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PRIMARY RESEARCH PAPER

Centimeter-scale stream substratum heterogeneity and metabolic rates

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Abstract Spatial heterogeneity of substrata in streams may influence dissolved oxygen (O_2) transport and nutrient forms. We studied the relationship between scales of substratum heterogeneity and O_2. Heterogeneous systems could have greater respiration rates as a result of increased interfacial surfaces in the biogeochemically active areas between oxic and anoxic zones. We used grids with twelve 7 × 3.5 cm cells; half the cells were filled with sand and the other half with gravel to quantify the effect of centimeter-scale heterogeneity on respiration. The sand and gravel cells were arranged within the grids to give low, medium, and high heterogeneity. Grids were incubated for 15–17 days in a prairie stream, and then whole grid respiration was analyzed in closed recirculating chambers. Depth to anoxia and substratum metabolism were calculated from O_2 microelectrode profiles measured in each cell of the grid and compared with data from natural stream transects from agricultural, urban, and prairie land use types. Shannon–Weaver (H') diversity and "probability of change" indices were also used to compare heterogeneity of the grids to the natural stream transects. No significant differences were found among grid heterogeneity levels for respiration rate, but the anoxic interface was deeper in the gravel of higher heterogeneity grids, probably due to greater transport rates of O_2 in the coarse-grained substratum. The H' and probability of change indices indicated that the grids had levels of heterogeneity within the range of real streams. Grid depth to anoxia and substratum metabolism rates were similar to those found in streams, though less variable. In streams, H' and probability of change values showed a slight difference among land use types, with some urban and agricultural sites displaying very low heterogeneity.

Keywords Stream · Substratum · O_2 microelectrodes · Nutrients · Dissolved oxygen

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Introduction

Spatial and temporal variation of dissolved oxygen (O_2) concentrations alters nutrient form and transformation rates in streams, but how small-scale variation influences whole-stream processes is not well understood. Kemp & Dodds (2001a) showed that centimeter-scale spatial and temporal variation of O_2 concentrations and nitrification rates occur by both substratum type and season in a prairie stream. Dent

et al. (2001) compared variation in nutrient concentrations across spatial scales ranging from 1 to 25 m and found the greatest variation in nitrate concentration at the smallest (1 m) scale in a Sonoran Desert stream. These studies focused on heterogeneity at spatial scales varying from reach to riffle/pool sequences.

In an effort to quantify biogeochemical implications of small-scale spatial heterogeneity, Jacinthe et al. (1998) used mesocosms (15 cm diameter × 40 cm long) to investigate the influence of patches of high microbial activity on groundwater nitrate removal. They found that random sampling of small amounts of stream substrata can miss patches or "hotspots" of organic matter and associated microbial activity. Mesocosms with patches of high microbial activity had greater groundwater nitrate removal than mesocosms without the patches. Thus, organic matter "hotspots" proved important to whole-system processes because they supported rates of microbial activity sufficient to consume enough O_2 to allow anaerobic processes such as denitrification to occur. Similarly, leaves in streams can be "hotspots" for respiration (Fuss & Smock, 1996).

Organic matter patches with high microbial activity often occur in fine-grained substrata. Substratum interstitial space can control the rate of O_2 transport (Dodds et al. 1996a), and spatial heterogeneity of nutrient and O_2 concentrations is partially dependent on substratum type and subsequently substratum heterogeneity. Microelectrode measurements of O_2 in the substrata of Kings Creek, a prairie stream in Kansas, showed concentrations that varied considerably among substrata within 10–20 cm (horizontal distance) of each other (Kemp & Dodds, 2001a). Comparable results have been found in other prairie streams in the area (Wilson, 2005). Many other studies using benthic cores analyzed in the laboratory (e.g., Revsbech et al., 1981; Revsbech & Jørgensen, 1986; Dodds, 1991) have shown that O_2 concentrations in substrata vary over spatial scales of <1 mm and that such small-scale variation is common.

