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Effects of groundwater flux on open-channel estimates of stream metabolism

Abstract—The open-channel oxygen method can produce precise estimates of photosynthesis (P) and respiration (R) over a wide range of stream conditions. It is widely recognized that flux of groundwater contributes to the oxygen mass balance for a stream. However, groundwater flux is rarely considered in open-channel estimates of stream metabolism, and no guidelines have been established regarding the conditions under which it can be ignored. The purpose of this paper is to describe a method for predicting the effect of groundwater flux on estimates of metabolism and thereby establish the conditions under which flux of groundwater can lead to large errors in estimates of metabolism. Estimation of P is not significantly affected by flux of groundwater. Ecosystem R , however, can be greatly overestimated where the oxygen concentration of groundwater is substantially lower than the concentration in the channel. Although the effects of groundwater flux on estimates of metabolism often are trivial, rates of flux can be sufficiently high in many streams, at least during some part of the year, to affect estimates of R where the oxygen concentration differs substantially between groundwater and surface water. Thus, the potential contribution of groundwater flux to oxygen mass balance should always be evaluated when the open-channel method is used.

The open-channel oxygen method can provide precise, system-level estimates of ecosystem metabolism over a wide range of stream conditions (McCutchan et al. 1998). The open-channel method also incorporates respiration in deep sediments, which often accounts for a large fraction of total respiration in streams and may be underestimated by chamber techniques (Grimm and Fisher 1984; Fellows et al. 2001). Application of the open-channel method has become

common since the advent of recording field oxygen meters and improvements to methods for measuring reaeration (exchange of oxygen with the atmosphere). Assumptions that are implicit in open-channel estimates of metabolism have come under scrutiny, however, as investigators have begun to test the limitations of the method.

Open-channel estimates of photosynthesis (P) and respiration (R) can be based on calculation of mass balance for carbon dioxide but most commonly are based on mass balance for dissolved oxygen. Changes in oxygen concentration of a stream over time or distance reflect the balance of metabolic processes (P and R) and reaeration. Flux of groundwater also must be considered in streams where the effect of groundwater on oxygen mass balance is large relative to rates of biological processes and reaeration, or metabolism will be estimated with error. Odum (1956) considered the potential effects of groundwater flux on the mass balance of oxygen in streams, and more recent work (Choi et al. 1998; Jones and Mulholland 1998) has demonstrated empirically that flux of groundwater can greatly affect gas concentrations in streams, but the effects of flux on estimates of stream metabolism have not been examined explicitly. Although practitioners of the open-channel method (e.g., Marzolf et al. 1994; Uehlinger and Naegeli 1998; Fellows et al. 2001) often have attempted to confine their work to reaches where rates of groundwater flux are low, the potential for error in open-channel estimates of metabolism has not been studied. The purpose of this paper is to establish the conditions under which flux of groundwater can lead to bias in estimates of metabolism and to describe a method for minimizing such errors.

When metabolism is estimated for a parcel of water flowing between two stations where oxygen concentration is measured, the mass balance for oxygen includes the sum of groundwater flux, metabolism flux, and reaeration flux, as follows:

$$\frac{dm}{dt} = C_g Q_g + (P + R)A + k(Sv[t] - m[t]) \quad (1)$$

where $m[t]$ is the mass of oxygen (units of m are g O₂) in the parcel at time t (time is measured in days), dm/dt is the rate of change in mass with respect to time (units are g O₂ d⁻¹), C_g is the concentration of oxygen in groundwater (units of concentration are g O₂ m⁻³), and Q_g is the rate of groundwater flux to the parcel (units of Q_g are m³ d⁻¹). P and R are rates of photosynthesis and respiration (units are g O₂ m⁻² d⁻¹; R is a sink for O₂ and is negative in sign), A is the area of the channel covered by the parcel (units of A are m²), k is the reaeration rate coefficient for oxygen at temperature T (units of k are d⁻¹), S is the saturation concentration for oxygen, $v[t]$ is the volume of the parcel at time t (units of volume are m³), and the rate of change in volume per unit time is equal to Q_g (i.e., $dv/dt = Q_g$). It is assumed that the parcel is well mixed and that barometric pressure, T , C_g , Q_g , P , R , A , and k are constant over the interval from time 0 to time t . If C_i and V_i are the oxygen concentration and volume of the parcel at time 0, solving Eq. 1 for $m[t]$ and dividing by $v[t]$ gives $c[t]$, the oxygen concentration for the parcel at time t , as follows:

