

Whole-stream metabolism in two montane streams: Contribution of the hyporheic zone

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Abstract

We used whole-stream and benthic chamber methods to measure rates of metabolism and determine the contribution of the hyporheic zone to ecosystem respiration (R) in two streams with differing surface–subsurface exchange characteristics, Rio Calaveras and Gallina Creek, New Mexico. We used the difference between whole-stream and benthic R to calculate the rate of hyporheic zone R and coupled this estimate to an independent measure of hyporheic sediment R to estimate the cross-sectional area of the hyporheic zone (A_H) for two reaches from each stream. Conservative tracer injections and solute transport modeling were used to characterize surface–subsurface hydrologic exchange by determining values of the cross-sectional area of the transient storage zone (A_s). The hyporheic zone contributed a substantial proportion of whole-stream R in all four study reaches, ranging from 40 to 93%. Whole-stream R , hyporheic R , and percent contribution of hyporheic R all increased as transient storage increased, with whole-stream and hyporheic R exhibiting significant relationships with A_s . All three measures of respiration and values of A_H were much greater for both reaches of the stream with greater surface–subsurface exchange. A_H is valuable for cross-site comparisons because it accounts for differences in rates of both benthic and hyporheic sediment R and can be used to predict the importance of the hyporheic zone to other stream ecosystem processes.

Aquatic ecologists are increasingly aware of the importance of interactions between surface water and groundwater to the functioning of aquatic ecosystems (Boulton et al. 1998; Winter et al. 1998; Jones and Mulholland 2000). The region of mixing between groundwater and stream water (i.e., the hyporheic zone, sensu Orghidan 1959; Triska et al. 1989b) influences ecosystem functioning because its sediments contain metabolically active microbial assemblages (Grimm and Fisher 1984; Pusch and Schwoerbel 1994; Jones et al. 1995b; Naegeli and Uehlinger 1997). Several recent studies have focused on the role of the hyporheic zone in the retention (Speaker et al. 1984; Triska et al. 1989b, 1990; Hendricks and White 1991; Triska et al. 1993; Valett et al. 1996) and the transformation (Duff and Triska 1990; Jones et al. 1995a; Holmes et al. 1996) of biologically important solutes. Far less work has focused on the influence of the hyporheic zone on whole ecosystem energetics (but see

Grimm and Fisher 1984; Mulholland et al. 1997; Naegeli and Uehlinger 1997).

In conceptual models presented by Findlay (1995) and Valett et al. (1996), the contribution of the hyporheic zone to stream ecosystem functioning depends on the types and rates of metabolic processes occurring in the hyporheic zone, the proportion of stream discharge routing through the hyporheic zone, and its impact on hydrologic residence time. As rates of metabolism in the hyporheic zone and the volume of subsurface sediment actively exchanging water with the stream channel both increase, the importance of the hyporheic zone to surface processes increases.

Studies investigating the relationship between surface–subsurface hydrologic exchange and stream ecosystem functioning have provided indirect evidence of the importance of the hyporheic zone. Valett et al. (1996) found a strong relationship between nitrate-nitrogen uptake length and exchange for three streams in catchments of differing lithology. Minshall et al. (2000) found that retention of fine particulate organic matter was correlated with hydrologic exchange across six sites of varying size and discharge. Ecosystem respiration (R) was greater in the stream with greater surface–subsurface exchange in a comparison of two Appalachian streams with similar hydrological and chemical characteristics (Mulholland et al. 1997). None of these studies quantified the contribution of the hyporheic zone, however. In contrast, Grimm and Fisher (1984) and Naegeli and Uehlinger (1997) quantified the contribution of the hyporheic zone to whole-stream R , but neither study included quantitative estimates of surface–subsurface exchange.

Coupled measures of metabolism and exchange provide links between ecosystem processes and hydrology that allow for comparisons among differing stream ecosystems. However, understanding the contribution of the hyporheic zone to stream ecosystem processes requires not only quantitative measures of hydrologic exchange, but also process measurements made both at the whole-stream level and at scales that will allow distinction between the surface and hyporheic

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zone. In this research, we address how differences in surface–subsurface exchange influence stream ecosystem metabolism with a focus on the relative contribution of the hyporheic zone to ecosystem R . Our approach is to use the difference between whole-stream and benthic R to determine the rate of R in the hyporheic zone. We then couple this estimate to an additional and independent measure of hyporheic R to estimate the size of the hyporheic zone. Further, we tie rates of metabolic processes and their distribution between surface and hyporheic subsystems to ecosystem hydrology by applying solute transport models to quantify features of surface–hyporheic exchange.

Study sites

The study was conducted in two headwater streams of north-central New Mexico, under baseflow conditions during the summers of 1996 and 1997. Previous work has shown that these streams differ greatly in the extent of groundwater–surface water exchange, with little exchange at Rio Calaveras and generally greater exchange at Gallina Creek (Valett et al. 1996; Morrice et al. 1997).