Our study focused on the in situ small-scale heterogeneity of substratum types and the effects of different levels of heterogeneity on metabolic rates. Our working hypothesis was that highly heterogeneous systems would have greater rates of respiration due to increased interfacial area between oxic and anoxic zones. We hypothesize this because steep redox gradients lead to high biogeochemical activity (Sheibley et al., 2003). We suggest that greater rates of biogeochemical activity will lead to higher aerobic respiration rates concentrated at interfaces between oxic and anoxic zones. Anoxic zones can serve as sources of dissolved organic compounds as well as reduced compounds such as NH_4^+, S^{2-}, Fe^{2+} that are oxidized. We tested our working hypothesis with a manipulative experiment in a stream where we altered the patch size of fine and coarse substrata, and by sampling six streams for microscale O_2 patterns in fine and coarse substrata. O_2 flux and depth to anoxic conditions were used as measures of relative metabolic rates. We then compared those measurements and estimates of whole stream metabolism to the results from the manipulative experiment.

Methods

Site description

Manipulative experiments were conducted on Kings Creek, which is entirely encompassed by Konza Prairie Biological Station (KPBS), ~10 km southeast of Manhattan, Kansas in the Flint Hills region of the Great Plains. KPBS is tallgrass prairie with streams characterized by low NO_3^- and NH_4^+ concentrations and little riparian cover in upstream reaches (Gray & Dodds, 1998; Gray et al., 1998; Dodds et al., 2000; Kemp & Dodds, 2001b; Dodds et al., 2004).

Additional streams were sampled on Konza and elsewhere to test a range of streams for heterogeneity effects with microelectrode and whole stream metabolism measures. These streams encompassed a nutrient gradient from upper to lower Kings Creek (Kemp & Dodds, 2001b) and agriculturally or urban influenced streams (O'Brien et al., 2007). One stream was a highly modified concrete channel receiving water from a city storm sewer system and was ultimately removed from the statistical analyses.

Small-scale heterogeneity grids

Sampling grids were created from plastic containers, partitioned with 6-mm hardware cloth (for stability) and 1-mm screen. Heterogeneity in the plastic containers was altered using equal amounts, by area, of sand and small gravel sediments arranged from small to large cell sizes to create a gradient. Each grid

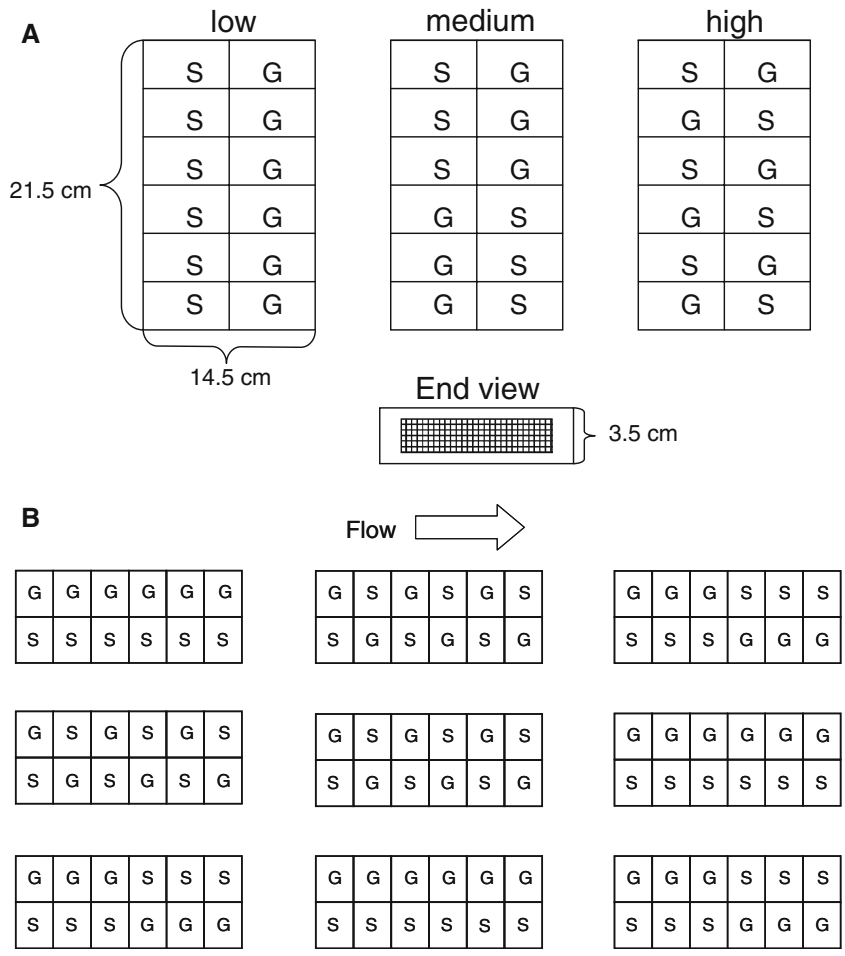

Fig. 1 **A** Organization of substratum into low, medium, and high heterogeneity levels. **B** Arrangement of grid replicates in the stream. *G* gravel, *S* sand

