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COMMUNITY METABOLISM IN MICHIGAN RIVERS: EFFECTS
OF INCLUDING HYPORHEIC SEDIMENTS IN ESTIMATES
OF PRODUCTION/RESPIRATION (P/R) RATIOS

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COMMUNITY METABOLISM IN MICHIGAN RIVERS: EFFECTS OF INCLUDING HYPORHEIC SEDIMENTS IN ESTIMATES OF PRODUCTION/RESPIRATION (P/R) RATIOS

By

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ABSTRACT

COMMUNITY METABOLISM IN MICHIGAN RIVERS: EFFECTS OF INCLUDING HYPORHEIC SEDIMENTS IN ESTIMATES OF PRODUCTION/RESPIRATION (P/R) RATIOS

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The hypothesis tested in this study was that inclusion of a small portion of the hyporheic zone could significantly alter production/respiration (P/R) values, possibly to the extent that some middle-order stream systems once believed to be autotrophic are actually heterotrophic. I designed an open-ended hyporheic community metabolism chamber and simultaneously measured metabolism using these hyporheic chambers and standard *in-situ* benthic chambers. The standard benthic chambers were similar to those used to develop the hypothesis of the river continuum concept (RCC) stating that P/R values of medium size rivers are expected to be greater than one, indicating autotrophy. The 100 cm long hyporheic chamber allowed water to flow freely through the top 20 cm of benthic sediments. A sediment transfer shovel, specially designed to maintain stratigraphic integrity was used to transfer sediments from the streambed to the chamber. The chambers were left in place for 30 days for recolonization after sediment transfer. Comparisons were made between the two chamber designs through a series of side by side comparisons. Results from 4th and 5th-order Michigan rivers demonstrated that P/R values using the traditional closed benthic chamber were always greater than one, as predicted by the River Continuum Concept, while results obtained using the hyporheic chamber were always less than one. These results, including a conservative 20 cm of the

hyporheic zone, lead to questions concerning P/R ratio changes along a river continuum. Further, this experiment emphasizes the need to include the hyporheic zone in studies of stream metabolism.

In a second set of studies, closed benthic chambers, whole system upstream-downstream measurements, and the hyporheic chambers were tested simultaneously. Several studies that had compared closed benthic chambers and whole system upstream-downstream methods had suggested conflicting results. However, statistical comparisons were not possible because the whole system method could not be replicated. The hyporheic chamber was used along with both the upstream-downstream and closed benthic chamber methods simultaneously at two sites on Augusta Creek, a third order Michigan stream. The hyporheic chamber and upstream-downstream methods estimated community respiration values higher than benthic chambers at both study sites. Hyporheic and benthic chamber estimates were significantly different. Gross community productivity was non-detectable using the hyporheic chamber at one site and was significantly higher than benthic chamber estimates at the other. The upstream-downstream estimates of gross community productivity tended to be higher than benthic chamber productivity estimates at both sites but tended to agree with hyporheic chamber estimates. These data suggest inclusion of hyporheic sediments strongly influences respiration estimates and indicate that whole system and benthic chamber methods should not be use interchangeably.

ACKNOWLEDGMENTS

I would like to thank Dr.'s Thomas Burton, Donald Hall, Stephan Hamilton, Daniel Hayes, and Robert King for input on the development of the hyporheic chamber protocol. Dr. Stephan Hamilton also provided technical support, field assistance, and the use of his lab and equipment during these studies. I would like to thank Dr. Donna King for the use of the closed benthic chambers, and Craig Stricker, Ted Siler, Mark Scalabrino, Keith Kintigh, Christy Lewis, Donna Kashian, and Archie Martell for assistance in the field. Electra •tec constructed and donated the hyporheic chambers. Funding came from The Kalamazoo Foundation, Kalamazoo Valley Trout Unlimited, and the U.S. Department of Defense.

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Including 20 cm of hyporheic respiration in estimates of production to respiration

INTRODUCTION

Many studies concerning hyporheic nutrient dynamics suggest that an extensive microbial community exists beneath the surface sediments (Grimm and Fisher 1984, Rutherford and Hynes 1987, Ford and Naiman 1989, Triska et al. 1989a, Triska et al. 1989b, Triska et al. 1990, Hendricks and White 1991, Stanford and Ward 1993, Hendricks and White 1995, Jones et al. 1995a). Until recently, this community has been largely ignored when measuring ecosystem metabolism (P/R). Grimm and Fisher (1984) suggested that the use of in-situ benthic chambers to estimate P/R values may overestimate autotrophy by underestimating hyporheic respiration. While the closed benthic chamber method, described by McIntire et al. (1964) and developed by Bott et al. (1978), provides good estimates of surface sediment metabolism, it does not take into account the potentially high respiration of the hyporheic zone. Pusch and Schwoerbel (1994) speculated that respiration in many streams may actually be twice as high as benthic chamber measurements suggest, if the hyporheic zone were included. Even bottomless benthic chambers do not account for hyporheic respiration since surface and interstitial waters do not readily mix once the chamber is put into place (Grimm and Fisher 1984, Pusch and Schwoerbel 1994).

Currently the most popular methods for measuring community metabolism are closed benthic chambers and diel oxygen curves or the upstream-downstream method. Air-water diffusion estimates for the upstream-downstream method are often imprecise and add major uncertainty to P/R measurements obtained using this technique (Marzolf et al. 1994). Closed system procedures are often favored because they eliminate the uncertainty associated with estimates of diffusion. However, closed systems are not without their shortcomings as ambient conditions are altered to some extent. Altered water velocity, temperature, nutrient concentrations, or dissolved oxygen (DO) concentrations have the potential to change the metabolism of a closed sediment sample (Horner and Welch 1981, Horner et al. 1990). An alternate procedure such as the upstream-downstream method (Odum 1956) has the potential to account for hyporheic respiration. Unfortunately, there are several problems associated with this method, including the lack of true replication, the restriction of applicability to reaches with little inflow, the uncertainty associated with oxygen flux reaeration corrections, and the limits of detecting small changes in DO concentrations (Marzolf *et al.* 1994).

