greater between time points than between sites, although the overall levels of variation wer generally comparable.

# Comparison to Amanda’s *Inland Waters* paper

The half saturation constant for equation [[eq:pi-curve]](#eq:pi-curve) is given by solving

for when , which yields

where is the product log function. This cannot be expressed in terms of elementary functions, but approximately evaluates as

To provide further context, we can make approximations by analogy to the hyperbolic tangent and Michaelis-mention PI curves, which have analytical expression for the half-saturation constant. For the hyperbolic tangeent, the half-saturation constant is

If we substitute in the exprssion for from equation [[eq:alpha]](#eq:alpha), we obtain

Suppose the half saturation constant for the Michaelis-Mention PI curve is . Then the initial slope of the curve is . If we set and solve for , we obtain

Therefore, the average half saturations for pelagic production from this analysis are 45, 38, and 69 for the direct, hyperbolic tangent, Michaelis-Mention approximations. These are pretty close to th value 46 that Amanda obtianed in her *Inland Waters* paper. That is not too suprising, since they use the same data. However, the results are also very close for benthic production: 104, 88, and 160 compared to 111. Amanda’s analysis used data from routine incubations, while mine used the light gradient incubations. It is quite comforting that they gave similar results.

c|ccc Pelagic  
& max GPP & opt PAR & Resp  
GPP & 1 & & & &  
opt PAR & -0.12 (-0.41, 0.21) & 1 & &  
Resp & -0.13 (-0.41, 0.20) & 0.04 (-0.32, 0.43) & 1

![[fig:nep-pel] Fits of the photoinhibition curves to the pelagic data. Ribbons are posterior standard errors. ](data:application/pdf;base64,)

[fig:nep-pel] Fits of the photoinhibition curves to the pelagic data. Ribbons are posterior standard errors.

![[fig:nep-ben] Fits of the photoinhibition curves to the benthic data. Ribbons are posterior standard errors. ](data:application/pdf;base64,)

[fig:nep-ben] Fits of the photoinhibition curves to the benthic data. Ribbons are posterior standard errors.

![[fig:par] Variation in the metabolism parameters between sites and sampling dates. max GPP and respiration are in units of \text{mg}~\text{O}_2~\text{m}^{-2}~\text{h}^{-1} and optimum PAR is in units of \mu\text{mol}~\text{photons}~\text{m}^{-2}~\text{s}^{-1}. Points are posterior medians and error bars are posterior standard errors. ](data:application/pdf;base64,)

[fig:par] Variation in the metabolism parameters between sites and sampling dates. max GPP and respiration are in units of and optimum PAR is in units of . Points are posterior medians and error bars are posterior standard errors.

![[fig:sd] Standard deviations for variation in the metabolism parameters. Points are posterior medians and error bars are posterior standard errors. ](data:application/pdf;base64,)

[fig:sd] Standard deviations for variation in the metabolism parameters. Points are posterior medians and error bars are posterior standard errors.

![[fig:var] Log F ratios calculated from ANOVA for each parameter. The ratio compares the variation between sites to the variation within, and a log-ratio of 0 indicates equal variation. This was calculated over the full posterior distributions for each parameter; the points are medians and error bars are standard errors from the resulting distribution of log F ratios. ](data:application/pdf;base64,)

[fig:var] Log F ratios calculated from ANOVA for each parameter. The ratio compares the variation between sites to the variation within, and a log-ratio of 0 indicates equal variation. This was calculated over the full posterior distributions for each parameter; the points are medians and error bars are standard errors from the resulting distribution of log F ratios.