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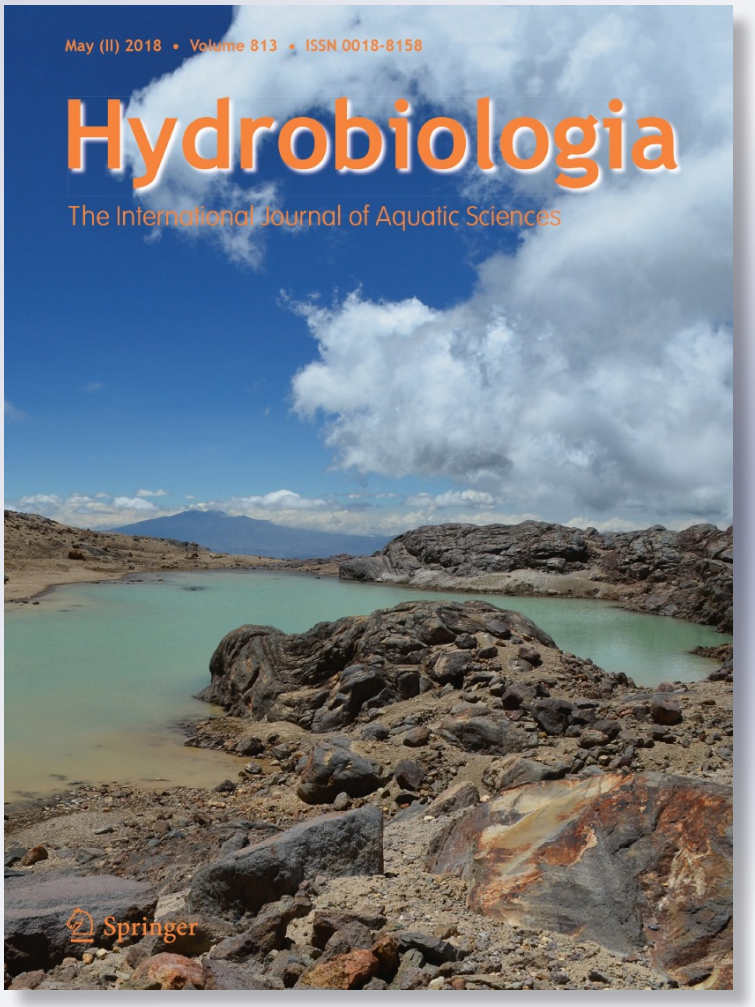

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PRIMARY RESEARCH PAPER

Spatial heterogeneity and controls of ecosystem metabolism in a Great Plains river network

Walter K. Dodds · Sophie A. Higgs · Margaret J. Spangler · James Guinnip · Jeffrey D. Scott · Skyler C. Hedden · Bryan D. Frenette · Ryland Taylor · Anne E. Schechner · David J. Hoeinghaus · Michelle A. Evans-White

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Abstract Gross primary production and ecosystem respiration together define ecosystem metabolism and help indicate the importance of internal and external carbon sources. Spatial variability of these processes is poorly characterized in rivers. We measured metabolism in the Kansas River: (1) at 10 locations over 100 s of km in tributaries within the watershed and (2) over 20 km with detailed sampling in the main stem. Whole-river metabolism at the larger scale was decoupled from light, algal growth, and nutrient limitation, and was positively related to nutrients. Smaller-scale main stem sampling revealed almost as much variance over a few kilometers as the larger scale sampling. Local processes seemed to dominate dissolved oxygen dynamics, since diurnal dissolved oxygen patterns were better correlated with absolute time than data corrected for travel times. A single-station method compared against two-station metabolism methods indicated that local hotspots of metabolism occur at scales less than 1 km and that single-station estimates average out this variance. The main stem data provide support to the idea that functional processing zones control characteristics used to estimate system metabolism, but the nutrient effect at the whole watershed level indicates that transport from upstream can also be important.

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Introduction

Ecosystem metabolism is a characteristic that controls food webs, biogeochemistry, and transport of organic materials and nutrients within and through rivers and streams. This set of metabolic processes includes net ecosystem production (NEP), the balance of gross primary production (GPP), and ecosystem respiration (ER). Aquatic food webs rely on a continuous input of energy in the form of organic matter originating either within (autochthonous) or outside of (allochthonous) the ecosystem (Wetzel, 2001). Thus, measures of metabolism within an aquatic ecosystem are instrumental in understanding interactions among organisms and their environment (Thorp & Delong, 2002; Marcarelli et al., 2011) and act as important indicators of trophic state (Dodds, 2006). Lotic waters are a unique system in which to study metabolism due to their unidirectional flow, dynamic geomorphology, spatial heterogeneity, and high variability in physical, chemical, and biological characteristics (Wetzel, 2001). Some of these highly variable parameters complicate the measurement and scaling of ecosystem rates, while others can inform models of metabolic control over dissolved oxygen.

Several factors interact to determine spatial patterns of metabolic rates locally and across watersheds. Light, temperature, and nutrient concentrations all can directly influence GPP by stimulating photosynthetic rates (Wetzel, 2001) while other factors, such as grazing, sloughing, or scouring, can influence loss rates (Dodds & Whiles, 2010). In large rivers, light availability can be spatially heterogeneous due to factors such as canopy cover or the interaction between depth and turbidity (Ochs et al., 2013). ER can be influenced by carbon availability (GPP alongside external inputs), as well as temperature and losses from grazing and scouring. Metabolic rates of aquatic organisms generally increase with temperature (Allen et al., 2005). Demars et al. (2011) found that NEP decreased exponentially with increasing temperatures across a 20°C gradient due to ER increasing at a faster rate than GPP. A better constrained study shows similar increases in ER and GPP (Demars et al., 2016). Nutrient availability also acts as a driver of metabolism in rivers and such effects are well documented (e.g., Karr & Dudley, 1981; Wetzel, 2001; Richards et al., 2008). While the impact of abiotic factors on river metabolism has received substantial attention, few studies, of which we are aware, have empirically measured metabolism in large rivers at multiple points within the network while paying explicit attention to scale of variance.

Most investigators measure whole-system metabolism at one or a few locations, with little understanding of how representative these measures are of the entire river (except see Williams et al., 2000; Reichert et al., 2009; Demars et al., 2011; Hunt et al., 2012; Hondzo et al., 2013; Houser et al., 2015; Siders et al., 2017). When investigating drivers of metabolism, we expect specific parameters to differentially affect GPP and ER and anticipate variation across scales. This variation in rivers has been represented mathematically (Reichert et al., 2009) but its assumptions have been questioned because results defying the laws of biophysics of the system can emerge (Demars et al., 2015), as previously found for other two-station models (Demars et al., 2011).

Lotic metabolism is sometimes measured at fine spatial scales or in controlled laboratory settings (Oviatt et al., 1986; Findlay et al., 2003; Wiegner et al., 2005), but these studies may not reflect whole ecosystem conditions and are therefore difficult to accurately scale up to larger aquatic systems (Carpenter, 1996). Studies that measure lotic metabolism across large spatial scales and incorporate heterogeneity are lacking (Reichert et al., 2009), especially those with the goal of understanding processes that contribute to variation both within a river and across a landscape (Hall et al., 2016). This heterogeneity could be important depending upon the extent to which rivers and streams link to their upstream components (Siders et al., 2017). In fact, influential concepts in river ecosystem ecology variously recognize the importance of upstream (i.e., River Continuum Concept; Vannote et al., 1980) and lateral (i.e., Flood Pulse Concept; Junk et al., 1989) linkages and modifications thereof (i.e., Serial Discontinuity Concept; Ward & Stanford, 1995) for local metabolism. Alternatively, local conditions can dominate ecosystem processes (i.e., Riverine Productivity Model; Thorp & Delong, 1994), and this idea was more explicitly formalized as functional processing zones in rivers (i.e., Riverine

Ecosystem Synthesis; Thorp et al., 2006). These competing perspectives of river metabolism call into question the specific applicability of river metabolism estimates. For example, if highly local processes dominate (e.g., Kupilas et al., 2017), but experimental methods measure metabolism on much greater spatial scales, incorrect inference is possible with respect to the interpretation of metabolic rate estimates (and vice versa). Methodology for metabolism measurements varies from small chambers at decimeter scales (e.g., Bott et al., 1985), to eddy covariance methods at tens of meters (Berg et al., 2016), and whole stream methods at 100 m or greater scales. Few studies link the scales (except see discussion in Tromboni et al., 2017).