Grimm and Fisher (1984) estimated respiration of the hyporheic zone by sealing both ends of a sediment core sample and monitoring DO consumption over time. Pusch and Schwoerbel (1994) used a similar method, in which tubes filled with sediment were buried parallel to flow at various depths. The tubes were retrieved from the streambed after an incubation period, but left submerged in the stream water to observe DO changes under recirculating conditions. Naegeli et al. (1995) used a similar system in the lab after tubes were retrieved. Jones et al. (1995b) removed cores from the stream and filled them with hyporheic water, sealed them and returned them to the hyporheic zone for a three to four-hour incubation period. These four studies of hyporheic respiration indicated that hyporheic respiration was similar to respiration measured at the surface on an areal basis. Thus, hyporheic respiration should be included in estimates of community metabolism. However, incubations of closed cores ex-situ may not produce representative values for hyporheic sediments in-situ.

To address this problem, a flow-through hyporheic chamber that allowed in-situ determination of community metabolism was designed. The objective of this study was to test this newly designed hyporheic chamber that included surface and hyporheic community metabolism in streams in side-by-side comparisons with the closed benthic community metabolism chambers built to the design developed by Bott *et al.* in 1978. The Bott *et al.* design has been used extensively since 1978 to measure P/R ratios for streams.

The hypothesis tested was that inclusion of 20 cm of hyporheic sediments would significantly alter P/R values, because of increased community respiration by hyporheic consumers. It was further hypothesized that inclusion of this hyporheic community respiration would reduce P/R values for middle-order streams from autotrophic values greater than one to heterotrophic values less than one.

MATERIALS AND METHODS

Study sites

Sites on the Jordan, AuSable, North Branch of the AuSable and the Red Cedar Rivers in Michigan were selected for this study. Measurements were made at the Jordan River, a designated wild and scenic river, on 5 September 1996. The Jordan was fifth-order, and heavily sand impacted at the study site located at T.30N. R.6W. Sec. 10, Antrim County, Michigan. The riparian zone at this site was forested and the stream channel investigated was 18 m wide. Community metabolism using the side-by-side comparison of methods was determined on the North Branch of the AuSable River on 16 May 1996 and 26 June 1997. Metabolic measurements were made on the main stem of the AuSable River on 17 May 1996 and again on 17 July 1996. The AuSable River and the North Branch AuSable River study sites were both located in Crawford County, Michigan at T.26N. R2W Sec. 6 and T.27N. R1W. Sec 8 respectively. Both were forested fourth-order stream reaches considered "quality trout fishery stream reaches" by the Michigan Department of Natural Resources. Stream width ranged from 15 to 20 m at both sites and substrates consisted of mainly gravel. Metabolism measurements were made on the Red Cedar River on 8 June 1997. The Red Cedar study site was a 3rd-order, 15 m wide reach of the river that drained predominantly urban and agricultural land. The site was located at T.4N. R.1W Sec. 27 in Ingham County, several kilometers downstream from a sewage treatment facility. Substrate consisted mainly of gravel with an underlying, heavily consolidated clay layer. Unlike the other sites located on cold water trout streams, the Red Cedar River was a warm water stream.

All measurements were made in riffle sections except for measurements on the Jordan River. Since riffles did not exist on this stream reach, a comparable run of rapid flow was selected. Riffle/run sections were chosen because they potentially support the most primary productivity and are therefore most likely to be autotrophic.

Hyporheic chamber design

Flow-through, one m long, 20 cm wide, 20 cm deep, hyporheic chambers were designed to include sediments that extended from the sediment surface to 20 cm deep. Chambers were constructed from galvanized sheet metal and were covered with 0.6 cm thick clear acrylic tops to allow light to penetrate to the sediments (Figure 1A). The design allowed uninhibited parallel flow through the entire length of the chamber. Sampling ports at upstream and downstream ends were encased in 500 mm mesh to keep sediments from filling around the stirrers and DO probes. Although the entire chamber, upstream , downstream, and between the sampling ports was filled and buried, metabolic measurements were made on sediments fit in the 0.765 m long area between sampling ports. Therefore, a sediment sample size of 0.765 m by 0.20 m by 0.20 m was used to estimate community metabolism.

With the top and bottom sealed, the flow-through hyporheic chamber was not subject to the uncertainty associated with estimates of air-water diffusion of oxygen into or out of the stream and/or with seepage of groundwater into the chamber between the upstream and downstream ports. Thus, this chamber combines some of the best features of the upstream-downstream technique of measuring stream metabolism with some of the best features of the closed benthic chamber. The downside to this chamber is that it is

