The Effect of an Extreme Rain Event on the Biogeochemistry and Ecosystem Metabolism of an Oligotrophic High-Elevation Lake

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Abstract

We characterized the effect of an extreme rain event on the biogeochemistry and ecosystem metabolism of an oligotrophic Sierra Nevada (California) lake. During a 10 hour period of an autumn season rainfall event, lake discharge increased from <1.0 L s^{-1} to over 3000 L s^{-1}, reaching a rate one order of magnitude higher than found during peak snowmelt. Large quantities of terrestrial particulate and dissolved organic matter were washed into the lake. An entire season of autochthonous dissolved organic carbon (DOC) was flushed and replaced by allochthonous DOC as light attenuation increased by $>300\%$. The resulting truncation of the photic zone, reduction of water column chlorophyll-*a*, and increase in particulate and dissolved organic matter available to microbes resulted in a 47% reduction in whole lake gross primary production and 30% increase in respiration relative to average autumn values. As a consequence, the lake went from being slightly autotrophic to strongly heterotrophic. If rain events increase in frequency, as many climate change models predict, increased terrestrial inputs to Sierran lakes may result in more frequent periods of reduced primary production, increased periods of hypoxia and anoxia, and an ecosystem shift toward net heterotrophy during the ice-free season.

Introduction

Large rain events are capable of transporting substantial amounts of terrestrial material into lakes. Because of this tendency, rainstorms often act as temporal ''hot-spots,'' accounting for a majority of terrestrial organic inputs and stimulating biogeochemical reactions (McClain et al., 2003; Raymond and Saiers, 2010). Such fluxes may be especially pronounced in high-elevation catchments, where steep slopes, thin soils, and large areas of impermeable rock rapidly channel runoff into lakes. Of the mechanisms capable of causing such flooding in the Sierra Nevada (California), rain on snow events and summer thunderstorms have the greatest capacity to inundate catchments, raise lake levels, and lead to overbank flows in streams (Kattelmann, 1990). The effect of these comparatively rare floods on lake and stream ecology has been characterized for high-elevation systems (Cooper et al., 1988; Engle and Melack, 2001). However, little is known regarding how these events broadly affect ecosystem function.

Non-winter rainfall, which occurs during the ice-free period of high biological activity in alpine lakes, has considerable potential to impact ecosystem function by altering ecosystem metabolic rates. Metabolic rates quantify the production and consumption of organic matter in a system and provide an index of overall biological activity (Carpenter et al., 2005). At the scale of a lake, ecosystem metabolism reflects the balance between gross primary production (GPP) and community respiration (CR). Lakes where primary production exceeds respiration are autotrophic; however, lakes with large contributions of organic matter from the surrounding landscape can be net heterotrophic. The net ecosystem production (NEP) of a system reflects its metabolic balance (NEP = GPP + CR) and is a product of the interaction between autotrophic and heterotrophic processes. These processes are, in turn, affected by a range of drivers, including weather patterns (Tsai et al., 2005), landscape inputs (Staehr et al., 2010), and aquatic biogeochemistry (Cole et al., 2000; Hanson et al., 2003). Consequently, NEP may be a good metric of environmental change, especially in systems where these drivers have large gradients or show strong seasonal patterns (Coloso et al., 2011).

Although there has been little published on the ecosystem metabolism of high-elevation lakes, recent work from Emerald Lake suggests some lakes are likely to be net autotrophic during the ice-free season (Sadro et al., 2011a, 2011b). While net heterotrophy might be predicted from the comparatively low levels of primary productivity found in these lakes (del Giorgio and Peters, 1994; Duarte and Agusti, 1998; Cole et al., 2000), because terrestrial inputs of organic matter are low, on a seasonal basis GPP is higher than CR, and NEP is positive. Low levels of dissolved organic carbon (DOC) have been associated with net autotrophy in other temperate lakes as well (Carignan et al., 2000; Prairie et al., 2002; Hanson et al., 2003). Although autotrophic on average during the ice-free period, NEP in Emerald Lake has a seasonal pattern (Sadro et al., 2011a, 2011b): The epilimnion is predominantly heterotrophic immediately after ice-off when snowmelt is tapering off, chlorophyll-*a* is at a seasonal minimum, and the fluorescence characteristics of lake water suggest dissolved organic matter is largely of terrestrial origin. The lake becomes autotrophic with the seasonal increase in chlorophyll-*a* that occurs during the period of stratification. After the onset of autumn mixing, when chlorophyll-*a* concentrations peak and fluorescence characteristics suggest dissolved organic matter is of autochthonous origin, the lake is predominantly autotrophic throughout the water column.

While few studies have quantified the effect of flooding on lake metabolism, there is ample indirect evidence to suggest impacts may be substantial. Climatic factors, such as precipitation, affect terrestrial inputs to lakes (Pace and Cole, 2002); in particular, the runoff from intense rain storms is capable of mobilizing large quantities of terrestrial material (Kattelmann, 1990). Allochthonous loading decreases water column transparency, which is important in structuring thermocline depth, the strength of stratification, and light climate (Houser, 2006). The availability of light throughout the water column affects the depth of the photic zone and, as a consequence, rates of primary production (Fee et al., 1996; Carpenter et al., 1998; Cole et al., 2000). The loading of terrestrial organic matter, which often increases in lability after photodegredation in aquatic environments (Moran and Zepp, 1997; Sulzberger and Durisch-Kaiser, 2009), stimulates increased rates of bacterioplankton respiration (Lennon and Pfaff, 2005) and may cause increased heterotrophy of the ecosystem (Hanson et al., 2003). Given the weak autotrophy found during the growing season in high-elevation lakes (Sadro et al., 2011a, 2011b), the changes to ecosystem function that result from flooding may substantially alter metabolic balance.