$$c[t] = \frac{e^{-kt}}{k(Q_g t + V_i)} \times ([C_g Q_g + A(P + R)](e^{kt} - 1) + Q_g S(1 + e^{kt}[kt - 1] + kV_i(C_i + S[e^{kt} - 1]))) \quad (2)$$

If flux of groundwater over the reach is equal to zero, Eq. 2 simplifies as follows:

$$c[t] = S + A \left(\frac{1 - e^{-kt}}{kV_i} \right) (P + R) - (S - C_i)e^{-kt} \quad (3)$$

When groundwater flux is ignored and rates of metabolism are calculated by Eq. 3, the absolute bias in nighttime R (b_R) is calculated as follows:

$$b_R = R_3 - R_2 = -\frac{Q_g}{A} \left((S - C_g) - (S - c[t]) \frac{kte^{kt}}{e^{kt} - 1} \right) \quad (4)$$

where R_2 is the rate of R calculated by Eq. 2, R_3 is the rate of R calculated by Eq. 3, and the quantity Q_g/A is the flux of groundwater per unit area (i.e., the vertical velocity of groundwater; units are m d⁻¹). Typically, photosynthesis is calculated as the difference between net flux of oxygen due to metabolism ($P + R$) and the estimated daytime rate of R . If temperature is constant and daytime R is not stimulated by photosynthesis, it can be assumed that daytime R equals nighttime R and the absolute bias in net production (b_{P+R}) is calculated as follows:

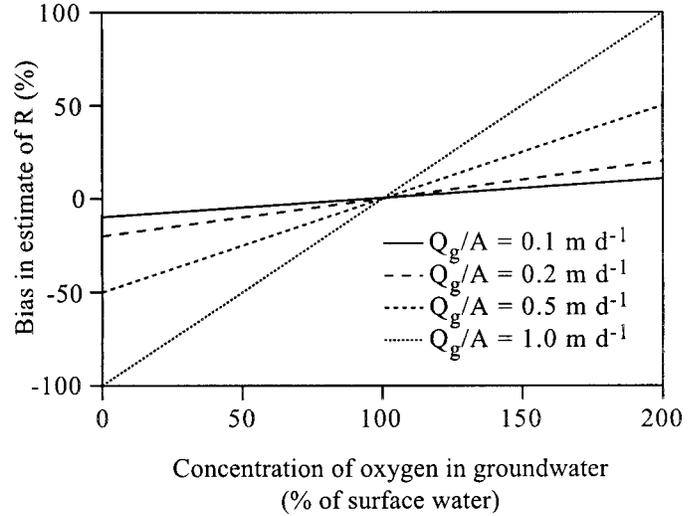


Fig. 1. Relative bias (B_R , as percentage of metabolic rate; because R is negative in sign, positive values of B_R represent underestimation of R and negative values represent overestimation) in estimates of respiration (R) as a function of the concentration of oxygen in groundwater relative to that in stream water ($C_g/c[t]$). Bias is calculated by Eq. 7, subject to the condition that $c[t]/R = 1$ d m⁻¹.

$$b_{P+R} = R_3 - R_2 = -\frac{Q_g}{A} \left((S - C_g) - (S - c[t]) \frac{kte^{kt}}{e^{kt} - 1} \right) = b_R \quad (5)$$

Because P is calculated as the difference between two values that include the same absolute error, P is estimated without bias when open-channel estimates of metabolism are based on Eq. 2.