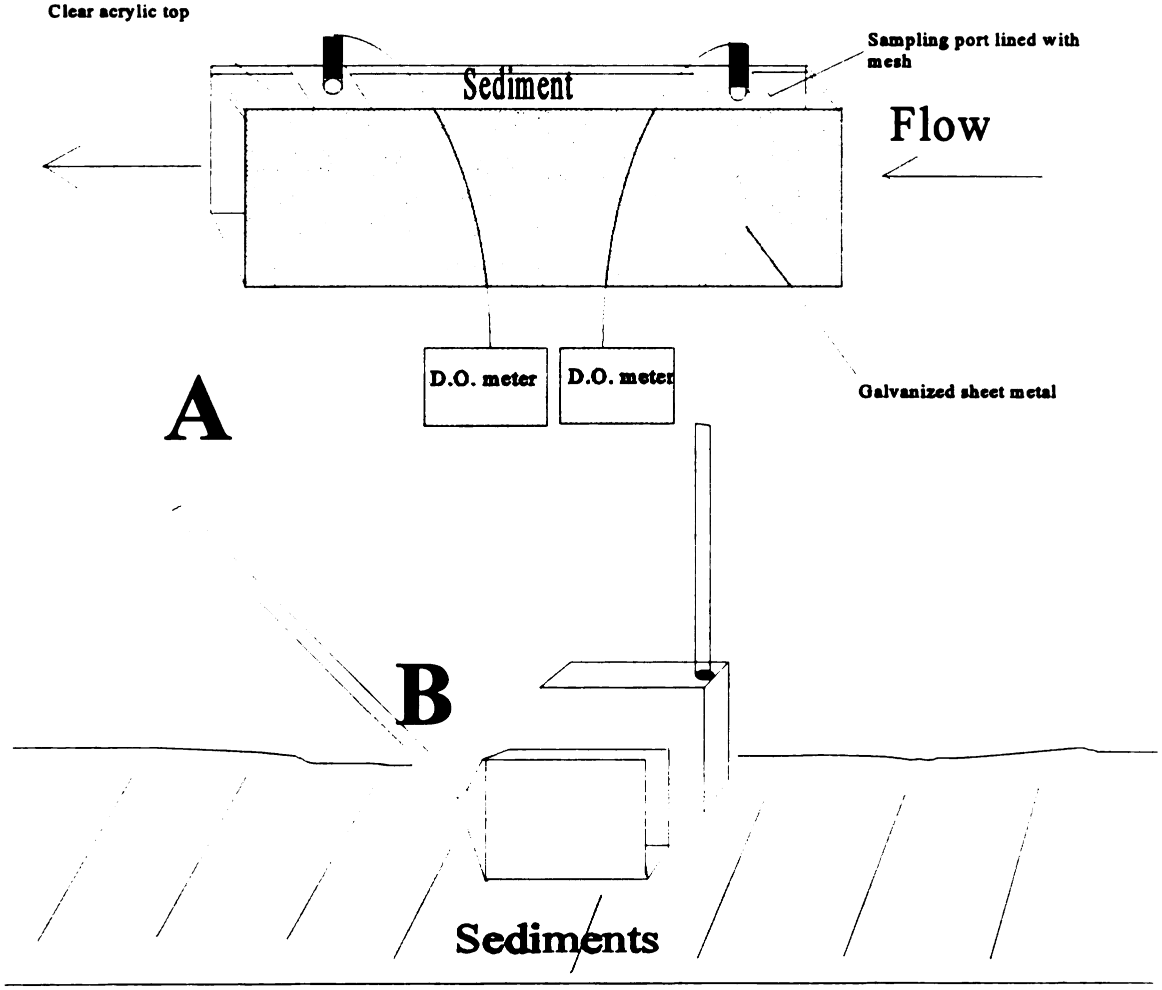

Figure 1. A. Design of the one m flow-through, in-situ hyporheic chamber for measuring community metabolism. B. The chambers were filled with sediment using a customized shovel and cover designed to fill the area between sampling ports with two shovels full of sediments. The lid was made of 0.6 cm clear acrylic and was sealed to the top of the chamber with a foam gasket and secured with spring clamps. Sample compartments were lined with 500 µm mesh netting and were not filled with sediments. Dissolved oxygen readings were taken from the sampling compartments using YSI dissolved oxygen probes. Twelve-volt DC stirrers were placed into the sampling compartments and directly beneath the probes (A). The sediment transfer shovel (B) was used to fill the hyporheic chambers. A depression was made downstream of a flat shovel driven into the streambed. The scoop was placed in the depression before removing the flat shovel and the scoop was driven upstream until it was full. The cover was driven into the streambed to enclose the block of sediments (B).

measuring metabolism on a very small spacial scale and the chamber itself can potentially alter natural flow paths since it is buried in the streambed. The chamber was made to measure a conservative 20 cm of hyporheic zone for the purpose of this study, but within reason, the size of the chamber is not limited by its design.

Filling Chambers

Four chambers were filled with 20 cm of sediment using a customized shovel and cover to maintain the stratigraphic integrity of the sediments (Figure 1B). The outer dimensions of the shovel matched the inner dimensions of the chamber, and each hyporheic chamber held two shovels of sediment. Once the covered shovel was lowered into the chamber, sediments were held in place as the shovel was removed from the chamber. Hyporheic chambers were buried in the streambed parallel to surface flow with the covers removed, and allowed to incubate for four weeks (Figure 2). Due to the unstable shifting sands of the Jordan River, the incubation period for both the hyporheic and benthic chambers was eliminated.

Metabolism measurement

After incubation, 12-volt DC stirrers were placed into the sampling compartments of three randomly chosen chambers. The chambers were covered by seating the lid gaskets in the grooved edge of each chamber and attaching spring clamps. Yellows Springs Instruments dissolved oxygen probes were securely sealed into the lid corresponding to the upstream and downstream sampling compartments of each chamber. Each replicate pair of probes was calibrated simultaneously before securing them in

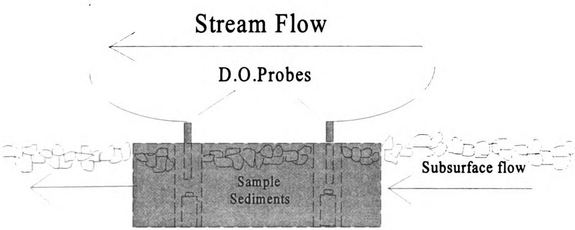

Figure 2. After being filled with sediments (see figure 1), the hyporheic chamber was buried in the streambed parallel to flow. Chambers were left in place with the covers off for a four-week incubation period before measurements were made.

sampling compartments.

The fourth chamber was used to determine hyporheic flow velocity by introducing a conductivity spike in the upstream sampling compartment with a concentrated sodium chloride solution. Velocity measurements were conducted in a separate chamber in order to avoid deleterious impacts to the biota. Velocity through all of the chambers was assumed to be comparable since the relatively small sediment samples for all four chambers were randomly taken from similar sized sediments from the same riffle. Preliminary observations, where flows through all four chambers were determined with conductivity spikes, during the development of the chamber design agreed with this assumption. A conductivity probe was used to detect the conductivity spike as it moved through the downstream sampling compartment. Mean water velocity was calculated from the time required for the conductivity spike to travel from the upstream to the downstream compartment.