In this study, we document the effect of an intense rain event that occurred at the end of the 2009 ice-free season on the ecosystem function of an alpine lake. We characterize the impact to lake physical and biogeochemical patterns and explore how overall changes in these patterns affect ecosystem metabolism. We demonstrate that the influx of terrestrial material into an alpine lake from a flood simultaneously suppresses primary production and stimulates respiration, causing a shift in metabolic balance toward net heterotrophy.

Methods

Emerald Lake is an oligotrophic, high-elevation lake located on the western slope of the Sierra Nevada (California, 36°35′49″N, 118°40′29″W, 2800 m a.s.l.). With a surface area of 2.7 ha, a maximum depth of 10 m, and volume of 16.2×10^4 m^3, it is representative of high-elevation lakes found throughout the Sierra (Melack and Stoddard, 1991). The theoretical residence time (i.e., the number of preceding discharge days necessary to equal lake volume) of Emerald Lake ranges from a few days during peak snowmelt to nearly a year during summer and autumn periods of low flow. Light attenuation in the lake is low; the attenuation coefficient for photosynthetically active radiation (PAR) typically ranges between 0.2 m^{-1} and 0.3 m^{-1} during the ice free-season (Sadro et al., 2011a), and the entire water column and benthic zone remain above the 1% irradiance level defining the euphotic zone. Its headwater catchment is steep and sparsely vegetated overall, though there are dense areas of willow and other woody shrubs (Rundel et al., 2009). Seasonally, dissolved organic matter inputs to the lake are typically low (Nelson et al., 2009). Emerald Lake's snowmelt-dominated hydrology and biogeochemistry have been well characterized for over two decades (Melack and Stoddard, 1991; Sickman et al., 2003), and spatial and temporal variability in its ecosystem metabolism have recently been described (Sadro et al., 2011a, 2011b, 2011c). On 13 October 2009 a large rainstorm inundated the catchment with 15–20 cm of rain in less than a 24 h period.

ENVIRONMENTAL DATA

Lake discharge was calculated hourly at the outflow using a calibrated weir and pressure transducer corrected for fluctuations in atmospheric pressure. Wind speed was measured with a microvane anemometer at 1 s intervals and recorded as 5 min averages using a Campbell Scientific meteorological station located 30 m from and 8 m above the lake shore. The attenuation coefficient for PAR was estimated by measuring light at 0.5 m intervals throughout the water column using a hand-held meter (LiCor LI-250A with a LI-192 quantum sensor).

WATER SAMPLING AND ANALYSIS

Seasonal sampling of Emerald Lake was conducted approximately monthly between June and early October 2009. Samples were collected at four depths (1, 4, 7, and 9 m) using a hand-operated peristaltic pump and processed in the field. Dissolved nitrate + nitrite (NO$_3$) and total dissolved nitrogen (TDN) were measured by cadmium reduction while soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) were measured by phosphomolybdate reaction (Strickland and Parsons, 1972). Total dissolved samples were oxidized prior to analysis (Valderrama, 1981), and all analysis were done using a Lachat autoanalyzer (Lachat Instruments Quickchem 8000). Dissolved organic nitrogen and phosphorus (DON and DOP) were computed as the difference between total dissolved and dissolved inorganic fractions. Particulate phosphorus samples were collected on glass fiber filters (Gelman A/E, 1.0 μm nominal) and processed the same as total dissolved samples. Chlorophyll-a (Chl-a) samples were collected on 0.45 μm nitrocellulose filters (Millipore) and extracted for 24 h in 90% acetone before analysis on a Turner AU-10 fluorometer. Water samples for dissolved organic carbon (DOC) and fluorescence were filtered through glass fiber filters (Whatman GF/F; 0.7 μm nominal) into amber borosilicate vials and immediately acidified with HCl to pH < 2 and analyzed on a Shimadzu Total Organic Carbon analyzer using high-precision methods adapted for low concentrations (Carlson et al., 2010). We measured the fluorescence index (FI), a relative measure of allochthonous and autochthonous fulvic acids in the dissolved organic matter pool based on the ratio of emission intensity between 450 and 500 nm at 370 nm excitation (McKnight et al., 2001), as described by Nelson et al. (2009). We computed the mass ratio between dissolved inorganic nitrogen (made up of NO$_3$ because ammonium is a small fraction of the total) and total phosphorus (DIN:TP μg:μg) as an index of nutrient limitation: > ~4 suggest P-limitation; < ~0.5 suggest N-limitation; and co-limitation occurring between the two (Morris and Lewis, 1988; Sickman et al., 2003).

MEASUREMENTS OF ECOSYSTEM METABOLISM

Paired days of metabolism measurements were made approximately monthly over the ice-free season from June to August 2009; post-flood metabolism was measured once on 24–25 October 2009, 11 days after the 13 October 2009 flood. Metabolic rates were estimated from diel dissolved oxygen (DO) profiles using a modified mass balance approach (Sadro et al., 2011a). We measured DO throughout the water column using optical dissolved oxygen sondes (D-opto, Zebra-Tech). Pre-flood 2009 and autumn 2008 DO

measurements were made manually at 1 m depth intervals from the lake surface to 9.75 m every other hour from sunrise to sunset over a 24 h to 48 h period. Post-flood 2009 DO measurements were recorded at 5 min intervals from 0, 1.0, 2.5, 3.5, 5.5, 6.5, 8.0, and 9.75 m depths over a 24 h period. NEP for each depth at each time interval was computed as