Rio Calaveras is located in the Jemez Mountains at an elevation of 2475 m, approximately 63 km west of Los Alamos, New Mexico. A 110 m reach of Rio Calaveras was chosen for study in 1996, and in 1997 the experimental reach was shortened to include only the lower half of the reach in order to decrease water travel time. The two lengths of the stream are referred to as the long and short reaches, respectively. Gallina Creek is in the Sangre de Cristo Mountains at an elevation of 2524 m, approximately 31 km northeast of Taos, New Mexico. The study reach used in 1997 was 400 m upstream of that used in 1996. The two reaches are referred to as the lower and upper reaches, respectively.

Methods

Solute injections—Solute injections were used to quantify aspects of surface hydrology and surface–subsurface water interactions within each stream reach. For a detailed description of these techniques, see Stream Solute Workshop (1990). We injected a conservative tracer (Br^- or Cl^-) and monitored solute concentrations at a station downstream using in-stream ion-specific electrodes (ISE, Orion) or an electrical conductivity meter (YSI or VWR). Solute was injected for 1 to 6 h, depending on the time required to generate complete mixing throughout the reach. Concentrations of the conservative tracer were measured directly on water samples by ion-chromatography (Dionex DX-100) or were determined through regression analysis relating results from the ISE probes or electrical conductivity to selected water samples analyzed by ion-chromatography. Solute injections for modeling were conducted once at each reach in conjunction with measures of whole-stream metabolism, generally in early to midafternoon.

Background-corrected plateau concentrations of conservative tracers were used to calculate stream discharge (Q) for each solute injection (Triska et al. 1989a; Gordon et al. 1992). Replicate stream water samples were taken at an up-

stream station (far enough below the solute addition to allow for complete mixing) and the downstream station to quantify lateral inflow (Stream Solute Workshop 1990). In general, Q was nearly constant along each of the chosen stream reaches and mean values of Q at the upstream and downstream stations were used in solute modeling and metabolism calculations. For the upper reach of Gallina Creek, Q was calculated as the average of four longitudinally distributed sampling points. A single tracer injection was conducted at each site in 1996, but multiple injections were performed in 1997 to resolve temporal changes in Q for more accurate whole-stream metabolism calculations. Nominal travel time (T_N) was calculated for each reach as the time required to reach half plateau concentration at the downstream station. Reported values of water velocity were calculated as nominal travel time divided by reach length.

Solute curves (downstream concentration vs. time) were used to visually fit model outputs from a one-dimensional transport with inflow and storage model (OTIS, Runkel 1998), a mathematical simulation based on the transient storage model presented by Bencala and Walters (1983). Surface–subsurface water exchange can be characterized using transient storage models that employ a hypothetical, non-advective storage zone to account for flow paths moving much slower than the advective velocity of the stream channel (Bencala and Walters 1983; Stream Solute Workshop 1990; D'Angelo et al. 1993; Harvey et al. 1996; Morrice et al. 1997; Runkel 1998). The ratio between the cross-sectional area of this storage zone (A_s) and of the above-ground stream channel (A) normalizes the extent of transient storage to stream size and has served as a useful comparative measure of hyporheic zone size (D'Angelo et al. 1993; Valett et al. 1996; Morrice et al. 1997; Mulholland et al. 1997). The parameters estimated through visual fitting were stream cross-sectional area (A , m^2), storage zone cross-sectional area (A_s , m^2), dispersion (D , $\text{m}^2 \text{ s}^{-1}$), and the storage zone exchange coefficient (α , s^{-1}). Additionally, after visual best fits were obtained, parameter estimates were entered into OTIS-P (Runkel 1998) for statistical determination of parameter values using nonlinear least squares analysis. The parameter estimates reported are those obtained from OTIS-P. Damkohler numbers ($Da_l = [\alpha \times \text{reach length} \times (1 + A_s/A)]/\text{velocity}$, Bahr and Rubin 1987) were calculated and evaluated after the experiments to assess the reliability of parameter estimates (Wagner and Harvey 1997).

Several hydrologic descriptors were calculated using output from solute modeling results. These variables included hydraulic residence times in the stream ($T_{\text{str}} = 1/\alpha$) and storage zone ($T_{\text{sto}} = A_s/[A \times \alpha]$); hydraulic uptake length in the stream channel ($S_{\text{hyd}} = Q/[A \times \alpha]$), a measure of the average distance a water molecule travels before entering the storage zone (Mulholland et al. 1994); and the hydrologic retention factor ($R_h = T_{\text{sto}}/S_{\text{hyd}}$), the storage zone residence time per unit of stream reach traveled (Morrice et al. 1997).

Metabolism—Whole-stream: Whole-stream metabolism was measured using a two station diel oxygen mass balance method similar to that described by Odum (1956) and modified by Marzolf et al. (1994). Dissolved oxygen (DO) concentrations were measured at both the upstream and down-

stream stations of each chosen reach for 36 h at 15-min intervals (YSI DO meters, Rio Calaveras both years, lower reach of Gallina Creek), or 5-min intervals (Orbisphere DO meters, upper reach of Gallina Creek). To account for exchange of oxygen between the stream and atmosphere, reaeration coefficients were determined from the longitudinal decrease in steady-state concentrations of a dissolved volatile tracer (propane) coinjected during the conservative tracer injections described above (*sensu* Marzolf et al. 1994, with modifications described in Young and Huryn 1998).

