

**Experimental and observational evidence that dissolved organic  
matter loading induces heterotrophy in a high elevation,  
oligotrophic lake**

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**Abstract**

Dissolved organic matter (DOM) is an important regulator of metabolism in aquatic ecosystems. The influx of DOM in oligotrophic, high alpine lakes during rain events has been shown to alter lake metabolism and increase net heterotrophy. DOM loading is expected to increase for high-elevation Sierra Nevada lakes as precipitation shifts from snow to rain. To explore the effects of DOM loading on ecosystem metabolism in high-elevation lakes, we characterize ecosystem metabolic response to DOM loading in both *in situ* incubation experiments and through whole lake measurements of dissolved oxygen made during a summer with unusually high levels precipitation. Experimental *in situ* incubations show net ecosystem production (NEP) decrease linearly as DOM increases, causing heterotrophy to grow stronger. Gross primary production (GPP) responded in a light-dependent manner, where GPP was stimulated across the DOM loading gradient during sunny, but not cloudy, weeks. ER was also stimulated and exceeded GPP across the entire DOM gradient, causing heterotrophy. ER was coupled to GPP in a light dependent manner, suggesting consumers continue to consume autochthonous carbon even when allochthonous carbon is present. Seasonal metabolism measurements support that DOM shifts a lake towards heterotrophy at the whole lake level, and a large rain event was sufficient to shift lake metabolism from autotrophy to heterotrophy for at least three weeks. Increased DOM loading due to climate induced changes in vegetation cover and the timing and magnitude of precipitation events could alter the amount of carbon cycled in these lakes.

**Introduction**

At a basic level, dissolved organic matter (DOM) is colored (Hongve et al., 2004; Haaland et al., 2010; Sadro and Melack, 2012) and bioavailable to consumers within a lake

(Williamson et al., 1999; Cole et al., 2000; Hanson et al., 2003; Carpenter et al., 2005; Solomon et al., 2015) The colored portion of DOM increases light attenuation within a lake, reducing the amount of light available for photosynthesis (Williamson et al., 1999; Solomon et al., 2013) and trapping heat, causing the epilimnion to rise within the lake (Houser, 2006). The bioavailable portion of DOM provides energy for both gross primary production (GPP) and ecosystem respiration (ER) (Cole et al., 2000; Hanson et al., 2003; Carpenter et al., 2005; Sanders et al., 2015; Seekell et al., 2015). The balance between GPP and ER reflects the energy an ecosystem either produces or consumes, and is defined as net ecosystem production (NEP) ( $NEP = GPP - ER$ ; Odum, 1956). We have long understood DOM's broad influence on seasonal lake metabolism (Del Giorgio & Peters 1994; Pace & Cole, 2002; Staehr et al., 2010), and recent research is beginning to describe the nuances and complexities present at smaller timescales (Sadro et al. 2011c; Kissman et al., 2013; Seekell et al., 2015; Jones & Lennon, 2015). Studies focusing on DOM's influence on lake metabolism have often compared a whole variety of lakes (Duarte and Agustí, 1998; Hanson et al., 2003; Staehr et al., 2010; Solomon et al., 2013, 2015; Seekell et al., 2015), but few have focused on DOM fluctuations within a lake. As climate change is expected to change DOM levels within lakes on a global scale (Hongve et al., 2004; Raymond & Saiers, 2010; Haaland et al., 2010), characterizing metabolic response to DOM fluctuations within an individual lake becomes increasingly important. High elevation, Sierra Nevada lakes are expected to receive more DOM as precipitation shifts from snow to rain in high elevation catchments (Miller et al., 2003) and vegetation migrates to higher elevations (Kelly and Goulden, 2008). In this study, we quantify the effects of DOM loading on ecosystem metabolism within Emerald Lake, an oligotrophic high-elevation lake, using both experimental *in situ* incubations and seasonal sampling data.

Metabolism is inherently linked to carbon cycling within a lake: primary producers fix carbon via photosynthesis, and consumers use carbon through respiration. Lake trophic status is defined by its carbon use. Autotrophic lakes produce more carbon through photosynthesis than they respire, and heterotrophic lakes respire more carbon than the primary producers can produce (Odum, 1956). An ecosystem's metabolic reliance on carbon not directly produced by the resident primary producers is inherently linked to the amount of carbon that enters a given lake.

Lakes receive DOM in two ways: as excreted matter by aquatic organisms, or as terrestrial runoff. Phytoplankton and photosynthate excretions, and aquatic plant excretions create autochthonous organic matter, or organic matter from within the lake itself. Terrestrial DOM, or organic matter of allochthonous origin, begins as terrestrial plant matter, is decomposed and altered to some degree in soil, then exported into the aquatic ecosystem (Solomon et al., 2015). The relative composition of DOM can vary widely between lakes and regions, and thus vary widely in bioavailability (Lennon & Pfaff, 2005). Usually, autochthonous DOM is more labile than allochthonous DOM (Sulzburger & Durisch-Kaiser, 2009; Perez & Sommaruga, 2006), but allochthonous DOM is still used by organisms. There is debate as to the extent to which DOM supports primary production and respiration. Though some studies indicate terrestrial support of food web biomass is low, (Brett et al., 2009; Francis et al., 2011) the highest estimates suggest over half of consumer biomass in some lakes relies on allochthonous support (Carpenter et al., 2005).

Allochthonous, or terrestrial loading varies widely across lakes, and is heavily influenced by precipitation character, frequency, and intensity (Hongve et al., 2004; Staehr et al., 2010; Sadro and Melack, 2012). Lakes that receive the majority of their precipitation as snowpack melting over long periods of time gradually release available water and slowly mobilize nutrients

over the spring season (Sickman et al., 2003, Ollesch et al., 2008). Though rain events contribute little total precipitation to snowmelt dominated lakes, they have the potential to mobilize much larger quantities of nutrients and organic material than snowmelt (Martínez-Castroviejo, 1990; Langlois et al., 2005; Haaland et al., 2010).

High alpine lakes are particularly susceptible to loading from rain events, given their short growing season, lack of nutrient rich, well-developed soils and thus DOM within the lake, and fast hydrologic flushing rates (Clow et al. 2003). An increase in precipitation falling as rain as opposed to snow has already been observed in the Sierra Nevada (Knowles et al., 2006), and current climate change models predict a continuation of this trend (Miller et al., 2003). An increase in precipitation is expected to increase DOM loading in Sierran lakes, and this may have significant consequences on ecosystem metabolism. Furthermore, vegetation is expected to migrate to higher elevations and increase vegetation cover for alpine catchments (Kelly & Goulden, 2008). This will increase DOM in the soil, and increase DOM concentration in rain runoff. DOM is a known driver of heterotrophy (Cole et al., 2000; Hanson et al., 2003; Staehr et al., 2010; Sadro and Melack, 2012; Forsström et al., 2013; Jones & Lennon, 2015), and a heterotrophic shift was observed in Emerald Lake after a large rainstorm (Sadro and Melack, 2012). As high-elevation lakes are normally autotrophic and thus produce more carbon than they consume (Cole et al., 2007), an increase in rain induced heterotrophic events in these lake may increase carbon fixation and sequestration in these lakes.

The goal of this thesis is to experimentally characterize Emerald Lake's metabolic response to increased DOM due to rain loading. As alpine, oligotrophic lakes have low baseline DOM levels, even small increases in DOM should affect both GPP and ER within the lake. We hypothesized that 1) ER will be stimulated across all concentrations of DOM; 2) GPP will be

stimulated at low DOM levels, but increasing light attenuation from DOM will cause GPP to eventually decline; and 3) NEP may increase at low levels as GPP exceeds ER, but as DOM and thus light attenuation increases, ER will exceed GPP and cause negative NEP, or heterotrophy.