$$NEP = \Delta DO + F_{GE}/MLD, \quad (1)$$

where ΔDO (g m^{-3}) is the measured change in DO, F_{GE} (g m^{-2}) is flux due to atmospheric gas exchange, and MLD (m) is the mixing layer depth. We did not include fluxes between strata in the water column in our mass balance because we lacked the thermistor data necessary to compute eddy diffusivities. Such fluxes accounted for 12% of the total mass balance in 2008, and while their inclusion improves the accuracy of metabolism estimates, their omission does not substantially alter interpretations and does not influence whole-lake, depth-integrated estimates (Sadro et al., 2011a). F_{GE} was computed as

$$F_{GE} = k_{DO} (DO_{water} - DO_{sat}), \quad (2)$$

where k_{DO} (m h^{-1}) is the gas exchange coefficient for DO, DO_{water} (g m^{-3}) is the concentration of dissolved oxygen in surface water, and DO_{sat} (g m^{-3}) is the saturation concentration of dissolved oxygen at ambient temperature and atmospheric pressure. The gas exchange coefficient was estimated based on wind speed (Cole and Caraco, 1998) and the relationship between Schmidt numbers (Jahne et al., 1987). Mixing layer depth (Brainerd and Gregg, 1995) was computed by identifying the depth where water density was 0.05 kg m^{-3} greater than surface density. Daily NEP was computed by summing NEP for each of the time intervals over a dawn-to-dawn 24 h period. CR was computed by summing nighttime NEP and dividing by the time interval over which it was summed to derive an average hourly nighttime rate, which was subsequently applied over an entire 24 h period. We computed GPP as the sum of NEP and CR (GPP = NEP + CR) where CR is treated as a positive value. We assumed constant diel respiration; while this likely caused us to underestimate CR and GPP, it does not affect our estimates of NEP (Sadro et al., 2011c).

Whole-lake depth-integrated metabolism was computed by integrating DO concentrations through the entire water column, where the concentration at each depth was first multiplied by the proportional area of that depth as determined from hypsographic curves (see Sadro et al., 2011a, for a more complete description).

PRE- AND POST-FLOOD ANALYSIS

We tested for the effect of the storm on biogeochemistry throughout the water column using paired *t*-tests. Additionally, we demonstrated the magnitude of change with respect to seasonal variability by plotting pre- and post-storm values in relation to the seasonal mean and standard deviation in the months preceding the storm. Pre-storm biogeochemical data are measurements from 4 October 2009, post-storm values were collected on 25 October 2009, ~10 d after the storm. Seasonal values are the mean of the four monthly samples preceding the flood, from June to October 2009. We used JMP (SAS Institute Inc., version 9.0) for all statistical analyses.

The closest pre-storm metabolism measurements made in 2009 were from August. Because metabolism measurements in Emerald Lake have a seasonal pattern of increase through mid-summer and decline into the autumn (Sadro et al., 2011a, 2011b), we compare post-storm rates with average autumn values from the comparable time period in 2008 rather than the August values from 2009. There are a number of reasons why this approach is justified. (1) Seasonal variability is larger than interannual variability between autumn periods (Sadro et al., 2011a). For example, while the average seasonal standard deviation for depth integrated CR and GPP from 2007 to 2008 was 14.6 mmol m^{-2} d^{-1}, the standard deviation between interannual autumn values for those years was ~55% lower. (2) Seasonal patterns in metabolism in Emerald Lake were consistent between 2007 and 2008 (Sadro et al., 2011a), and the few measurements we made in 2009 fall within that range. (3) Despite interannual variability in mean NEP, autumn values were typically positive in 2007 and 2008 (Sadro et al., 2011a, 2011b).

Results

The late season rain of 13 October 2009 caused discharge at the outflow of Emerald Lake to increase from <1.0 L h^{-1} to >3000 L h^{-1}, an order of magnitude higher than peak spring snowmelt flows (Fig. 1). The total storm runoff was equal to 1.3 times the volume of the lake, causing the theoretical residence time to drop from 300 d to <1 d. There was evidence that floodwaters exceeded bankfull levels and overtopped the outlet weir for some period of time during the event, possibly introducing error in our discharge measurements. We evaluated our estimates by comparing the sum of discharge during the flood event to theoretical discharge based on simple water mass balance. Using the 18.5 cm total rainfall amount measured at Panther Gap near Emerald Lake (P. Kirchner, personal communication) and assuming a runoff coefficient of 0.8 for the predominantly granitic and wetted catchment soils, we estimated a discharge of ~178,000 m^3 for Emerald Lake's 1.2 km^2 catchment area. This amount is about the same as our cumulative total discharge following the storm (172,100 m^3), suggesting measurement error of less than 3%.

Relatively large amounts of terrestrial material were mobilized within the catchment during the flood. Pea-size granite fluvial deposits were evident at lake margins fed by even the smallest of seasonal meltwater streams, and the benthic zone was littered with organic debris. Concentrations of dissolved and particulate carbon and nutrients increased (Fig. 2). As a result of these inputs, light transmittance throughout the water column was reduced; the attenuation coefficient of photosynthetically active radiation (K_d) doubled from 0.3 to 0.6 (Fig. 2, Part A). The 1% light depth, which typically exceeds the maximum depth of the lake throughout the ice-free season, decreased by 70% to 7.5 m after the flood. As a result of the reduced transparency, solar heating within the water column caused the lake to weakly re-stratify by ~0.2 °C during a period when diel convective turbulence typically keeps the water column well mixed on a daily basis (Fig. 3).