Upstream and downstream DO values along with Q , reach travel time, and exchange with the atmosphere were used to calculate net rates of oxygen change due to metabolism (net ecosystem production) for each 5- or 15-min time interval (Marzolf et al. 1994). Daily rate of ecosystem R was calculated as the sum of the values of net ecosystem production for all the time intervals during the night plus an estimate of daytime R for each interval during the day derived from linear regression of predawn and postdusk R values (Marzolf et al. 1994). The sum of the daytime intervals plus estimated daytime R was used to calculate gross primary production (P_G). To obtain areal metabolism rates, values were divided by the bed surface area of the reach. Bed surface area was calculated by taking the average value of wetted channel width (taken every one or two meters along each reach) multiplied by reach length.

Metabolism values from periods of rain were substituted with values from a regression of prestorm and poststorm intervals to determine the degree to which whole-stream metabolism calculations were affected. The resulting calculations using modified values were then compared to original values.

Light was measured as photosynthetically active radiation (PAR) photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (LI-COR quantum sensor). Readings were taken at 5- or 15-min intervals and values were integrated over daylight hours.

Linear regression was used to assess relationships between hyporheic R , whole-stream R , and the percentage (arcsine square root transformed) of whole-stream R contributed by hyporheic R , and transient storage as both A_i and A_i/A (proc REG, SAS release 6.12 1996). For whole-stream R , the analysis was repeated using two sites from Mulholland et al. (1997, incorporating corrections based on Marzolf et al. 1998) in addition to the four reaches from this study.

Benthic: Benthic metabolism was measured using light and dark incubations of benthic sediment in traditional recirculating chambers (*sensu* Bott et al. 1978). Plastic trays ($n =$ three or four per site) were filled with approximately the top 2 cm of benthic sediment and inserted back into the stream bed at least 1 month prior to being used in chamber metabolism measurements. In 1996, the planar area of each tray was 350 cm² and the circulating volume of each chamber was 4 liters. Truckee River model benthic chambers (Al-iquot) with a volume of 2 liters were used in 1997 with 85 cm² trays. Chambers were submerged in the stream during all incubations, and dark conditions were achieved by covering the chambers with opaque reflective material. Chambers were run for approximately 2 h in the dark followed by 2 h in the light during late afternoon. Winkler titrations

(1996) or Orion DO meters (1997) were used to measure DO concentrations every 30 or 5 min, respectively. Three chambers were run simultaneously and the resulting values were averaged to obtain a value for the reach. A single chamber at each site was run without benthic sediment in 1997. Neither chamber showed measurable change in DO concentration during light or dark incubation, and therefore water column metabolism was considered negligible.

Rates of metabolism were calculated from the slope of the linear regression of DO concentration and time, resulting in units of mg O₂ m⁻² h⁻¹. Respiration was calculated from the dark incubations and net primary production (P_N) was calculated from the light incubations. Gross primary production was calculated by assuming a constant rate for R and adding R to P_N . Respiration values were scaled to 24 h and P_G values were scaled to the total number of daylight hours to calculate P_G/R ratios. To account for the fact that rates of P_G measured in late afternoon might not be representative of rates over the entire day, levels of irradiance were taken into account in scaling light incubation rates. We assumed photosaturation occurred at 400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ for periphyton in the four study reaches. This value was chosen to result in a conservative estimate of daily P_G and was based on a review of multiple periphyton studies that found that photosaturation typically occurred between 200 to 400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Hill 1996). Mean PAR during all light chamber incubations except the lower reach of Gallina Creek was greater than 400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (data not shown), and we therefore assumed that rates obtained represented photosaturated conditions. Chamber rates were considered representative of the period of daylight during the whole-stream measurements in which PAR exceeded 400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. For the remaining daylight hours, values of P_G were assumed to be 50% lower. During light incubations at the upper reach of Gallina Creek in 1997, the DO probe in one chamber did not function properly, and resultant values were omitted from analyses. Sediment from the trays was analyzed for organic matter content by combustion and chlorophyll a content using an acetone extraction (Wetzel and Likens 1991) followed by measuring absorbance on a spectrophotometer (Hewlett-Packard HP8452A).

To test for significant differences among reaches, benthic chamber data were analyzed using one-way analysis of variance (ANOVA), with reach as the factor (four levels) and R , P_G , P_N , organic matter content, and chlorophyll a content as the dependent variables. These analyses were followed by Bonferroni multiple comparisons where appropriate (Sokal and Rohlf 1981).

Hyporheic: Hyporheic sediment R was measured as carbon dioxide generation and/or oxygen consumption in sediment microcosms. Values for Rio Calaveras were taken from rates of aerobic R obtained in autumn 1997 by Baker et al. (2000, table 4, interface microcosms, $n = 4$) and determined for Gallina Creek sediment for this study in September 1997 ($n = 3$). Hyporheic sediments and unfiltered stream water from Gallina Creek were brought back to the lab and stored at 4° C for less than 24 h before incubations were performed. Approximately 0.4 L of wet sediment was put into a 0.7 liter Plexiglas cylinder, and stream water was

Table 1. Measured physical characteristics of study reaches and parameters from solute transport modeling of conservative tracer injections. Discharge, width, and depth are reach averages.