Experimentally, we show increasing DOM shifts the lake towards heterotrophy, as ER exceeds GPP at all concentrations. However, both GPP and ER were stimulated across all DOM concentrations. Furthermore, seasonal metabolism measurements show the lake shift towards heterotrophy after a typical summer rain event, supporting our experimental measurements. As a changing climate shifts precipitation from rain to snow, our results suggest an increase in DOM loading and thus heterotrophic moments in high elevation Sierran lakes will result. This may shift seasonal metabolic balance within these lakes towards heterotrophy, reducing their capacity to act as carbon sources and altering their role in the global carbon cycle.

## Methods

*Site Description*—Emerald Lake is a high-elevation, oligotrophic lake located in the south central Sierra Nevada (California, 36°35'49"N, 118°40'29"W, 2800 m a.s.l). It has a 2.7 ha surface area, a maximum depth of 10m, and a volume of  $16.2 \times 10^4 \text{ m}^3$ , and is representative of alpine lakes in the Sierra (Melack and Stoddard, 1991). Emerald Lake has low groundwater inputs and a snowmelt dominated hydrology. Its catchment is a sparsely vegetated, glacially scoured cirque comprised of granitic and granodioritic rock, and only small amounts of terrestrial dissolved organic matter enter the lake (Nelson et al., 2009). Emerald Lake ecology, hydrology, and biogeochemistry have been studied for over three decades (Sickman et al., 2003).

*Environmental Data*— Air temperature was measured by a Viasala thermistor (Vantaa, Finland). Downwelling shortwave radiation (285-2800 nm) was measured by an Eppley

Precision Spectral Pyrometer (Newport, Rhode Island). Total rainfall was measured by a tipping bucket rain gauge. Wind speed was measured with an R.M. Young propeller anemometer with a  $1.0 \text{ m s}^{-1}$  threshold  $\pm 0.3 \text{ m s}^{-1}$  (Traverse City, Michigan). All environmental data were collected at 10 second intervals and recorded at 5 minute averages at the station maintained  $\sim 30 \text{ m}$  from and  $\sim 8 \text{ m}$  above the southeastern shore of Emerald Lake.

*Temperature and Oxygen Profiles*—Temperature and dissolved oxygen profiles were collected about every 2 hours from dawn to dusk each sampling day and at least once between sunset and sunrise the following morning. Profiles were collected approximately weekly between June 3, 2015 and August 6, 2015. Two additional, individual profiles were collected at 14:00 April 17, 2015 and 10:00 May 28, 2015. Inlet temperatures were collected 0-3 days before lake profiling each week. Measurements were made using YSI ProODO high precision optical DO sensors (Yellow Springs, OH) calibrated in 0% and 100% saturation solutions prior to sampling. Measurements were made at the surface (0.05m) and at 1m intervals from 1m to 10m deep. The logger was allowed to equilibrate for 1-2 minutes at each depth before recording a measurement.

*Water Sample Collection and Analysis*—Water samples were collected at weekly intervals between June 3, 2015 and August 6, 2015. Samples were collected at four depths (1, 4, 7, and 9m) using a Van Dorn bottle and stored in low-density polyethylene containers cubitainers for  $< 4\text{h}$  before being filtered or decanted into sample bottles. Dissolved organic carbon (DOC) samples were filtered through pre-combusted (2h at  $450^\circ\text{C}$ ) Whatman glass fiber filters (GF/F,  $0.7\text{-}\mu\text{m}$  nominal pore size) (Maidstone, United Kingdom) into pre-combusted (12h at  $450^\circ\text{C}$ ) amber borosilicate vials and immediately acidified with HCl to  $\text{pH} \sim 2$ . DOM samples were analyzed on a Shimadzu Total Organic Carbon analyzer (Kyoto, Japan) using high precision methods adapted for low concentrations (Carlson et al., 2010).

*Extraction of soil DOM*—DOM was extracted from soil samples collected from ten locations within the catchment to proportionally represent the following soil types: wet meadow soils, drained meadow soils, drained tree/shrub vegetated soils, and drained mineral rich meadow soils. Soils were air dried at 20°C for six weeks before extraction. Soils were manually broken up and run through a 2mm sieve before being added to Milli-Q (Darmstadt, Germany) ultrapure water in a 0.27 ratio by weight. The water/soil slurry was stirred for 5 min and stored at 4°C for 24 hours for extraction. The slurry was stirred for 5 min every 2 hours for the first 12 hours of extraction, then stirred again before filtering at 24 hours. Extraction water was decanted from the slurry and centrifuged at 40,000 rpm for 10 min at 10°C in 50ml tubes before serial filtration through Whatman GF/F (vacuum) and 0.2 micron nitrocellulose (peristaltic pump, ~1m/sec) filters (hereafter referred to as soil extract).

*Experimental Incubations*—Incubations were carried out in 1.9L borosilicate glass incubation chambers that were deployed at 4m four consecutive days. Water was collected from 4m in a Van Dorn bottle and filtered through 122µm Nitex mesh into low-density polyethylene cubitainers. Soil extract was added directly to cubitainers aiming for the following amendment concentrations: 0µM (control), +10 µM, +20 µM, +50 µM, +150 µM, +400 µM, +600 µM. Actual dissolved organic carbon (DOC) concentrations can be found in Table 1. After DOM amendment was added, each jar received a single randomly assigned Zebra Tech D-Opto (Lincolnshire, Illinois) or PME MiniDOT (Vista, California) optical oxygen logger. Each chamber was inspected to ensure no air bubbles remained after being sealed and dissolved oxygen was measured at 5 min intervals. All incubations were deployed in the lake within an hour of collection. Water samples from each amendment level were collected for nutrient and DOC analysis as indicated above.



*Metabolism Measurements*—Whole lake metabolism estimates were calculated using a modified mass balance approach from 24 hour DO profiles. Briefly, whole lake metabolism was computed from DO concentrations integrated through the water column for each time interval. NEP was calculated as  $NEP = \Delta DO + F_{GE}$ , where  $\Delta DO$  ( $g\ m^{-3}$ ) is measured change in DO,  $F_{GE}$  ( $g\ m^{-2}$ ) is flux due to atmospheric gas exchange,  $F_{GE}$  was computed as  $F_{GE} = k_{DO} (DO_{water} - DO_{sat})$ , where  $DO_{water}$  ( $g\ m^{-3}$ ) is the measured concentration of dissolved oxygen in surface water, and  $DO_{sat}$  ( $g\ m^{-3}$ ) is the saturation concentration at ambient temperature and atmospheric pressure.  $k_{DO}$ , the gas exchange coefficient, was estimated from wind speed (Cole and Caraco, 1998) and the relationship between Schmidt numbers (Jahne et al., 1987). Estimating metabolism from whole water column integrated DO concentrations accounts for any vertical fluxes that occur during the duration of sampling (Sadro et al., 2011a). Summing net ecosystem production (NEP) from each time interval over the 24 hour sampling period gives daily NEP. Summing nighttime NEP and dividing by the nighttime time interval gives an hourly rate of ecosystem respiration (ER), which was then applied over the entire 24 hours. Gross primary production (GPP) was computed as the sum of NEP and ER ( $GPP = NEP + ER$ ) when ER is positive. Assuming constant diel respiration likely underestimates CR and GPP but does not affect NEP estimates (Sadro et al., 2011b). Incubation metabolism estimates were computed as  $NEP = \Delta DO$ , as closed incubations do not experience lake-atmosphere gas flux. GPP and ER were calculated as described above.

*Data analysis*—Correlation analysis using Pearson Correlation Coefficients (PCC) was used to analyze relationships between metabolism data and environmental conditions. Dunnett's tests were used to compare DOM levels at 1, 4, 7, and 9m during rain events with mean seasonal DOM levels at each depth. Data was log-transformed to meet homoscedacity of variance and

normality of residuals. A linear regression was fitted to NEP for experimental incubation data (Fig. 5), and exponential regressions were fitted to weekly experimental NEP data (Fig. 7A). All statistical analyses, and regressions were performed using JMP (version 12; SAS Institute, Cary, North Carolina, jmp.com).