The flood substantially altered lake biogeochemistry. Nearly all variables we measured changed significantly from pre-flood values (Table 1; Fig. 2; in the following text we report means ± standard deviation), and in many instances average post-flood
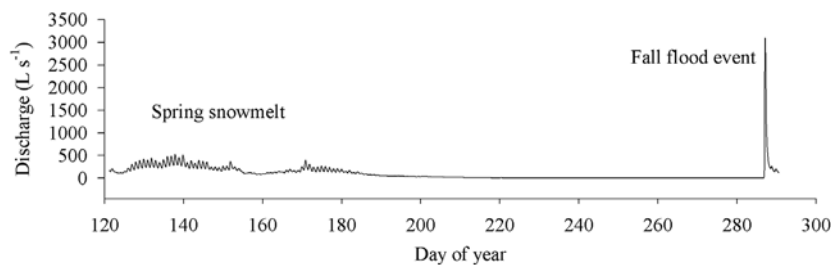
FIGURE 1. Discharge measured at the outflow of Emerald Lake starting with the onset of snowmelt in May through late October 2009.

values fell well outside the range of seasonal variability (Fig. 2). NO_3 increased 100-fold from 0.14 ± 0.06 to 14.33 ± 0.04 μmol L^{-1}. DON more than doubled to 8.8 ± 1.8 μmol L^{-1}, resulting in an almost sixfold increase in TDN. Although there was no measurable change in SRP, DOP increased 50% causing TDP to increase 27%. PP nearly doubled to 0.22 ± 0.01 μmol L^{-1}, which together with the increases in the other phosphorus species, caused TP to increase by 61%. A pre-flood DIN:TP ratio of 0.6 indicates the likelihood of co-limitation of the phytoplankton prior to the flood. Despite the post-flood increase in TP, however, the proportionally larger increase in nitrate caused DIN:TP to increase substantially, resulting in a shift to P-limitation after the flood.

The increase in dissolved and particulate organic matter appears to have been driven largely by terrestrial material. While some resuspension of sediments near the inlets is possible, the areal extent of the littoral zone in Emerald Lake is small, and the steep gradient in the bathymetry at the inlets, where depth drops to >6 m within about 5–25 m of shore, further reduces the likelihood of much sediment resuspension. Although PP increased, there was a corresponding 40% decline in Chl-*a*, suggesting the simultaneous flushing of autochthonous organic matter and delivery of terrestrial organic matter. Similarly, as DOC nearly doubled to 127 ± 2.3 μmol L^{-1}, a concentration well outside the seasonal range of variability, there was a corresponding 0.20 unit decline in FI. FI in
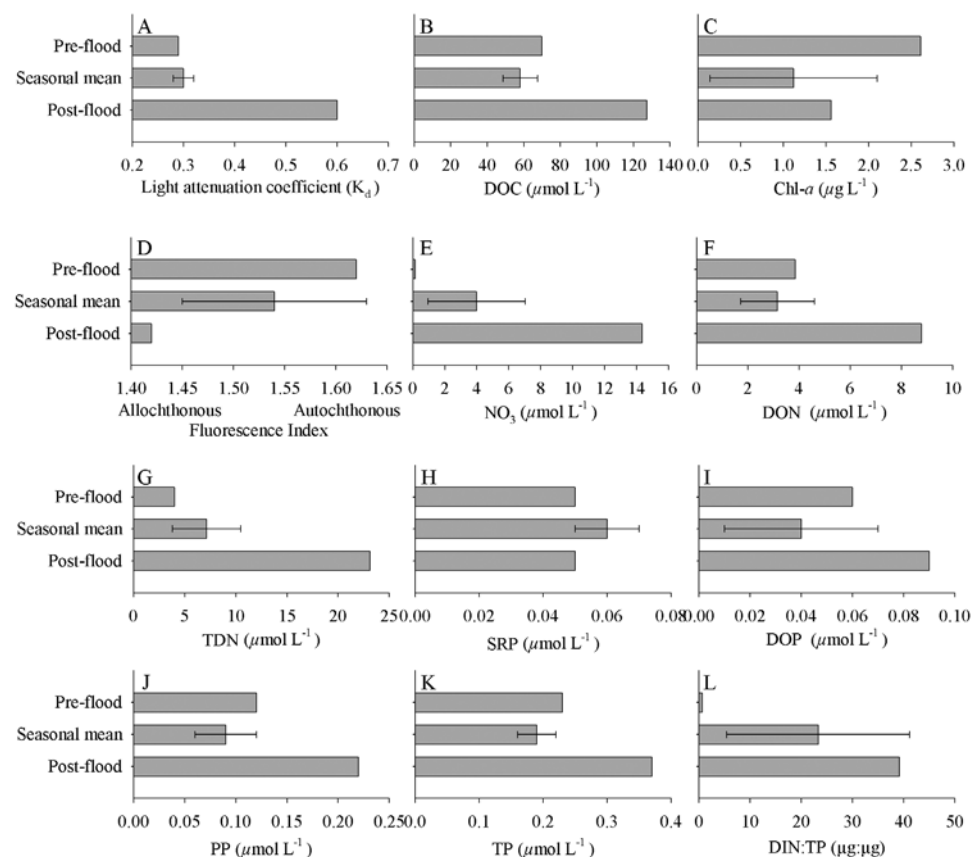