Relative bias in estimates of R (B_R) is calculated as follows:

$$B_R = \frac{R_3 - R_2}{R_3} = -\frac{Q_g}{A} \left(\frac{1}{R_3} \right) \left((S - C_g) - (S - c[t]) \frac{kte^{kt}}{e^{kt} - 1} \right) \quad (6)$$

Over short intervals of time, relative bias in R can be approximated by a linear function of $C_g/c[t]$ and is proportional to Q_g/A and $c[t]/R$, as follows:

$$B_R \approx -\frac{Q_g}{A} \left(\frac{c[t]}{R_3} \right) \left(1 - \frac{C_g}{c[t]} \right) \quad (7)$$

The magnitude of B_R can exceed 50% when Q_g/A and $c[t]/R$ are high and the oxygen concentration of groundwater differs substantially from that of surface water (Fig. 1).

Estimates of bias presented here are based on the assumption that T , R , and k are constant over space and time. For small intervals of time, variation in the reaeration rate coefficient has little effect on the bias in estimates of metabolism. Because temperature affects the saturation concen-

Table 1. Estimates of the average vertical velocity of groundwater (Q_g/A) and physical parameters for stream reaches described in published studies. L is length of the study reach, A_{reach} is surface area for the reach, Δt is water travel time for the reach, Q_i is discharge at the upper end of the reach, and $Q_{g, \text{reach}}$ is the flux of groundwater to the reach.

Reference	Stream	Date	L (m)	A_{reach} (m ²)	Δt (d)	Q_i (m ³ d ⁻¹)	$Q_{g, \text{reach}}$ (m ³ d ⁻¹)	Q_g/A (m d ⁻¹)
Fellows et al. (2001) and C. Fellows unpubl. data	Rio Caleveras	18 Jul 96	110	84	0.063	39	4.8	0.057
		11 Sep 97	59	53	0.015	97	1.2	0.022
	Gallina Creek	24 Jul 96	41	15	0.028	49	45	3.1
Marzolf et al. (1994)		27 Aug 97	80	64	0.017	156	-86	-1.4
	Walker Branch	10 Apr 92	62	81	0.012	534	51	0.63
		29 Jul 92	62	81	0.017	262	12	0.14
		16 Nov 92	62	81	0.028	227	19	0.23
Mulholland et al. (1997)	Walker Branch	16 Jun 93	62	136	0.017	363	19	0.14
	Hugh White Creek	12 Jul 94	78	218	0.019	423	140	0.64
Ortiz-Zayas (1998)	Q. Bisley 3	11 Apr 95	50	88	0.035	259	69	0.79
		13 Sep 95	50	76	0.024	1,990	300	4.0
		22 Nov 95	50	74	0.029	950	78	1.1
		10 Jan 96	50	76	0.027	2,250	190	2.5
	Rio La Mina	2 May 95	120	274	0.024	9,500	10	0.038
		26 Sep 95	120	237	0.013	10,900	390	1.7
		7 Dec 95	120	281	0.015	5,880	300	1.1
Rio Mameyes	1 Dec 95	260	1,920	0.017	62,200	2,700	1.4	

tration of oxygen and the rate of metabolism, changes in temperature may affect the bias in estimates of R when flux of groundwater is ignored. Although not presented here, a simulation analysis similar to the one described in McCutchan et al. (1998) showed that when t is small, changing temperature does not contribute substantially to the bias in estimates of R when groundwater flux is ignored.

For many streams, groundwater flux is likely to be important in open-channel estimates of metabolism. Dissolved oxygen in groundwater often is low relative to surface water (Gibert et al. 1994), although C_g can exceed the oxygen concentration in surface water (e.g., below an effluent outfall). Most estimates of Q_g/A derived from published studies are greater than 0.1 m d⁻¹, and many exceed 0.5 m d⁻¹ (Table 1). Thus, the values of Q_g/A and $C_g/c[t]$ considered here (see Fig. 1) are relevant (i.e., values given represent real and common occurrences).