	Rio Calaveras long reach 1996	Rio Calaveras short reach 1997	Gallina Creek lower reach 1996	Gallina Creek upper reach 1997
Reach length (m)	110	59	41	80
Discharge (Q , L s ⁻¹)	0.5	1.2	0.8	3.2
Velocity (m s ⁻¹)	0.02	0.05	0.02	0.05
Width (m)	0.76	0.90	0.36	0.80
Depth (m)	0.03	0.03	0.16	0.11
Reach travel time (T_N , min)	90	21	41	25
Channel cross-sectional area (A , m ²)	0.024	0.024	0.035	0.082
Storage zone cross- sectional area (A_s , m ²)	0.0042	0.0015	0.0583	0.0068
A_s/A	0.18	0.06	1.67	0.08
Storage zone exchange coefficient (α , min ⁻¹)	0.006	0.053	0.038	0.025
Hydraulic residence time in the stream (T_{str} , min)	181	19	27	41
Hydraulic residence time in the storage zone (T_{stor} , min)	32	1	44	3
Water uptake length (S_{hyd} , m)	223	56	41	137
Hydraulic retention factor (R_h , s m ⁻¹)	8.4	1.2	64.8	1.4
Damkohler number (Dal)	0.6	1.2	4.3	0.7

added to fill the remaining volume. Water was circulated through the microcosms using a peristaltic pump. Water samples were taken and analyzed for dissolved carbon dioxide concentration every 30–60 min, and the slope of the regression of concentration versus time was taken as the rate of R . A respiratory coefficient of 1.0 was used to express rates of carbon dioxide production as DO consumption. Microcosm incubations were similar for Rio Calaveras sediment, except the microcosms were filled and buried in the field for a period of time prior to measuring R , and changes in DO were also measured (*see* Baker et al. 2000 for details). Porosity was estimated for each sediment sample (Fetter 1994), and organic matter content was quantified by combustion. Rates in units of DO consumption per volume of

dry sediment from Baker et al. (2000) were multiplied by $(1 - \text{porosity})$ for conversion to units of wet sediment, and results from both sites are reported as volumetric rates with units of g O₂ m⁻³ wet sediment d⁻¹. Differences in volumetric hyporheic R rates and organic matter content were assessed using t -tests to compare Rio Calaveras and Gallina Creek sediments.

Calculation of hyporheic zone contribution and size—The areal rate of hyporheic zone R ($R_{\text{hyporheic}}$) was calculated as the difference between areal rates of whole-stream R and benthic chamber R (similar to the method described by Naegele and Uehlinger 1997). For a given reach, the mean rate

Table 2. Water temperature, photon flux density of photosynthetically active radiation (PAR), and whole-stream metabolism values based on 24-h measures of open-system oxygen balance.

	Rio Calaveras long reach 1996	Rio Calaveras short reach 1997	Gallina Creek lower reach 1996	Gallina Creek upper reach 1997
Average water temperature (°C)	15.2	11.1	13.7	12.6
PAR (mol quanta m ⁻² d ⁻¹)	41	15	13	7
R (g O ₂ m ⁻² d ⁻¹)	2.9	2.3	14.7	6.7
P_G (g O ₂ m ⁻² d ⁻¹)	0.5	0.6	1.7	0.2
P_G/R	0.19	0.25	0.11	0.03

Table 3. Benthic sediment characteristics and metabolic rates for the four study reaches. Values are means of three chambers \pm SE. P_G/R values were calculated from scaling chamber rates to 24 h (see text for details). Means within a row are significantly different (ANOVA, Bonferroni $p < 0.05$) if superscripts differ.

	Rio Calaveras long reach 1996	Rio Calaveras short reach 1997	Gallina Creek lower reach 1996	Gallina Creek upper reach 1997
Chlorophyll <i>a</i> (mg m ⁻²)	60.2 \pm 6.9 ^{ab}	86.7 \pm 7.2 ^{ab}	120.0 \pm 19.0 ^a	49.4 \pm 5.1 ^b
Percentage organic matter by weight	0.8 \pm 0.2 ^a	1.3 \pm 0.2 ^a	1.2 \pm 0.03 ^a	1.7 \pm 0.4 ^a
<i>R</i> (mg O ₂ m ⁻² h ⁻¹)	49.4 \pm 8.2 ^a	57.5 \pm 13.5 ^a	41.0 \pm 6.7 ^a	42.2 \pm 1.7 ^a
<i>P_N</i> (mg O ₂ m ⁻² h ⁻¹)	57.7 \pm 0.43 ^b	160.3 \pm 27.3 ^a	98.0 \pm 5.4 ^{ab}	44.3 \pm 27.4 ^{b†}
<i>P_G</i> (mg O ₂ m ⁻² h ⁻¹)	107.2 \pm 8.5 ^{ab}	217.8 \pm 39.1 ^a	139.1 \pm 2.6 ^{ab}	84.8 \pm 27.2 ^{b†}
<i>P_G/R</i>	0.9 \pm 0.1	1.2 \pm 0.1	1.2 \pm 0.2	0.6 \pm 0.2 [†]

† $n = 2$.

of *R* from the benthic chambers was scaled to 24 h and hyporheic zone *R* was calculated with units of g O₂ m⁻² d⁻¹.

