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Multi-year measurement of wholestream metabolism in a snowmelt-dominated montane ecosystem

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MULTI-YEAR MEASUREMENT OF WHOLE-STREAM METABOLISM IN A SNOWMELT-DOMINATED MONTANE ECOSYSTEM

by

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PROFESSIONAL PROJECT

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Preface

Warming temperatures, reduced precipitation, and earlier snowmelt are predicted for the mountains of the southwestern U.S due to climate change. In addition, inter-annual variability in precipitation, partially linked to the El Niño-Southern Oscillation phenomenon (ENSO), also will impact stream-flow and ecosystem processes. Whole-stream metabolism was modeled using continuous data for selected time periods ranging from 2005 to 2012. This eight-year study explores temporal trends in whole-stream metabolism parameters; as well, it links the potential impact of climate variability on these temporal trends. Gross primary production (GPP) and community respiration (CR) rates are comparable to other open-canopy lotic systems and remain predominantly autotrophic with P/R > 1 with a few exceptions where P/R < 1. GPP ranged from 2.35 to 18.54 (g O_2 m^{-2} d^{-1}). CR ranged from 2.63 to 16.29 (g O_2 m^{-2} d^{-1}). GPP and CR rates were significantly greater in the summer (July) compared to spring (May) and fall (September) time periods for all years analyzed. Seasonal trends were strongly apparent. Statistical differences between spring and fall rates among years studied were not significant. Similarly, overall inter-annual rates showed no clear trend amongst years. Total snowmelt discharge (TSQ) as a proxy for effects from the El Niño-Southern Oscillation (ENSO) phenomenon explained 74% of the variation in GPP and 68% of the variation in CR during peak production periods, defined as the maximum diurnal amplitude of dissolved oxygen for a year. The negative linear relationship was statistically significant, suggesting a link between ecosystem function and global scale climate patterns. This research builds upon known large-scale environmental relationships to relate ENSO-influenced climate patterns with rates of whole-stream metabolism.

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ABSTRACT

Warming temperatures, reduced precipitation, and earlier snowmelt are predicted for the mountains of the southwestern U.S due to climate change. In addition, inter-annual variability in precipitation, partially linked to the El Niño-Southern Oscillation phenomenon (ENSO), also will impact stream-flow and ecosystem processes. Whole-stream metabolism was modeled using continuous data for selected time periods ranging from 2005 to 2012. This eight-year study explores temporal trends in whole-stream metabolism parameters; as well, it links the potential impact of climate variability on these temporal trends. Gross primary production (GPP) and community respiration (CR) rates were comparable to other open-canopy lotic systems, and remained predominantly autotrophic with P/R > 1 with a few exceptions where P/R < 1. GPP ranged from 2.35 to 18.54 (g O_2 m^{-2} d^{-1}). CR ranged from 2.63 to 16.29 (g O_2 m^{-2} d^{-1}). GPP and CR rates were significantly greater in the summer (July) compared to spring (May) and fall (September) time periods for all years analyzed. Seasonal trends were strongly apparent. Statistical differences between spring and fall rates among years studied were not significant. Similarly, overall inter-annual rates showed no clear trend amongst years. Total snowmelt discharge (TSQ) as a proxy for effects from the El Niño-Southern Oscillation (ENSO) phenomenon explained 74% of the variation in GPP and 68% of the variation in CR during peak production periods, defined as the maximum diurnal amplitude of dissolved oxygen for a year. The negative linear relationship was statistically significant, suggesting a link between ecosystem function and global scale climate patterns. This

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INTRODUCTION

Whole-stream metabolism serves as an indicator of ecosystem function for rivers (Young et al. 2008) and provides quantification of stream energy budgets (Fisher and Likens 1973), particularly carbon in the form of biomass production and consumption. Aquatic carbon sources are derived from two main sources: autochthonous (in-stream primary production) and allochthonous (terrestrial organic matter), depending on catchment characteristics such as the degree of riparian vegetation (Dodds 1997). Ecosystem processes that contribute to the production and consumption of carbon, like autotrophic and heterotrophic activity, affect *in situ* production and decomposition and the downstream transport of carbon and nutrients: ultimately, this transport has important implications for eutrophication of downstream lakes, reservoirs, and marine systems. Hence, ecosystem health is a concern for natural resource managers and can be assessed by performing measurements of ecosystem function, such as stream metabolism (Grace and Imberger 2006). As a metric of ecosystem health, estimates of stream metabolism are applicable across systems and biomes. Comparing ecosystem processes across climate regimes (Lamberti and Steinman 1997, Mulholland et al. 2001) and catchments (Hall and Tank 2003) with variable physical features provides a better understanding of primary driving factors of ecosystem metabolism.

Studies measuring whole-stream metabolism have expanded since the late 1950s with increasing numbers of these studies in the 21st century (Tank et al. 2010). Measuring whole-stream metabolism through the use of diel (24-hour) change in dissolved oxygen in the water column (Odum 1956) has progressed from taking discrete samples to making continuous, high-resolution time series measurements with *in situ* sensors and data loggers. Such technological advances in automated sensoring allow researchers to identify the direct effects of temperature dependent parameters (Butcher and Covington 1995) and groundwater (Hall and Tank 2005) on gross primary production (GPP) and community respiration (CR) estimates. Additionally, these improvements in time series data increase the accuracy in estimating GPP and CR (Roberts et al. 2007), which has implications for evaluating ecosystem function. Yet, analysis of stream metabolism across multiple-year time scales is relatively unexplored (but see Uehlinger 2006) even though such studies would aid our understanding of long-term trends and disturbance impacts on ecosystem dynamics. Further benefits of autonomous sensors include exploring diurnal biogeochemical dynamics (Nimick et al. 2011, Sherson 2012) and the capture of significant environmental events such as snowmelt (Pellerin et al. 2011) and flow disturbance (Uehlinger 2000). As a result, ecosystem dynamics can be recorded with automated sensors under a variety of environmental conditions.

Researchers have expanded their knowledge of ecosystem dynamics in part due to advances in automated sensor equipment. For instance, researchers have been able to study the environmental variables that change in space and time and to identify with greater accuracy the controls on rates of GPP and CR. Better measuring equipment has revealed that in-stream primary productivity is notably driven by light availability or photosynthetically active radiation (PAR) in the 400 to 700 nm spectral range. Local effects of riparian coverage of the channel or surface water turbidity (Izagirre et al. 2008) often regulate light availability necessary for autotrophic activity (Young and Huryn

1996). Roberts et al. (2007) found that changing leaf coverage in the riparian canopy influenced in-stream primary production by reducing GPP rates in the summer when canopy was dense. However, light limitation is less restrictive for open canopy systems, which are predicted to be dominated by autotrophic production. Lamberti and Steinman (1997) found that semi-arid and desert streams are typically open-canopied and contain some of the highest rates of in-stream GPP compared to other biomes partly due to light availability. Furthermore, Lamberti and Steinman (1997) identified stream discharge and watershed area as predictors of GPP because the predictor variables integrate ecosystem processes.

Research to date is more limited in linking climate variability with stream metabolism or ecosystem function. Marcarelli et al. (2010) modeled shifts in the hydrologic regime that produced substantial effects on stream metabolism in the face of climate change. Some studies have looked at global drivers (e.g., Mulholland et al. 2001) and hydrologic regimes (e.g., Lamberti and Steinman 1997) that control GPP and CR. Young and Huryn (1996) linked temporal patterns of hydrologic variability induced by oceanic climates with fluctuating rates of GPP. However, climate patterns remain relatively unexplored in relation to whole-stream metabolism. In particular, the ENSO phenomenon as manifested in the southwestern United States displays predictable changes in stream flow associated with snowmelt in spring and summer monsoonal rainfall events. Molles and Dahm (1990) have shown that total snowmelt discharge in catchments in New Mexico is linked to ENSO categories. The impact of snowmelt on stream discharge is reflected in seasonal and inter-annual variability in flows for this region. Moreover, stream discharge influences stream metabolism (Uehlinger 2000, Young and Huryn 1996). Given predictable patterns in the snowmelt-dominated hydrology for streams and rivers in New Mexico linked to the ENSO phenomenon in the Pacific Ocean, I hypothesized in this paper that stream metabolism parameters will respond to varying snowmelt intensity, and hence, climate patterns. El Niño (EN) years, associated with high snowpack, will reduce whole-stream metabolism because an increase in stream discharge during snowmelt will scour the stream channel and biological communities. La Niña (LN) years, associated with reduce snowpack, will not have as great of an impact on whole-stream metabolism because stream discharge during snowmelt is not as high as EN years.