To date, metabolism is more commonly measured or estimated in smaller streams relative to large rivers due in part to the logistic constraints associated with field measurements in larger channels (Dodds et al., 2008, 2013; Hall et al., 2016). Thus, we have few data to understand how spatial scale affects metabolism in rivers and we have a need for research that integrates large spatial scales and takes into account metabolism estimates at smaller scales (however, see Houser et al., 2015; Williams et al., 2000). Our primary objectives were to determine if metabolism varies spatially across a 20 km length of the Kansas River and to compare metabolism among numerous tributaries in the Kansas River basin at a larger scale. A recent approach taken in small streams was to see if sequential two-station estimates of metabolism matched single-station estimates (Siders et al., 2017) and we take this approach and apply it to a larger river system. Our initial predictions on how various factors interact with scale to control metabolism in each system led us to hypothesize that (1) metabolism (NEP, ER, and GPP) will be spatially heterogeneous in the Kansas River as driven by variation in light and external carbon input; (2) differences in nutrients and nutrient limitations among broadly distributed sites will influence GPP and ER and interact with the first prediction (Schade et al., 2011); and (3) local processes will dominate GPP and upstream processes will have more influence on ER (Fuß et al., 2017). First, we made metabolism and habitat measurements at 10 streams distributed across the Kansas River watershed coupled with physical and chemical measurements and associated nutrient diffusing substrata experiments. Second, we completed a detailed set of deployments of dissolved oxygen (O_2), temperature, and light sensors along a 20-km stretch of the main stem of the Kansas River coupled with multiple measurements of physical habitat.

Materials and methods

Study system

The Kansas River system originates in eastern Colorado and flows east to the Missouri River. The main stem of the Kansas River forms at the confluence of the Smoky Hill and Republican Rivers in northeastern Kansas (Quist et al., 1999). The total drainage covers approximately 159,000 km^2 of land in portions of Colorado, Nebraska, and Kansas (Metcalf, 1966). Shallow side channels, vegetated islands, and sandbars (Quist et al., 1999) characterize the Kansas River. In 2007, we used ten sites throughout northern Kansas for a comparison of metabolism across tributaries of the Kansas River (Fig. 1). We then selected a 20-km stretch of the Kansas River between Ogden and Manhattan, Kansas, for a detailed study of within-reach river metabolism heterogeneity in 2015 (Fig. 1).

2007 Large-scale comparison; sites, physical, chemical, and habitat variables

The ten small streams for our large-scale comparison of metabolism were selected because they all lie within the Kansas River drainage basin and represent a range of characteristics including size, substrata composition, and canopy cover (Table 1). The average discharge of these streams at the time of the study ranged from 0.03 to 0.97 $m^3\ s^{-1}$. Discharge at these sites for the month prior to the sampling period was relatively low with no major floods or spates. All channel data within the small streams were collected during the summer of 2007.

Dissolved oxygen (O_2), water temperature, and turbidity were measured using YSI 6920 V2 sondes with Clark-type sensors (Yellow Springs Instruments, Yellow Springs, Ohio). Data were logged at 10-min intervals at one location in each stream and probes were carefully calibrated for drift in the O_2 reading. Three Winkler titrations (Eaton & Franson, 2005) were performed at each site during initial calibration

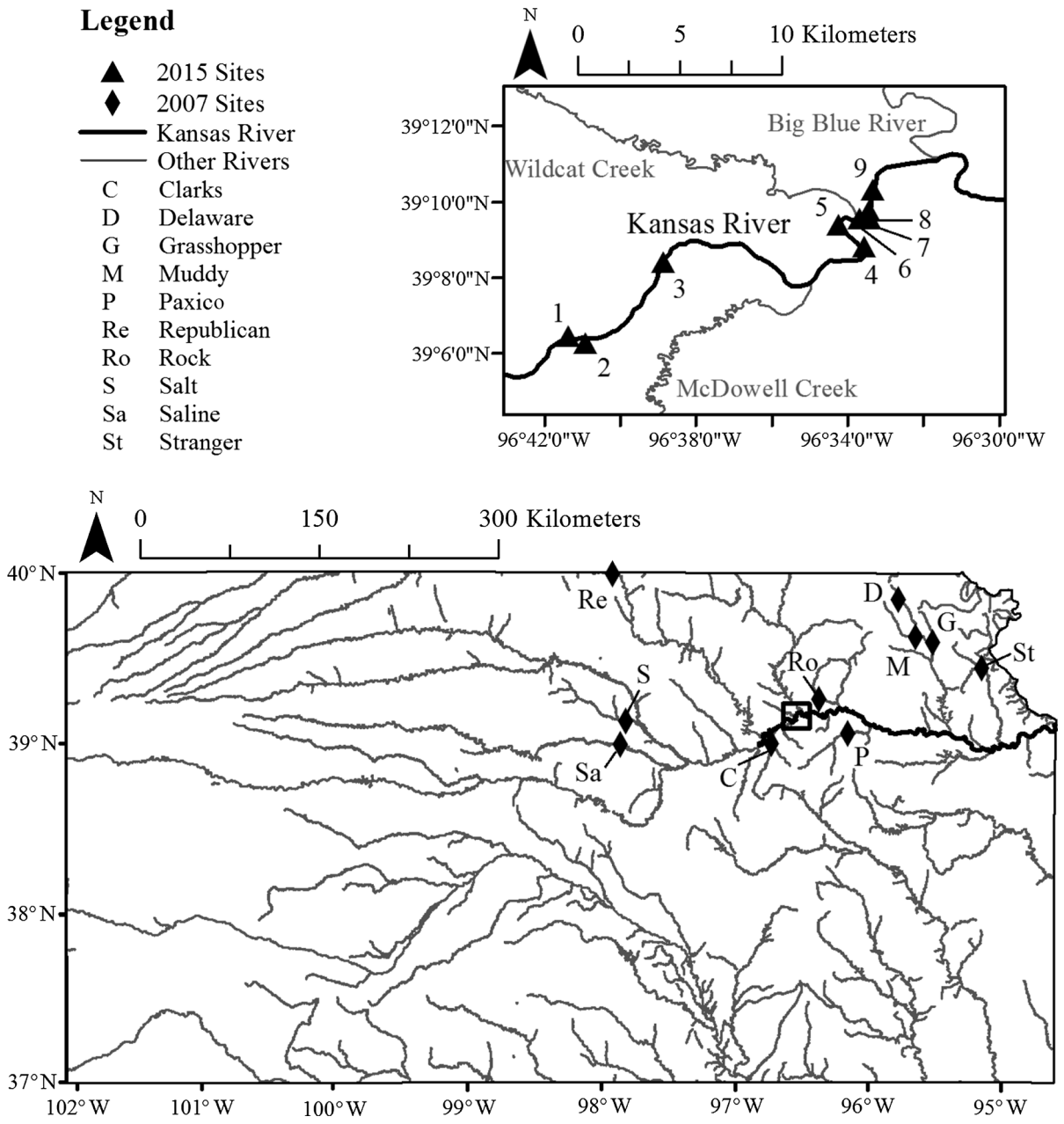


Fig. 1 [ArcMap] Map of Kansas including all study sites. Square in the northeastern quarter of Kansas represents the river reach studied in 2015 and is magnified above. Triangles represent DO probe locations. Diamonds represent 2007 sites

of the sonde and at the end of the deployment period to test for drift and absolute calibration. The beginning sonde value was taken from a Winkler titration after the sonde readings had stabilized (temperature equilibration and stabilization required about 30 min). This calibration procedure was repeated after deployment and deviation of O_2 from the Winkler was used to correct assuming linear drift over time. Individual probes drifted at different rates, and drift was generally less than 0.5 mg l^{-1}. We retrieved barometric pressure data for each site from historical weather data using Weather Underground (www.