(14.5 cm W × 21.5 cm L × 3.5 cm D), with one of three levels of substratum heterogeneity (low, medium, and high), had a 2 × 10 cm opening covered with 1-mm screen at each end to allow for water flow-through and was divided into 12 cells measuring ~7 cm × ~3.5 cm (Fig. 1A). Each cell of the grid was filled in situ with sand (<1 mm) or small gravel (>4 mm) from the stream. Substrata were removed from the stream bottom, well mixed, and sieved to separate sand and gravel. Heterogeneity levels were assigned to grids arranged in rows of 3, with 3 replicates/level (Fig. 1B). Grids were placed in the stream so that the tops were in level with the surrounding large gravel substratum in a run at a mean depth of 0.26 m and a mean water velocity of 0.05 m/s. Nine grids were incubated in lower Kings Creek for 15–17 days. This was a sufficient time to develop a substantial biofilm following the initial disturbance of the substrata (Murdock & Dodds, 2007).

Dissolved oxygen microprofiles

Cathode-type O_2 microelectrodes (Revsbech & Jørgensen, 1986) were used to measure subsurface O_2 concentrations in each cell of the heterogeneity grids using a method similar to Kemp & Dodds (2001a). Electrodes were glass coated with a gold-plated platinum wire tip ~10 μm in diameter. They were not sensitive to water velocity and therefore were suitable for use in the benthic substrata of lotic waters. The sensing tip of each microelectrode was placed inside a 16-mm gauge hypodermic needle and held in place with epoxy to avoid breakage during field measurements. O_2 microelectrode profiles were done in situ, during daylight hours, on each grid cell ($N = 108$) on day 14 of the experiment.

Measurements were taken in each grid vertically using a micromanipulator every 1 mm beginning 2 mm above the substratum surface until anoxic

conditions, the bottom of the grids, or a rock (in stream transects) were reached, or to a depth of 20 mm. Anoxia was defined as <0.1 mg/l, which is the detection limit of the O_2 microelectrodes. Calibration was conducted as in Kemp & Dodds (2001a) by using open water and anoxic mud at the beginning of each grid. This calibration was checked repeatedly during microelectrode use by measuring water column O_2 and comparing it to routine water column measurements with a conventional YSI O_2 meter (Yellow Springs Instruments, Yellow Springs, Ohio, USA).

Microelectrodes were also used to measure subsurface O_2 concentrations during daylight hours along transects in six streams located in and around Manhattan, KS, or on KPBS (Table 1). These measurements were done in the same way as in the experimental grids. Lateral transects were established 5–20 m apart along a 50–70 m stream reach, depending on benthic substratum diversity. Points for O_2 gradient measurements were spaced 10 cm apart with gradients measured at each transect point across the width of the stream. About 50–100 gradient measurements were made per stream. Calibration was conducted as described above, performed at the beginning of each transect, and reassessed several times in each transect by measuring water column O_2.

Data from each O_2 profile were analyzed for O_2 diffusion flux using Fick's first law of diffusion:

$$J = \mathrm{DC} * \Delta C/\Delta X \quad (1)$$

where DC = diffusion coefficient (5.18×10^{-6} $m^2\ h^{-1}$; Glud et al., 1992), ΔC = change in O_2 concentration, and ΔX = change in distance. Calculations were based on measurements taken every 1 mm above the substrata until a constant water column value was obtained (the slope of the change in O_2 was used to indicate O_2 flux). A positive flux indicated net photosynthetic production, and negative flux indicated net respiration. A substratum specific average of O_2 flux was taken for each grid to estimate metabolism by substratum type at each heterogeneity level. We recognize that transport in the water column could cause us to assume the DC is less than it really is. However, the trend of O_2 concentration immediately above the bottom of the streams and the grids indicates that molecular diffusion was predominating (i.e., turbulent transport into the sediment would likely destroy concentration gradients).