This study analyzes continuous measurements of water quality parameters during the spring, summer, and fall over an eight-year period (2005-2012) to identify temporal trends in whole-stream metabolism in a high elevation stream. In addition, this report provides seasonal and inter-annual whole-stream metabolism estimates and compares these estimates to rates that have been made for similar open-canopy systems. Finally, the study explores global climate patterns, specifically the ENSO phenomenon, as potential predictors for GPP and CR and provides a multi-year, ecosystem-scale evaluation of in-stream carbon fluxes (primary production and respiration) for this snowmelt-dominated, montane grassland stream.

METHODS

Site and climate conditions

The East Fork Jemez River (EFJR) is a low-gradient, third-order stream that displays high sinuosity throughout the Valles Caldera National Preserve (VCNP) in New Mexico, USA (Figure 1). EFJR’s characteristics include an average stream gradient of

0.05% with substrate of organic matter in pools and gravel in riffle zones (Simino 2002). Vegetation within the catchment is composed primarily of montane grassland. Dominant sources of carbon for the EFJR are derived from in-stream primary producers (i.e., benthic algae and aquatic macrophytes) that exhibit seasonal shifts in community biomass and composition. Benthic algal species are dominant immediately following snowmelt and three main macrophytes (*Elodea canadensis, Ranunculus aquatilis, and Potamogeton richardsonii*) are prevalent at the onset of summer (June) through early fall (September) when light and temperature are favorable (Thompson, unpublished data). Nitrogen is the limiting nutrient for in-stream primary production for this stream ecosystem based on previous solute injection experiments (Van Horn et al. 2012).

Bimodal precipitation patterns result from winter snowfall and summer monsoonal rainfall, characteristic of montane environments in New Mexico. Baseflow conditions in the EFJR are typically two to three cfs (57 to 90 $l\ s^{-1}$). The 2005-2012 annual hydrograph is derived from a stream gauge on the Jemez River that is downstream from the confluence of the EFJR and Rio San Antonio (Figure 2A). The multi-year hydrographs show that snowmelt influences peak stream discharge in years with a substantial snowpack. Summer monsoonal precipitation affects discharge with short, discrete flow peaks occurring in July and August. The timing and magnitude of snowmelt for the Jemez Mountains is influenced by ENSO climate patterns. EN years typically produce higher peak and total discharge from snowmelt while LN years generally show reduced snowmelt peaks and discharge (Figure 2B and 2C).

Data source and collection

A water quality sonde from Yellow Spring Instruments (YSI) was installed on the EFJR in 2005 at an elevation of 2583 m with site coordinates of N 35.83667, W – 106.501. The sonde was maintained yearly from April to November by the Valles Caldera Trust (2005-2010) and the NM Experimental Program to Stimulate Competitive Research (EPSCoR, 2011-2012). A suite of field parameters were measured every 15-minutes including: dissolved oxygen (DO – mg l^{-1}), water temperature (°C), pH, turbidity (NTU) and specific conductance (mS cm^{-1}). The sensors were maintained and calibrated regularly (monthly) to prevent probe biofouling and ensure data quality. The DO probe was switched from a membrane-based probe to an optical probe in 2011. Raw data received quality assurance and quality control assessment using Aquarius software (Aquatic Informatics™) to apply drift corrections from biofouling and to delete suspicious data.

Nearby Eddy Co-variance flux towers for quantifying water vapor and carbon dioxide fluxes provided estimates of photosynthetically active radiation (PAR µmol m^{-2} s^{-1}), barometric pressure (kPA), and air temperature (°C) taken at half hour time intervals during years 2007-2012. An additional flux tower located in the Valle Grande provided additional flux data to extend the historical time record for analysis of stream metabolism to 2005 and 2006. A third source of meteorological data was accessed from the Los Alamos National Laboratory (LANL) weather station. Flux data from all sources were interpolated by applying a cubic spline function to match fifteen-minute time interval sampling performed by the YSI sonde. In addition, barometric pressure was corrected for elevation differences between the flux towers and stream site using the hydrostatic equation (Barry and Chorley 2003).

The long-term record of stream discharge from the Jemez River was gathered from the US Geological Survey (USGS) stream gauge number 08324000 located on the Jemez River near Jemez, Sandoval County, New Mexico (35.6620, -106.7434). This gauge is located at an elevation of 1714 m and has a drainage area of 1217 km^2. Historical data exists back to 1924 and the gauge is currently active. Daily average stream discharge was used to 1) identify inter-annual trends in stream discharge, 2) identify the length of seasonal snowmelt for years 2005-2011 from the hydrograph, and 3) calculate total annual snowmelt as the total volume of water passing through the system from February 10^{th} through June 10^{th} (Figure 3). Baseflow conditions were accounted for by averaging discharge two weeks prior to the beginning of snowmelt and by subtracting that amount from total snowmelt discharge (TSQ).

ENSO index and category

Stream discharge was used as a proxy for the ENSO-related precipitation inputs to explore potential relationships with estimates of stream metabolism. Total snowmelt discharge, in units of million cubic meters (MCM), was correlated with maximum dissolved oxygen amplitude and corresponding GPP and CR to describe inter-annual trends in whole-stream metabolism. Stream discharge data were collected from the USGS Jemez River site and the ENSO category was determined from the National Oceanographic and Atmospheric Administration (NOAA) (http://elnino.noaa.gov/observ.html). Sea surface temperature (SST) fluctuations along the Eastern and Central equatorial region in the Pacific Ocean were used as a diagnostic tool to classify the ENSO category. Definitions for EN and LN were taken from the Ocean Niño Index (ONI) on the NOAA web site (http://elnino.noaa.gov/observ.html). In southwest New Mexico, EN winter conditions are associated with larger than normal snowpack while LN winter conditions are associated with lower than normal snowpack at high elevations (Molles and Dahm 1990). Three EN (2005, 2007, 2010), four LN (2006, 2008, 2011, 2012), and one medial or neutral (M; 2009) winter seasons occurred during the eight years recorded in New Mexico (Table 1). Year 2008 was not used for analysis of peak primary production due to a substantial data gap from July to August. Similarly, 2012 results was not used in the seasonal data set when comparing EN and LN years for reasons explained later in this paper.

Model Fitting

Diurnal DO profiles and ancillary environmental variables (water temperature and PAR) were transferred into Model Maker 4.0 (AP Benson, Wallingford, UK) to derive instantaneous gross primary production (GPP) and community respiration (CR) along with reaeration (E) following the procedures described by Grace (2011). For additional details on the modeling procedures see Atkinson et al. (2008). Briefly, Equation 1 explains how the change in DO concentration over time is controlled by three parameters [GPP, CR, and E], which are calculated from the model outputs. Net ecosystem production (NEP) is the difference between daily GPP and CR.

$$\Delta DO = GPP - CR \pm E \qquad \text{Equation 1}$$

Reaeration accounts for the exchange of oxygen between the atmosphere and the water column and is the product of the reaeration constant and the oxygen deficit. The model requires input parameters of water temperature (°C), PAR (Einsteins m^{-2} s^{-1}) and percent dissolved oxygen saturation corrected for water temperature and barometric pressure (Grace and Imberger 2006) recorded in 15-minute time intervals. This suggested time interval improves the accuracy of modeled estimates. The model accounts for the temperature dependency of the respiration and reaeration constants by using mean daily temperature during the model fitting.

The modeled runs require a series of optimization steps where model parameters are selected to represent high and low values to improve calculated estimates. These optimized parameters include: A (a constant), K (reaeration coefficient), R (community respiration), and p (degree of light saturation). Light saturation was tested at high and low values to determine what influence this saturation has on the overall model. I concluded that light saturation was common at the EFJR site due to the high elevation (2,590 meters) and open-canopy. Optimization statistics were used to determine convergent parameters that provide a goodness of fit, accepted under conditions when $r^2 > 0.90$. Two cases showed r^2 was less than 0.90 (May 2005 and 2009; $r^2 = 0.89$). GPP was then calculated from the optimized model parameters mentioned above and I (or PAR) shown in Equation 2 by following the daytime regression method (Kosinski 1984).

$$GPP = AI^p \qquad \text{Equation 2}$$

Due to the dependency of respiration and reaeration on temperature (Butcher and Covington 1995; Kilpatrick et al. 1989), both instantaneous R and K values were corrected with corresponding water temperature values (Grace and Imberger 2006). Daily estimates of whole-stream metabolism represented by GPP and CR were converted from volume (mg O_2 l^{-1} d^{-1}) to area (g O_2 m^{-2} d^{-1}) using a rating curve from a derived relationship between Jemez River and EFJR discharge and stage parameters. A linear regression model was used to derive EFJR discharge from the independent variable, Jemez discharge. EFJR stage data were derived from a nonlinear function, with EFJR discharge as an independent variable. EFJR stage calculations were compared to discrete measurements of mean depth from Van Horn et al. (2012), and the comparison confirmed that stage calculations were appropriate estimates of mean depth.