Table 1 Physical characteristics of 2007 streams listed in order of increasing discharge

	Latitude (N)	Longitude (W)	Date	Width (m)	Mean depth (m)	Velocity (m min^{-1})	Discharge (m^3 min^{-1})	k (min^{-1})	Peak lag (min)	k from peak (d^{-1})	Mean canopy cover (%)	Canopy cover SD (%)	Mud (%)
Delaware	39°84′14″	95°78′41″	8/28/2007	2.5	0.06	13.5	2.0	0.0006	330	0.07	76	21	0
Grasshopper	39°35′04″	95°31′36″	5/8/2007	5.2	0.07	7.3	2.9	0.0043	50	30	70	29	0
Stranger	39°26′52″	95°9′43″	5/8/2007	3.7	0.10	8.0	3.1	0.0032	10	100	13	8	14
Republican	39°59′03″	97°55′56″	12/8/2007	7.9	0.14	15.3	16.8	0.0037	260	2.5	27	37	0
Salt	39°08′21″	97°50′12″	12/8/2007	6.0	0.30	9.4	16.8	0.0025	220	5.1	25	23	100
Clarks	39°00′02″	96°44′20″	3/8/2007	14.2	0.33	5.2	35.1	0.0012	220	5.1	67	35	8
Saline	39°00′14″	97°52′25″	12/8/2007	6.4	0.31	17.7	35.7	0.0009	290	0.8	49	30	60
Rock	39°15′53″	96°22′47″	5/8/2007	9.4	0.38	6.9	39.1	0.0010	220	5.1	26	25	22
Paxico	39°03′53″	96°10′08″	28/8/2007	12.2	0.20	18.3	44.2	0.0018	190	6	48	28	10
Muddy	39°37′43″	95°39′28″	3/9/2007	13.0	0.44	6.9	58.3	0.0023	290	0.6	83	19	52

Physical stream measurements represent those characteristics at the time of the study. Aeration (k) represents a modeled value. Peak lag is the number of minutes the peak dissolved oxygen occurs after the peak in light. Aeration (k) from peak is calculated by equations in Chapra & Di Toro (1991) from peak lag and day length data

wunderground.com) at the closest airport to each respective site for the days of data collection. Water chemistry samples were taken on the day that the sondes were deployed for analyses of total nitrogen (TN) and total phosphorus (TP). Samples were taken from an area of active flow and kept on ice until they were returned to the laboratory (within 5 h), where they were immediately frozen until analyses. Samples were analyzed by a persulfate digestion (Ameel et al., 1993) followed by analysis for phosphate and nitrate on a continuous flow auto analyzer. Photosynthetically active radiation (PAR) was measured at each site using a single Odyssey logger (PAR Recorder, Data flow systems, Christchurch, New Zealand) mounted adjacent to the sonde to estimate PAR at the water surface. Data were logged at 10-min intervals for approximately 48 h.

Five of the ten sites (Stranger, Salt, Saline, Republican, and Mill Creek at Paxico) had United States Geological Survey (USGS) gaging stations immediately above the site of O_2 measurement. Stream discharge, width, and velocity data were accessed online from the USGS (USGS, www.usgs.gov). Only discharge data were available at each site during the dates of our study so we modeled width and velocity using simple regressions made from a year of USGS data. All width and velocity values from 2006 through 2007 were plotted against corresponding discharge values and the equations from the resulting lines of best fit were used to model the average widths and velocities for each stream on each day of sonde deployment (equations in Supplementary Table S1). Average depth was then calculated by dividing the discharge by the product of width and velocity.

For those sites without a nearby gaging station (Delaware, Grasshopper, Clarks, Rock, and Muddy), stream discharge calculations were made with the handheld current meter method as described by Gore (2006). Depth and velocity measurements were taken for at least twenty points along a transect on the day of sonde deployment and on the day of sonde retrieval. The two resulting discharge calculations were used to monitor discharge changes, and periods of time during which discharge changed drastically were not used in metabolism modeling.

We assessed physical habitat characteristics along five transects in each stream spaced approximately 50 m apart (i.e., 200-m reach). We measured canopy cover using a convex densiometer at four points on

each transect (each bank facing riparian zone and middle of the transect facing each side). Dominant substrata were determined by particle size (bedrock and large boulders > 45 cm, boulders – 25 to 45 cm, cobble − 6 to 25 cm, gravel − 2 to 60 mm, sand − 0.06 to 2 mm, mud and silt < 0.06 mm) assessed by grab samples and/or sight at each of 10 equally spaced points on each transect. Relative frequency of substratum types at the reach scale was simply the number of occurrences of each substratum class divided by 50 (i.e., 10 points on each of 5 transects).

2007 Nutrient diffusing substrata deployments

Nutrient diffusing substrata (NDS) were ammended with inorganic nitrogen (0.5 M as KNO_3) only, with inorganic phosphorus (0.5 M as NaH_2PO_4) only, or with both N and P (0.5 M each) according to previously published methods (Tank et al., 2006; Tank & Dodds, 2003). This two-factor design allows for examination of independent and interactive effects of N and P amendment. We drilled holes in the caps and placed either glass-fritted filters or cellulose sponge circles in the cap hole on the surface of the agar and exposed them to stream water. Replicate NDS with either glass frits or cellulose (5 of each for each nutrient treatment or control) were placed on the stream bottom in areas of modest flow in plastic racks at each site for 21 and 10 days, respectively, in July and August of 2007. The incubation time was shorter for cellulose sponges because we found that sponges were decomposing completely within 21 days in a preliminary deployment. We collected glass frits and spectrophotometrically measured chlorophyll *a* after ethanol extraction to assess benthic algal nutrient limitation (Sartory & Grobbelaar, 1984). We estimated heterotrophic microbial nutrient limitation by measuring respiration rates on collected cellulose sponges. Sponges were placed in a full vial of room temperature stream water from the appropriate site with no atmospheric air. Dissolved oxygen concentrations were measured in the stream water at time zero and after a known incubation time (1.5–3 h), and these values were used to estimate respiration rates. A two-way analysis of variance was used to assess nutrient limitation according to Tank & Dodds (2003).

2015 Reach-scale heterogeneity: physical and chemical methods

Physical and chemical measurements were conducted at nine sites along a 20-km reach of the Kansas River (Fig. 1). In the upstream portion of the reach (sites 1–3), channel measurements and physical and chemical data were collected starting 11 October 2015, during which the average discharge was 16.7 $m^3\ s^{-1}$ (Table 2). Data were collected in the downstream portion (sites 4–9) over 3 days beginning 25 October 2015, during which the average discharge was comparatively lower (8.2 $m^3\ s^{-1}$). A third deployment along the entire reach was attempted, but dam operation during this time period caused discharge to nearly double, so these data were only used for analyses of spatial autocorrelation. Fifty-one years of data from a nearby gaging station on the river (USGS 06879100) reported discharge values for October with a median of 37 $m^3\ s^{-1}$ with 10.3 and 19.4 $m^3\ s^{-1}$ as the lower 10th and 25th percentiles, suggesting that all of our measurements in 2015 on the Kansas River were made during extremely low discharge.