Dissolved oxygen concentrations in the upstream and downstream compartments were monitored hourly for a 24-hour period. Stirrers were connected to a 12-volt DC battery until dissolved oxygen meters stabilized. Immediately following each reading, stirrers were disconnected. The interval of time determined by the sodium chloride tracer was used to separate upstream and downstream readings to ensure a measurement of the same water mass. The rate of change of oxygen between the upstream and downstream compartments was calculated using the formula modified from McDiffett et al. (1972):

(1) $X = \Delta C\ (F/A)$, where
X = rate of change ($g\ O_2\ m^{-2}\ hr^{-1}$)
C = dissolved oxygen ($mg\ l^{-1}$)
F = discharge ($m^3\ hr^{-1}$)
A = area of surface sediments (m^2)

The upstream-downstream calculations were applied to the chamber since it is essentially a small scale upstream-downstream technique without diffusion. Like the upstream-downstream method, results from the hyporheic chamber were expressed per meter square of surface sediment to compare results with the closed benthic chamber. Discharge through the sediments was determined using water velocity, the cross-sectional area of the chamber, and a conversion factor estimating the interstitial spaces of the sediment. The conversion factor was calculated from an estimate of the sediment porosity, the volumetric (V/V) ratio of water to sediment. Three sediment samples from each site were dried at 105° C for 24 hours, and porosity was determined via volume displacement (Fetter 1994). The area occupied by the interstitial spaces was determined by multiplying the mean ratio of water to sediments by the chamber volume. Net community productivity (NCP) was determined by calculating the mean rate of change during the daylight period. Community respiration (CR_{24}) was determined by calculating the mean rate of change from sundown to sunrise and extrapolating to a 24-hour period. Gross community productivity (GCP) was determined by multiplying CR per hour by the number of daylight hours and adding the NCP. Community metabolism (P/R) was determined by dividing GCP by CR_{24} (Bott et al. 1978).

Hyporheic chambers were used simultaneously with standard chambers, as described by Bott et al. (1978) and Bott in Hauer and Lamberti (1996). Results produced by each type of chamber were compared using analysis of variance. Chambers were also compared on an individual stream basis using Mann-Whitney U tests. The software package SYSTAT 5.0 was used for the analysis.

RESULTS

Gross community productivity

GCP values (± SE) obtained from the flow-through hyporheic chambers ranged from 1.57 ± 0.812 g O_2 m^{-2} day^{-1} at the AuSable River during the spring to 4.39 ± 0.29 g O_2 m^{-2} day^{-1} at the North Branch of the AuSable during midsummer (Table 1). Closed benthic chamber estimates were lower and ranged from 0.78 ± 0.04 g O_2 m^{-2} day^{-1} at the AuSable River in the spring to 2.11 ± 0.14 g O_2 m^{-2} day^{-1} at the Jordan River during the early fall. Measurements of GCP were significantly different between chambers on three of the six occasions with the hyporheic chamber always higher (Figure 3). The general trend from site to site appeared to be similar between chambers with the exception of the North Branch of the AuSable River. The hyporheic GCP values observed at the North Branch of the AuSable River were the highest values measured over the course of the investigation. This was not the case with the benthic chamber. When all sites were combined for analysis of variance, blocking for river, there was a significant difference ($p < 0.05$) in GCP between the two chamber types (Table 2). The flow-through hyporheic chamber measured higher GCP on every occasion, although variance between replicates was also higher.

Community respiration

Mean CR_{24} (± SE) measured with the flow-through hyporheic chamber ranged from 32.75 ± 22.71 g O_2 m^{-2} day^{-1} at the AuSable River during the spring to 7.13 ± 0.13 g O_2 m^{-2} day^{-1} at the Red Cedar River in early summer (Table 1).

Table 1. A comparison of values determined with the flow-through hyporheic chamber with values obtained for Bott et al. Standard benthic chambers. Values are means and standard errors for community respiration (CR_{24}), gross community productivity (GCP), and P/R values for sites on four Michigan Rivers.

20 cm deep hyporheic chambers with flow through the sediments

	CR_{24} ($g\ O_2\ m^{-2}\ day^{-1}$)	standard error	GCP ($g\ O_2\ m^{-2}\ day^{-1}$)	standard error	P/R (GCP/CR_{24})	standard error
AuSable R. (5/17/96) n=3	32.75	±22.71	1.57	±0.812	0.06	±0.01
AuSable R. (7/17/96) n=2	11.32	±2.47	2.44	±0.61	0.21	±0.07
N.B.AuSable (7/16/96) n=3	23.18	±7.6	4.39	±0.29	0.22	±0.05
Jordan R. (9/5/96) n=3	9.60	±2.39	3.58	±0.60	0.42	±0.13
N.B.AuSable (6/26/97) n=3	19.89	±11.23	3.82	±1.12	0.26	±0.07
Red Cedar R. (6/8/97) n=2	7.13	±0.70	2.97	±0.80	0.41	±0.07

Bott *et al.* (1978) recommended benthic chambers with flow over the sediments

	CR_{24} ($g\ O_2\ m^{-2}\ day^{-1}$)	standard error	GCP ($g\ O_2\ m^{-2}\ day^{-1}$)	standard error	P/R (GCP/CR_{24})	standard error
AuSable R. (5/17/96) n=5	0.65	±0.04	0.78	±0.04	1.2	±0.05
AuSable R. (7/17/96) n=4	1.45	±0.19	1.43	±0.09	1.02	±0.11
N.B.AuSabe (7/16/96) n=4	1.00	±0.04	1.34	±0.12	1.34	±0.14
Jordan R. (9/5/96) n=3	0.57	±0.05	2.11	±0.14	3.78	±0.52
N.B.AuSabe (6/26/97) n=3	0.94	±0.22	1.11	±0.33	1.16	±0.06
Red Cedar (6/8/97) n=3	0.63	±0.23	0.96	±0.39	1.56	±0.21

Table 2. Analysis of variance, blocking for the effects of river and date, for community respiration (CR) and gross community productivity (GCP) calculated using SYSTAT version 5.0. CR and GCP measured using hyporheic chambers were significantly different ($p < 0.05$) from values measured with closed benthic chambers. Hyporheic chambers estimated higher CR and GCP.