Data Analysis

Continuous time-series data were analyzed within years and among years to identify potential seasonal and inter-annual trends in whole-stream metabolism. Temporal GPP and CR data were tested for comparison of means by using repeated measures analysis of variance (ANOVA) and Tukey's post-hoc tests to analyze variance among 1) seasons within a year and 2) multiple years within the same season. Statistical computations were done in RStudio (v0.97.318). The maximum DO amplitude period was explored for potential relationships with hydrologic characteristics, specifically total snowmelt discharge. Maximum DO amplitude was calculated as the difference between daily maximum DO concentration and minimum DO concentration and was representative of the period of peak productivity within each year. Peak productivity was calculated as an average of a consecutive three-day run and analyzed across years (2005-2012) to compare inter-annual rates. The goal was to explore relationships between whole-stream metabolism parameters at peak productivity and the ENSO category (EN, M, LN) using total spring snowmelt discharge as a proxy. Analyses of total snowmelt for 1954 through 2011 were performed to test assumptions of equal variance and normality across ENSO categories using the Bartlett test of homogeneity of variances and the Shapiro-Wilks normality test, respectively. Furthermore, a one-way ANOVA and multiple comparisons Bonferroni allowed for testing the null hypothesis of equal means of log transformed snowmelt data across ENSO categories. A fire disturbance in the EFJR catchment occurred late-June through July 2011 and was taken into consideration when analyzing trends in these data. Peak period estimates of stream metabolism for year 2012 were analyzed with an awareness of potential effects due to forest fire in the EFJR catchment.

RESULTS

Temporal scales of stream metabolism

For all years maximum values for percent saturation of dissolved oxygen (DO) occurred in July. Daytime maximum values ranged from 161% in 2005 to 215% in 2009 and occurred during 11:00 AM and 15:00 PM. Supersaturation during sunny days happened consistently on daily and seasonal time scales. Furthermore, nighttime minimum values for percent saturation of DO also occurred in July for all years and ranged from a low of 23% in 2005 to a minimum high of 54% in 2010. Overall seasonal rates for estimates of stream metabolism ranged from a minimum of 2.4 g O_2 m^{-2} d^{-1} in September 2008 to a maximum of 18.5 g O_2 m^{-2} d^{-1} in July 2009 for GPP. Seasonal minimum and maximum estimates of CR were 2.6 g O_2 m^{-2} d^{-1} in September 2008 and 16.3 g O_2 m^{-2} d^{-1} in July 2009, respectively. Seasonal trends across years resulted in statistically greater rates of GPP and CR in July compared to May and September (Figure 4). July also had larger spread in the distribution of GPP and CR values and a higher sample mean compared to other months (Table 2). Additionally, GPP showed greater seasonal and diurnal variability compared to CR. Overall, net ecosystem production (NEP) was predominantly positive across seasons.

Comparison of inter-annual estimates of both GPP and CR exhibited variability in the spread of seasonal rates across years; however, when comparing GPP to CR across years the trend is similar regarding the variance of observations (Figure 5). Mean and standard deviation values of seasons grouped by year were variable for both GPP and CR but NEP remained predominantly positive across years (Table 3). Furthermore, ANOVA and Tukey post-hoc tests for inter-annual trends in both GPP and CR mean rates showed some statistical significance ($P < 0.05$). Total snowmelt discharge explained some of the variation in inter-annual rates of GPP ($r^2 = 0.374$) but was not significant ($P = 0.19$). There was no correlation between total snowmelt discharge and CR ($r^2 = 0.050$).

Annual peak productivity

Maximum DO amplitude varied in magnitude and time of occurrence among years (2005-2012) during peak productivity (Figure 6). Baseflow conditions were present during periods of maximum DO amplitude that occurred during June or July in all years. Maximum DO amplitude was highest in 2012 (17.0 mg l^{-1}) and lowest in 2005 (7.0 mg l^{-1}). Stream metabolism estimates at peak productivity expressed as GPP was greatest in 2006 (15.5 g O_2 m^{-2} d^{-1}) during a LN year and lowest in 2005 (7.1 g O_2 m^{-2} d^{-1}) during an EN year. Similarly, peak metabolism expressed as CR were greatest in 2006 (13.5 g O_2 m^{-2} d^{-1}) and lowest in 2012 (7.8 g O_2 m^{-2} d^{-1}); 2006 and 2012 were associated with LN conditions. Results from a two-sample t-test showed GPP did not differ significantly between EN and LN years ($p > 0.05$, $df = 4$). Similar results were found with CR when comparing the ENSO categories ($p > 0.05$, $df = 4$). Inter-annual variation in peak GPP and CR rates occurred (Table 4), but NEP was predominantly positive showing that autotrophic production exceeded decomposition during these periods of time in all years.

Snowmelt

Total snowmelt discharge (TSQ) for the Jemez River differed significantly between EN, LN, and M categories from 1954 through 2011 (one-way ANOVA, P = 0.0411, F= 3.386). Furthermore, EN and LN years were statistically different (Bonferroni multiple comparisons, adjusted P = 0.039), but M years did not differ from EN or LN years with P = 1.00 and 0.276, respectively (Figure 7). During the study period (2005-2012), TSQ was significantly greater for EN years compared to LN years (two-sample t-test, P = 0.0258, df = 4).

Maximum amplitudes of dissolved oxygen from daytime maxima to nighttime minima (ΔDO) showed seasonal and annual variation across years. Maximum daily ΔDO had a negative linear correlation with TSQ explaining 76% of the variance in maximum ΔDO (Figure 8). The negative linear correlation between TSQ and stream metabolism parameters (GPP and CR) resulted in significant relationships (Figure 8). Total snowmelt discharge explained the greatest amount of variance for GPP (r^2 = 0.74) and was statistically significant (P = 0.027). TSQ explained 68% of the variance for CR and was statistically significant (P = 0.043). High snowmelt years resulted in reduced GPP and CR, and vice versa with low snowmelt years resulting in high GPP and CR rates.

Because 2012 followed a major fire disturbance, the linear regression analyses were done including and excluding 2012 to test the impact of removing this outlier from the statistical analysis (Table 5). With 2012 included in the correlation plots, the relationship between TSQ and stream metabolism parameters (GPP, CR, and DO amplitude) were not significant and had poor correlation coefficients. The correlations between TSQ and stream metabolism parameters were much improved by removing 2012

(Table 5). The assumption that 2012 is an outlier year was validated given 2012 falls statistically outside the 95% confidence interval in the correlation plots (Figure 8).

DISCUSSION

This study follows the progression of whole-stream metabolism by analyzing seasonal stages from continuous water quality data. This study also shows that the magnitude of gross primary production (GPP) and community respiration (CR) rates peak at predictable times of the year. In addition, total snowmelt discharge (TSQ) was found to be a good predictor variable of GPP and CR. Overall, it appears that inter-annual rates of GPP and CR were reduced during El Niño (EN) years compared to La Niña (LN) years.

Diurnal dissolved oxygen profiles showed variability on inter-annual, seasonal, and diurnal time scales. The strong diurnal patterns in EFJR result from high rates of primary production during the daytime and high sustained respiration rates. Strong oscillations in dissolved oxygen minima and maxima improved the ability of ModelMaker 4.0 to model whole-stream metabolism. Both primary production and community respiration are drivers of dissolved oxygen profiles with a pronounced effect in the summer when environmental conditions are highly favorable for both primary production and community respiration.

Temporal trends in stream metabolism

Seasonal shifts in GPP and CR values had clear patterns of reduced spring and fall rates compared to summer maxima. Spring GPP was low immediately following spring snowmelt. Snowmelt discharge and anchor ice may have scoured the channel bottom, physically dislodging autotrophic organisms under high flow conditions or autotrophs were not present because the stream was under ice. Alternatively, snowmelt flushed terrestrial sources of nutrients into the stream that may have enhanced metabolic processes following snowmelt. The varying rates of GPP and CR in the spring were not correlated to total snowmelt discharge. However, rates of GPP and CR in the summer and fall months showed some correlation to total snowmelt discharge but these relationships were not significant. These result suggests other exogenous factors contribute to seasonal fluctuations of whole-stream metabolism, such as water temperature (Acuña et al. 2008) and light (Uehlinger et al. 2000), which were less favorable in the spring and fall compared to summer at the East Fork Jemez site.