A separate indicator of metabolic O_2 demand, depth to anoxia, was indirectly related to rate of metabolism and did not require knowing the DC or porosity. When depth to anoxia was not reached within 20 mm, it was estimated using linear regression. Slightly greater r^2 values for some concentration gradients could be attained using an exponential model, but this model implies that anoxia is never reached and therefore was not appropriate for our study. Substratum-specific and heterogeneity-level averages were calculated from these estimates for experimental treatments. Substratum (all data for each substrata type) and reach (all data for each stream regardless of substrata type) averages were calculated for the stream transect data.

Table 1 Site description and location of streams used for lateral transect measurement with O_2 microelectrodes

Site	Date sampled	Stream type	Site description	Location
Natalie's Creek	May 2004	Agricultural	Surrounded by lightly grazed pasture, typical of Flint Hills streams	39°13.716′ N 96°39.536′ W
Lower Kings Creek	August 2004	Agricultural	Surrounded by row crop with undisturbed prairie upstream	39°06.343′ N 96°36.344′ W
Maintenance Creek	May 2004	Urban	Shaded stream in forested area	39°12.396′ N 96°38.134′ W
Wal Mart Ditch	May 2004	Urban	Concrete raceway surrounded by roads and businesses	39°11.062′ N 96°33.491′ W
Kings Creek watershed N1B	July 2004	Prairie	Low order reach in protected prairie preserve, shaded, and grazed by bison	39°05.183′ N 96°34.591′ W
Kings Creek downstream from USGS Gage	July 2004	Prairie	Mid-order reach in protected prairie preserve, shaded, and ungrazed	39°06.132′ N 96°35.665′ W

Whole grid chamber metabolism estimates

On days 15–17, following microelectrode measurements, three grids were removed and transported back to the laboratory. Each grid was immediately placed in one of three recirculating chambers filled with stream water collected at the time of grid removal from the stream. Recirculating chambers were housed in a controlled environment chamber with a mean water temperature of 26°C and a mean light intensity of 11.75 mol quanta m^{-2} day^{-1} with illumination provided by mixed fluorescent and halogen sources. Chambers were made of UV-transparent acrylic with a volume of 24.5 l. More detailed description of the chambers can be found in Dodds & Brock (1998). Open channel chamber water velocity was calibrated the first day at 0.05 m/s and maintained throughout the experiment. The chambers were sealed and all air bubbles removed before the start of data collection. YSI O_2 probes were sealed into a hole in the lid of each chamber after air calibration and connected to a data logger (Campbell 21x) that recorded 5 s averages of O_2 and temperature every 5 min. The experiment ran for 2 h in the light and 2 h in the dark and was repeated with the remaining grids for the next two consecutive days. Oxygen flux from the recirculating chambers was determined by the rate of change of O_2 in the light. Respiration (R) was determined by the rate of change of O_2 in the dark. Gross primary production (GPP) was calculated as net O_2 flux + R.

Whole-stream metabolism estimates

Oxygen flux for each of the six stream reaches was measured using the upstream–downstream diurnal O_2 change technique (Marzolf et al., 1994, with modifications suggested by Young & Huryn (1998). These metabolism and aeration measurements were made at baseflow, and within 1 week of the instream microprofiles of O_2. Measurements of O_2 and temperature were made at 5-min intervals over a 48-h period using logging O_2 probes (YSI model 600XLM or 6920). Probes were calibrated in the laboratory within 12 h prior to deployment. Both probes were placed side-by-side in the reach for the first 15 min to 1 h of logging time to correct for differences in recorded O_2 measurements between probes; this procedure was repeated at the end of the 48-h logging period.

Reaeration rate determined immediately before or after whole-stream metabolism was measured from the decline in dissolved propane or acetylene concentration during a steady-state injection (at plateau) coincident with a conservative tracer (NaBr) release to account for dilution caused by groundwater inflow (Mulholland et al., 2001). The reaeration rate was converted to O_2 using a factor of 1.39 for propane (Rathbun et al., 1978) and 0.867 for acetylene (unpublished data). In 2003, duplicate gas samples were taken at six to seven sites along the reach. In 2004, four to five replicates were taken at three locations along each reach to better account for variability among samples at each individual location. Upstream (background) samples were taken first and subsequent samples were taken from downstream to upstream to minimize possible contamination. Samples were kept at 4°C until analysis. Analysis was completed within 3 days on a Shimadzu gas chromatograph (model GC-14A) equipped with a flame ionization detector.

