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Robert O. Hall
*University of Wyoming*

Jennifer L. Tank
*University of Notre Dame*

Michelle A. Baker
*Utah State University*

Emma J. Rosi-Marshall
*Institute of Ecosystem Studies*

Michael R. Grace
*Monash University of Wyoming*

*See next page for additional authors*

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Authors
Robert O. Hall, Jennifer L. Tank, Michelle A. Baker, Emma J. Rosi-Marshall, Michael R. Grace, and Erin R. Hotchkiss
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ROBERT O. HALL, JR. ✤ UNIVERSITY OF WYOMING ✤ LARAMIE
JENNIFER L. TANK ✤ UNIVERSITY OF NOTRE DAME ✤ NOTRE DAME
MICHELLE A. BAKER ✤ UTAH STATE UNIVERSITY ✤ LOGAN
EMMA J. ROSI-MARSHALL ✤ INSTITUTE OF ECOSYSTEM STUDIES ✤ MILLBROOK NY
MICHAEL R. GRACE ✤ MONASH UNIVERSITY OF WYOMING ✤ MELBOURNE AU
ERIN R. HOTCHCKISS ✤ UNIVERSITY OF WYOMING ✤ LARAMIE

INTRODUCTION

Primary production and respiration are core functions of river ecosystems that in part determine the carbon balance. Gross primary production (GPP) is the total rate of carbon fixation by autotrophs such as algae and higher plants and is equivalent to photosynthesis. Ecosystem respiration (ER) measures the rate at which organic carbon is mineralized to CO₂ by all organisms in an ecosystem. Together these fluxes can indicate the base of the food web to support animal production (Marcarelli et al. 2011), can predict the cycling of other elements (Hall and Tank 2003), and can link ecosystems to global carbon cycling (Cole et al. 2007).

Much of the work in estimating metabolism of lotic ecosystems is from small streams (Bernot et al. 2010), including several from streams in and around Grand Teton National Park (Hall and Tank 2003; Hall et al. 2003). We know much less about metabolism in larger rivers (Figure 1); one reason is that methods have not been worked out for them. As part of our larger project examining carbon and nutrient cycling in large rivers, we measured GPP and ER from 5 regional rivers in summer 2010.

METHODS

We studied 5 rivers: Buffalo Fork of the Snake River east of Grand Teton National Park in the Teton National Forest; Snake River below the confluence of the Buffalo Fork; Green River below Fontenelle Dam in Seedskadee National Wildlife Refuge; Henry’s Fork of the Snake downstream of Warm River, Idaho; and Salmon River upstream of Challis, Idaho. In each river we identified a 5-12 km study reach for which to estimate metabolism and nutrient uptake.

We estimated two-station metabolism (Hall et al. 2007) which budgets dissolved oxygen. We use oxygen as a surrogate for carbon; GPP produces
oxygen and ER consumes oxygen. We varied the classic two-station approach by modeling oxygen concentrations and solving for GPP and ER as best fit parameters in a model as inspired by Van de Bogert et al. (2007) and Holtgrieve et al. 2010, though these papers used 1 station methods which would not have worked as well in our reaches (M. R. Grace and R. O. Hall, unpublished manuscript). Our two station approach modeled oxygen concentration between an upstream and downstream station in a Lagrangian framework. Controls of oxygen concentration were GPP, ER and gas exchange with the atmosphere.

The equation for the model is in Figure 2 (Equations A) where $O_2$ is oxygen concentrations (mg L$^{-1}$ or g m$^{-3}$) at upstream and downstream locations. Reach travel time is $\tau$ (d). GPP is gross primary productivity and ER is ecosystem respiration (g O$_2$ m$^{-3}$ d$^{-1}$), $z$ is mean river depth (m), $K$ is gas exchange coefficient (1/d). The expression to the right of $K\tau$ is the reach average saturation deficit, where $O_{2\text{sat}}$ is upstream oxygen saturation. We normalized GPP to the fractional amount of light (PAR, µmol photoms m$^{-2}$ s$^{-1}$) received in the reach following Van de Bogert (2007). Note that $O_2$ is on both sides of equation (1), thus we rearranged that equation (see Figure 2 Equation B).

We estimated the parameters (GPP, ER and sometimes $K$) as those that minimized the negative-log likelihood of predicted oxygen from equation 2 relative to the downstream oxygen data.

We measured oxygen at 5 min intervals at the top and bottom of the reach using recording optical sensors. We measured travel time as nominal transport time from pulse addition of sodium bromide. Mean depth was estimated assuming hydraulic continuity (discharge=velocity*depth*width). Light was measured nearby the reach. We estimated $K$ as either a free parameter or used the nighttime regression method (Hornberger et al. 1977).

### RESULTS

Modeling procedure produced close fits between modeling and data (Figure. 3) and subsequently low estimates of uncertainty on parameters GPP and ER. Using likelihood ratio tests GPP error was 6% for Buffalo Fork, the least productive river and 1.3% for Henry’s Fork, the most productive river.

Metabolism varied widely among the 5 rivers (Figure 4). Green River and Henry’s Fork had the highest rate of metabolism; both rivers had stable discharge due to dams and spring inputs (Henry’s). The other 3 rivers were snowmelt-driven alluvial rivers and had much lower GPP and ER.

![Figure 3. Downstream oxygen concentration for Henry’s Fork (black points) and model (red line). Note large diel excursion in oxygen concentration in this productive river.](image-url)
DISCUSSION

We developed a two-station, Lagrangian modeling approach that fit the data well and produced low estimates of uncertainty on metabolism parameters. We emphasize that parameter uncertainty does not represent the true variation; metabolism measured at another location in the river or during the following week may have been different. However, we suggest that our approach holds promise for estimating metabolism in large rivers. Because these rivers had low rates of oxygen exchange ($K$), they had high diel oxygen excursion which likely allowed more constrained parameter estimates.

GPP and ER in the Green River and Henry’s Fork were among the highest ever measured. The fact that GPP exceeded ER shows that these rivers were autotrophic (producing more carbon than consuming) on the measurement days. Autotrophy is uncommon for streams (Marcarelli et al. 2011, Figure 5). Three of the 5 rivers we studied, plus a tailwater on the Colorado River, were autotrophic; this fraction is much higher than that for most streams and rivers. This finding supports predictions of the river continuum concept (Vannote et al. 1980) where mid order river have high GPP:ER ratios. However, we worked in clear rivers. Further research in more sediment-filled rivers in the Southwest and Midwest should provide more variability; work in these other two regions is ongoing.

Figure 4. GPP (top panel) and ER (bottom) from 5 rivers. Boxplots show mean and distribution of data from 4 estimates each day for 2 days.

Figure 5. GPP tends to be much smaller than ER for most streams and rivers. Black points are from Marcarelli et al. (2011) and Bernot et al. (2010). Red points are this study plus one unpublished point from the Colorado River below Glen Canyon Dam (R. O. Hall et al. unpublished). Line is where GPP=ER. Note log$_{10}$ scale of both axes.
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LITERATURE CITED