Dependent Variable: Community Respiration n=38 Multiple R: 0.631 Squared Multiple R: 0.399

Source	Sum-of-Squares (Type III)	DF	Mean-Square	F-Ratio	P
Block	0.894	5	0.179	0.635	0.675
Chamber	4.948	1	4.948	17.567	0.000
Error	8.731	31	0.282		

Dependent Variable: Gross Community Productivity n=38 Multiple R: 0.802 Squared Multiple R: 0.643

Source	Sum-of-Squares (Type III)	DF	Mean-Square	F-Ratio	P
Block	11.520	5	2.304	2.851	0.031
Chamber	29.813	1	29.813	36.888	0.000
Error	25.054	31	0.808		

Values were much lower when measured with the closed benthic chamber, ranging from 1.45 ± 0.19 g O_2 m^{-2} day^{-1} at the AuSable River during midsummer to 0.57 ± 0.05 g O_2 m^{-2} day^{-1} at the Jordan River in early fall. The hyporheic chamber measured CR_{24} significantly higher on every occasion and like GCP measurements, variance was also much higher (Figure 4). There did not seem to be a similar general trend between chambers from site to site although this would be difficult to detect because it may be masked by the variance of the hyporheic chamber. When all sites were combined for

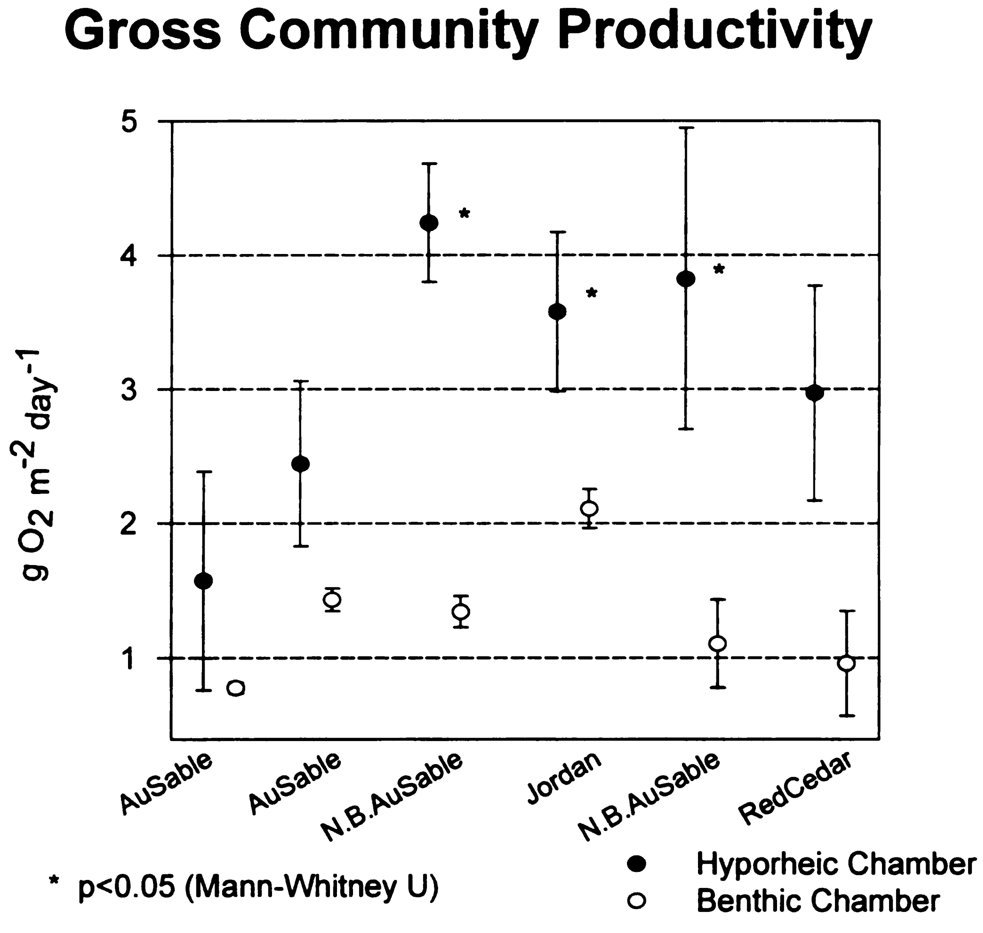

Figure 3. Gross community productivity (GCP) was measured using hyporheic and benthic chambers simultaneously on six occasions. Results from individual streams were compared using Mann-Whitney U tests. There were significant differences between chambers at the N.B. of the AuSable River and the Jordan River.