Dissolved O_2, water temperature, and barometric pressure were measured using YSI Professional Optical Dissolved Oxygen (ProODO) instruments (Yellow Springs Instruments, Yellow Springs, OH). O_2 was logged with each sensor calibrated on the day of deployment with water-saturated air until readings stabilized. We did not need to use the Winkler approach taken in 2007 as the optical probes are much more stable and thus exhibit less drift. Water temperature and barometric pressure at the surface were measured by sensors within the probe and handheld instrument, respectively. Probes were placed by canoeing down the channel and identifying areas where the stream channel was coherent and natural features allowed them to be placed in the thalweg (i.e., the channel is sandy so the occasional log jams provided good locations to place probes). There were two modestly sized confluence channels and probes were placed above and below them to account for potential differences related to their input. Distance between ProODO instruments was variable (mean = 2.0 km, range = 0.27–10.1 km). Data were logged at 10-min intervals for approximately 48 h. PAR was logged at 10-min intervals at four points along the river with Odyssey Photosynthetic Irradiance Loggers (Model Z412). The channel was broad

Table 2 Kansas river sites are listed from upstream to downstream

Site	Distance downstream (km)	Width (m)	Mean depth (m)	Velocity (m min^{-1})	Discharge (m^3 min^{-1})	Aeration (min^{-1})	Alpha at 20°C (mg l^{-1} min^{-1} μE^{-1})	P_{max} (mg l^{-1} min^{-1})	Daily ER (g O_2 m^{-2} d^{-1})	Daily GPP (g O_2 m^{-2} d^{-1})	GPP:ER	Daily NEP (g O_2 m^{-2} d^{-1})
1	0	67.3	0.42	19.7	1001.5	0.00337	1.30E−05	2.29	− 1.25	2.38	1.90	1.12
2	0.8	70.5	0.40	19.2	1001.5	0.00279	1.25E−05	10.00	− 1.43	2.19	1.53	0.76
3	6.0	105.1	0.20	13.6	1001.5	0.00351	1.86E−05	10.00	− 1.09	1.67	1.53	0.59
4	16.2	123.0	0.10	10.7	490.6	0.00370	1.65E−05	10.00	− 0.28	0.37	1.32	0.09
5	17.7	113.5	0.15	12.3	490.6	0.00416	1.72E−05	1.51	− 0.46	0.6	1.30	0.15
6	18.7	113.1	0.16	12.3	490.6	0.00343	1.15E−05	1.51	− 0.22	0.4	1.82	0.18
7	19.2	93.7	0.27	15.5	490.6	0.00401	1.51E−05	1.51	− 0.79	0.91	1.15	0.12
8	19.6	74.4	0.38	18.6	490.6	0.00409	2.14E−05	0.88	− 2.57	1.82	0.71	− 0.75
9	20.6	104.3	0.21	13.7	490.6	0.00399	1.78E−05	0.88	− 0.66	0.82	1.24	0.16

Distance downstream represents the distance from the first site. Physical stream measurements represent those characteristics modeled from physical measurements taken at the time of the study. Aeration, alpha, P_{max} (maximum photosynthetic rate), daily GPP (gross primary production), daily ER (ecosystem respiration), and daily NEP (net ecosystem production) represent modeled values and GPP/ER is the ratio of those modeled daily values. Alpha and P_{max} are parameters used to fit the irradiance curve for GPP

and sandy, and had little influence of riparian vegetation, so four points were adequate.

Habitat parameters were measured along 42 transects from 1 km above the uppermost O_2 probe down to the lowermost probe. Parameters measured include stream width (m), stream depth (m), velocity (m s^{-1}), and discharge (m^3 s^{-1}). Depth and velocity were measured along 22 shallow, wadeable transects using a handheld flow meter (Hach FH950), and data were used to calculate average discharge across the 22 transects according to Buchanan & Somers (1969). Measurements were dispersed evenly across a given transect using a range finder and each measurement of velocity was taken at 0.6 stream depth. For 20 deeper (non-wadeable) transects, stream width, average depth, and average discharge were measured directly across the width of transects using a RiverSurveyor model M9 Acoustic Doppler Velocimeter (ADP, Sontek, YSI instruments, Yellow Springs, OH).

2015 River characteristic modeling

We used our field measurements in regression models to predict velocity and depth based on width for each of the 16.7 and the 8.2 m^3 s^{-1} discharge conditions (data in supplementary Table S2, equations in Supplementary Materials Table S3). Four historical Google Earth images were selected to represent a range of discharges as recorded by the nearby gaging station (USGS 06879100) and we used the ruler tool to measure wetted river widths (excluding sandbars) along the Kansas River centerline every 200 meters from the lowermost station to 14-km upstream above the uppermost site. These data were used to predict depth and velocity every 200 m in the study area.

Modeling metabolism

We used a single-station method (Dodds et al., 2013) to model daily metabolism at the nine different locations along the Kansas River and at single locations in each of the 10 small streams. We compared this to the output of two-station models sequentially calculated upstream to assess the role of heterogeneity on the single-station results. We employed two similar but differently coded methods for fitting the data. The Bayesian method of Grace et al. (2015) corrected for light approximation according to Song et al. (2016,

downloaded on 6 September 2016 from https://github.com/dgiling/BASE) and a Microsoft Excel-based model (Dodds et al., 2013). Both methods yielded similar results ($R^2 = 0.98$, slope not significantly different from 1, linear regression) so we only present the results from the Dodds et al. (2013) model (Bayesian data in supplementary materials).

We also used a two-station method to estimate metabolism in defined reaches between the probes for the 2015 data (Riley & Dodds, 2013). In this method, a curve-fitting approach similar to the one described by Holtgrieve et al. (2010) is used to model daily O_2 patterns from expected changes in O_2 due to production, respiration, and aeration as calculated by physical measurements and equations described by Riley & Dodds (2013).

With the single-station estimates, we were interested in determining the appropriate upstream distance along which to measure physical characteristics (Demars et al., 2015). We adopted the procedure used by Hall et al. (2015) to determine the length of approximately 80% O_2 turnover based on the equations in Demars et al. (2015) to calculate the 80% distance $O_{2,80}$:

$$O_{2,80} = \frac{1.61 \times v}{k}, \quad (1)$$

where v is average velocity (m d^{-1}) and k is aeration (d^{-1}). We used a multi-step procedure to determine physical characteristics above each probe. First, we modeled k assuming physical characteristics for one km above the probe. We then used the modeled k and measured average velocities to estimate how far upstream we should be estimating depth, width, and average velocity (Eq. 1). The rates of GPP and ER were then re-modeled using these physical characteristics. We also compared aeration rates obtained from our models to the method of Chapra & Di Toro (1991) based on time lags of O_2 after peak light. We felt that the time-lag could be related to factors in addition to aeration, and wanted to verify this independent method and find out if it matched.

Additional calculations and statistics

Statistical analyses were performed in Statistica (Statsoft Inc., Tulsa, OK). Non-parametric Spearman's Rank Correlation was used as an initial step of data exploration, to test if O_2 concentrations in the 2015 measurements were more strongly correlated by time or space, and to test for the relationships among GPP, ER, and k. Spatial autocorrelation was checked by correlating all sites among each other after correcting for travel time and observing if correlation was a function of distance of sites from each other. Temporal autocorrelation was tested by correlation among all sites with time not corrected for travel time. Regression and multiple regression analyses were used to assess the relative importance of potential independent variables influencing metabolism.

Calculated values for the 2007 data included chlorophyll *a* accrual, degree of nutrient limitation, and available light. Chlorophyll *a* accrual was calculated from the mass of chlorophyll *a* on the control glass frits from the 2007 NDS deployments divided by the number of days of deployment. The relative total nutrient limitation was calculated as the log response ratio in the N + P additions relative to the controls. Relative available light was calculated as the turbidity measured with the sondes multiplied by the average depth from habitat characterizations.

The downstream-most single-station estimate was compared to two-station estimates upstream that were summed by distance-weighting two-station results upstream sequentially for the 2015 data. This approach was taken to investigate the zone of influence on single-station estimates. Distance-weighted metabolism for the more detailed 2015 measurements was calculated from two-station estimates of metabolic rates as

$$M_d = \sum_i^n M_i \times \frac{D_i}{D_t}, \quad (2)$$

where M_d is the distance or aeration footprint-weighted metabolic estimate (GPP or ER), with n measures of two-station metabolism (M_i) over individual lengths of each two-station method (D_i) scaled by the total distance of summed two-station models (D_t). Equation 2 was also used with aeration scaled by the proportion of the footprint accounted for by each individual two-station measurement relative to the entire footprint accounted for with all sequential measures.