Techniques are available for measurement of the key variables (Q_g/A , C_g) in Eq. 2. Groundwater flux often is estimated from the dilution of a conservative tracer added to the stream (Triska et al. 1989) or from the increase in the streamwater concentration of a tracer added to groundwater, and the oxygen concentration of groundwater can be estimated from measurements in alluvial wells that intercept important flowpaths for groundwater. Once estimates of Q_g/A and C_g have been made, it is relatively simple for investigators to reach a conclusion about the potential for bias due to groundwater flux and thus to make informed decisions about which equation should be used to estimate metabolism.

If groundwater flux is included in the mass balance for oxygen (i.e., estimates are based on Eq. 2), investigators will be faced with examining the accuracy of estimates for groundwater flux and concentration as well as the validity

of assumptions such as the constancy of Q_g/A and C_g over space and time. Flux of groundwater can vary in magnitude (Rutherford 1994), in response to physical characteristics of the channel and processes within the watershed (e.g., evapotranspiration or variation in snowmelt related to the daily thermal cycle), and concentrations of oxygen in groundwater can be very heterogeneous. Although localized variations in flux have been measured by a variety of methods and at different scales (Triska et al. 1989; Cey et al. 1998; Hinkle et al. 2001), the effects of spatial and temporal variability in flux on estimates of metabolism have not been addressed. Furthermore, the flux-weighted average concentration of oxygen for groundwater entering a stream may be very difficult to determine. If variation in Q_g/A or C_g over a reach is large relative to net flux over the reach, open-channel estimates of metabolism may be subject to errors that are not considered here, and such errors may be large.

When the open-channel method is used to estimate stream metabolism between two stations, estimates of photosynthesis are not affected by groundwater flux but, for many stream reaches, estimates of R are subject to substantial bias when groundwater flux is ignored. Under some conditions, such bias can far exceed estimates of precision for the open-channel method (McCutchan et al. 1998). The analyses presented here relate to two-station applications of the open-channel method, but they also can be applied to estimation of metabolism based on measurements at a single station if it can be assumed that the factors affecting the mass balance for oxygen (e.g., Q_g/A , k , P , and R) are spatially homogeneous upstream. It is not difficult to determine in advance whether significant bias is likely if groundwater flux is ignored. Therefore, the potential for such bias always should be evaluated when the open-channel method is used.

James H. McCutchan, Jr.¹, James F. Saunders, III,
William M. Lewis, Jr., and Matthew G. Hayden

Center For Limnology
Cooperative Institute for Research in Environmental Sciences
University of Colorado
Boulder, Colorado 80309-0216

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¹ Current address: Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545-0129.

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Seasonality of in situ respiration rate in three temperate benthic suspension feeders

Abstract—Natural respiration rates of suspension feeders in temperate ecosystems are still poorly known. This lack of information constrains our understanding of the functioning and dynamics of benthic marine ecosystems in temperate areas. We examined the in situ seasonal variation in respiration rate of three benthic suspension feeders (a sponge, an ascidian, and a gorgonian) in northwestern Mediterranean sublittoral communities using a recirculating flow respirometry system. The in situ technique is shown to be highly applicable to seasonal studies of the physiological energetics of benthic suspension feeders. Respiration rates of the three species varied two- to threefold through the annual cycle, exhibiting a marked seasonal pattern but showing no daily cycle or significant day-to-day variability within months. The respiration rate of the sponge and ascidian, active suspension feeders, increased with temperature. The respiration rate of the gorgonian, a passive suspension feeder, did not correlate with temperature. We estimated a Q_{10} of 1.1, which indicates that respiration rate in

this species is not highly dependent on temperature. Synthesis of new tissue of some Mediterranean benthic suspension feeders, such as gorgonians, does not correlate with temperature, which allowed us to isolate the effects of temperature and synthesis of new tissue on respiration rate. Synthesis of new tissue increased respiration rate of the gorgonian by ~40%. The low rate of synthesis of new tissue during summer, together with the contraction of polyps and the low Q_{10} , explains the low respiration rates of the gorgonian observed during the period of highest temperature. These low respiration rates support the hypothesis that energy limitations may underlie summer dormancy in some benthic suspension-feeding taxa in the Mediterranean.

Respiration is the metabolic process by which organic substances are broken down to simpler products with the release of energy (Lucas 1996). Oxygen consumption is a