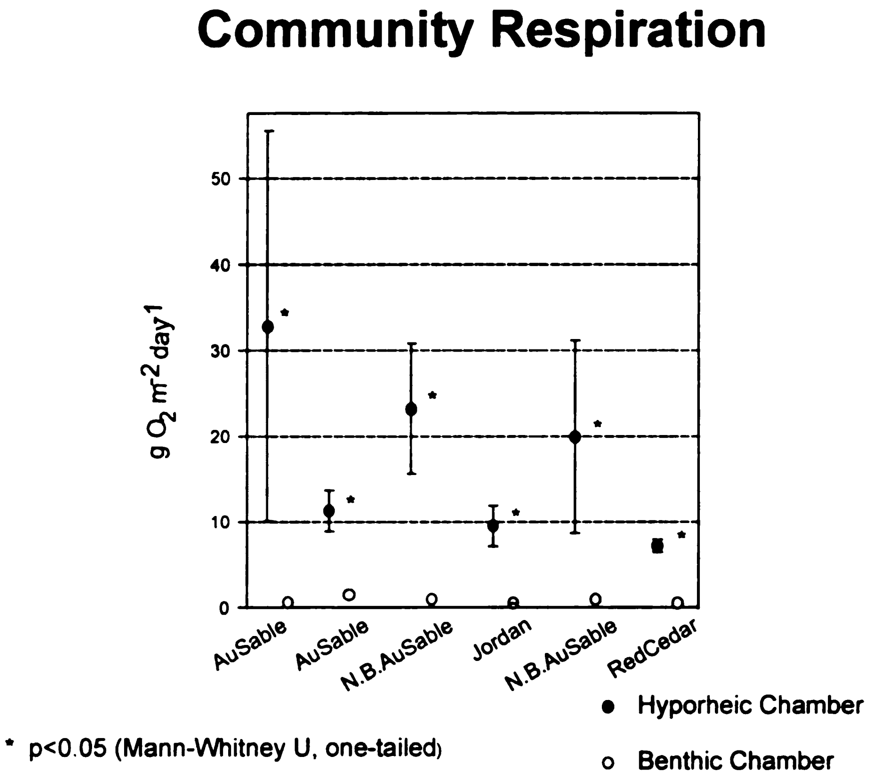

Figure 4. Community respiration (CR_{24}) was measured using hyporheic and closed benthic chambers in a series of side-by-side experiments. Results were compared using Mann-Whitney U tests. On every occasion, hyporheic chambers estimated significantly higher CR_{24} values.

analysis of variance, blocking for river, there was a significant difference ($p < 0.05$) in measured CR_{24} between the two chambers (Table 2).

P/R values

P/R values always suggested heterotrophy when measured with the flow-through hyporheic chamber. Values ranged from 0.42 at the Jordan River in early fall to 0.06 at the AuSable River during spring (Table 2). Conversely, benthic chambers predicted autotrophy on every occasion with values ranging from 3.78 at the Jordan River in early fall to 1.02 at the AuSable River during midsummer. P/R values were significantly different ($p < 0.05$) on every occasion (Figure 5). The two chambers seemed to produce similar trends with respect to P/R values from site to site with the exception of the AuSable River during the summer.

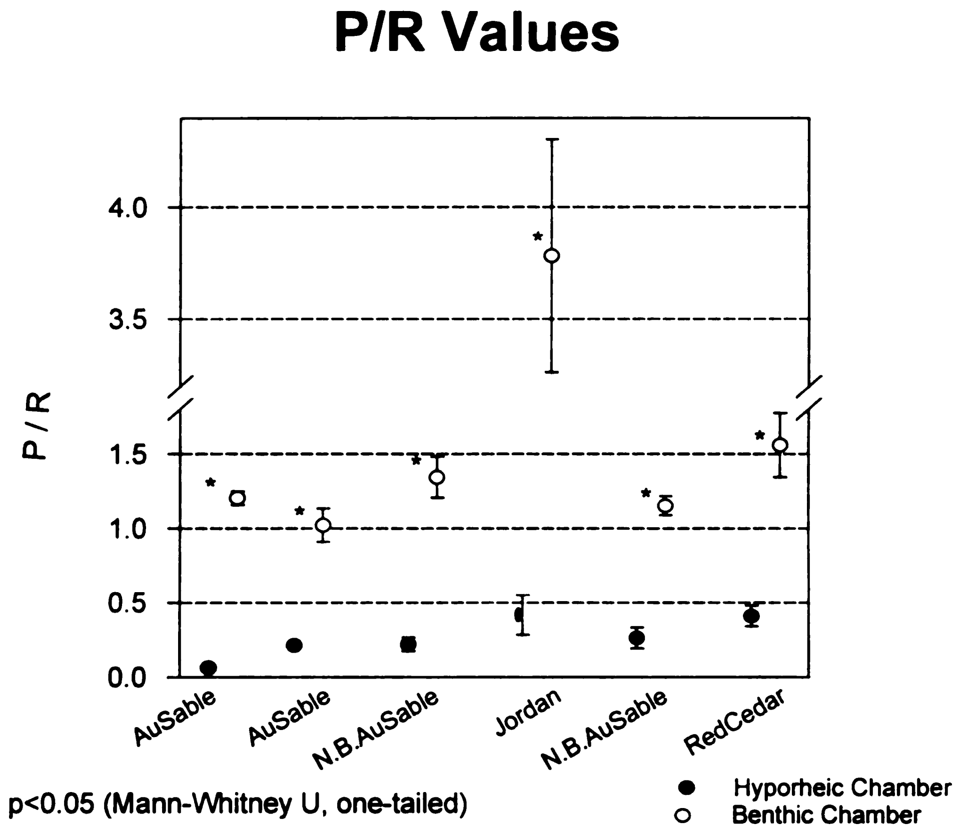

Figure 5. P/R values were estimated using hyporheic and closed benthic chambers simultaneously in a series of side-by-side experiments. Significant differences ($p < 0.05$) in measured values using each type of chamber were observed on all occasions. Hyporheic chambers always predicted heterotrophy while closed benthic chambers predicted autotrophy.

DISCUSSION

Gross community productivity

Estimates of GCP produced by each type of chamber were significantly ($p < 0.05$) different on three of the six occasions. When the sites were combined for analysis of variance, there was a significant ($p < 0.05$) difference between chambers. Hyporheic chamber estimates of GCP were higher on every occasion. However, differences between chamber estimates of GCP did not increase hyporheic chamber P/R estimates with respect to Benthic chamber estimates as might be expected. In fact, higher GCP estimates measured using the hyporheic chamber still resulted in significantly lower P/R estimates. Therefore, the hyporheic chamber estimates of P/R were conservative with respect to autotrophic benthic chamber estimates since the hyporheic chamber measured higher GCP.