FIGURE 2. Dissolved nutrient concentrations in Emerald Lake measured before (4 Oct) and after (25 Oct) the fall 2009 flood (14 Oct) with respect to 2009 seasonal mean and standard deviation. Data are for: (A) attenuation coefficient (Kd) for photosynthetically active radiation; (B) dissolved organic carbon (DOC); (C) chlorophyll-*a* (Chl-*a*); (D) fluorescence index (FI); (E) nitrate (NO_3); (F) dissolved organic nitrogen (DON); (G) total dissolved nitrogen (TDN); (H) soluble reactive phosphorus (SRP); (I) dissolved organic phosphorus (DOP); (J) particulate phosphorus (PP); (K) total phosphorus (TP); and (L) the μg:μg ratio between dissolved inorganic nitrogen and total phosphorus (DIN:TP), an index of nutrient limitation. Not shown is total dissolved phosphorus (TDP), which has the same pattern as TP. Flood effects were statistically significant for all variables but SRP (see Table 1).
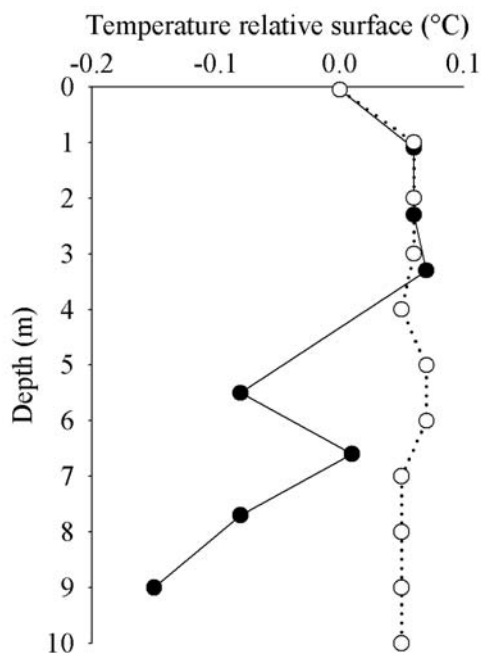
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FIGURE 3. Water column temperatures in Emerald Lake. Values are a comparison between a typical autumn day (25 October 2008, see Sadro et al., 2011a; open circles and dotted line) and ~10 days after the 2009 flood (25 October 2009; closed circles and black line). Profiles were collected at dawn on each day and temperatures are shown as °C relative surface temperatures to facilitate comparison.

Emerald Lake has a distinct seasonal pattern of increase that, not surprisingly, is correlated with the seasonal increase in Chl-a (Sadro et al., 2011b). The scale of change we observed in FI after the flood represents a shift toward allochthony approximately equal to the entire range of seasonal change, indicating near complete flushing and replacement of autochthonous lake DOC with terrestrial DOC.

Diel dissolved oxygen patterns were impacted by the flood, although the magnitude of the effect differed with depth. Under typical autumn conditions (Sadro et al., 2011a, 2011b), DO increases during the day throughout the water column before overnight respiratory drawdown, and there is relatively little variability in metabolic rates with depth (Fig. 4, Part A). However, with the changes to water column transparency and Chl-a concentration that accompanied the flood, DO only showed a diel pattern of increase within the epilimnion. In the metalimnion and below, DO decreased continuously throughout the day despite the relatively even distribution of Chl-a and nutrients throughout the water column (Table 1).

The effect of the flood on lake biogeochemistry and Chl-a concentrations caused significant changes in the magnitude of metabolic rates throughout the water column (Fig. 4). Rates of GPP at the depths we sampled ranged from 0.98 μmol L^{-1} d^{-1} to 2.50 μmol L^{-1} d^{-1}. These rates were 26% to 92% lower than typical autumn values, representing a statistically significant reduction (Table 2). Rates of CR ranged from 1.22 μmol L^{-1} d^{-1} to 7.64 μmol L^{-1} d^{-1}, between 48% lower than and >400% higher than typical autumn water column values. However, despite the substantially higher rates near the bottom of the lake (Pearson correlation coefficient between CR and depth: $r = 0.69$, $p = 0.0593$), and 41% higher water column rates on average, volumetric rates of CR were not significantly different from autumn values overall. The cumulative effect of the lower GPP and slightly higher CR was to cause NEP to drop significantly relative to autumn values. NEP throughout the water column ranged from -0.21 μmol L^{-1} d^{-1} to -6.55 μmol L^{-1} d^{-1}. Relative to typically positive autumn values this represents a 119% to 881% decline and a substantial shift toward heterotrophy (Fig. 5): the mean post-flood GPP:CR ratio throughout the water column (0.48) was well outside the 95% prediction interval surrounding typical autumn values (1.25).

TABLE 1

Flood effect throughout the water column on biogeochemical variables in Emerald Lake. SD is the standard deviation among the four depths water samples were collected on each date. Statistical comparisons were made using paired t-tests with seven degrees of freedom for each sample. NO_3 is nitrate + nitrite; SRP is soluble reactive phosphorus; TDN and TDP are total dissolved nitrogen and phosphorus; DON and DOP are dissolved organic nitrogen and phosphorus; PP is particulate phosphorus; TP is total phosphorus; DIN:TP, an index of nutrient limitation, is the μg:μg ratio between dissolved inorganic nitrogen and total phosphorus; FI is the fluorescence index, a relative measure of allochthonous and autochthonous fulvic acids in the dissolved organic matter pool (McKnight et al. 2001); Chl-a is chlorophyll-a; and DOC is dissolved organic carbon.