A Michaelis-Menten curve, initially developed to model enzyme kinetics, was used to describe GPP and ER. This model has been previously used to describe GPP response to irradiance due to dissolved inorganic carbon in lakes (Adams et al., 1978; Turner et al., 1982) and to describe ER response to substrate availability in marine bacteria (Aguilar-González et al., 2011). Michaelis-Menten curves were fitted using JMP (version 12; SAS Institute, Cary, North Carolina, jmp.com).

## Results

*Environmental and limnological conditions prior to and during the experiment* — At the beginning of May, the lake was weakly stratified and average lake temperature was  $<6^{\circ}\text{C}$  (Fig. 2). Over the course of the ice-free season, stratification strengthened and average lake temperature increased to reach a maximum of  $15.0^{\circ}\text{C}$  (Fig. 2). Temperature gradient through the water column reached a maximum  $8.3^{\circ}\text{C}$  in early July (Fig. 2). After stratification, thermocline depth gradually deepened from 3-5m (Fig. 2). Conditions during the 2015 icefree season were similar to conditions recorded during 2007, a similar low snow year for Emerald Lake (Sadro et al., 2011a). Mean daily epilimnetic temperature was correlated with mean daily air temperature (Pearson Correlation Coefficient (PCC)=0.551, Table 2) but not correlated with total daily rainfall (PCC=0.079, Table 2), suggesting rain events must be of a certain magnitude to alter lake temperature.

There were eleven rain events during the ice-free season, five of which occurred during regular lake sampling (Fig. 1A). These rain events were mostly brief, lasting a few hours (Fig. 1B), and ranged in magnitude from 5 mm to 45mm of rain, characteristic of summer rainstorms at Emerald Lake. Total seasonal rainfall was 219mm. Total daily rainfall was highly correlated with a reduction in daytime shortwave radiation (PCC=-0.509, Table 2) and lower average daily temperature (PCC=-0.278, Table 2), both known drivers of ecosystem metabolism (Staeher et al., 2010; Solomon et al., 2015).

*Lake DOM levels*—Dissolved organic material within the lake fluctuated greatly during the sampling season at all depths (Fig. 3A). At iceoff, DOM levels were high before quickly declining at the beginning of the summer season. Values generally increased as the season progressed.

Often, rainstorms did not significantly elevate DOM at any depth. Only two of seven storms significantly elevated DOM (Table 4). When 5.6 mm of rain fell on July 1, DOM at 9m was elevated ( $p < 0.05$ , Dunnett's test), though this elevated value is most likely caused by sediment disturbance during sampling rather than rain. When 45.0mm of rain fell on July 21, DOM at 4m was significantly elevated on July 23 ( $p < 0.05$ , Dunnett's Test). Despite sampling after multiple rainstorms similar in size to the July 21 rainstorm, no other DOM values were elevated. This suggests rain events can significantly load DOM in the epilimnion as long as they are of a certain magnitude.

DOM at 1m was never elevated, despite numerous loading events and one sample taken during a rainstorm. Inlet water was colder than water at 1m for all but three measurements (Table 3). In fact, the greatest difference in temperature (4.3°C, Day 204, Table 3) between the inlet and 1m depth occurred two days after the largest rainstorm of the season (45.0mm). High DOM inlet

water is colder, and therefore less dense, than water 1m deep during rainstorms. This causes DOM loaded inlet water to enter the lake and sit below the 1m band, explaining lack of elevated DOM at 1m.

*Experimental Incubation Response to Experimental Loading*—Experimental DOM loading had a profound effect on ecosystem metabolism across the entire DOM gradient (Fig. 5). Averaging GPP, ER, and NEP across all three experiments presents a clear picture of metabolic response to DOM loading. GPP and ecosystem respiration both increased in a nonlinear fashion across the DOM gradient (Fig. 5B, C). GPP showed a rapid increase at low concentrations of DOM that tapered to a gradual increase with higher DOM concentrations. A Michaelis-Menten curve weakly fit GPP data ( $r^2=0.188$ ), but removal of the outlier at 450  $\mu\text{M}$  DOM (x on plot, Fig. 5B) greatly improved the fit of the model ( $r^2=0.66$ ). ER was also best described by a Michaelis-Menten curve ( $r^2=0.65$ ), with a rapid increase over lower concentrations tapering to a gradual increase at high concentrations (Fig. 5C). Importantly, the magnitude of the ER curve was greater than the GPP curve for all DOM concentrations, causing heterotrophy in all incubations (Fig. 5D). NEP was negatively, linearly correlated with the amount of allochthonous DOM in the incubation ( $r^2=0.964$ ) (Fig. 5A), indicating increasing DOM causes heterotrophy.

*Environmental Factors Regulating Ecosystem Metabolic Response to Soil DOM* — Though metabolism averaged across all three experiments provides a good overview of how DOM effects NEP, GPP, and ER, comparing metabolism from each experiment individually highlights how changes in environmental conditions affect metabolism. Shortwave radiation, which contains photosynthetically active radiation (PAR), was low for experiment 2 (22,801  $\text{w}/\text{m}^2$ ) and normal for experiments 1 and 3 (25,987  $\text{w}/\text{m}^2$ ; 25,767  $\text{w}/\text{m}^2$ ) (Fig. 6C). A large rainstorm (45.0 mm) ended two days before the first experiment (Fig. 6A), causing significant

DOM loading at 4m in the lake (Table 4) and lakewater used in the first experiment (Table 1). A much smaller rainstorm (6.3mm) occurred before experiment 3, possibly, but not significantly, causing DOM loading in lakewater used for experiment 3 (Fig. 6A).

GPP and ER showed complex, nonlinear responses to DOM loading. GPP increased until about 200  $\mu\text{M}$  DOM in experiment 1, and declined at higher concentrations (Fig. 7B, blue line). Light limited experiment 2 showed GPP decrease for all DOM concentrations (Fig. 7B, red line), suggesting GPP is light dependent. Experiment 3 showed GPP increase along the entire DOM gradient (Fig. 7B, green line), indicating GPP is stimulated along the entire DOM gradient with sufficient sunlight. ER somewhat mimicked GPP, but the magnitude of each ER curve was greater than the curve for GPP, causing experiment wide heterotrophy (Fig. 7C). Experiment 1 shows ER increase until around 200  $\mu\text{M}$  DOM, at which point ER declined and then flattened out (Fig. 7C, blue line). Experiment 2 showed ER remain unstimulated with less than 450  $\mu\text{M}$  DOM, suggesting ER is indirectly regulated by light availability. Experiment 3 shows ER increase continuously along the DOM gradient (Fig. 7C, green line), demonstrating consumers continue to utilize DOM across all concentrations tested.

GPP:ER ratios also varied between experiments. For experiments 1 and 3, as GPP increased, ER increased (Fig. 7D, blue and green lines). The slope of both lines was less than 1, indicating net heterotrophy, as ER exceeded GPP. However, GPP and ER were coupled in both experiments (Exp 1,  $r^2=0.63$ ; Exp 3,  $r^2=0.98$ ), suggesting consumers continue to rely on GPP for energy despite added DOM. In experiment 2, ER increased along the DOM gradient while GPP remained unstimulated (Fig. 7D, red line). GPP and ER were uncoupled during experiment 2 ( $r^2=0.00$ ), suggesting GPP and ER couple in a light dependent manner.

NEP declined for all three experiments, and this result supports that DOM pushes a lake towards heterotrophy (Fig. 7A). Experiment 1 was the most heterotrophic across all DOM gradients, and experiment 3 was the least heterotrophic. Exponential curves fit these data well (Exp 1,  $r^2=0.82$ ; Exp 2,  $r^2=0.99$ ; Exp 3,  $r^2=0.86$ ).