Once baseflow conditions were established following snowmelt, the dissolved oxygen amplitude becomes larger. Maximum and minimum percent saturation of dissolved oxygen (DO) was seen on a daily basis in summer when compared to spring and fall seasons. The strong oscillation in DO indicates primary production was high during daylight hours while community respiration is high throughout the night in the summer. Further, this saturation suggests that carbon cycling rates (primary production and decomposition) were elevated during the summer. As expected, GPP is reduced in the fall when aquatic organisms begin to senesce due to cooling environmental conditions. Temporal patterns of CR were similar to GPP in that maxima rates occurred in summer months. In an open-canopy, grassland system like the East Fork Jemez River (EFJR), GPP is not seasonally suppressed by overhanging riparian vegetation and can attain higher autotrophic rates due to the lack of light limitation. The EFJR is a highly productive stream; specifically, high rates of in-stream primary production support high rates of secondary consumption. As a result, net ecosystem production (NEP) is predominately positive regardless of season: spring, summer, and fall.

Our research assesses seasonal and inter-annual time scales of ecosystem metabolism that clearly display variability in rates as site conditions, such as water temperature and sunlight intensity, change. Seasonal rates of whole-stream metabolism did show some correlation with snowmelt, a predictable disturbance in this montane ecosystem. Fisher et al. (1982) used GPP and CR to characterize temporal dynamics of carbon following a flood disturbance. Yet, most studies concerning stream metabolism are limited by the availability of data to explore temporal relationships in greater depth (but see Uehlinger 2006). Thus, the seven-year period of continuous stream monitoring reported in this study is highly unusual when compared to other steam metabolism studies. This research advances temporal analyses of ecosystem metabolism and provides better temporal understanding of carbon dynamics in stream ecosystems.

Comparison among open-canopy systems

Whole-stream metabolism estimates reported in the literature vary among open-canopy stream and river ecosystems (Table 6). The EFJR stream metabolism estimates during peak production reach high rates supported by observations of high biomass for aquatic macrophytes and benthic algae (Thompson and Bixby, unpublished data). The EFJ estimates of metabolism are comparable to the highest rates reported by Johnson and Tank (2009) and Acuña et al. (2011). Furthermore, similar estimates of GPP and CR have been made in open-canopy systems in the Grand Tetons, Wyoming (Hall and Tank 2003; Johnson and Tank 2009), the Pampean streams of Argentina (Acuña et al. 2011), and in the Taieri River, New Zealand (Young and Huryn 1996). These open-canopy lotic ecosystems also represent a range of stream discharge rates (10l s^{-1}- 347 l s^{-1}) by three orders of magnitudes (Table 6). Other similarities specifically between the EFJR and streams in the Grand Tetons include semi-arid and snowmelt-driven climates with relatively low baseflow discharge ranging from 79 - 118- l s^{-1}. Open-canopy sites, where riparian vegetation cover is reduced, are characterized as being dominated by autrotrophic activity and exhibiting P/R ratios greater than one (Vannote et al. 1980). P/R ratios were largely net autotrophic for the EFJR, even though this ratio was largely net heterotrophic for other open-canopy streams (Table 6).

Fire disturbance

Inter-annual patterns of stream metabolism estimates were complicated due to the 2011 Las Conchas fire occurring in the headwaters of the EFJR. I observed smoke plumes shielding sunlight during the day and, therefore, expect this decrease in sunlight to have negatively impacted summer productivity similar to the effect of riparian shading in a forested stream. As a result, whole-stream metabolism in 2012 may be reduced due to light inhibition from the smoke plumes (Table 4). Studies of post-fire impacts on aquatic ecosystems have observed changes in lake metabolism and carbon dynamics (Marchand et al. 2009), as well as shifts in lotic autotrophic and heterotrophic community structure due to changing stream substrate (Earl and Blinn 2003). However, no studies have captured the effects of fire disturbance on stream metabolism. Further analysis of the fire disturbance needs to be quantified in order to determine the impact of this fire on ecosystem metabolism in the EFJR.

Annual peak productivity

This study is the first to link estimates of stream metabolism with meteorological variables. High and low rates of GPP during the peak period corresponded to a LN year and EN year, respectively. Similarly, high and low rates of CR during the peak period corresponded to LN and EN years, respectively. Overall, two out of the three EN years had lower rates of GPP and CR compared to LN years. The timing of peak production occurred later in the summer season during EN years while peak production occurred earlier in the summer during LN. This relationship between climate patterns and stream metabolism may be complicated by additional meteorological driving forces not analyzed in this study. For example, summer monsoon activity reduces DO concentrations through flow disturbance from rainfall or blocking of sunlight from cloud coverage. This complication is seen in the DO profile when the buildup of monsoons typically forms as increased cloud coverage in the late afternoon and reduces available light needed for photosynthetic activity. A study by Gutzler (2000) showed summer monsoons in New Mexico to be negatively related to winter snowpack or the El Nino-Southern Oscillation (ENSO) phenomena. High winter snowpack (EN) was correlated with reduced summer monsoon season; and the opposite is true also (Gutzler 2000). The monsoon patterns in the summer may impact the timing and/or magnitude of the period of peak stream metabolism; although this relationship should be explored further. A benefit of quantifying peak stream metabolism is such that it provides a measure of carbon cycling at full capacity at an ecosystem scale.

Snowmelt correlated to ENSO phenomena

EN and LN cycles were indirectly related to GPP and CR peak annual rates through the predictor variable of total snowmelt discharge. Rates of GPP and CR are significantly correlated to total snowmelt discharge during peak periods of ecosystem metabolism. Total snowmelt explained 74% and 68% of the variance for GPP and CR, respectively. Both of these correlations were negative linear relationships indicating that higher total snowmelt resulted in lower GPP and CR rates during summer peak period. Based on the results in this study, total snowmelt is a good predictor of summer GPP and CR. Physical disturbances are episodic in this snowmelt-dominated montane system due to both global and regional climate patterns. In particular, the ENSO and the North American Monsoon phenomena impact winter and summer precipitation, respectively. For example, EN years show significantly greater total snowmelt discharge than LN years using the Jemez River long-term stream discharge record. The identification of greater total snowmelt during EN years in New Mexico and lower snowmelt totals during LN years is supported by Molles and Dahm (1990). Changing climate patterns are known to impact temperatures and snowpack in montane ecosystems (Knowles et al. 2006). In addition, Hall et al. (2012) found decadal trends are shifting towards earlier spring snowmelt. These changes in climate influence the flow regime of montane streams and may impact stream metabolism patterns as well.

Studies have explored the effects of flow disturbance (e.g. bed moving spates) on stream metabolism (Uehlinger 2006) and nutrients (Marti et al. 1997). Initial responses of stream metabolism parameters to flow disturbance are found to be suppressed (Roberts et al. 2007) but exhibit resiliency such that seasonal patterns are not diminished (Uehlinger 2006). Acuña and Tockner (2010) found flow alterations to have a greater impact on carbon fluxes compared to water temperature on carbon fluxes, and ultimately increase export rates. Models of hydrologic flow alterations are being performed to forecast potential effects on ecosystem function, in the face of climate change (Marcarelli et al. 2010). The balance of carbon export and retention will have implications for downstream ecosystems. Thus, monitoring ecosystem compartments as well as developing predictor variables will increase our awareness of how ecosystems respond to disturbances.

SUMMARY

Gross primary production (GPP) and community respiration (CR) show seasonal and inter-annual variation in this multi-year study. Summer was significantly higher than spring and fall for both GPP and CR, as predicted from the dissolved oxygen profile (Figure 4). Furthermore, this open-canopy stream ecosystem is not light restricted by dense riparian vegetation that typically forms in the summer and that allows for high rates of in-stream primary production. As a result, this stream is extremely productive and predominately net autotrophic on seasonal and interannual time scales. Biogeochemical and hydrological cycles are increasingly being monitored with high-resolution, in situ, continuous sensors. These tools expand our understanding of how biogeochemical and hydrological cycles interact dynamically over multiple time scales.