Gross primary productivity was obtained by summing O_2 production and calculated R (net ecosystem respiration) after correction for aeration. Whole-stream O_2 production was determined at 5-min intervals from the change of O_2 between stations corrected for aeration as determined by the propane or acetylene injection. Respiration was obtained from net O_2 exchange rate corrected for aeration for night, and daily R was calculated by summing net O_2 nighttime exchange rate.

Statistical analyses and indices of spatial heterogeneity

For the grid data, Kendall tau correlation analyses ($\alpha = 0.05$) were used to test for differences in O_2 production, R, and GPP as correlated with heterogeneity levels at the whole-grid level. Respiration and O_2 production data were cube-root transformed to establish normal distributions while maintaining positive or negative net metabolism rates. For the microscale grid data, ANCOVA, with heterogeneity as the continuous covariate and substrata as the categorical predictor ($\alpha = 0.05$), was used to test for differences in depth to anoxia and O_2 production between sand and gravel as influenced by heterogeneity.

The Shannon–Weaver (H') index (Shannon & Weaver, 1963) and a "probability of change index" were also used to assess the differences in substratum heterogeneity among stream types. These indices were calculated for the same six streams on which O_2 microelectrode transect measurements were made. The probability of change index was calculated by counting how frequently substratum type changed when moving from point to point across each transect (with 10 cm between points for the stream measurements). The Shannon–Weaver index was calculated by the relative proportion of each type of substrata encountered in a stream. One-way ANOVA ($\alpha = 0.05$) was used to test for differences in these indices among stream types. Linear regression was used to relate H' and probability of change values to depth to anoxia in sand and gravel, microelectrode-measured O_2 flux and whole-stream O_2 production, GPP and R in the natural streams.

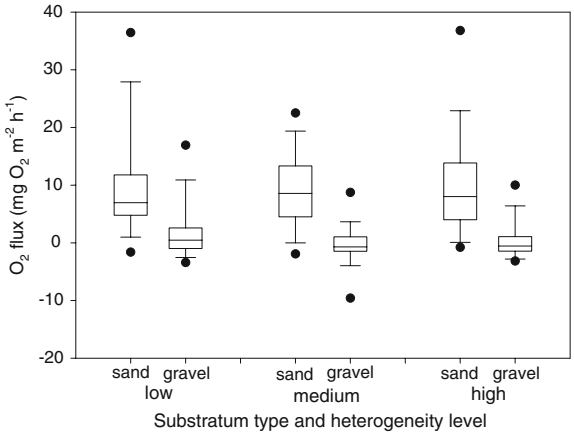

Fig. 2 O_2 flux as measured with microelectrodes across heterogeneity levels and substratum types from the grid experiment. The *line* shown in the *box* is the median; the *top* and *bottom* of the *box* represents the 25th and 75th percentiles; the *whiskers* represent the 10th and 90th percentiles; and any points beyond these percentiles are shown as *solid circles*

Results

There was no significant difference in R (Kendall tau correlation, $P = 0.18$) or GPP ($P = 0.46$, Table 2) among heterogeneity levels at the whole-grid level, but O_2 production was greater as heterogeneity increased ($P = 0.02$). Daytime net O_2 flux as measured with microelectrode profiles within cells of the grids (Fig. 2) was not significantly influenced by heterogeneity level ($P = 0.50$) but was greater for sand than for gravel ($P = 0.00001$). Greater depth to anoxia was measured within each grid cell with the microelectrode (Fig. 3) at high heterogeneity ($P = 0.0006$). Depth to anoxia increased in gravel with increasing substratum heterogeneity so that the greatest depth to anoxia was found in the gravel of high heterogeneity grids.

Natural stream transect gravel and sand O_2 flux rates (Fig. 4A) and depth to anoxia (Fig. 4B) as measured with microelectrodes were not significantly different across streams of various land use types. Values of H' and probability of change indices were not significantly different among stream types (Fig. 5).