| Variable	Pre-flood mean	Pre-flood SD	Post-flood mean	Post-flood SD	t-ratio	p
NO_3 μmol L^{-1}	0.14	0.06	14.33	0.04	1025.6	<.0001
SRP μmol L^{-1}	0.05	0.01	0.05	0.00	0.6909	0.5393
TDN μmol L^{-1}	4.00	1.25	23.11	1.78	39.42	<.0001
TDP μmol L^{-1}	0.11	0.01	0.14	0.01	2.680	0.0751
DON μmol L^{-1}	3.86	1.24	8.78	1.78	10.45	0.0019
DOP μmol L^{-1}	0.06	0.01	0.09	0.01	3.434	0.0414
PP μmol L^{-1}	0.12	0.01	0.22	0.01	10.98	0.0016
TP μmol L^{-1}	0.23	0.02	0.37	0.01	18.70	0.0003
DIN:TP	0.62	0.26	39.17	1.21	72.96	<.0001
DIN:DON	0.04	0.02	1.69	0.39	8.824	0.0031
DIP:DOP	0.78	0.14	0.59	0.09	-3.695	0.0344
FI	1.62	0.03	1.42	0.01	-12.64	0.0011
Chl-a ug L^{-1}	2.61	0.19	1.56	0.09	-9.21	0.0027
DOC μmol L^{-1}	69.9	3.4	127.3	2.3	69.27	<.0001
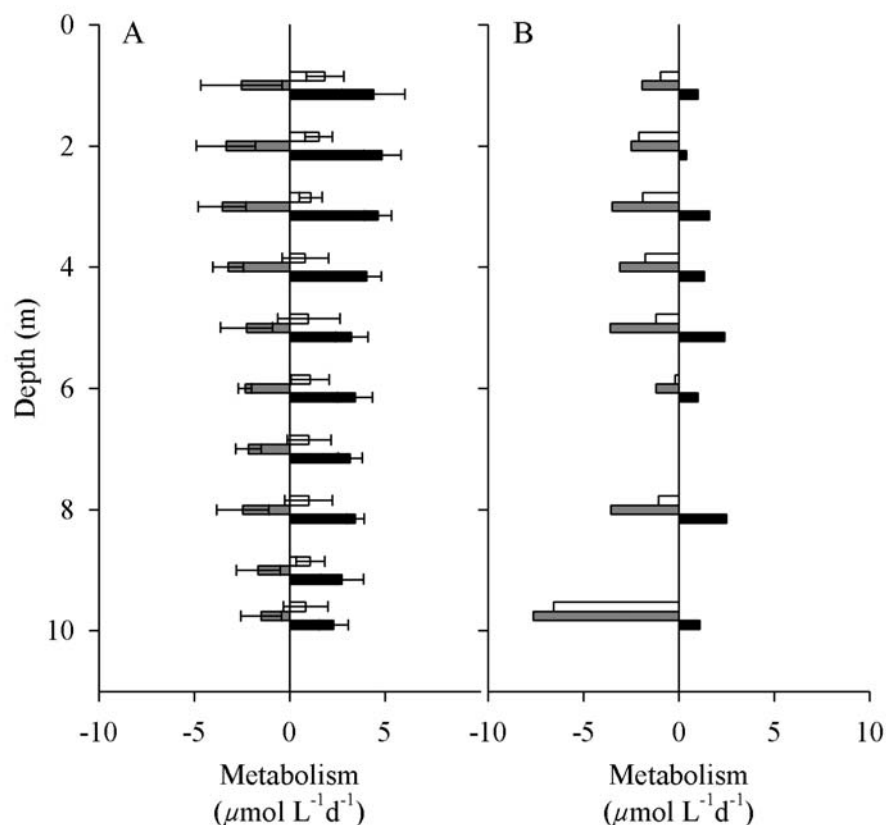
FIGURE 4. Flood effect on volumetric metabolic rates throughout the water column. (A) Average autumn values (2008; see Sadro et al., 2011a). (B) Post-flood values (25 October 2009). Black bars are gross primary production (GPP), gray bars are community respiration (CR), and white bars are net ecosystem production (NEP).

Similar patterns are seen when volumetric metabolic rates are integrated through the water column and scaled to the whole lake level (Fig. 6). At 13.3 mmol m^{-2}, post-flood whole lake GPP was 47% lower than typical autumn values, and 79% lower than during the stratified period of 2009. Post-flood whole lake CR was 21.7 mmol m^{-2}, 30% higher than autumn levels, but 52% lower than higher rates measured during the period of stratification when lake temperatures were warmer. The cumulative effect of reduced primary production and increased respiration at the whole lake level resulted in negative NEP. Post-flood whole lake NEP was −8.4 mmol m^{-2}, 202% and 151% lower than typical autumn values and the 2009 summer average, respectively. The GPP:CR ratio at the whole lake scale was 0.68, ~60% lower than typical autumn or summer 2009 values.

Discussion

We characterized the effect of a flood event in a high-elevation lake (Fig. 1) on thermal structure (Fig. 2), transparency (Fig. 3,

Part A), biogeochemistry (Fig. 3, Parts B–L), and ecosystem metabolism (Figs. 4–6) in the context of typical autumn values. The cumulative effect of the changes we illustrate was a shift toward heterotrophy (Figs. 5 and 6) in a lake that has been found to be seasonally autotrophic (Sadro et al., 2011a, 2011b), and where episodes of heterotrophy are uncommon during the period of autumn mixing when the flood occurred (Fig. 5). While the lack of additional post-flood sampling affects our ability to characterize variability around the rates we measured, previous studies in Emerald Lake (Sadro et al., 2011a, 2011b, 2011c) have demonstrated that metabolism measurements from an individual day, especially during the period of autumn turnover, are good estimates of seasonal means. The magnitude of change in lake biogeochemistry that we demonstrate to be associated with the flood was large relative to seasonal means, underscoring our interpretations.