The size of the hyporheic zone was estimated by coupling the areal rates of hyporheic *R* calculated by the difference method with independently measured rates of *R* obtained from sediment microcosm incubations. This calculation assumes that incubating three or four samples of hyporheic sediment per site accurately represents hyporheic *R*, a process that is spatially heterogeneous (Jones et al. 1995b). We provide these calculations as initial assessments of hyporheic dimensions (sensu Harvey and Wagner 2000). Areal hyporheic *R* determined from whole-stream measures was converted to a linear measure with units of g O₂ m⁻¹ d⁻¹ by multiplying areal rates by mean wetted channel width. The cross-sectional area of the hyporheic zone (*A_H*, m²) was calculated by dividing this linear measure of hyporheic *R* by the volumetric measure from the sediment microcosm incubations (g O₂ m⁻³ d⁻¹).

In this manner, *A_H* represents the cross-sectional area of the alluvial aquifer that is functionally within the boundaries of the lotic ecosystem. To compare *A_H* to *A_s*, *A_H* was multiplied by sediment porosity to obtain a measure of the cross-sectional area of the saturated interstices in the hyporheic zone. To obtain a maximum estimate of hyporheic depth for a reach, *A_H* was divided by the mean wetted width of the channel. This approach provides a spatial resolution of the

hyporheic zone as a rectangular unit beneath the wetted perimeter (similar to calculations using *A_s* described in Harvey and Wagner 2000) and is an adequate comparative estimate for these reaches in which stream depth is a relatively small proportion of width.

Results

Solute injections and modeling—The lower reach of Gallina Creek exhibited the most surface–subsurface exchange with the greatest values of *A_s*, *A_s/A*, *T_{stor}*, *R_h*, and the lowest value of *S_{hyd}* (Table 1). In contrast, the lowest values of *A_s*, *A_s/A*, *T_{stor}*, and *R_h* were at the short reach of Rio Calaveras and were more than an order of magnitude lower than those at the lower reach of Gallina Creek. Values of *A_s/A*, *T_{stor}*, and *R_h* for the upper reach of Gallina Creek were low and similar to those of the short reach of Rio Calaveras. The rate of exchange between the surface water and the storage zone, α , was lowest for the long reach of Rio Calaveras, with the other three values four to nine times greater. Discharge was greatest at the upper reach of Gallina Creek and was more than six times greater than that of the long reach of Rio Calaveras, which had the lowest value of *Q* and the highest value of *S_{hyd}*. Damkohler numbers varied from 0.6 to 4.3, within the range of values likely to yield reliable parameter estimates (Wagner and Harvey 1997).

Table 4. Values relating to calculations of hyporheic zone site. *A_H* is the cross-sectional area of the hyporheic zone, calculated by dividing the rate of hyporheic *R* determined by the difference between whole-stream *R* and benthic *R* by the rate *R* determined by hyporheic sediment microcosm incubations. *A_H* is multiplied by hyporheic sediment porosity for conversion to the cross-sectional area of interstitial water for comparison with *A_s*.

	Rio Calaveras long reach 1996	Rio Calaveras short reach 1997	Gallina Creek lower reach 1996	Gallina Creek upper reach 1997
<i>A</i> (m ²)	0.024	0.024	0.035	0.082
<i>A_H</i> (m ²)	0.18	0.12	0.73	0.70
Depth of hyporheic zone (m)	0.24	0.14	2.04	0.84
<i>A_H</i> \times porosity/ <i>A</i>	2.9	1.9	8.2	3.2
<i>A_s/A</i>	0.18	0.06	1.67	0.08
<i>A_H</i> \times porosity/ <i>A_s</i>	16	30	5	39