*Seasonal Metabolism*—Depth integrated metabolism estimates for Emerald Lake show net autotrophy during much of the sampling season (Fig. 4). GPP rate exceeded ER rate from the beginning of weekly sampling in June through late July (Fig. 4). The lake transitioned from autotrophy to heterotrophy around July 22 and was heterotrophic for the rest of the sampling season, through August 6. This transition occurred just after the largest rain event of the season, with 44.6 mm of rain falling between five and two days prior to sampling. This supports our experimental results, and suggests rain loaded DOM can shift the metabolic balance of an ecosystem towards heterotrophy.

ER was correlated with NEP (PCC=-0.967) and GPP (PCC=-0.875), and GPP was also correlated with NEP (PCC=-0.875) (Table 5). Though GPP and ER inherently define NEP, correlation between GPP and ER supports GPP:ER coupling shown in our experimental incubations. Other known drivers of metabolism (total rainfall in the proceeding week, total weekly shortwave radiation, DOM levels) were correlated with NEP, GPP, or ER (Table 5).

## **Discussion**

*Sensitivity of High Elevation Lakes to dissolved organic matter (DOM) loading*—Both our experimental incubations and seasonal metabolism measurements show that even small amounts of allochthonous DOM are sufficient for inducing heterotrophy in a high-elevation oligotrophic lake. In all three experimental incubations, regardless of environmental conditions,

increasing DOM concentrations induced greater heterotrophy (Fig. 7A). Furthermore, we observed that a typical summer rain event was sufficient to drive the lake from autotrophy to heterotrophy and remain heterotrophic for at least the following three weeks (Fig. 4). Agreement between our experimental incubations (Fig. 7) and our seasonal metabolism measurements (Fig. 4) suggest the metabolic balance in oligotrophic lakes is highly sensitive to DOM loading.

Metabolism in Emerald Lake normally relies on little support from allochthonous organic matter. For the majority of our sampling, Emerald Lake was autotrophic, (Fig. 4, blue line) supporting previous studies that suggest the lake is net autotrophic during the icefree season (Sadro et al., 2011a; 2011b). Our last three metabolism measurements (July 28, August 2, August 6), however, show the lake transition to heterotrophy. These measurements were taken after a 44.95mm rainstorm that ended on July 27. DOM levels were elevated in the epilimnion following this rain event. We designed our experimental incubations to explore how elevated levels of DOM affect ecosystem metabolism. Our experimental incubations demonstrate even small amounts of loaded DOM is sufficient for inducing heterotrophy (Fig. 7), and validate the idea that Emerald Lake's observed shift from autotrophy to heterotrophy is a result of rain loading.

Breaking metabolism down into how GPP and ER relate to each other clarifies how this lakewide shift towards heterotrophy occurred. DOM loading from the large rainstorm likely pushed the lake towards heterotrophy by increasing both nutrient stimulation and light attenuation, which affect GPP and ER (Seekell et al., 2015). In many lakes, GPP and ER are linked at both seasonal and diel time scales due to consumers' reliance on autochthonous carbon assimilation from photosynthesis (Hanson et al., 2003; Staehr et al., 2010; Solomon et al., 2015; Sadro et al., 2011c). Though the shape of GPP and ER response to increasing DOM in our

experiments follow the same curve (Fig. 5D), our data show that ER exceeds GPP for all DOM concentrations. DOM reduces photosynthetically active radiation and increases nutrient availability (Seekell et al. 2015), and thus stimulates ER more so than GPP (Fig. 5A).

Alternatively, ER stimulation may exceed GPP stimulation because respiratory processes have a lower net activation energy (Yvon-Durocher et al., 2010) and organisms can more readily utilize allochthonous inputs to support ER than GPP. Likely, both limiting photosynthetically active radiation and a lower activation energy for ER allowed ER to exceed GPP.

Interestingly, we also observe DOM stimulate ER to a greater extent than GPP in our seasonal metabolism measurements. For the majority of the sampling season, GPP exceeds ER (Fig. 4). However, after the rainstorm on July 27, ER exceeds GPP for the remainder of sampling and the lake becomes heterotrophic (Fig. 4). The lake never fully recovered to autotrophy during the rest of our sampling, adding to a growing amount of evidence that increasing levels of DOM causes heterotrophy (Carpenter et al., 2005).

As climate change models predict increased precipitation for the Sierra Nevada and much of the Western United States show increased and more intense rainfall, and thus increased DOM loading events for high-elevation lakes (Clow et al., 2003; Knowles et al., 2006), heterotrophic moments for these lakes may occur more frequently. Interestingly, Emerald Lake never recovered to autotrophy after the rain event on July 27, and was heterotrophic when sampling terminated on August 4. With a large enough rain event, loaded DOM is sufficient for inducing heterotrophy for extended periods of time (Fig. 4). Enough large rain events could then shift the seasonal metabolic balance in Emerald Lake towards heterotrophy. These lakes normally produce more carbon than they respire ( $GPP > ER$ ; Sadro et al., 2011b). As DOM stimulates GPP, increasing DOM should increase the amount these lakes fix and sequester carbon. Interestingly,



temperature increase has already been shown to drive heterotrophy in some lake experiments (Yvon-Durocher et al., 2010), and alongside increased precipitation, average ambient temperature is expected to increase in the Sierra Nevada (Klow et al., 2003; Miller et al., 2003, Knowles et al., 2006). We show another climate driven factor, DOM, is sufficient for altering a lake's metabolic balance. However, to understand the extent that climate change will alter global carbon cycling, all drivers of metabolism impacted by climate change must be examined. Furthermore, despite sampling after a multitude of rain events, only the largest recorded rain event during the sampling season significantly altered DOM levels and lake metabolism. Rain intensity, then, appears as important as rain frequency in its capacity to alter a lakes metabolic balance. Understanding exactly how precipitation will change is important in understanding potential metabolic changes in these lakes.

Our experimental incubations present strong evidence that DOM is the limiting factor to respiration in oligotrophic lakes and suggests low baseline DOM levels cause high sensitivity to DOM loading. A low baseline level of DOM is also likely why we see NEP continue to decline across our entire DOM concentration gradient (Fig. 4). Our highest incubations contained more DOM than the highest observed DOM concentration in Emerald Lake (Sadro & Melack, 2012), and still NEP declined, suggesting that even at high concentrations DOM still limited respiration. Clearly, consumers can and will use organic matter that enters the lake. At some concentration of DOM higher than we tested, though, NEP may level off as DOM is no longer the limiting factor to respiration. However, DOM is readily utilized by consumers in all lake types, ranging from DOM poor oligotrophic lakes to high DOM humic lakes (Hanson et al., 2003; Karlsson et al., 2003; Kelley et al., 2014). As increasing DOM levels changes lake structure (Houser, 2006) and causes significant change to other biological processes, such as GPP (Hanson et al., 2003) and

bacterial production (Karlsson et al., 2009), focusing on DOM as a limiting factor to respiration in isolated incubations misses important broad scale implications of DOM loading.

Understanding that consumers will continue to use DOM across normal levels of loading for Emerald Lake suggests that future increases in precipitation will continue to drive the lake towards heterotrophy.