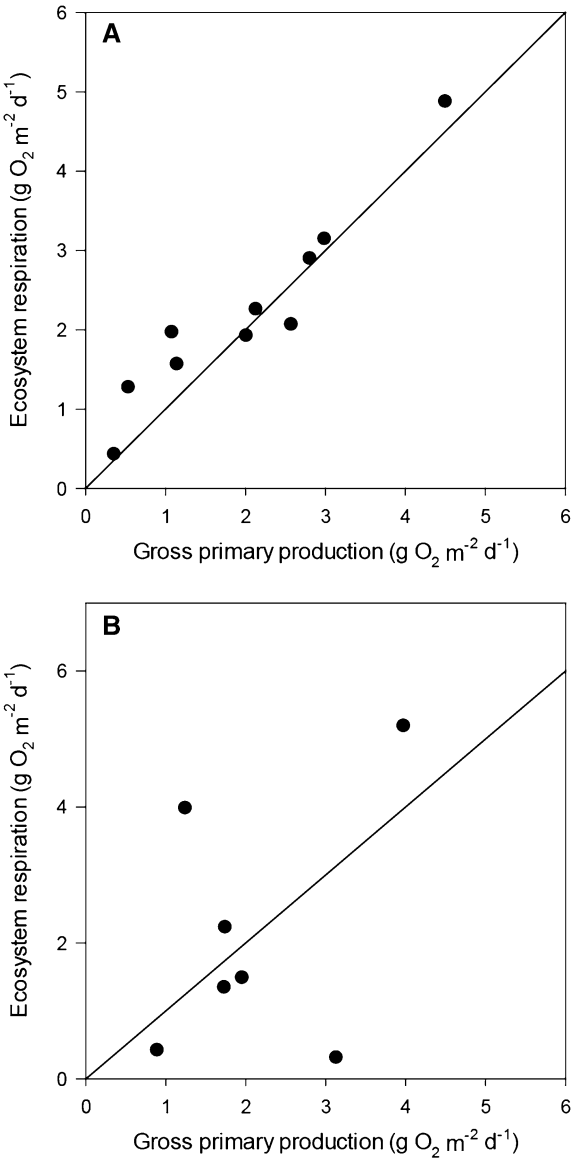


Fig. 2 Relationship between Gross Primary Production (GPP) and ecosystem respiration (ER) from ten locations in the Kansas River basin as estimated by a single-station model in 2007 (**A**) and within a 20-km reach of the main stem of the Kansas River estimated with the two-station method in 2015 (**B**). Line represents 1:1 ratio

Results

2007 Broad scale comparison

Values of GPP and ER varied several-fold among sites. The values for GPP ranged from 0.36 to 4.50 g O_2 m^{-2} d^{-1}, and the range in values for ER

Table 3 Biological and chemical characteristics of 2007 Kansas River sites

	Daily ER (g O_2 m^{-2} d^{-1})	Daily GPP (g O_2 m^{-2} d^{-1})	GPP:ER	Daily NEP (g O_2 m^{-2} d^{-1})	Total N (μg L^{-1})	Total P (μg L^{-1})	Turbidity (NTU)	Chlorophyll accrual (μg chl cm^{-2} d^{-1})	Nutrient response (log response ratio)
Delaware	− 0.43	0.36	0.83	− 0.07	NC	NC	NC	NC	NC
Grasshopper	− 1.97	1.08	0.55	− 0.89	1164	280	6	0.11	0.18
Stranger	− 1.27	0.54	0.42	− 0.73	1089	59	20	0.12	0.14
Republican	− 2.26	2.13	0.94	− 0.13	1337	566	105	NC	NC
Salt	− 4.88	4.50	0.92	− 0.37	1760	211	132	NC	NC
Clarks	− 2.07	2.57	1.25	0.51	705	132	17	0.15	− 0.19
Saline	− 2.90	2.81	0.97	− 0.09	1506	232	94	NC	NC
Rock	− 1.57	1.14	0.73	− 0.42	825	117	25	0.07	0.32
Paxico	− 1.92	2.01	1.05	0.09	658	274	36	0.16	0.38
Muddy	− 3.15	2.99	0.95	− 0.15	2035	259	66	0.04	0.18

Daily GPP (gross primary production), daily ER (ecosystem respiration), are modeled values, and NEP (net ecosystem production) and GPP:ER are calculated from modeled values

NC not collected or sample lost

Table 4 Spearman's rank correlation of variables associated with ecosystem respiration (ER), gross primary production (GPP), and net ecosystem production (NEP) for the basin-wide 2007 measurements

	Daily ER (g O_2 m^{-2} d^{-1})	Daily GPP (g O_2 m^{-2} d^{-1})	Daily NEP (g O_2 m^{-2} d^{-1})
Width (m)	− 0.406	0.564	0.455
Mean depth (m)	− 0.527	**0.697**	0.152
Velocity (m min^{-1})	0.055	− 0.049	0.274
Discharge (m^3 min^{-1})	− 0.401	0.578	0.274
Aeration (min^{-1})	− 0.248	0.042	− 0.588
Mud cover (%)	− 0.546	**0.669**	− 0.141
TN (µg/l)	− **0.783**	0.617	− 0.250
TP (µg/l)	− 0.350	0.133	0.150
N:P (molar)	− 0.050	0.133	− 0.433
Canopy cover (%)	0.006	0.333	0.167
Depth × turbid	− **0.783**	**0.850**	0.283
Temperature (°C)	0.483	− 0.433	− 0.233
Avg. Chl *a* accrual (µg cm^{-2} d^{-1})	0.257	− 0.143	0.429
NP Chl *a* response log (NP:C)	0.257	− 0.086	− 0.143

Values significant at $P < 0.05$ are bold

Note higher respiration rates (ER) are more negative, so negative correlations signify greater respiration with increase of the other value

was similar (from − 0.43 to − 4.88 O_2 m^{-2} d^{-1}). GPP and ER were closely linked at each site (Fig. 2A) and most sites had NEP close to zero (GPP/ER close to 1), with slightly higher ER rates at some sites (Table 3). One concern with model fitting with aeration is that ER and aeration can trade off against each other (i.e., a high GPP, ER, and aeration give a very similar model fit to a low GPP, ER, and aeration). We found no significant correlation between modeled aeration and either GPP or ER ($P = 0.90$ and 0.49, respectively). This suggests that modeled aeration did not control ER, or vice versa, and that the estimates are independent.

Mean rates of chlorophyll *a* accrual per day were 0.11 µg cm^{-2} d^{-1}, and were not correlated with either GPP or ER ($P > 0.05$, Table 4). Similarly, nutrient limitation was significant across sites (the 95% confidence interval did not include zero), but the degree of nutrient (N, P, or both) limitation was not significantly correlated with GPP or ER, or even TN, TP, or their molar ratio (TN:TP). However, our correlations from the nutrient diffusing substrata are incomplete because we lost several experiments (4 of 10, Table 3).

Metabolic rates were linked to our estimate of relative light (Fig. 3), but not as expected. As depth × turbidity increased, GPP increased, and ER became more negative (increased). Rates of GPP and ER increased with total N (Fig. 3) but were not significantly related to TP, potentially suggesting nitrogen limitation of ecosystem rates. Percent mud substratum was also positively correlated with GPP; other substrata types were not. In general, nutrients had stronger correlations with ER than with GPP.

Lags of O_2 after the times of maximum PAR were not driven by aeration. Aeration rates obtained from our models and from the method of Chapra & Di Toro (1991) indicated no significant correlation between aeration and time lag of peak O_2 ($P > 0.05$, data not shown).

2015 Local metabolism heterogeneity measures

Two-station estimates of GPP in the 2015 localized measures were correlated with ER, but the estimates fell further from the 1:1 line than did those in our among-stream comparisons (Fig. 2B). This suggests that ER and GPP were less tightly coupled locally than in more broadly dispersed sites (but could also be related to two-station method bias, Demars et al., 2011).