A weak relationship between probability of change values and whole-stream R was indentified. More interesting, however, is that the slope of the relationship changed sign depending on the inclusion or exclusion of concrete-channel Wal Mart Ditch data. With Wal Mart Ditch data included (Fig. 6A), R

Table 2 Whole-grid net O_2 flux in the dark, in the light, and gross primary production under lighted conditions for substratum heterogeneity grids

Heterogeneity level	Dark (mg O_2 l^{-1} h^{-1})	Light (mg O_2 l^{-1} h^{-1})	Gross primary production (mg O_2 l^{-1} h^{-1})
Low	−0.27	−0.13	0.14
Low	−1.27	0.00	1.27
Low	−0.14	−0.16	0.00
Medium	−0.11	0.04	0.15
Medium	−0.15	0.16	0.32
Medium	−0.42	−0.08	0.34
High	−0.23	0.13	0.36
High	−0.16	0.08	0.24
High	0.00	0.08	0.08

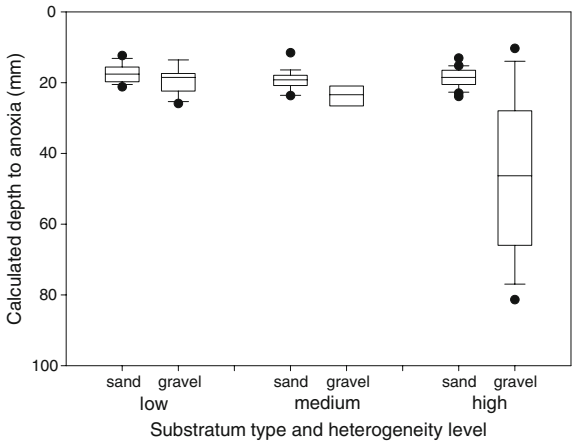

Fig. 3 Calculated depth to anoxia by heterogeneity level and substratum type from grid experiment. The *line* shown in the *box* is the median; the *top* and *bottom* of the *box* represents the 25th and 75th percentiles; the *whiskers* represent the 10th and 90th percentiles; and any points beyond these percentiles are shown as *solid circles*. *Whiskers* are not shown if there were not enough data to calculate them

decreased with increasing probability of change. Without Wal Mart Ditch data (Fig. 6B), there was a stronger, positive relationship between probability of change and whole-stream R. No significant relationships between H' and probability of change indices and depth to anoxia in sand or gravel, and microelectrode primary production were indicated.

Discussion

While increased levels of heterogeneity had no statistically significant whole-grid effect on respiration rates, there were significant differences among the substrata of the grids with respect to depth to anoxia. Sand substratum showed no significant difference in depth to anoxia among heterogeneity levels while gravel substratum did. The significant difference for gravel could indicate that fine-grained sand had lower inward transport rates of O_2 than large-grained gravel, as shown by the shallower depth to anoxia in sand, regardless of heterogeneity level. Alternatively, respiratory activity could have been greater in sand than in gravel, but this was not true in similar experiments done on Konza Prairie in groundwater mesocosms (Dodds et al. 1996b); so, we suggest variations in transport rates are the most likely explanation for the differences in depth to anoxia in the grids.