*Light Conditions and Metabolic Response to DOM Loading*—While averaging GPP, ER, and NEP rates across all three experiments gives us a general understanding of the effect of DOM on metabolism, looking at each experiment individually shows the how various environmental conditions affect metabolism. GPP responded differently in each set of incubations (Fig. 7A). Experiment 1 revealed a nonlinear response to DOM that peaked around 200 $\mu$ M, for experiment 2, NEP slightly declined as DOM increased, and with experiment 3, GPP increased along the whole DOM gradient (Fig. 7A). Experiment 3's constant increase in GPP shows irradiance due to added DOM did not limit light enough to negate the stimulatory effects of DOM on GPP. Experiment 2 was light-limited by the environment, though, and the decline in GPP during experiment 2 supports many studies showing GPP as light dependent (Williamson et al., 1999; Staehr et al., 2010; Seekell et al., 2015; Jones & Lennon, 2015). Interestingly, these studies suggest irradiance due to high DOM levels inhibits GPP, contrasting our experiment 3 result. Our incubations only contained a small portion of high DOM water. Instead of increasing light attenuation throughout the whole water column, like it would after a rainstorm, we only increased light attenuation within our incubations itself. In mesocosm experiments or whole lake experiments, however, reduction in photosynthetically active radiation throughout the water column inhibits GPP (Batt et al., 2015). Our incubations, then, may not be sufficient to model DOM's inhibitory effect on GPP. However, recent whole lake experiments found DOM

additions did not change the light climate in the photic zone and showed GPP stimulation with added DOM (Zwart et al., 2016). Additions of DOM to high-elevation lakes may not significantly increase light attenuation, and GPP stimulation will outweigh light attenuation in these lakes.

ER roughly mirrored the response of GPP in each incubation. GPP and ER remained tightly coupled in experiments 2 and 3 (Fig. 7D), and both indicate stimulation across all levels of DOM. This supports our averaged values across experiments (Fig. 5D) and the idea that GPP is coupled to ER in low DOM lakes (Staeher et al., 2010; Hanson et al., 2003; Solomon et al., 2015). Interestingly, GPP and ER completely uncoupled in the light-limited experiment 2. At high concentrations, ER increased as GPP remained unstimulated. This suggests a light-independent threshold concentration above which DOM can stimulate ER. Our data suggest this threshold lies between 200 $\mu$ M and 450  $\mu$ M DOM for Emerald Lake. Interestingly, this threshold is well below the 700 $\mu$ M DOM used in a study that found ER to be completely light dependent (Kragh et al., 2008). This apparent disagreement suggests that the light-independent threshold observed in our study may vary between lake types. While concentrations of DOM as high as 450  $\mu$ M this are rarely found in oligotrophic lakes, knowing exactly where this threshold occurs may help clarify lakes' response to large DOM loading events. Furthermore, while GPP and ER are coupled seasonally (Solomon et al., 2015), our study shows that complexities in this model exist on a smaller timeframe, as GPP to ER coupling is light dependent. With DOM loading and low light conditions, GPP and ER may uncouple briefly after a rain event yet remain seasonally coupled. Increasing frequency and intensity of rain events, thus increasing periods high DOM, may cause GPP and ER to be less coupled on a seasonal basis and allow consumers to be less

reliant on autochthonous carbon, shifting the metabolic balance within the lake towards heterotrophy.

GPP:ER coupling likely occurs because consumers preferentially consume autochthonous organic matter in many lakes (Lennon & Pfaff, 2005; Pérez & Sommaruga, 2006; Berggren et al., 2010). While our data cannot conclusively determine whether consumers have a preference between allochthonous and autochthonous organic matter, GPP:ER coupling across all DOM concentrations indicates that consumers continue to eat autochthonous organic matter despite the presence of allochthonous DOM. Furthermore, autochthonous DOM appears to stimulate consumption of allochthonous DOM in some lakes (Guillemette et al., 2015). In our light-limited experiment 2, we see a reduction in both ER and GPP compared to sunny weeks (Fig. 7B,C), supporting the idea that consumption of autochthonous material provides the necessary energy for consumption of recalcitrant allochthonous material. Furthermore, sunlight driven photoreactions increase DOM lability and allow DOM to more easily be used by consumers (Moran & Zepp, 1997; Kragh et al., 2008), further bolstering sunlight's role in regulating metabolic processes. Our experiment 2 strongly demonstrates ER is stimulated by sunlight, and through either DOM photoreactions or stimulation by autochthonous organic matter ER is regulated by light availability.

*Bacterial Dynamics and Metabolic Response to Loading*—GPP and ER both responded nonlinearly along the DOM gradient in experiment 1, with a peak in roughly the same place (Fig. 7B, C, blue line). DOM causes ecosystem wide changes in bacterioplankton and phytoplankton composition (Pérez & Sommaruga, 2006; Kissman et al., 2013) and biomass (Carpenter et al., 1998; Kissman et al., 2013; Forrström et al., 2013). Bacterioplankton biomass was elevated 4 days after DOM addition in mesocosm experiments, after which it begins to decline (Sanders et

al.,2015). We began incubating our first experiment roughly 4 days after the start of a rainstorm, which coincides with peak bacterial biomass. The nonlinearity in our ER response could be explained by bacterial dynamics. If high concentrations of DOM additions caused biomass to continue to increase to an unsustainable point, a large bloom and dieoff of bacterioplankton during the experiment may lower respiration estimates overall. Smaller amounts of DOM may not have pushed biomass to unsustainable levels, hence the increase in both GPP and ER among lower concentrations of DOM. Chl-A and bacterial abundance samples have yet to be analyzed for our experiment, and will clarify this hypothesis.

*Conclusions*—Using both experimental incubations and seasonal metabolism measurements, we demonstrate that DOM loading is sufficient for inducing heterotrophy in a high-elevation lake. Furthermore, our data indicate loading from a large enough rain event can shift the metabolic balance of the lake toward heterotrophy for an extended period of time. This dramatic shift to heterotrophy suggests high-elevation lakes are sensitive even to small amounts of loaded DOM, and climate induced shifts in precipitation frequency and intensity will alter the extent that these lakes act as carbon sources.

Our incubations demonstrate how GPP and ER response to DOM is highly dependent on environmental factors. Both ER and GPP were readily able to utilize added DOM, and both increased across the DOM gradient. However, ER increased at a greater rate than GPP, either because of increased light attenuation from DOM or because respiration is a more efficient process than photosynthesis. Furthermore, we show DOM and ER couple in a light-dependent manner, suggesting consumers continue to use autochthonous DOM alongside allochthonous DOM as long as both are present.

Rainfall is expected to increase in both frequency and intensity as a result of climate change (Knowles et al., 2006). Increased rainfall will increase DOM loading events for high alpine lakes (Clow et al., 2003). Our data demonstrate that increasing DOM loading events will shift the metabolic balance towards heterotrophy. As these lakes play a significant role in global carbon dynamics (Cole et al., 2007), a greater frequency of heterotrophic moments during the ice-free season may alter the amount of carbon cycled in these lakes. The biogeochemistry of high-elevation lakes is likely to change with altered precipitation patterns due to climate change.

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**DOM Concentrations by Experiment ( $\mu\text{M}$ )**

Experiment	Control	+10	+20	+50	+150	+400	+600
1	87.73	95.74	105.25	138.2	230.44	456.56	680.54
2	81.23	95.98	101.05	130.39	235.51	449.75	722.87
3	82.46	93.27	99.16	133.31	245.53	475.59	644.2

Table 1. Starting dissolved organic matter (DOM) concentrations for each jar during experiments 1, 2, and 3. DOM is reported in  $\mu\text{M}$ .