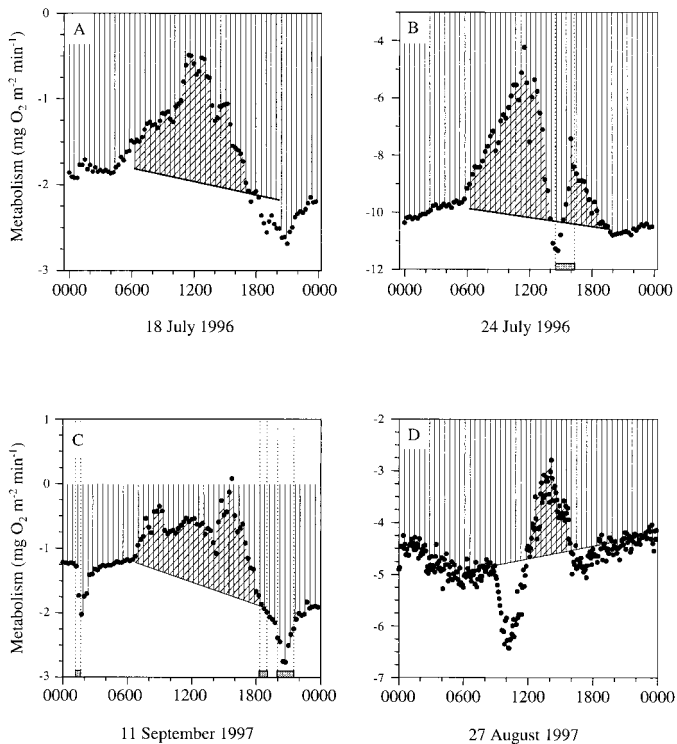


Fig. 1. Whole-stream metabolism data for the four study reaches. Each point represents the net rate of change in dissolved oxygen concentration due to metabolism (reaeration-corrected) for a (A)–(C) 15-min or a (D) 5-min interval. The area integrated to obtain a value for total respiration (R , $\text{mg O}_2 \text{ m}^{-2} \text{ d}^{-1}$) is indicated by the vertical lines and extends up to 0 for each interval. The cross-hatched area represents the area integrated to obtain a value for gross primary production (P_G). The duration and timing of precipitation are indicated by gray bars along the horizontal axes and vertical dashed lines. The date of the measurements is indicated below each plot. (A) long reach of Rio Calaveras, (B) lower reach of Gallina Creek, (C) short reach of Rio Calaveras, (D) upper reach of Gallina Creek.

Whole-stream metabolism—All four reaches exhibited strong daytime signals of P_G as evidenced by increased values of net change of oxygen concentration during daylight hours (Fig. 1). Nevertheless, metabolism was dominated by respiration, with only a single 15-min interval having a positive value of net ecosystem production (Fig. 1C). All whole-stream P_G/R ratios were much less than 1 (Table 2), with a mean value among sites of 0.15. Whole-stream R ranged from 2.3 to $14.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with the Rio Calaveras reaches having the two lowest values and the lower reach of Gallina Creek having the highest value. Gross primary production ranged from 0.2 to $1.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, with the lowest value at the upper reach of Gallina Creek and the highest value at the lower reach of Gallina Creek. The lowest value of PAR corresponded to the reach with lowest P_G , at $7 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ for the upper reach of Gallina Creek, whereas the highest value was $41 \text{ mol quanta m}^{-2} \text{ d}^{-1}$ for the long reach of Rio Calaveras (Table 2).

Several apparent increases in respiration associated with precipitation events can be seen as dips in the plots of metabolism for the lower reach of Gallina Creek and the short

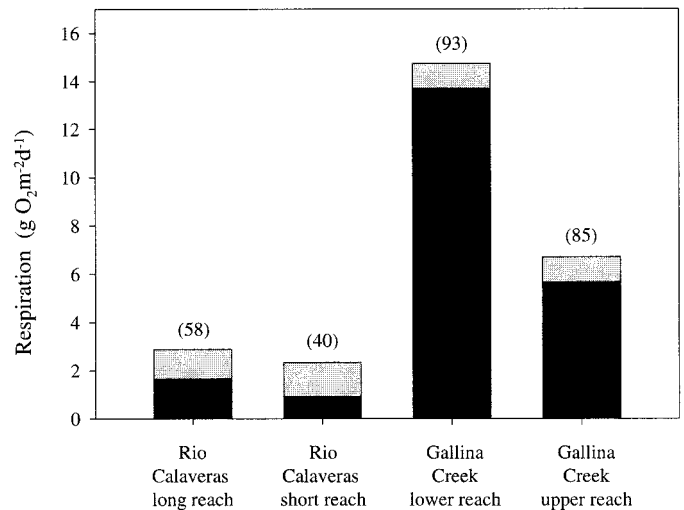


Fig. 2. Contribution of the hyporheic zone to whole-stream respiration (R) for the four study reaches. The height of each bar represents the value of whole-stream R , the light portion represents benthic chamber R , and the dark portion represents hyporheic R (calculated by difference). Percent of whole-stream R contributed by the hyporheic zone is shown above each bar in parentheses.

reach of Rio Calaveras (Figs. 1B and 1C, respectively). However, these events did not affect 24 h integrated metabolism values substantially. Metabolism values were calculated both as the shaded areas shown in Fig. 1 and with the intervals affected by precipitation replaced with values from a regression from a point 30 min before each storm and a point 60 min after, P_G for the lower reach of Gallina Creek increased by 5%, and R for the short reach of Rio Calaveras was reduced by 6%. Metabolism values generated without using regressions across storms were used for further analyses.

Benthic chamber metabolism—Benthic production varied substantially across reaches, whereas rates of R were relatively similar (Table 3). Mean chamber P_G/R ratios for all reaches were greater than the corresponding whole-stream ratios. Reach values of P_N , P_G , and chlorophyll a content were different (ANOVA, $p = 0.010$, $p = 0.026$, and $p = 0.016$, respectively). The short reach of Rio Calaveras had the greatest values for both P_N and P_G , whereas the upper reach of Gallina Creek had the lowest values. The upper reach of Gallina Creek also had the lowest value of benthic sediment chlorophyll a , and this value was significantly lower than that of the lower reach of Gallina Creek. Neither benthic R nor percent organic matter differed significantly among the four reaches (ANOVA, $p = 0.58$ and $p = 0.12$, respectively).