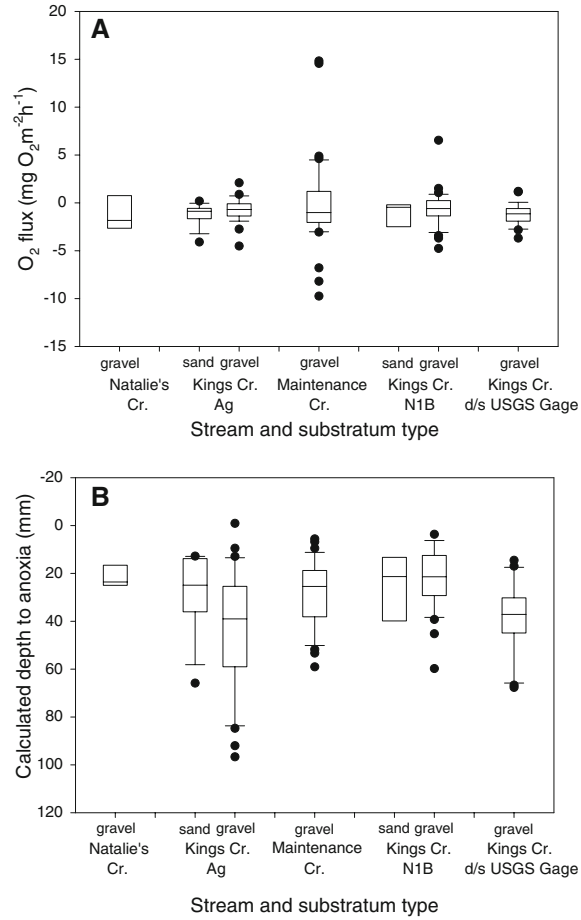

Fig. 4 **A** O_2 flux (as measured with microelectrodes) and **B** calculated depth to anoxia by stream and substratum type from natural stream transects. Sand substratum was not found in all streams. Neither sand nor gravel was found in Wal Mart Ditch. The *line* shown in the *box* is the median; the *top* and *bottom* of the box represents the 25th and 75th percentiles; the *whiskers* represent the 10th and 90th percentiles; and any points beyond these percentiles are shown as *solid circles*. *Whiskers* are not shown if there were not enough data to calculate them

As heterogeneity level increased in the grids, depth to anoxia became deeper and more variable in gravel. At the most heterogeneous level, depth to anoxia in gravel had greater variation and a deeper depth than gravel in grids at the least heterogeneous level. This variation was not present in sand; however, sand had greater O_2 flux rates than gravel at all heterogeneity levels. At greater heterogeneity levels, the close proximity of the two substrata types could have allowed O_2 generated at the surface of the sand substrata to be transported to the gravel, resulting in deeper depth to anoxia in gravel at higher heterogeneity

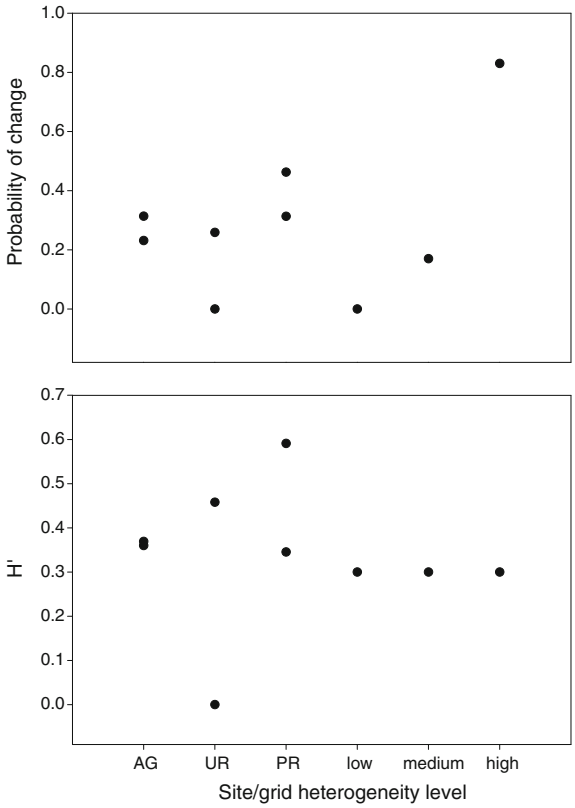

Fig. 5 Shannon–Weaver (H') and probability of change index values as a function of stream type for each of the six natural streams and the three levels of grid heterogeneity