This study also attempts to link global climate patterns that affect precipitation regimes with key ecosystem functions like primary production and decomposition. Total snowmelt in the East Fork Jemez was negatively correlated to GPP and CR and explains 74% and 68% of the variation, respectively. Total snowmelt discharge varied significantly between El Niño (EN) and La Niña (LN) years with higher total snowmelt discharge associated with EN. Thus, the response of ecosystem function to the snowmelt disturbance is related to the El Niño-Southern Oscillation (ENSO) cycle. The influence of global climate phenomenon like the ENSO phenomenon in a montane system offers insight on the interaction of multiple temporal scales that influence ecosystem function. A shift in hydrologic regimes induced by climate change has been predicted for the hydrology of the western U.S. (Barnett et al. 2008). This study aids in bridging gaps in scientific research considering linkages between global climate change and ecosystem function in aquatic ecosystems (Marcarelli et al. 2010)**.** The increase use of long-term data will improve our understanding of these complex relationships.

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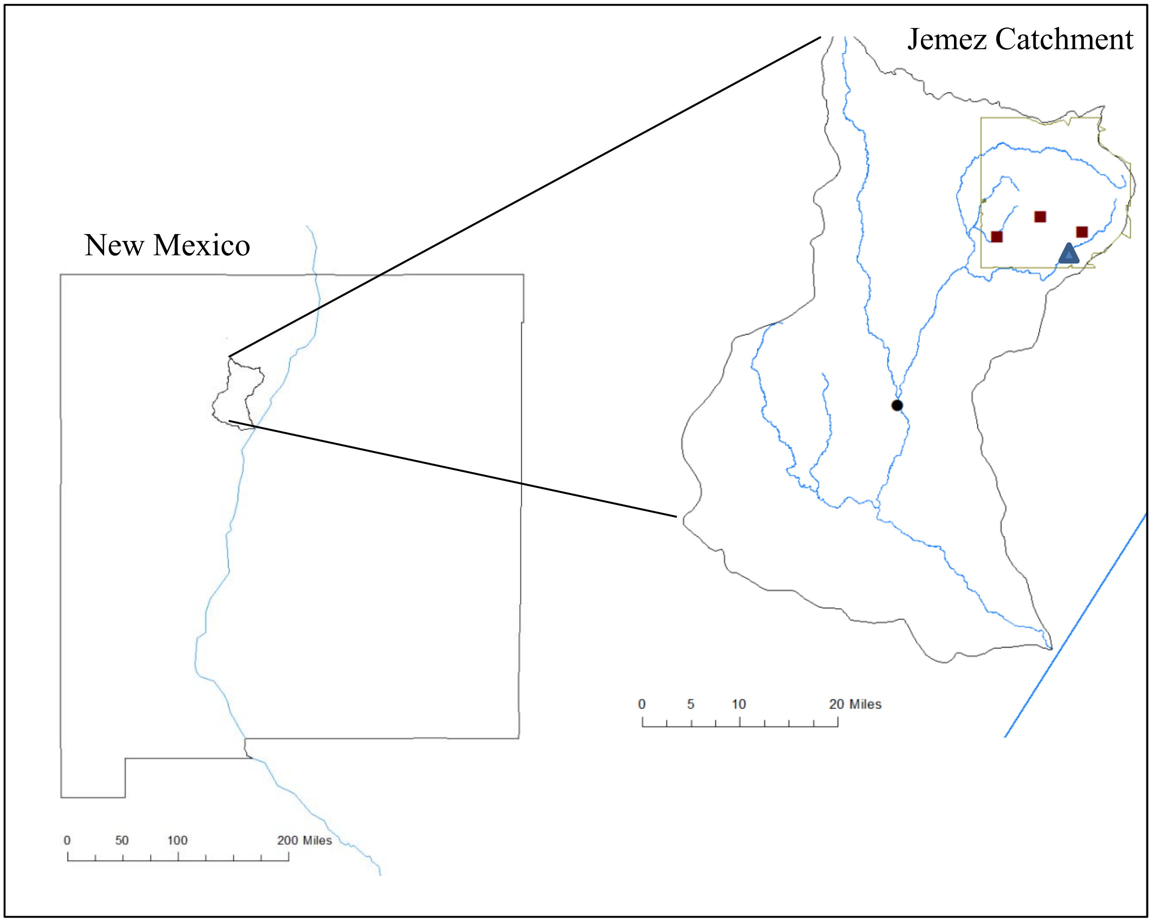

Figure 1: The Jemez River catchment (in black outline) is located in north-central New Mexico. The study site is the East Fork of the Jemez River (N 35° 50.2'; W 106° 30.083') inside the Valles Caldera National Preserve outlined in brown in the Jemez catchment. Symbols: square (solar flux towers), circle (Jemez stream gauge), and triangle (water quality sensor).

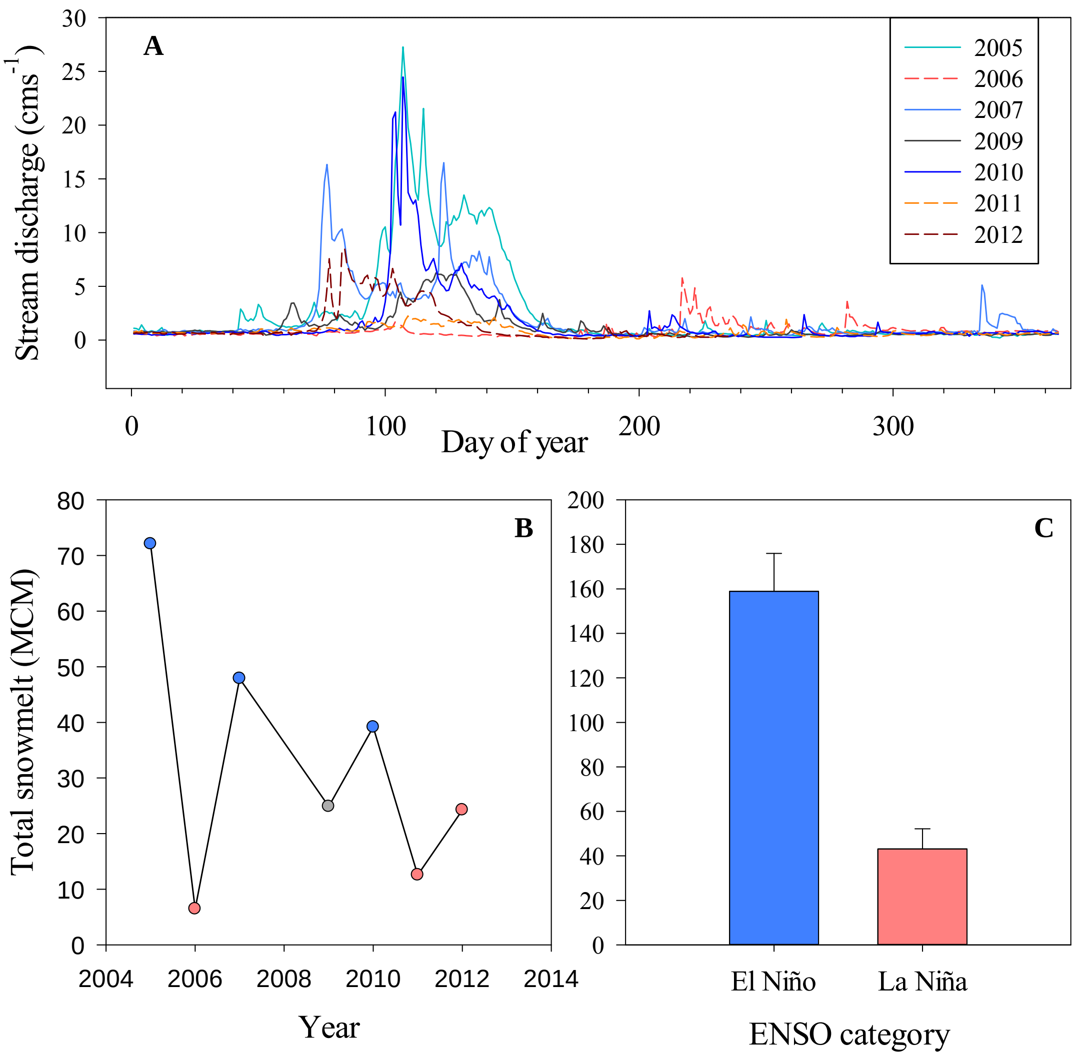

Figure 2: Jemez River discharge as total snowmelt (MCM) is delineated by A) year and B) ENSO category. C) Inter-annual variability in Jemez hydrograph derived from daily average discharge for the Jemez River collected by USGS gauge #08324000. Coloration for the lines and dots represents ENSO category; blue (EN), red (LN), grey (M).