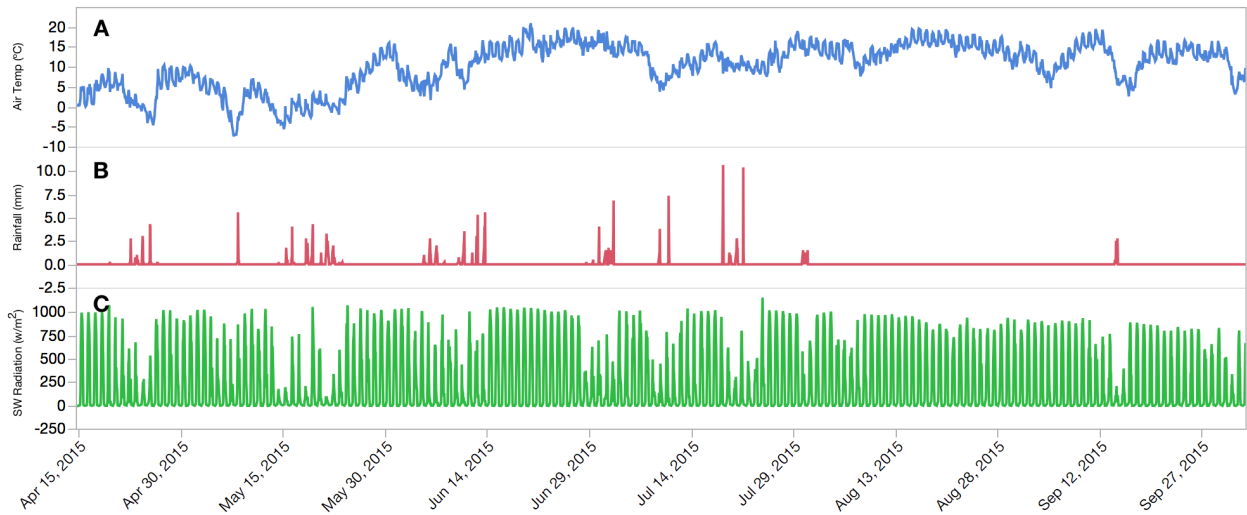


Fig. 1. Environmental conditions during the 2015 ice-free season for Emerald Lake. (A) Mean daily air temperature. (B) Total daily rainfall. (C) Shortwave radiation, reflecting availability of photosynthetically active radiation.

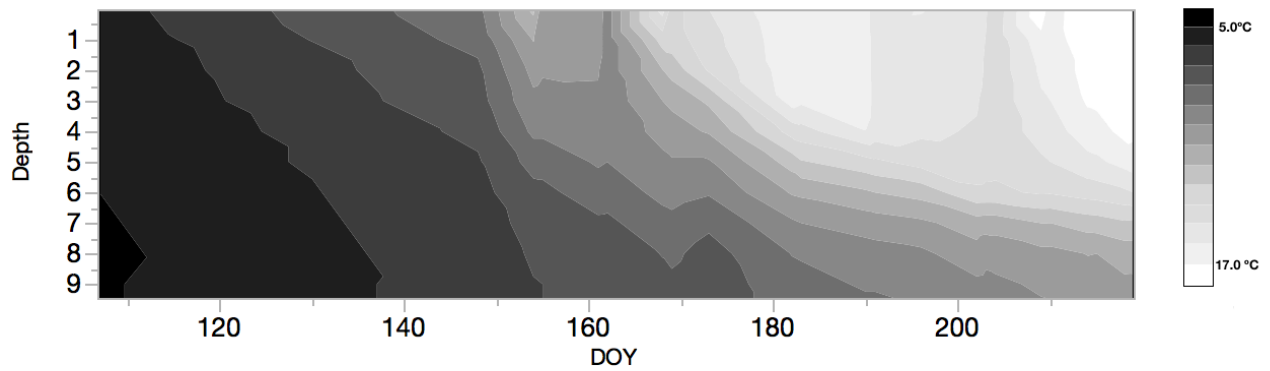


Fig 2. Time-depth contour plot of lake temperature for the sampling season (April 15 to August 6, 2015). DOY is day of year. Contours represent 1°C.

	Mean Lake Temp (°C)	Mean Air Temp (°C)	Total Rainfall (mm)	Total SW Radiation (watt/m2)
Mean Lake Temp (°C)	1.000	<b>*0.551</b>	0.079	-0.148
Mean Air Temp (°C)	<b>*0.551</b>	1.000	<b>*-0.278</b>	<b>*0.464</b>
Total Rainfall (mm)	0.079	<b>*-0.278</b>	1.000	<b>*-0.509</b>
Total SW Radiation (watt/m2)	-0.148	<b>*0.464</b>	<b>*-0.509</b>	1.000

Table 2. Correlation coefficients between daily mean epilimnetic lake temperature, daily mean air temperature, total daily rainfall, and total shortwave radiation for Emerald Lake. Bold and starred values indicate  $p < .05$ .

DOY	Inlet (°C)	1m (°C)
147	8.1	8.3
159	9.2	10.2
166	12.6	14.1
173	15.3	.
181	14.3	16.8
188	19.2	16.4
196	12.7	15.5
204	10.8	15.1
209	18.2	17.1
214	18.7	18.6
218	17.1	17.6

Table 3. Temperature measurements from the inlet and 1m depth. Gray boxes represent inlet temperature greater than temperature measured at 1m. DOY reflects 1m measurements. Inlet measurements occurred 0-3 days before 1m measurements, but at the same time of day.



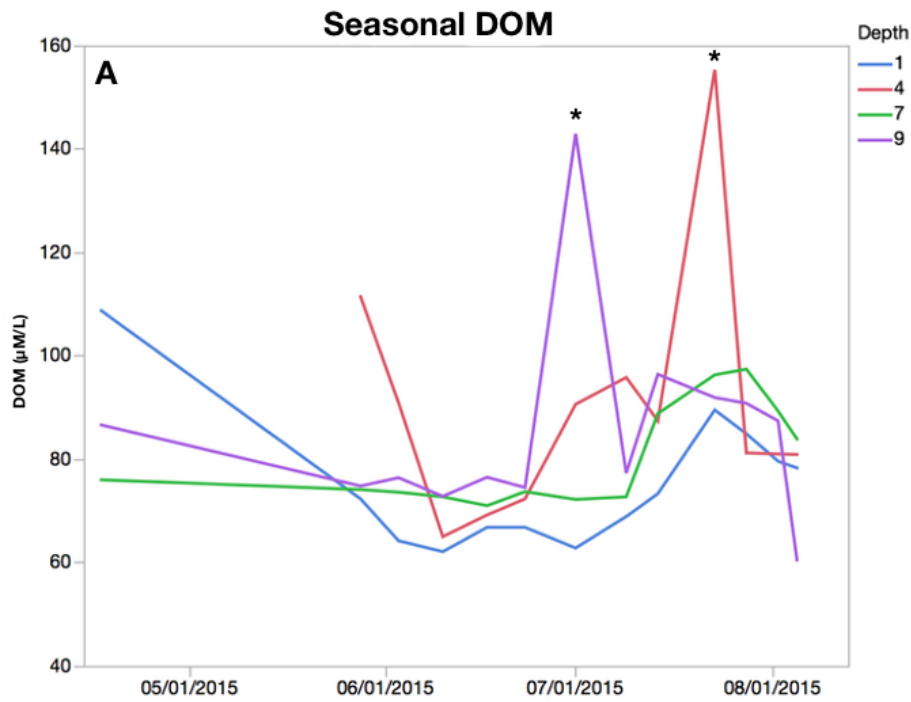


Fig. 3. Dissolved organic matter (DOM) concentration at different depth intervals in Emerald Lake. (A) DOM measurements made over the course of the sampling season. Starred spikes are significantly elevated DOM levels compared to mean DOM levels for that depth ( $p < .05$ ). No 4m sample was recorded during the first day of sampling.

Date of Rainstorm	Date of Sampling	Total Rain (mm)	1m DOC ( $\mu\text{M}$ )	4m DOC ( $\mu\text{M}$ )	7m DOC ( $\mu\text{M}$ )	9m DOC ( $\mu\text{M}$ )
Seasonal Mean	-	0	76.4	85.3	78.5	87.0
5/22/15	5/28/15	51.1	72.3	111.4	74.1	74.8
6/6/15	6/10/15	13.0	62.1	65.0	72.7	72.8
6/13/15	6/17/15	38.1	66.8	69.2	71.0	76.5
7/1/15	7/1/15	5.6	62.8	90.6	72.2	<b>*142.9</b>
7/10/15	7/14/15	17.8	73.3	87.4	88.8	96.4
7/21/15	7/23/15	45.0	89.5	<b>*155.3</b>	96.3	91.9
7/31/15	8/2/15	9.3	79.6	81.0	89.3	87.4

Table 4. Mean dissolved organic carbon (DOC), a measure of DOM, at each depth compared to DOC in the sample following summer rainstorms. Rain totals reflect total rainfall before sampling. Starred and bold values reflect  $p < 0.05$  (Dunnett's method).