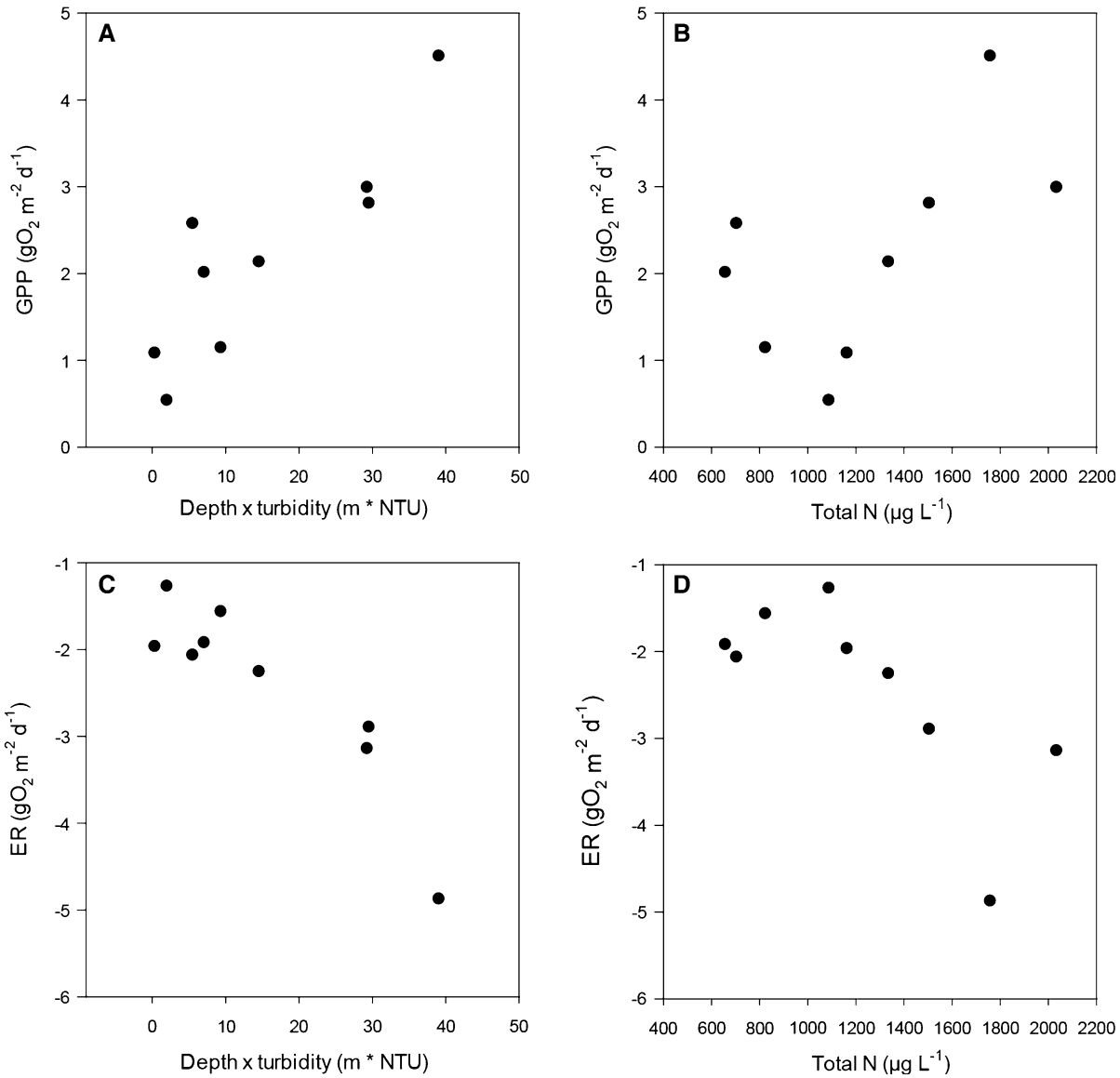


Fig. 3 Relationships between gross primary production and water light transmittance (turbidity × depth, **A**) and total nitrogen (**B**), and ecosystem respiration and light transmittance (**C**) and total nitrogen (**D**) for sites around the Kansas River basin in 2007

We used these data in two ways to investigate the relationship between spatial scale and heterogeneity in stream metabolism. First, we compared correlation of O_2 values taken at each time point among all stations corrected by travel time between each pair (Fig. 4A). Second, we performed the correlation without time correction so all points were matched by the exact time they were collected, regardless of where they were on the river (Fig. 4B). Specific locations upstream that are hotspots of metabolic activity would be expected to correlate better with a downstream station when time corrected. If the system is homogenous and all stations respond to variation in light over time in the same way, then metabolic activity should correlate well with space and not with time. There was a clear decrease in correlation with distance between stations when distance is corrected for travel time. There was not a decrease in correlation with distance up river when there was no travel time correction.

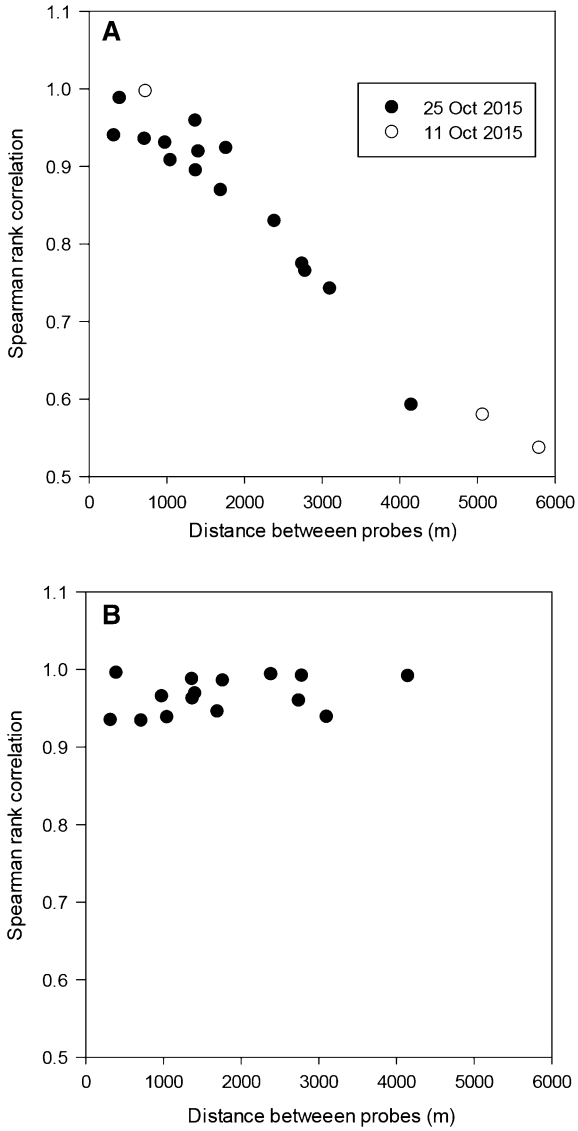


Fig. 4 Spearman's rank correlations between dissolved oxygen concentrations with all pairs of probes as a function of distance between probes for 2015 data on sites within a 22-km section of the Kansas River with correlations of O_2 offset by travel time between the stations (**A**) and with no time offset (**B**)

The zone of upstream influence based on the 80% O_2 turnover was generally greater than the distance to the next station upstream (Fig. 5). However, these zones were not longer than the length of the entire study area. These estimates indicate the value of comparing one and two-station spatially weighted estimates.

We compared one and two-station estimates to dissect out the potential effect of spatial heterogeneity on single-station estimates. Several interesting patterns emerge with the approach of comparing single-station results to sequentially distance-weighted upstream two-station results (Fig. 6). There is noticeable heterogeneity in the two-station estimates. For example, there is one short segment (between 2500 and 3000 m upstream of the downstream probe (Fig. 6A) where ER is quite high, but GPP is not (Fig. 6B). This particular segment modestly influences the distance-weighted estimate and somewhat more strongly the aeration footprint-weighted estimate relative to the downstream segment length. Furthermore, the distance-weighted metabolism measurement over multiple upstream segments generally causes the calculated value to come closer to the single-station method from the bottom of the contiguous segments. The distance and aeration footprint-weighted methods do not exactly correspond, with the aeration-footprint method being less sensitive to high values further from the downstream station.

Discussion

We investigated stream metabolism at two scales: comparing sites on streams distributed across the Kansas River watershed (2007) as well as among sites within a single reach of the main stem Kansas River (2015). As expected, GPP, ER, and NEP were spatially heterogeneous at both scales of study. We hypothesized that open-canopy systems with clearer water would be dominated by GPP but this was not supported. We only found modest support for hypothesized nutrient effects, suggesting that heterogeneity is not primarily driven by nutrient availability at the larger scale.