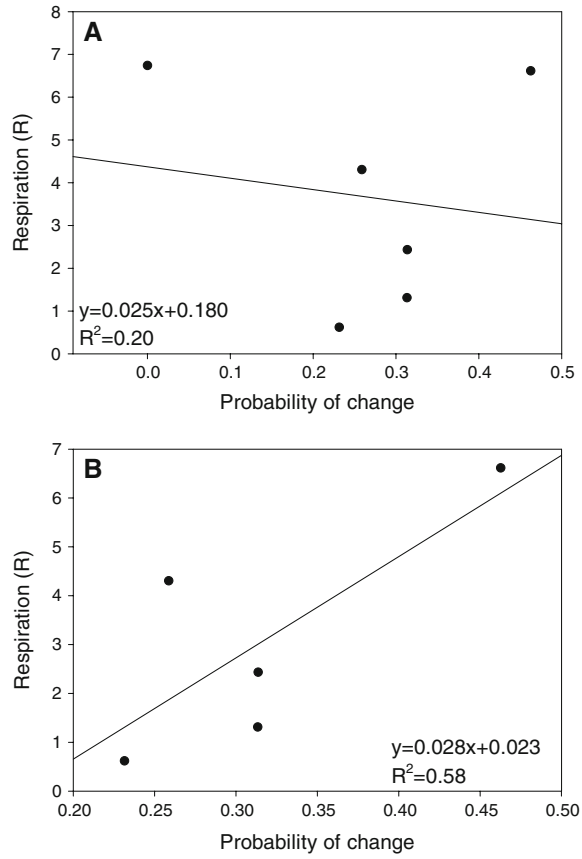

Fig. 6 Probability of change and whole-stream R with Wal Mart Ditch data included (**A**) and excluded (**B**). The relationship was similar for H' and is not presented here

levels. Greater O_2 penetration could have allowed larger interstitial spaces in gravel, whereas in the sand, O_2 could not infiltrate as deeply, resulting in a consistently shallower depth to anoxia. Contact time of water with subsurface sediment can be negatively correlated with O_2 water content (Findlay, 1995).

Natural stream O_2 flux rates were similar to grid O_2 flux rates, in that they showed little variation between sand and gravel substratum types, but natural stream substrata had lower O_2 flux rates overall. Depth to anoxia in natural stream substrata was generally deeper in gravel than sand, but there was more variation in values for both sand and gravel in the natural streams than in the grids. Depth to anoxia values were similar between the natural stream transects and the grids.

These data on microscale O_2 flux surveys and depth to anoxia surveys are among the first ever published employing large numbers of in situ measurements for streams. Most measurements for freshwaters have been made on artificial substrata or cores removed from the laboratory (e.g., Carlton & Wetzel, 1987; Gallon et al., 2008). The only measurement surveys we are aware of in situ for streams were made in pristine streams (Kemp & Dodds, 2001a) and provided similar results, though less detail.

H' and the probability of change indices suggest that streams in different land use types in this study do not differ significantly with regard to substratum heterogeneity. Prior research has demonstrated that human impact on agricultural and urban watersheds can influence substratum diversity (Stevens & Cummins, 1999; Paul & Meyer, 2001). One of the urban streams, Wal Mart Ditch, is a concrete lined drainage channel with virtually no heterogeneity ($H' = 0$). In contrast, our research segment of Maintenance Creek ($H' = 0.46$) drains an area with suburban residences and a golf course, but the studied reach flows through a geologically heterogeneous area with intact natural riparian vegetation. Our results (e.g., Natalie's Creek and Wal

Mart Ditch H' and probability of change values) do show less substratum diversity in some agricultural and urban than prairie streams, but the differences are not significant by land use classification.

Scaling up from our small-scale grids to whole-stream processes proved difficult. There was a positive relationship (albeit with weak statistical significance) between probability of change and whole-stream respiration, supporting our hypothesis that increased heterogeneity leads to increased R rates. However, that relationship only held true without Wal Mart Ditch data. Wal Mart Ditch is an extreme example of an urban stream: a drainage ditch with constant inputs of nutrient-rich water from the storm sewer system, and high light availability, is essentially a big "hotspot" of activity. Given that we needed to remove it from the analysis, we only cautiously linked metabolism to heterogeneity. Depth of metabolic activity has previously been linked to whole-stream metabolism (Atkinson et al., 2008).

Small-scale substratum heterogeneity may influence stream processes at larger scales. Small-scale heterogeneity grids showed that increased heterogeneity of fine and coarse-grained substrata resulted in a deeper depth to anoxia in the coarse-grained substratum, likely due to faster transport rate of O_2 in gravel than in sand. H' and probability of change values were similar between the grids and natural stream substratum heterogeneity.

Few surveys of microscale O_2 patterns determined in situ in streams have been published. Our results suggest that substratum heterogeneity may control O_2 heterogeneity in an experimental setting. In natural streams, many other factors may influence O_2 heterogeneity. Further research is required to link small-scale heterogeneity to metabolism and ultimately trophic state of streams (Dodds, 2006).

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