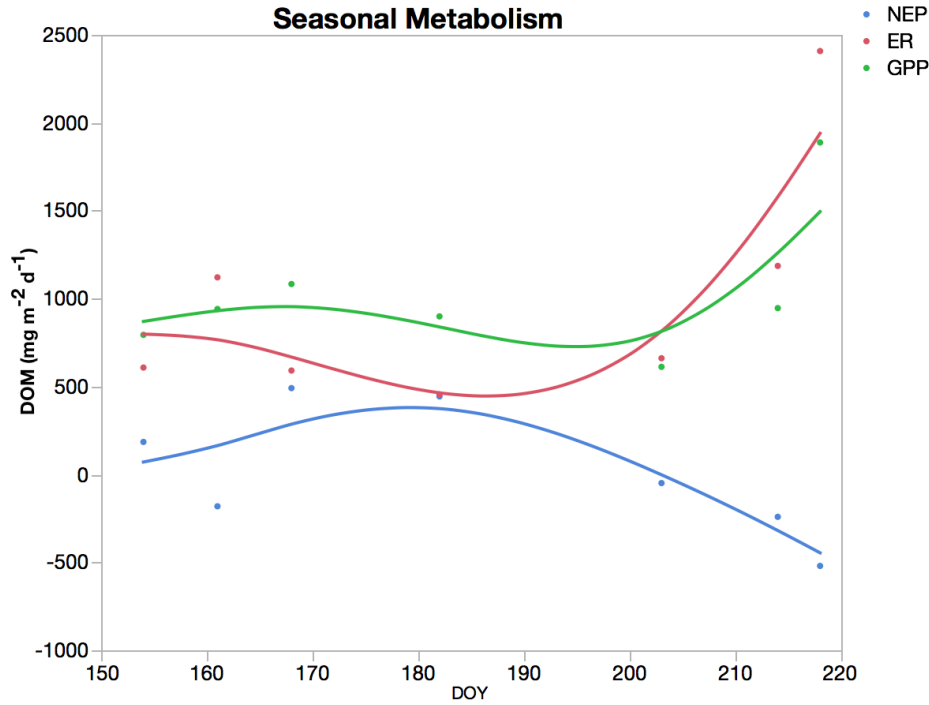


Fig 4. Depth integrated metabolism measurements for each DO profile recorded during the sampling season. Blue line is NEP, green line is GPP, red line is ER.

	NEP	GPP	ER
NEP	1.000	<b>*-0.875</b>	<b>*-0.967</b>
GPP	<b>*-0.875</b>	1.000	<b>*0.969</b>
ER	<b>*-0.967</b>	<b>*0.969</b>	1.000
Tot. Rain (mm)	0.421	<b>*-0.713</b>	-0.588
Total SW (watt/m <sup>2</sup> )	<b>*0.854</b>	<b>*-0.797</b>	<b>*-0.852</b>
Total column DOC ( $\mu\text{M}$ )	0.324	-0.121	-0.228

Table 5. Correlation coefficients between environmental conditions and daily metabolism measurements. NEP is net ecosystem production, GPP is gross primary production, ER is

ecosystem respiration, *SW* is shortwave radiation, and *DOC* is dissolved organic carbon.

Starred and bold values indicate  $p < .05$ .

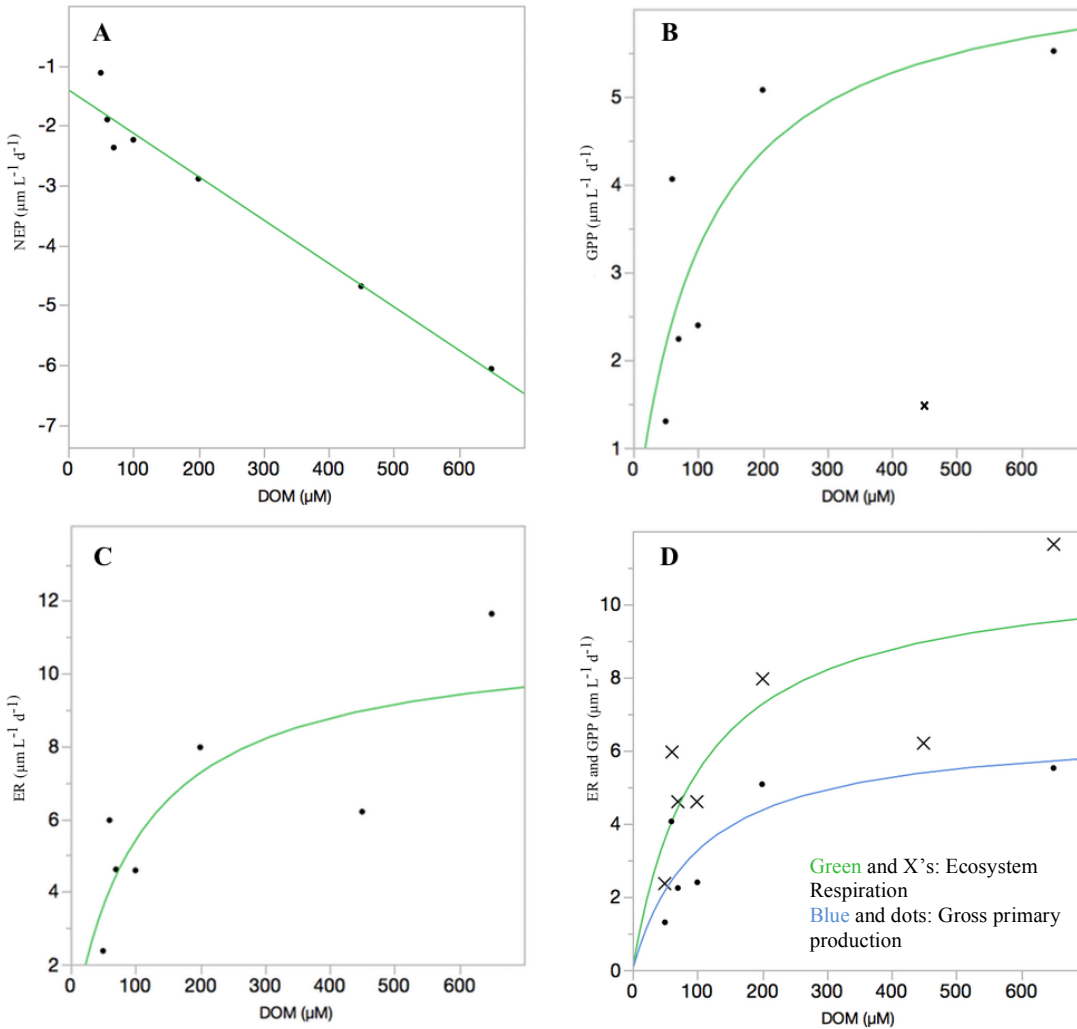


Fig 5. Metabolism estimates averaged for all three sets of experimental incubations. (A) NEP estimates. (B) GPP estimates. **x** on plot represents outlier eliminated from analysis. (C) ER estimates. (D) Blue line and black dots represents GPP. Green line and Xs represents ER.