Data collected from different streams across the watershed can be used to broadly address factors that might influence whole-system metabolism. In contrast, many of the potential factors affecting stream metabolism cannot be directly assessed using our within-reach data because nutrients, turbidity, and flow regime did not vary greatly along the 20-km reach. Some factors that potentially affect GPP and ER can be mostly ruled-out as driving differences among streams in this study. Nutrient enrichment bioassays did yield variable levels of chlorophyll accrual related to N and P additions, indicating some nutrient limitation of algal growth (N, P, or N and P co-

limitation); however, GPP was not linked to chlorophyll accrual, degree of nutrient limitation, TN, or TP (Table 4). Depth correlated with GPP in the opposite direction than expected, as did the product of depth and turbidity. This result could be related to development of phytoplankton blooms in slower moving deep rivers, but we did not take water column chlorophyll samples so we cannot confirm this speculation. Flow was relatively low during this study, and most of these sites were shallow enough that they did not have obvious phytoplankton blooms.

What does modeled aeration really represent?

Aeration is a key factor controlling how far upstream processes influence O_2 concentration at any particular point downstream. It is therefore important to understand the influence of aeration on whole-system metabolism estimates and how aeration estimation may influence the ability of various methods to detect spatial heterogeneity. In extreme cases, very high rates of aeration make it impossible to measure whole stream metabolism because any deviation from saturation is immediately equilibrated. In the other extreme, with no aeration, O_2 deficit or super saturation would propagate over long periods (or distance in flowing waters).

Chapra & Di Toro (1991) use the time lag of the peak O_2 following the light peak to indicate aeration. Our data suggest that this is an incorrect interpretation of the peak lag because our modeled aeration rates do not match aeration rates estimated with this method. There are other indicators that the lag is predominantly reflective of aeration. Much of the GPP and ER is probably associated with benthic microorganisms occurring within the flow diffusion boundary, and the rate that O_2 enters or leaves the water column from these biofilms could be limited by diffusion, causing the observed lag. Similarly, the exchange between shallow side pools and the main channel could cause delays in response to light when the probes are placed in the thalweg. As such, the time lag in our study is probably an indicator of spatial segregation within the habitat rather than aeration.

We also recognize that one aeration value for a 24 h or greater period may be incorrect. For example, changes in wind speed and direction could alter the rates. This change could be particularly significant in

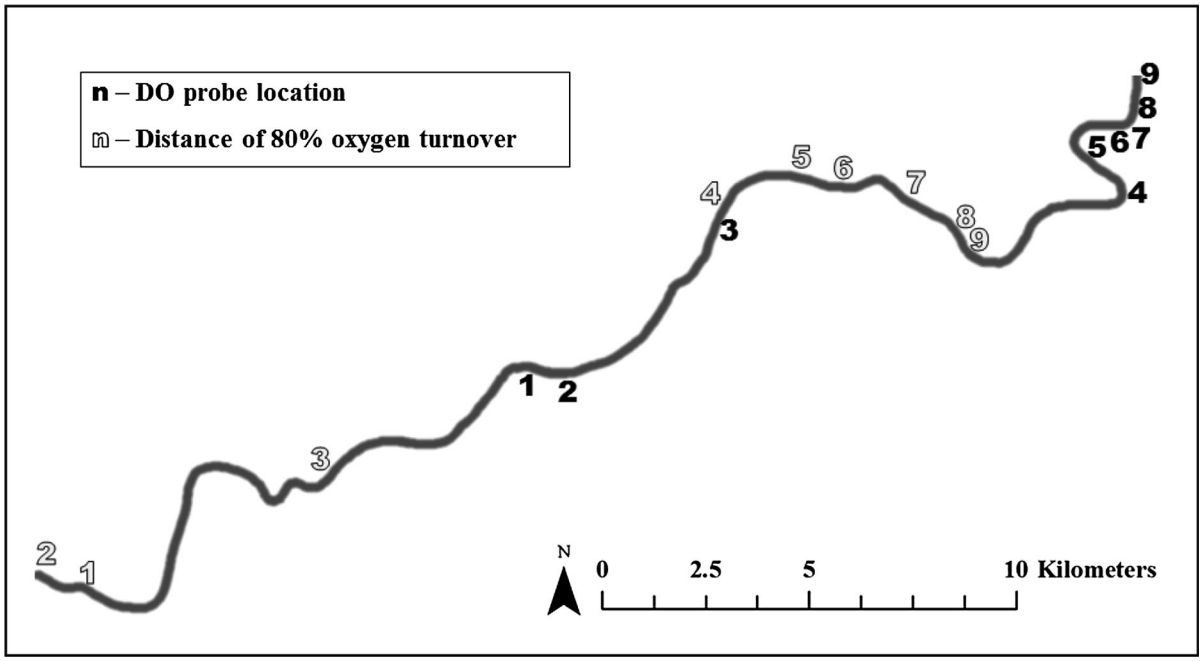
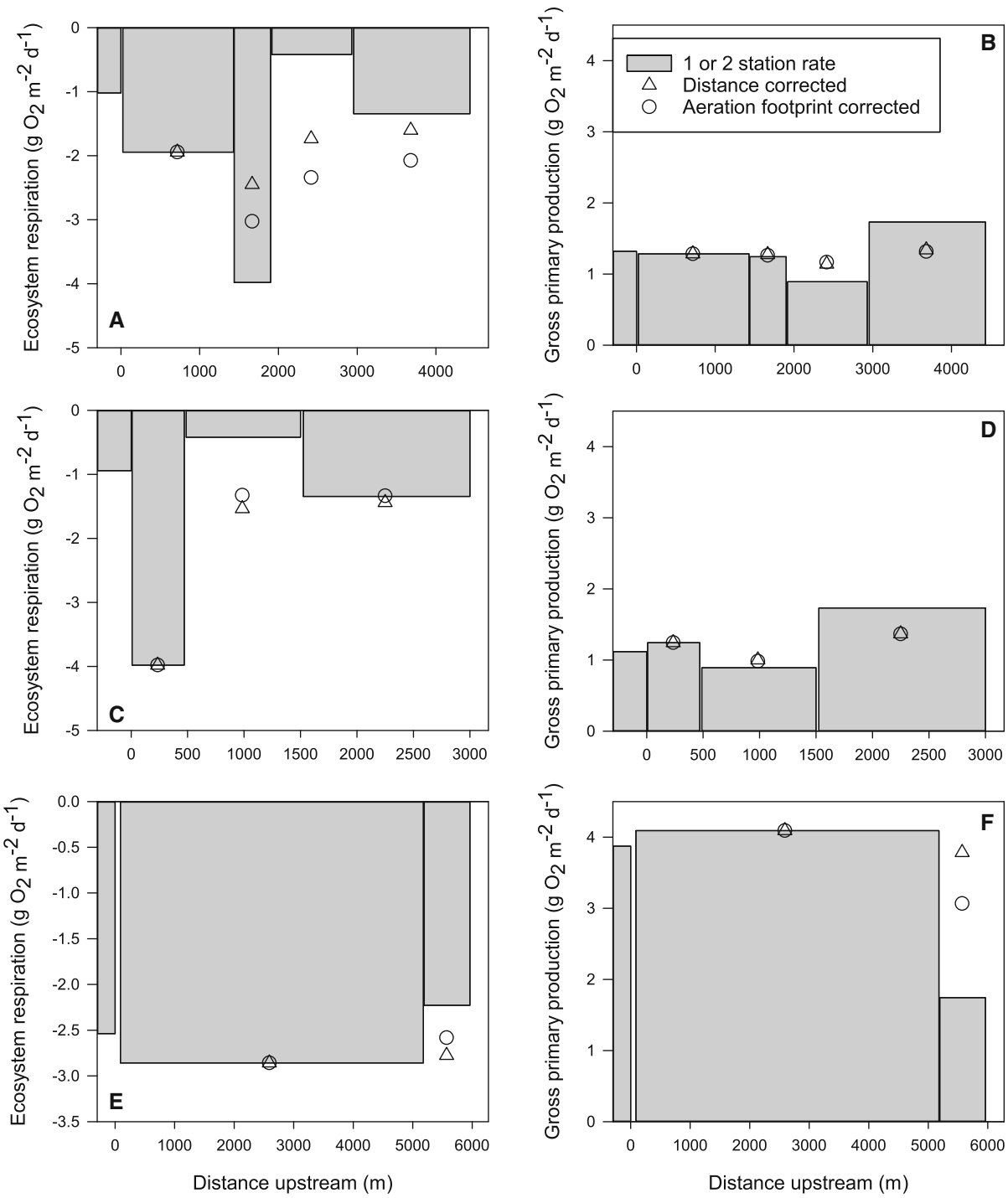