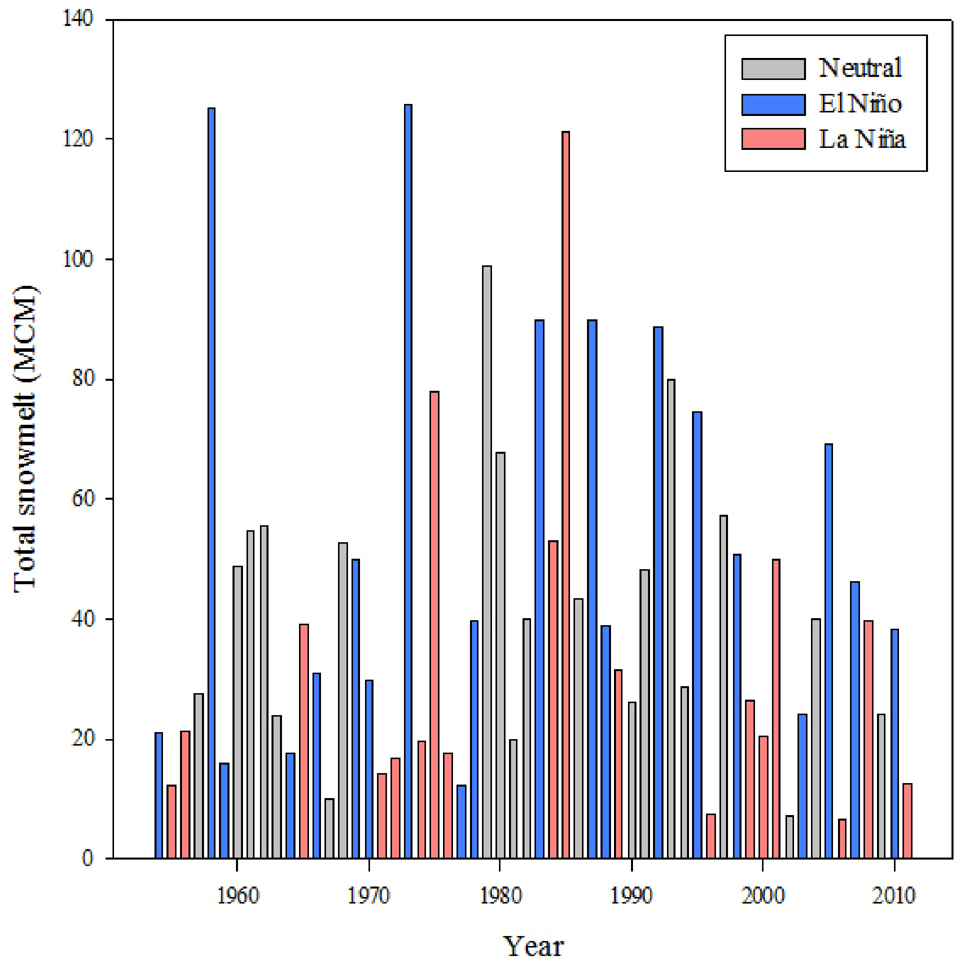

Figure 3: Long-term discharge for Jemez River taken from USGS gauge #08324000. Total snowmelt period in million cubic meters (MCM) represents the sum of monthly discharge for February through May for 1954 - 2011. El Nino-Southern Oscillation category (El Niño, Neutral or Medial, La Niña) was indicated using the Oceanic Niño Index for the three-month running mean of December through February. Total snowmelt is statistically different between EN and LN cycles (Bonferroni adjusted P = 0.039).

Table 1**:** El Niño-Southern Oscillation categorized by the Oceanic Nino Index (ONI) taken from the National Oceanographic and Atmospheric Administration (NOAA) based on five overlapping seasons.

	NM time period	ENSO	ONI value
JJA 2004 – DJF 2004/05	2005	El Niño	0.7
OND 2005 – FMA 2006	2006	La Niña	-0.9
ASO 2006 – DJF 2006/07	2007	El Niño	1
JAS 2007 – MJJ 2008	2008	La Niña	-1.5
JJA 2009 – MAM 2010	2010	El Niño	1.6
JJA 2010 - MAM2011	2011	La Niña	-1.5

El Niño-Southern Oscillation (ENSO); Oceanic Niño Index (ONI). Year 2009 is assumed to be medial not meeting ONI criteria for El Niño/ La Niña classification; however it may be considered weak La Niña based on the Southern Oscillation Index (SOI).

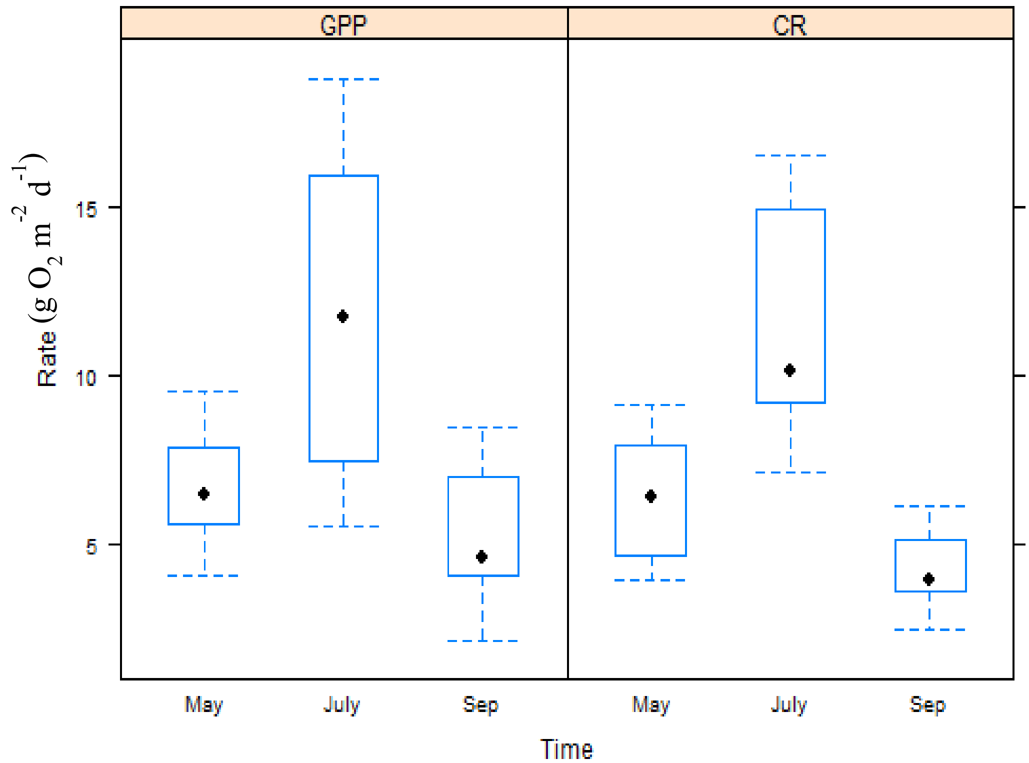

Figure 4: Comparison of seasonal estimates of GPP and CR with multiple years 2005-2011 pooled by season. Sample sizes for seasons are n=21 with the exception for July where n=18 due to a data gap in year 2008. Diamond symbol indicates the median value.