Community respiration

CR was always at least an order of magnitude higher when measured with the flow-through hyporheic chamber. These measurements only included 20 cm of the hyporheic zone. Many studies suggest that the hyporheic zone often extends to much greater depths than 20 cm in many streams (Grimm and Fisher 1984, Rutherford and Hynes 1987, Ford and Naiman 1989, Triska et al. 1989a, Triska et al. 1989b, Triska et al. 1990, Hendricks and White 1991, Stanford and Ward 1993, Hendricks and White 1995, Jones et al. 1995) which may make these estimates of CR_{24} extremely conservative. The estimates of CR_{24} at the Red Cedar likely included the entire hyporheic zone. A uniform layer of heavily consolidated clay was found below five cm in all sediment samples used in hyporheic chambers at the Red Cedar. These data support the fact that the hyporheic zone did not contribute as much to CR_{24} at this site since CR_{24} measured using hyporheic chambers was lowest at this site even though it undoubtedly had the most associated anthropogenic disturbance and probably the highest nutrient concentrations. The pronounced differences in CR_{24} between the two chamber types may be an indication of a very active but not extensive hyporheic zone. Evidence provided by this study and Mulholland et al. (1997) indicates that the extent of the hyporheic zone seems to be an important determinant of CR_{24} within stream reaches.

P/R values

On every occasion hyporheic chambers predicted heterotrophy ($P/R < 1$) while benthic chambers predicted autotrophy ($P/R > 1$). GCP and CR_{24} measured with the hyporheic chambers showed a great deal of variance between replicates within a single riffle. When the two parameters were put together as P/R values the variance was greatly decreased, this remained true, even when an arcsine squareroot transformation was used. It was noted that when a single replicate showed high GCP, CR_{24} was also high. The converse was also true when GCP was low for a given chamber. Jones et al. (1995) also concluded that hyporheic respiration was tightly linked to surface production. This may be due to leaching of streamwater DOC, as a result of surface productivity, into the sediments locally stimulating hyporheic respiration.

These data suggest that even relatively unimpacted medium size alluvial rivers in Michigan may be heterotrophic. This observation leads to questions concerning the reliability of current predictions regarding P/R ratio changes along a river continuum, and emphasizes the need to include the hyporheic zone in studies of stream metabolism.

CHAPTER 2

Metabolism in a 3rd-order stream: a comparison of Methods

INTRODUCTION

Closed benthic chambers as described by Bott et al. (1978) and diurnal oxygen curves or the upstream-downstream method (Odum 1958) are both widely accepted methods of measuring stream metabolism. The two methods have often been used interchangeably. In fact, the study reach of interest or availability of specialized equipment often dictates which method is used (Bott 1996). Benthic chambers are often favored where lateral inflow is high, oxygen diffusion across the air-water interface is expected to be high, or an indication of variance is required. The upstream-downstream method may be favored where a range of habitat types are to be incorporated in the measurement, or a nutrient limitation is expected to occur if closed benthic chambers are used. Unfortunately, the two methods can give conflicting results when used in conjunction (Bott et al. 1978; Grimm and Fisher 1984; Pusch and Schwoerbel 1994). In light of recent findings of significant respiration in the hyporheic zone, it is not surprising that results would conflict. After all, the two methods measure different portions of the stream. Bott et al. (1997) suggest selecting a method most consistent with the experimental objectives ranging from micro- to macro-habitats.

The upstream-downstream method should theoretically include hyporheic respiration so long as there is return flow from the hyporheic zone within the study reach.

However, the upstream-downstream method has been criticized because it relies heavily on estimates of reaeration and much uncertainty accompanies these estimates. Recently improvements have been made to the upstream-downstream method. Marzolf et al. (1994) used both a conservative and volatile tracer, thus increasing confidence associated with reaeration calculations. In an attempt to produce an indication of variance associated with this method, McCutchan et al. (1998) suggested the use of a Monte Carlo approach to estimate the overall uncertainty by incorporating error associated with each individual measurement made to calculate metabolic parameters.

I developed a chamber technique that accounts for streambed metabolism including hyporheic respiration to a depth specified by the dimension of the chamber (chapter 1). The purpose of this experiment was to compare the results obtained simultaneously using the closed benthic chambers recommended by Bott *et al.* (1978) with results from the hyporheic chambers that I developed, and with results obtained using the upstream-downstream technique with the improvements recommended by Marzolf *et al.* (1994).

MATERIALS AND METHODS

Study Site

The study sites were located on the third-order Augusta Creek in Kalamazoo County, Michigan. The site studied in July 1997 and July 1998 was located at T. 1S. R. 9W. Sec 10. The stream is considered to be relatively pristine for the ecoregion. The 35 m reach of stream was approximately 10 m wide with a forested riparian zone providing a fairly dense canopy. The mean water depth of the reach was 0.10 to 0.15 m and flowed over a gravel/pebble streambed.

The Kellogg Forest site studied in September 1997 and September 1998 was located at T. 1S. R. 9W. Sec 22. This 30 m reach was approximately 10 m wide and also had a forested riparian zone, however, the canopy was not as dense as the site studied in July. The reach could be described as a very sandy low gradient run. The mean depth was approximately 0.41 m.

Methodology

The hyporheic and benthic chamber methods were used as described in chapter I. I used the upstream-downstream method slightly modified from Marzolf *et al.* (1994). Dissolved oxygen (D.O.) probes were placed in the thalweg and at the upstream and downstream ends of the study reach. Downstream D.O. concentration were measured one reach travel time following each upstream measurement. Measurements were made hourly for 24 hours. The difference between the upstream and downstream concentrations are thought to be caused by dilution, chemical oxygen demand, metabolism and reaeration flux of oxygen. Rhodamine-WT, a conservative tracer, showed that dilution was insignificant within the reach. Lateral inflow was less than 1% in either study reach. Chemical oxygen demand was considered to be insignificant leaving only metabolism and reaeration to account for changes in D.O. Therefore, hourly readings were corrected for reaeration using calculations developed with a continuous injection of a conservative tracer and propane, a volatile tracer of air-water gas exchange.