Fig. 5 Schematic of site locations for the work on the Kansas River in 2017. Solid numbers refer to O_2 probe locations with 9 being the furthest downstream. Non-filled in numbers indicate the respective location of 80% oxygen turnover for each probe. Flow is from lower left to upper right. Note that, sites 1–3 were measured on a different day and at a higher discharge than sites 4–9



larger water bodies with slow flow. It is also possible common corrections for changes in temperature are not correct as temperature variation also influences water viscosity and subsequently turbulent mixing.

Spatial scale and metabolism

Data at the largest scale (2007 data) can be used to assess if metabolic rates are a function of position in

◀**Fig. 6** Metabolism estimates for single-station (bottom station) and two-station estimates from above (bar width reflects distance between stations moving upstream (except left-most bar which is the single-station estimate), as well as the distance-weighted (open triangles) and aeration footprint-weighted (open circles) values for each sequentially weighted estimate including the segments below as calculated from Eq. 2. See methods for calculation methods **A** and **B** match, **C** and **D** match, and **E** and **F** match. The lowermost station in **A** and **B** is station 9, with successive two-station estimates from 9–7, 7–6, 6–5, and 5–4. The lowermost station in **C** and **D** is station 8, with successive two-station estimates from 7–6, 6–5, and 5–4. The lowermost station in **E** and **F** is station 3 with 3–2 and 2–1 single-station estimates

the watershed. The River Continuum Concept (Vannote et al., 1980) proposes that upstream sites have closed canopy resulting in net heterotrophy due to low light and high inputs of terrestrial organic material. Mid-order streams are predicted to be net autotrophic as light allows for photosynthesis. Downstream turbid sites are net heterotrophic, driven by organic material transported from above. We found no clear relationships between any of the modeled daily metabolism estimates for 2007 (GPP, ER, or NEP) and stream discharge or stream width, which can serve as surrogates for stream order. This is in contrast to Demars et al. (2016) who found that metabolism was significantly related to discharge, and Hotchkiss et al. (2015) who saw decreases in net ecosystem production as river size increased. Individual metabolism estimates can be highly variable even amongst rivers of similar discharge in the temperate steppe/mountainous regions of the western U.S. (Hall et al., 2016) and small native grassland streams in the Kansas River watershed (Riley & Dodds, 2012). However, ER was related to total N, which is most likely delivered from upstream. This indicates that the River Continuum Concept is a weak predictor of whole-system metabolic characteristics based on position in the watershed along an upstream to downstream continuum, at least over the almost three orders of magnitude discharge between our smallest and our largest systems. This leaves us seeking alternative explanations for factors influencing spatial heterogeneity in metabolism.

High correlation between GPP and ER may suggest that autotrophs, as opposed to heterotrophs, are the primary contributors to these aspects of river metabolism (Huryn et al., 2014). We therefore expect that light would be the primary driver of metabolic heterogeneity given prior research on the role of light in controlling GPP in streams (Mulholland et al., 2001; Bernot et al., 2010). However, variance in metabolic rate estimates was similar when comparing the spatially explicit two-station means and standard deviations for the 2015 within-reach study (Table 1) to the single-station means by sites for the 2007 among streams study (Table 3). This occurred even though light was much more variable for the more broadly distributed streams. In addition, proxies for light availability (canopy, turbidity, and depth) had the opposite of expected relationship with GPP.

An important aspect of examining spatial heterogeneity in stream metabolism is checking for heterogeneity in dissolved O_2 values along the studied reach (Hondzo et al., 2013; Demars et al., 2015). This allows for identification of inflows that may be delivering low-oxygen water to the stream, resulting in an overestimation of ER (Demars et al., 2011). High statistical correlation of O_2 values measured at various points on the Kansas River suggest that inflows of deoxygenated water do not affect our metabolism estimates (Hall & Tank, 2005; McCutchan et al., 1998; McCutchan et al., 2002), as do the relatively constant estimates of discharge across our numerous transects of depth and velocity.

Prior research on a small nearby stream (Siders et al., 2017) documented sharp spatial segregation in diurnal O_2 signals (thalweg compared to the bottom of pools or side pools). These conditions would be expected to lead to lack of spatial correlation when time is not corrected for. If there were hotspots of metabolic activity upstream from a station that were highly influential on downstream O_2, then we would expect high correlation upstream stations to emerge with time-correction. We saw a strong spatial autocorrelation of O_2 with no time correction, indicating that all stations are reacting simultaneously to abiotic drivers and that nearby stations (those within the 80% zone of influence calculated from aeration) behave in very similar ways.

In contrast, the upstream weighting of two-station estimates compared to the lowermost one-station estimate also informs scales of inference and suggests that the two-station method detects smaller-scale heterogeneity. However, this concept is somewhat at odds with the idea that distance (travel time) weighting of O_2 for correlation becomes consistently weaker

over longer distances. Even more fine-scale estimates of metabolism could help understand this discrepancy. Biases inherent in the two-station estimates could lead us to conclude heterogeneity at this scale occurred falsely (see Demars et al., 2011, 2015). Finer scale methods may resolve this issue.

Models from Dodds et al. (2013) of metabolism for the Mississippi River showed that during certain times of the year there were distinct diurnal swings in O_2 that could be related to light as expected with GPP. This occurred even though the upstream zone of influence was calculated to be 500–800 km upstream. Given the median estimates of velocity of 1.2 m s^{-1} from the Dodds et al. (2013) paper, the travel time for the zone of influence would be 4.8–7.7 days. If the average travel time for a parcel of water was even half of that rate, the diurnal O_2 signal should be completely obliterated. The diurnal swings must come from relatively local processes that are more influential on O_2 concentrations and with substantially shorter travel times to the point of sampling. These data agree with our observations that contiguous two-station estimates can be quite heterogeneous, and that O_2 concentrations corrected for travel time do not correlate well with each other.

Conclusion

Our data provide some support for the idea of functional processing zones for river metabolism as presented in the Riverine Ecosystem Synthesis (Thorp et al., 2006) along reaches of several hundreds of meters in the Kansas River. As GPP can significantly influence food webs, even in systems with relatively restricted carbon inputs from GPP (Brett et al., 2017), future research is required to link metabolic heterogeneity with food web heterogeneity. We found metabolic heterogeneity both among tributaries across the Kansas River watershed and within a reach of the Kansas River itself. Local heterogeneity in metabolism is not confined to larger flowing waters in this system. For example, Siders et al. (2017) documented considerable heterogeneity in a small stream near our 20-km reach on the Kansas River.

The ability to detect heterogeneity is directly influenced by the method chosen to measure metabolism, consistent with Reichert et al. (2009). Most previous research on river metabolism is based on measurements at a single location, but the observed spatial variability within the Kansas River suggests that collecting data at multiple locations along the river may be required to make realistic estimates of metabolism. This would be consistent with the recommendation of Demars et al. (2015) to average results of several O_2 probes arrayed along a stream. Our data further suggest that such averaging should not occur with corrections for travel times between stations. Our two-station results indicate that there were hotspots of metabolic activity at scales smaller than those integrated by single-station approaches. Estimates of GPP, ER, and aeration based on diurnal O_2 dynamics verified that single-station methods average across considerable heterogeneity in the system. We demonstrate that there are some undefined processes that lead to O_2 dynamics in flowing waters, such as time lags in O_2 peaks, which cannot be attributed to aeration.

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