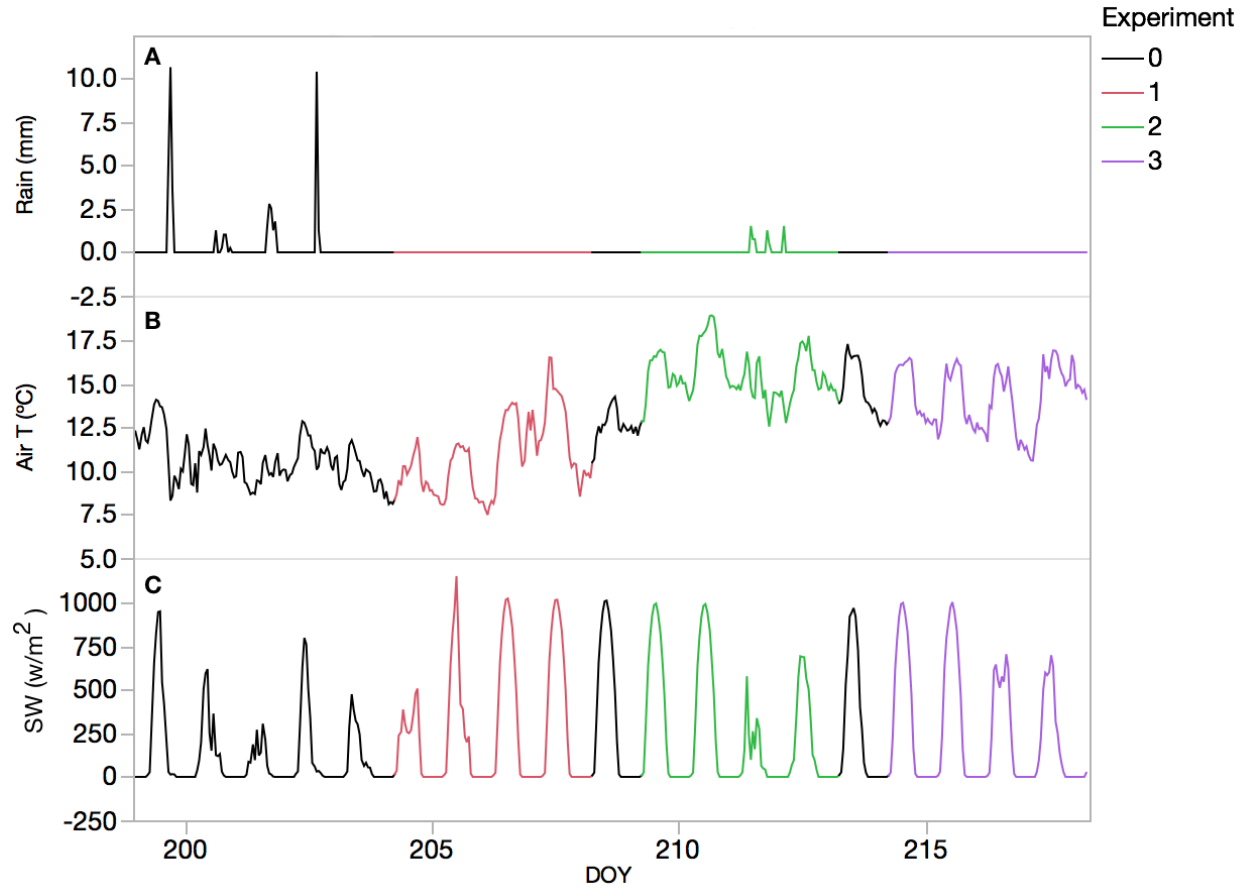


Fig. 6. Environmental data for experimental weeks only. Experiment 1 is red in all sections, experiment two is green, experiment 3 is purple. Black represents days that no experiments were in the water. (A) Rainfall amount. Note that water for incubations was collected at the start of each experiment and reflective of the rainfall the week prior. Incubations were closed and not affected by rainfall while in the water. (B) Air temperature. (C) Shortwave radiation, an indicator of PAR.

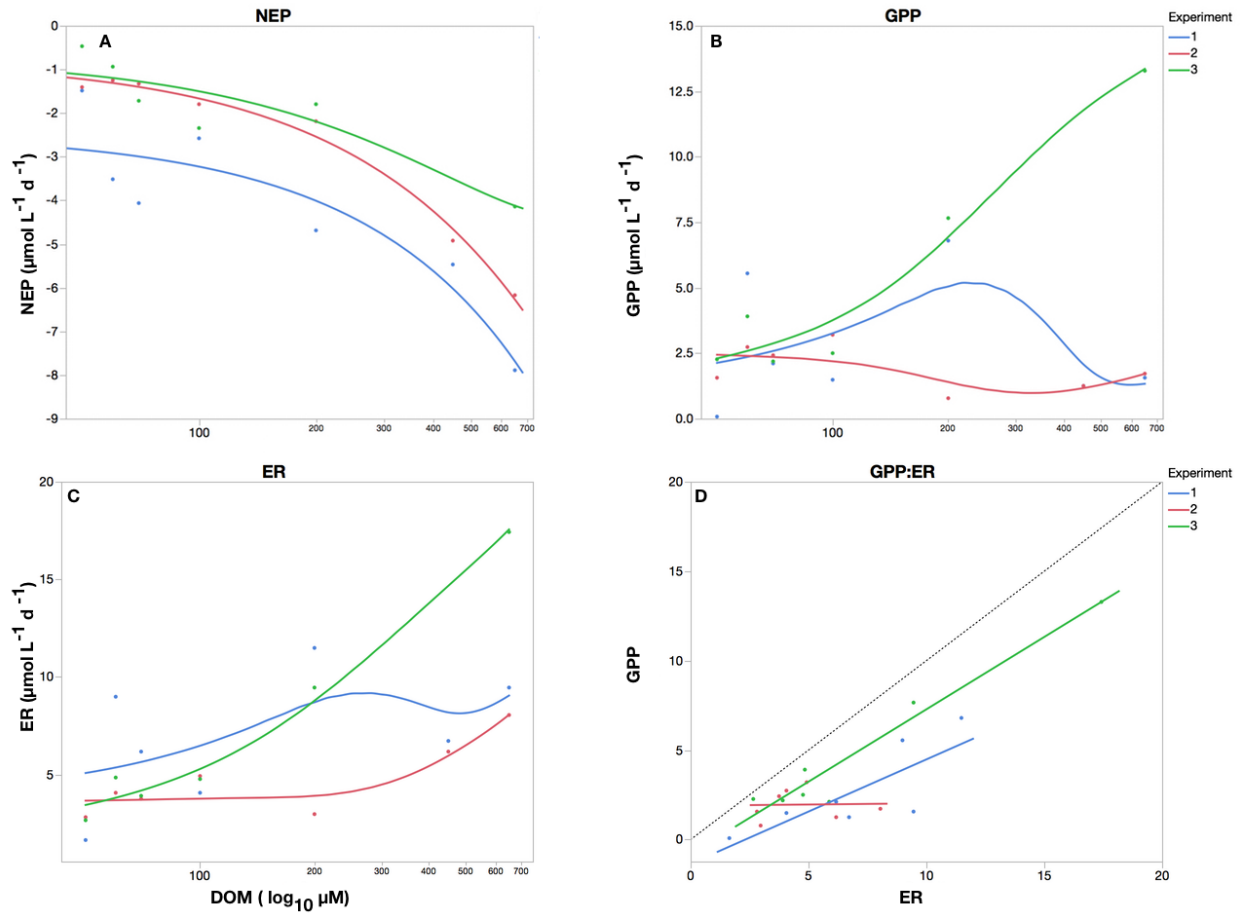


Fig 7. (A, B, C) Metabolism estimates for each individual experiment across the gradient of DOM tested. Note x-axes are log transformed to meet assumptions of homoscedasticity. (A) NEP. (B) GPP. (C) ER. (D) GPP versus ER rates. Dotted line is 1:1 ratio, above which indicates autotrophy and below which indicates heterotrophy. Blue lines represent experiment 1 in all plots, red lines represent experiment 2, and green lines represent experiment 3.

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