Hyporheic respiration—Areal hyporheic R was greater at both reaches of Gallina Creek than those of Rio Calaveras and ranged from $0.9 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $13.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 2). Similarly, the proportion of whole-stream R contributed by the hyporheic zone was much greater for both reaches of Gallina Creek than those of Rio Calaveras and ranged from

40% to 93% (Fig. 2). Mean organic matter content of hyporheic sediment was statistically similar between sites at $0.8 \pm 0.2\%$ for Rio Calaveras and $1.1 \pm 0.1\%$ for Gallina Creek (t -test, $p = 0.28$). Microcosm respiration rates were also similar between sites at $7.0 \pm 0.9 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$ for Rio Calaveras sediment (mean \pm SE, Baker et al. 2000) and $6.7 \pm 0.8 \text{ g O}_2 \text{ m}^{-3} \text{ d}^{-1}$ for Gallina Creek sediment and were not significantly different (t -test, $p = 0.87$).

Cross-sectional area of the hyporheic zone, A_H , ranged from 0.12 to 0.73 m^2 (Table 4), representing 5 to 21 times the area of the above-ground stream channel. A_H was much greater at both Gallina Creek reaches than the Rio Calaveras reaches, with values at Gallina Creek approximately 4 times those at Rio Calaveras. When A_H was divided by the average wetted width of each reach, estimates of hyporheic depth ranged from 0.14 m at the short reach of Rio Calaveras to 2.04 m at the lower reach of Gallina Creek (Table 4). Porosity of Rio Calaveras sediments was 37% ($n = 3$) (Baker et al. 2000) and Gallina Creek was 39% ($n = 3$). Porosity-corrected A_H still represented from 1.9 to 8.2 times the area of the surface stream channels. In addition, porosity-corrected A_H was much greater than A_s , with values ranging from 5 to 39 times greater (Table 4).

Relationships between surface–subsurface exchange and metabolism—All three measures of R generally increased as transient storage increased (Fig. 3). Whole-stream R and areal hyporheic R both exhibited significant relationships with A_s (proc REG, $r^2 = 0.93$, $p = 0.04$; $r^2 = 0.92$, $p = 0.04$, respectively). These measures of R also increased as the magnitude of A_s/A increased, but the relationships were not significant ($r^2 = 0.87$, $p = 0.07$; $r^2 = 0.86$, $p = 0.07$, respectively). The proportion of whole-stream R contributed by the hyporheic zone (arcsine square root transformed) was not significantly correlated with A_s ($r^2 = 0.57$, $p = 0.25$) or A_s/A ($r^2 = 0.49$, $p = 0.30$). For analyses including the two sites from Mulholland et al. (1997), the relationship between whole-stream R and A_s/A was significant ($r^2 = 0.84$, $p = 0.01$), but that between R and A_s was not ($r^2 = 0.52$, $p = 0.11$).

Discussion

Contribution of the hyporheic zone—Few studies have investigated the effects of the hyporheic zone on stream ecosystem metabolism, but all to date have demonstrated that the hyporheic zone is a major contributor to whole-stream respiration. Grimm and Fisher (1984) found that the hyporheic zone contributed 40–50% of total ecosystem R in Sycamore Creek, a desert stream. Fuss and Smock (1996) estimated the annual contribution of the hyporheic zone to be 70% in Buzzards Branch, a sand bottom, black water coastal plain stream. Naegeli and Uehlinger (1997) found that the proportion of hyporheic contribution was even greater, at 74–92% of ecosystem R in the Necker, a sixth-order gravel bed river. The hyporheic zone contributed a substantial proportion of whole-stream R in all four reaches of this study (40 to 93%) with a range very similar to that delineated by previous studies.