The changes in ecosystem metabolism we documented resulted from the flushing and replacement of lake waters with terrestrially influenced floodwaters and subsequent reduction in transparency within the lake. The lake was flushed by a volume of

TABLE 2

Flood effect throughout the water column on volumetric rates of metabolism. Statistical comparisons of rates measured throughout the water column were made between average autumn values (2008) and post-flood values (2009) using paired *t*-tests. CV is coefficient of variation, NEP is net ecosystem production, CR is community respiration, and GPP is gross primary production.

Metabolic rate (μmol L^{-1} d^{-1})	Autumn mean	Autumn CV	Post-flood mean	Post-flood CV	*t*-ratio	*p*
NEP	1.14	355	−2.02	108	−4.768	0.001
CR	2.50	364	3.51	187	0.888	0.4039
GPP	3.63	437	1.48	227	−5.253	0.0006

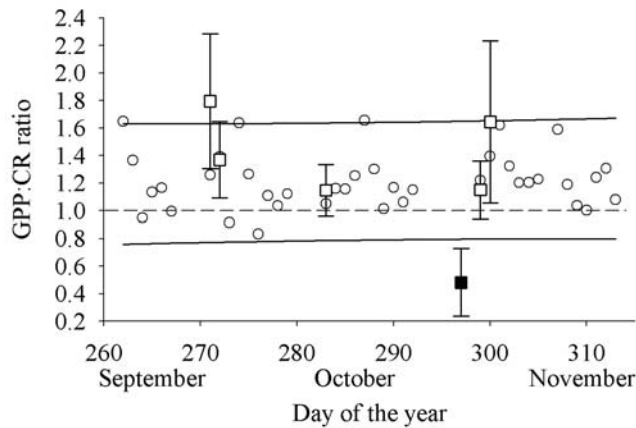STEVEN SADRO AND JOHN M. MELACK / 227

FIGURE 5. Flood effect on the balance between gross primary production and community respiration (GPP:CR) with respect to typical autumn values (see Sadro et al., 2011a, 2011b). Values of GPP:CR (>1 indicate autotrophy and values <1 heterotrophy) computed from volumetric metabolic rates for post-flood water column averages and standard deviation (black square), autumn 2008 water column averages and standard deviations (white squares), and autumn 2008 epilimnetic values (white circles). Black lines are 95% prediction intervals surrounding 2008 values.

floodwater in excess of lake volume causing Chl-*a* concentrations, which typically peak during the period of fall overturn (Sadro et al., 2011a), to decline by over half. The loss of phytoplankton biomass and concomitant truncation of the photic zone caused water column GPP to decline and NEP to become negative. In addition, the shift to P-limitation in the lake may have placed an
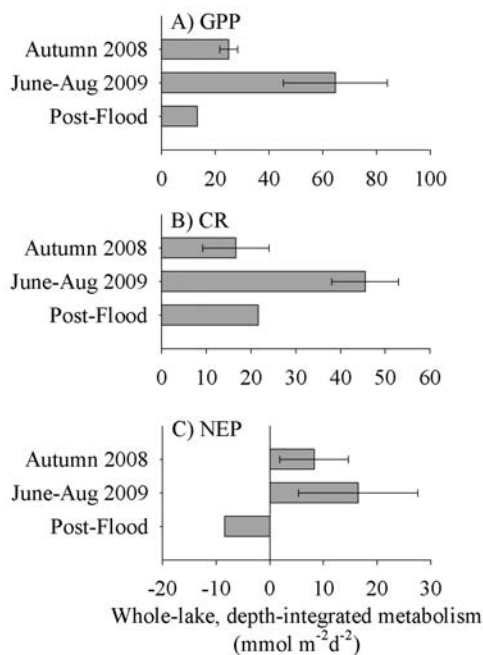

FIGURE 6. Flood effect on whole-lake, depth-integrated areal metabolic rates. Comparison is between 2008 average autumn values (Autumn; see Sadro et al., 2011a), 2009 seasonal average, (Seasonal) and post-flood values (25 October 2009; Post-Flood) for: (A) gross primary production (GPP), (B) community respiration (CR), and (C) net ecosystem production (NEP).

additional constraint on the growth of the phytoplankton that remained in the water column after the flood. Although flood effects on ecosystem metabolism are rarely documented, similar patterns to these have been observed in other aquatic systems: typhoon flooding in a subtropical humic lake (Tsai et al., 2008) and the experimental flooding of a stream (Uehlinger et al., 2003) both caused a reduction in primary producer biomass that reduced GPP and resulted in NEP becoming more negative. In neither of these cases, however, was the relative magnitude of the impact as substantial as we characterize here.

In contrast to the direct hydrologic effect of flooding on GPP and NEP, flood effects to CR in Emerald Lake were more complex to interpret. Despite the influx of terrestrial organic matter and rapid replacement of autochthonous with allochthonous DOM, except for the depth strata near the lake bottom, rates of respiration remained relatively unchanged throughout the water column (Fig. 4). Higher rates of respiration in the water column of Emerald Lake have been associated with higher concentrations of particulate matter, as when a deep Chl-*a* maxima is present (Sadro et al., 2011a), but post-flood concentrations of particulate matter did not vary much with depth, and we did not observe an increase in water column respiration rates that experimental evidence suggests might be expected with such a large influx of terrestrial dissolved organic matter (Lennon and Pfaff, 2005). Such material is thought to fuel higher respiration rates, in part, because high carbon to nitrogen and phosphorus ratios result in lower overall bacterial growth efficiency, leading to elevated rates of respiration (del Giorgio and Cole, 1998; Lennon and Pfaff, 2005; Perez and Sommaruga, 2006), and, in part, because soil organic matter increases in lability upon entering aquatic environments as a result of photo-oxidative reactions (Moran and Zepp, 1997; Sulzberger and Durisch-Kaiser, 2009). While soil DOM amendments have not been done in Emerald Lake, the respiration rates of bacterioplankton there are known to decrease on a diel basis in relation to changes in DOC (Sadro et al., 2011c), illustrating the responsiveness of bacterioplankton respiration to changes in organic matter.