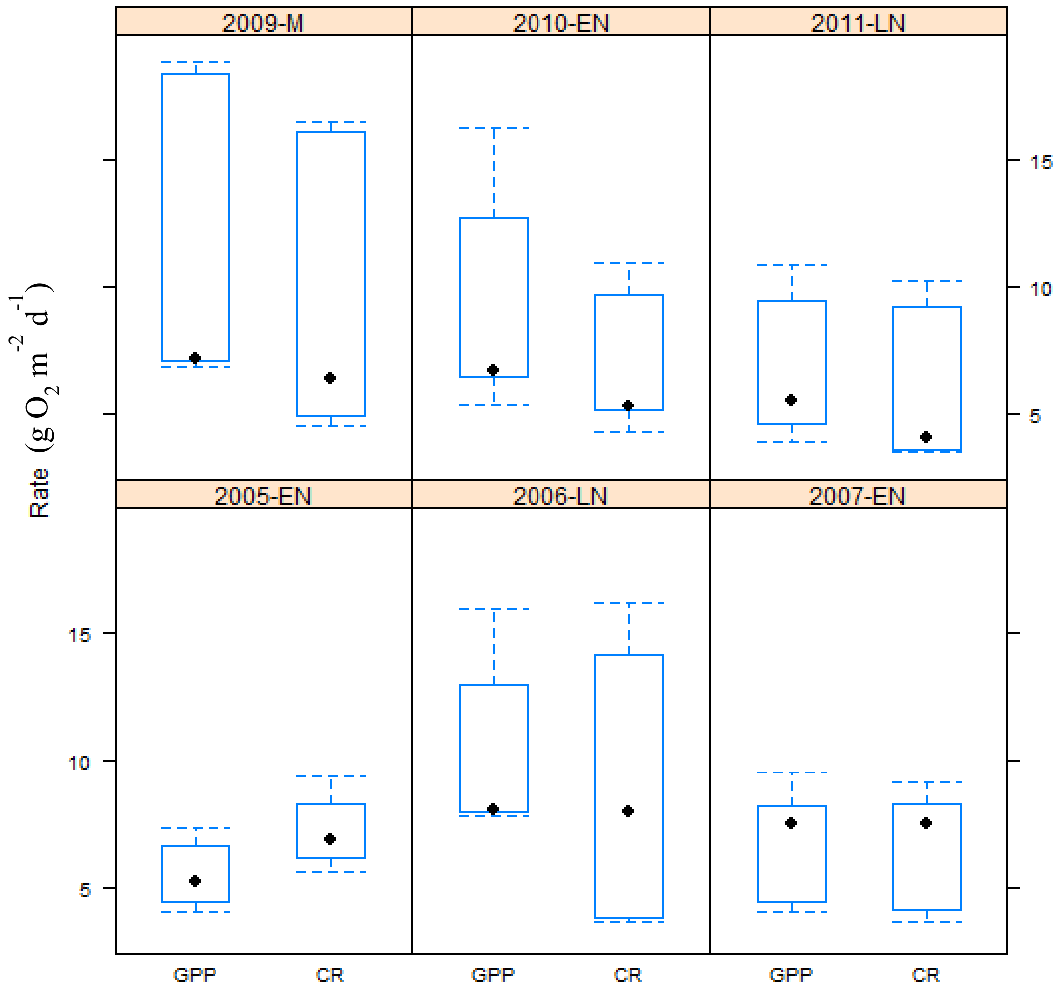

Figure 5: Inter-annual comparison of stream metabolism estimates (GPP and CR) ranging from 2005-2010 with El Niño (EN) and La Niña categories identified. Diamond represents sample median. Each year has a total sample size of n=9 with three months having three observations. Year 2008 was not included due to a data gap during July.

Table 2: Mean and standard deviation (SD) of GPP, CR, and NEP (g O_2 m^{-2} d^{-1}) for 2005 - 2011. The month of July has n = 18 due to data gap in 2008, May and September have n = 21.

Variable	month	mean	SD
GPP	MAY	6.65	1.26
	JULY	11.95	4.60
	SEPT	5.32	2.04
CR	MAY	6.36	1.70
	JULY	11.35	3.51
	SEPT	4.26	1.11
NEP	MAY	0.29	1.16
	JULY	0.60	2.15
	SEPT	1.06	1.92

Table 3: Inter-annual comparison of GPP and CR mean (g O_2 m^{-2} d^{-1}) and standard deviation (SD). Each year is composed of three seasons (spring, summer, and fall) with a three-day running mean for each month. Note n = 9 for all years except for year 2008 when n = 6 due to data gap during the summer month

variable	year	mean	SD
GPP	2005	5.60	1.38
	2006	10.16	3.68
	2007	6.62	2.14
	2008	4.09	NA
	2009	11.04	6.50
	2010	9.03	4.70
	2011	6.67	3.05
CR	2005	7.40	1.53
	2006	8.88	5.71
	2007	6.75	2.51
	2008	3.90	NA
	2009	9.21	6.20
	2010	6.83	3.15
	2011	5.84	3.46
NEP	2005	-1.79	0.21
	2006	1.28	2.70
	2007	-0.13	0.39
	2008	0.18	NA
	2009	1.82	0.86
	2010	2.20	1.55
	2011	0.83	0.62

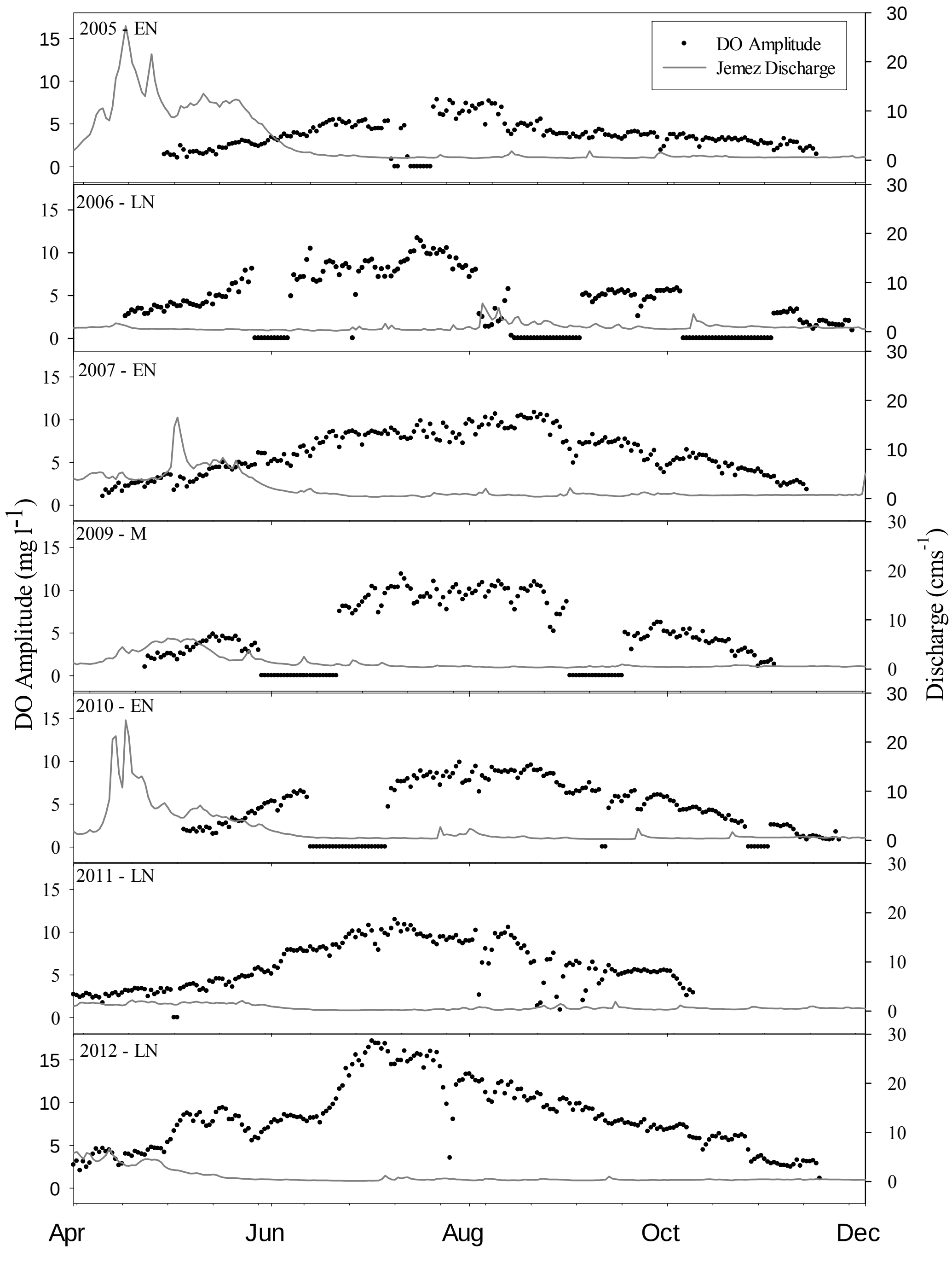

Figure 6: Continuous dissolved oxygen concentration expressed as DO amplitude calculated from daily minima and maxima values with El Nino-Southern Oscillation categories (EN, M, LN) identified (2005-2012). Peak productivity occurs at maximum DO amplitude during baseflow conditions. Year 2008 was not included due to numerous data gaps.

Table 4: Estimates of whole-stream metabolism (g O_2 m^{-2} d^{-1}) are reported as a three-day average during annual peak production periods. The date column indicates the beginning of the peak period when DO amplitude was greatest for each year.