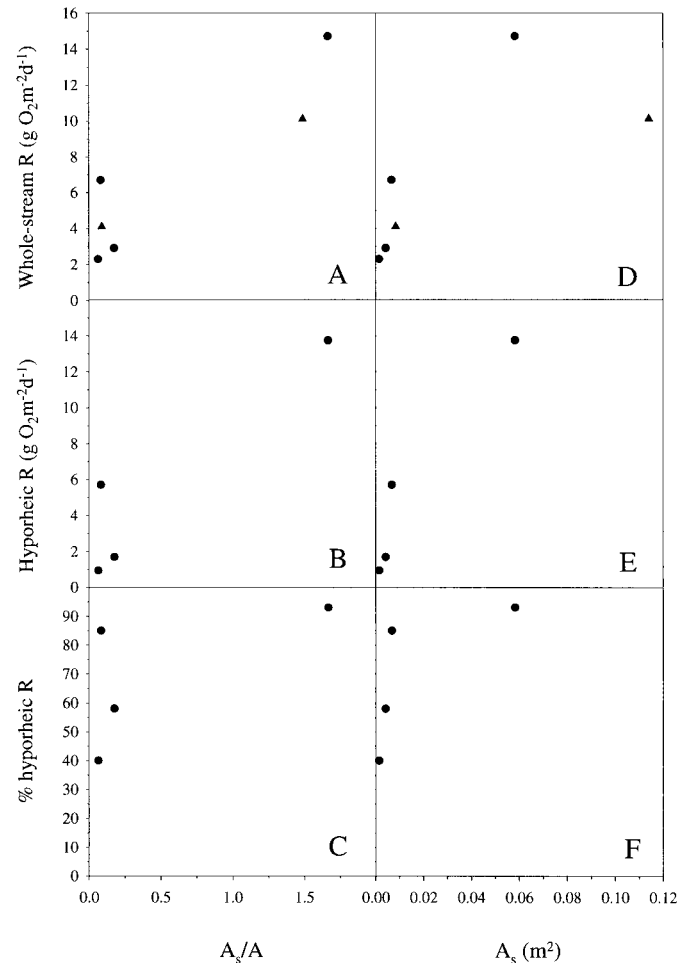


Fig. 3. Plots of different measures of respiration against (A)–(C) normalized size of the transient storage zone (A_s/A) or (D)–(F) cross-sectional area of the transient storage zone (A_s). Whole-stream and hyporheic R are areal rates, and percentage hyporheic R is the portion of whole-stream R contributed by the hyporheic zone. Values for the four study reaches are shown as circles, and values for two sites from Mulholland et al. (1997) are shown as triangles.

Surface–subsurface exchange and stream ecosystem respiration—As pointed out by Findlay (1995), there are few data in the literature with which to examine relationships between ecosystem functioning and hyporheic zone hydrodynamics. Our work supports the conclusion of Mulholland et al. (1997) that the magnitude of whole-stream R is related to the extent of surface–subsurface exchange. Whole-stream R may not be the best functional variable with which to examine the influence of surface–subsurface exchange on ecosystem metabolism given the capacity for benthic rates to obscure differences in hyporheic contributions. The relationship between hyporheic R and exchange may be more robust than that with whole-stream R , but since our study is the first to specifically measure hyporheic R and surface–subsurface exchange, there are even fewer data with which to make an evaluation than for whole-stream R . The relationship between whole-stream R and A_s/A provided in Fig. 3A links the fluvial nature of streams to their functional sta-

tus as ecosystems and will continue to be tested as more data become available.

The relative magnitude of hydrologic exchange at the two study sites can also be evaluated independently of solute transport modeling results. The contribution of the hyporheic zone to whole-stream R was greater at Gallina Creek than Rio Calaveras, whereas the volumetric rates of hyporheic sediment R were similar between sites. If the contribution of the hyporheic zone is a function of the rate of a process and the proportion of surface water routing through the hyporheic zone (Findlay 1995), this suggests that the proportion of stream water routing through the hyporheic zone was greater at Gallina Creek. Similarly, since calculations of A_H standardize for volumetric hyporheic sediment R rates, larger values of A_H mean that a greater volume of hyporheic zone sediments were contributing to whole-stream metabolism per unit stream length at the Gallina Creek reaches.

Estimates of hyporheic zone size using metabolic versus solute tracer technique—Although the hyporheic zone has been clearly indicated as a source of transient storage in stream ecosystems, it may be that transient storage values determined from short-term tracer injections do not adequately reflect hydrologic processes that affect metabolism over the period of days (Harvey et al. 1996). Porosity-corrected values of A_H were substantially greater than corresponding values of A_s (5–40 times). The duration of a solute injection determines the scale at which information about surface–subsurface exchange is obtained (Harvey et al. 1996), and our injections generally lasted a few hours. When metabolism measurements integrate longer duration flow paths that do not influence short duration tracer injections, values of A_H will be much greater than A_s . A_H therefore can be used in calculating the contribution of the hyporheic zone to other processes of interest of similar timescales, such as nutrient cycling, if the rate of the process is known for a defined volume of hyporheic sediment. A_H , alone or standardized for stream size using A_s , should be a valuable cross-site variable because it takes into account differences in rates of both benthic and volumetric hyporheic sediment R rates.

Our work provides additional evidence of the importance of extending stream ecosystem boundaries to include the region of surface water–groundwater exchange. The hyporheic zone contributes substantially to ecosystem functioning in the four reaches we studied and in many other streams (Jones and Holmes 1996; Brunke and Gonser 1997; Boulton et al. 1998; Dahm et al. 1998). Both A_s and A_H are indirect measures of the size of the hyporheic zone and are useful for cross-site comparisons and in predicting the contribution of the hyporheic zone to whole-system measures of metabolism and other processes. Since rates of benthic R and volumetric hyporheic sediment R were similar across reaches, hydrology was a significant factor determining the contribution of the hyporheic zone to whole-system processes at these sites. The importance of surface water–groundwater interactions to stream ecosystem functioning highlights the need for combining studies of ecosystem process with measures of hydrology and hydrologic modeling.

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