The patterns in water column CR we observed may be explained by a differential effect of the flood to free-living and particle-attached bacteria. Similar to phytoplankton biomass, it is likely that free-living bacterioplankton biomass also decreased as a result of the flushing of the lake. Bacterial abundance has been shown to be negatively correlated with flood frequency in some arctic lakes (Spears and Lesack, 2006), and in Emerald Lake it is seasonally lowest during and immediately after snowmelt (Nelson, 2008) when lake waters are diluted by the high volume of inflowing meltwaters. Given that respiration in Emerald Lake is dominated by bacterioplankton (~73% on average; Sadro et al., 2011c) and that seasonal variability in CR is largely a function of their abundance (Sadro et al., 2011b), a lack of significant increase in post-flood CR may simply be due to fewer cells contributing to ecosystem rates. Under such circumstances, the lack of a decline in CR may be masking the expected cell specific increases in bacterioplankton respiration.

Particle-attached bacteria, which were less likely to be diluted by flood waters, probably increased in conjunction with the increase in particulate terrestrial material washed into the lake during the flood. Although we did not quantify sediment accumulation

related to the flood, signs of new sedimentation were observed, both as fluvial deposits at inlets and as a visible distribution of particulate matter and plant material over the lake bottom. Particle-attached bacteria, with their higher per cell production rates, account for a majority of bacterial production in aquatic systems (Kirchman and Mitchell, 1982; Crump et al., 1998). Because their production is positively correlated with particle concentrations (Crump et al., 1998), it is likely that the higher post-flood respiration rates we measured near the lake bottom resulted from the settling of particles over the ~10 d period prior to our sampling.

The seasonal timing of storms will affect the magnitude of their overall impact on ecosystem metabolism. Large amounts of precipitation deposited as rain will mobilize more terrestrial material than snowmelt because of the higher energetic dynamics of rainfall-related flooding and the greater spatial availability of transportable material under snow-free conditions (Martinez-Castroviejo, 1990). Even in years with unusually large winter snowpacks, spring snowmelt dynamics ultimately constrain the rate of inundation of lakes by meltwaters. For example, differences in summer DOC concentrations in Emerald Lake between years with above and below normal snowpack were negligible, yet heavy afternoon summer thundershowers mobilized enough organic matter to cause a ~20–30 μM increase in surface water concentrations of dissolved organic carbon (Sadro et al., 2011a).

During the ice-free period, when the majority of precipitation falls as rain, the exact timing of these large events may have important implications for seasonal net metabolic balance. For example, the flood we characterized occurred near the end of the ice-free season. Assuming that fall productivity in the year of the flood would have been similar to values in 2008 had the flood not occurred, we estimate that the flood reduced ice-free seasonal NEP in Emerald Lake by ~75%. The magnitude of that decline in NEP is substantial, but not enough to overcome the net autotrophy of summer metabolism. Had the flood occurred earlier, however, it is possible that cumulative impacts would have been large enough to alter seasonal metabolic balance. Because the flood occurred at the end of the ice-free season, we were unable to characterize rates of recovery in ecosystem function (i.e., ecosystem resilience). However, we may still estimate the seasonal metabolic inflection point: that time during the ice-free season when, were the flood to occur, seasonal metabolic balance would be tipped toward heterotrophy. Using the post-flood metabolic rates, and assuming they remain constant until the end of the ice-free season, we estimate that floods occurring before late August or early September in Emerald Lake would most likely tip the seasonal metabolic balance toward negative NEP. Storm events that occur soon after spring mixing may affect seasonal metabolic balance the most by reducing primary productivity throughout the water column for a larger proportion of the growing season. Late autumn storms, although they may have a smaller effect on seasonal net metabolic balance, are capable of promoting periods of over-winter hypoxia or anoxia (Melack et al., 1989).

CONCLUSIONS

Alpine lakes are sentinels for global-scale perturbations (Psenner, 2003). Their remote location isolates them from many other anthropogenic impacts, and high transparency and low nutrient con-

centrations make their ecosystem function sensitive to change. Our results demonstrate this sensitivity by characterizing a significant shift in the ecosystem metabolism of a high-elevation lake toward net heterotrophy following a rain-induced flood event. Altered precipitation patterns are only one of a number of climate change effects that may alter ecosystem function of alpine lakes; climate modeling and recent trend analyses suggest that snowmelt will occur earlier, winter discharge will increase while summer flows will decrease, and more precipitation will fall as rain (Dettinger and Cayan, 1995; Melack et al., 1997; Knowles et al., 2006; Maurer, 2007). Although uncertainty remains high, the frequency and severity of storms capable of causing flooding may also increase (Cayan et al., 2008; Dettinger, 2011). While the magnitude of the flood we characterized may have been unusually large, our data support the notion that increases in the amount of precipitation that falls as rain will increase fluxes of terrestrial material (Raymond and Saiers, 2010; Einola et al., 2011). Given the weak autotrophy of these lakes during the ice-free season, it is possible that even a small increase in terrestrial inputs may cause a shift in metabolic balance toward net heterotrophy—possibly affecting carbon dynamics and net atmospheric fluxes (Rantakari and Kortelainen, 2005; Einola et al., 2011; Ojala et al., 2011).

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