Year	Date	ENSO	TSQ (MCM)	GPP	CR	NEP	P/R
2005	7/25/2005	EN	71.99	7.13	8.96	-1.83	0.80
2006	7/16/2006	LN	6.39	15.54	13.51	2.04	1.15
2007	8/21/2007	EN	47.80	8.69	8.12	0.57	1.07
2009	7/11/2009	M	24.79	13.49	9.64	3.85	1.40
2010	7/27/2010	EN	39.06	14.22	10.32	3.90	1.38
2011	6/30/2011	LN	12.51	12.81	12.37	0.45	1.04
2012	7/2/2012	LN	24.22	7.74	7.76	-0.03	1.00

Note: El Niño-Southern Oscillation (ENSO); El Niño (EN); La Niña (LN); Medial (M); Total snowmelt discharge (TSQ); Gross primary production (GPP); Community respiration (CR); Net ecosystem production (NEP); Primary production to community respiration ratio (P/R)

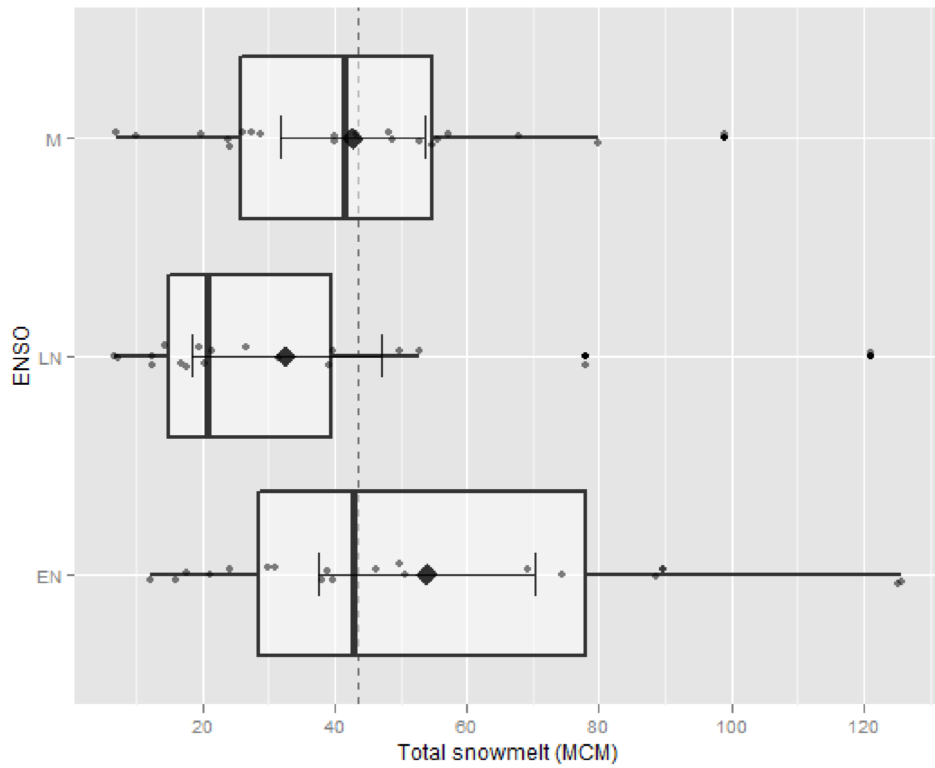

Figure 7: Annual total snowmelt discharge (MCM) during the time period February 10 through June 10 was measured in the Jemez River between 1954 and 2011 (USGS stream gauge #08324000). Box plots are grouped by ENSO category (M, EN, LN) where the diamond symbol displays sample mean with associated error bars and the dashed line represents global mean. The mean values were statistically different between EN and LN (P = 0.039).

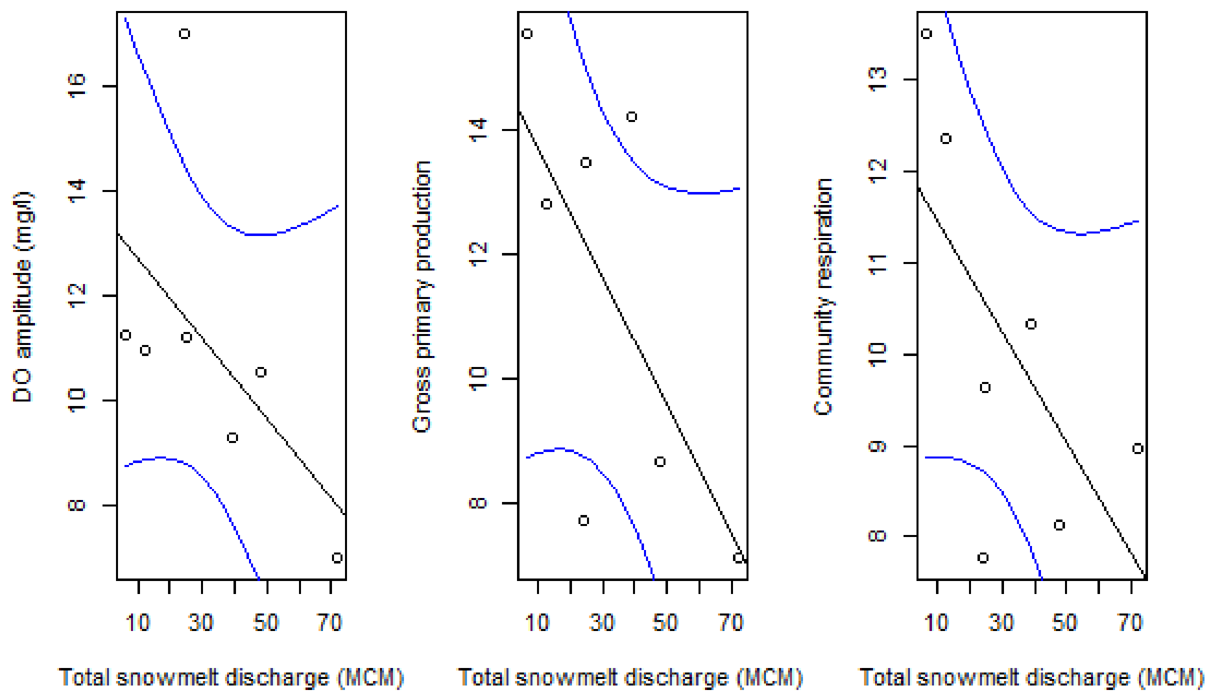

Figure 8: Daily DO amplitude (mg l^{-1}), GPP and CR (g O_2 m^{-2} d^{-1}) responses to total snowmelt discharge (MCM) during time of maximum dissolved oxygen amplitude. Statistics show a negative linear relationship in black and 95% confidence intervals (CI) in blue. Year 2012 falls outside the CI in all three correlation plots.

Table 5: Testing the effects of year 2012 on correlation coefficients and p-values for linear regression relationships among total snowmelt discharge (TSQ) and GPP and CR. A linear model was used in Rstudio. Symbol * denotes statistical significance at α = 0.05 level and correlation coefficient reported as multiple R-squared.

		Including 2012	Excluding 2012
GPP	r^2	0.46	0.74
	p-value	0.095	0.027*
CR	r^2	0.41	0.68
	p-value	0.123	0.043*
DO amplitude	r^2	0.32	0.76
	p-value	0.184	0.024*

Table 6: Comparison of whole-stream metabolism (g O_2 m^{-2} d^{-1}) estimates among systems using one-station (1) and two-station (2) methods.

Location	Discharge ($l\ s^{-1}$)	Canopy cover	GPP	CR	P/R	Method	Paper
East Fork Jemez, NM	90	open	2.4 - 18.5	2.6 - 16.3	0.8 - 1.4	1	This study
Sycamore Creek, AZ	10	open	9.4	10.1	0.9	2	Grimm and Fisher 1984
Taieri River, New Zealand	6600 - 76800	open	0.3 - 9.6	0.7 - 9.8	.5 - 7.0	1	Young and Huryn 1996
Rio Calaveras- long reach, NM	0.5	headwater	0.5	2.9	0.2	2	Fellow et al. 2001
Gallina Creek- lower reach, NM	0.8	semi-closed	1.7	14.7	0.1	2	Fellow et al. 2001
Gallina Creek- upper reach, NM	3.2	semi-closed	0.2	6.7	0.0	2	Fellow et al. 2001
Creightons Creek, Australian		open	0 - 0.5	0.6 - 3.7	0.0- 0.41	1	Atkinson et al. 2008
Teton Pines, WY	11	open	2.7	1.5	1.8	2	Johnson and Tank 2009
Two Ocean, WY	35	open	2.9	12.6	0.2	2	Johnson and Tank 2009
Spread, WY	347	open	3.2	9.8	0.3	2	Johnson and Tank 2009
Headquarters, WY	122	open	3.3	7.1	0.5	2	Johnson and Tank 2009
Kimball, WY	118	open	13.6	12	1.1	2	Johnson and Tank 2009
Giltner, WY	79	open	16.2	11.4	1.4	2	Johnson and Tank 2009
La Choza Pampean Stream, Argentina	30	open	16.34 ± 10.07	21.45 ± 8.00	0.93	2	Acuña et al. 2011