Rhodamine-WT was used to determine in-stream flow rate, lateral inflow, and the reach water travel time (τ). Reach water travel time determined the sampling interval between the upstream and downstream stations, and the length of time required for propane concentrations to reach steady-state (four times τ). A solution of 1.14 g/L Rhodamine-WT was dripped into the stream from an 18-L Mariotte bottle at four ml/sec 150 m upstream of the sample reach. Water samples were taken simultaneously at the upstream and downstream stations every 15 seconds beginning at the time of injection. Sampling continued until steady- state was achieved. Grab-samples were collected in six-dram glass sample vials at six tenths the depth and in the thalweg. Samples were left standing until sediments settled and a constant temperature was achieved before they were measured using a Turner Designs fluorometer. Percent lateral inflow was determined as the percentage decrease in dye concentrations between upstream and downstream sites at steady-state . Reach water travel time was determined by the difference in half-height concentration at steady-state. Discharge measurements were made using a Marsh-McBirney flow meter. The Rhodamine-WT procedure was carried out one to two days before the upstream-downstream technique was administered during base-flow conditions between storm events, when stream depths were relatively constant from day to day. Thus, reach travel time was assumed to have changed very little from the time the Rhodamine-WT procedure was carried out to the time of the community metabolism study.

Propane was bubbled into the stream from a 20-lb tank containing HD-5 (the common commercial propane containing 96% propane and 4% ethane) through two-m long perforated hoses. Most of the ethane was bled off before starting. Propane was injected for four times τ to reach steady-state concentration before water samples were collected. Water samples from the upstream and downstream sites were collected one τ interval apart. This ensured that the same water mass was sampled, guarding against fluctuations in injection rates. Grab samples were collected using horizontal bottle samplers. Water was transferred to 125-ml Boston round screw-cap bottles, overflowing the bottle three times its volume. Bottles were then sealed using open-hole caps equipped with a TFE/silicone liner. Samples were immediately taken to the lab and propane concentrations were determined using gas chromatography. An eight-ml helium headspace was added to each sample before they were shaken to allow dissolved propane to equilibrate with the helium headspace. A portion of the headspace was injected into a gas chromatograph equipped with a flame ionization detector, using helium as a carrier. The integrated areas of the propane peaks were used directly in the reaeration coefficient (RC) calculations, instead of actual concentrations. The conservative and volatile tracers were not injected into the stream simultaneously. The following equation was used to calculate the propane exchange coefficient,

$$(1)\ (k_{propane}):\ k_{propane}\,(\text{min}^{-1}) = \tau^{-1} * \ln\left\{(G_1 * C_2)/(G_2 * C_1)\right\}$$

where τ is the water travel time through the riffle, G_1 is the steady-state concentration of propane at the upstream station, G_2 is the steady-state concentration of propane at the downstream station, C_1 is the steady-state concentration of the conservative tracer at the upstream station, and C_2 is the steady-state concentration of the conservative tracer at the downstream station. The oxygen exchange coefficient (k_{oxygen}) was calculated as (2) $k_{oxygen} = 1.39 * k_{propane}$. Rathbun et al. (1978) demonstrated that the relationship between $k_{propane}$ and k_{oxygen} is independent of mixing conditions, temperature, and water quality.

The instantaneous oxygen flux into or out of the stream is calculated using, (3) Reaeration flux = $DO_{deficit} * -k_{oxygen} * \tau$ (Young and Huryn 1998; Marzolf et al. 1998) where k_{oxygen} = RC (min^{-1}), $DO_{deficit} = DO_{Saturated} - DO_{measured}$ (mg of O_2 per L), and τ = stream water travel time (min). The $DO_{deficit}$ is the difference between the calculated oxygen saturation value and the mean of the upstream and downstream measurements. Saturation value was calculated using the water temperature and the atmospheric pressure.

The following day, in-stream DO concentrations were measured using YSI oxygen meters and polarographic sensors. The meters were air calibrated before being placed side by side in the stream where fine adjustments were made to ensure that each meter read identical concentrations. Probes were fastened to stakes placed in the thalweg at the upstream and downstream stations. Time, temperature, and dissolved oxygen concentrations were recorded hourly for 24 hours. $DO_{Saturated}$ was calculated using the average stream temperature, barometric pressure, and elevation. The $DO_{deficit}$ was calculated as the difference between $DO_{Saturated}$ and the averaged upstream and downstream concentration. The following metabolic parameters were calculated: Dark metabolism = ΔDO_{dark} - reaeration; Net community productivity (NCP) = ΔDO_{light} - reaeration; Gross community primary productivity (GCP) = NCP + $respiration_{light}$; Community respiration (CR_{24}) = Average night Resp. scaled for 24 hours; Net daily metabolism (NDM) = GCP - CR_{24}; and P/R = GCP/CR_{24}. The change in D.O. (ΔDO) was calculated as the difference between the upstream and downstream values.

RESULTS AND DISCUSSION

Net Community Productivity

All three techniques directly measured net community productivity (NCP) during daylight hours. Using oxygen as a surrogate for photosynthesis, NCP can be defined as the amount of oxygen either produced or consumed during the period from sunrise to sunset. This parameter is free from error associated with extrapolating either gross production or 24-hour respiration estimates. Every data point recorded during the daylight period using the closed benthic chamber was a direct measure of NCP for a one-hour period. Data points recorded using the upstream-downstream and hyporheic chamber techniques were instantaneous NCP readings and were used to represent an average for a particular hour.

Net community productivity estimates made in 1998 were very similar to estimates made in 1997 for each method (Figure 6). The greatest difference between 1997 and 1998 was observed using the upstream-downstream technique at Kellogg Forest in September. This difference may be due to increased error associated with this method when it is reduced to a single station. The 1997 September upstream-downstream method had to be reduced to a single station technique since there was not a significant difference between upstream and downstream dissolved oxygen concentrations. Differences were detected using a paired t-test at that site in 1998 and therefore, the two-station technique was employed as recommended by Bott (1996). Two-station upstream-downstream calculations were possible during both July 1997 and 1998 measurements.

I re-calculated all of the NCP values using the single-station equations and found

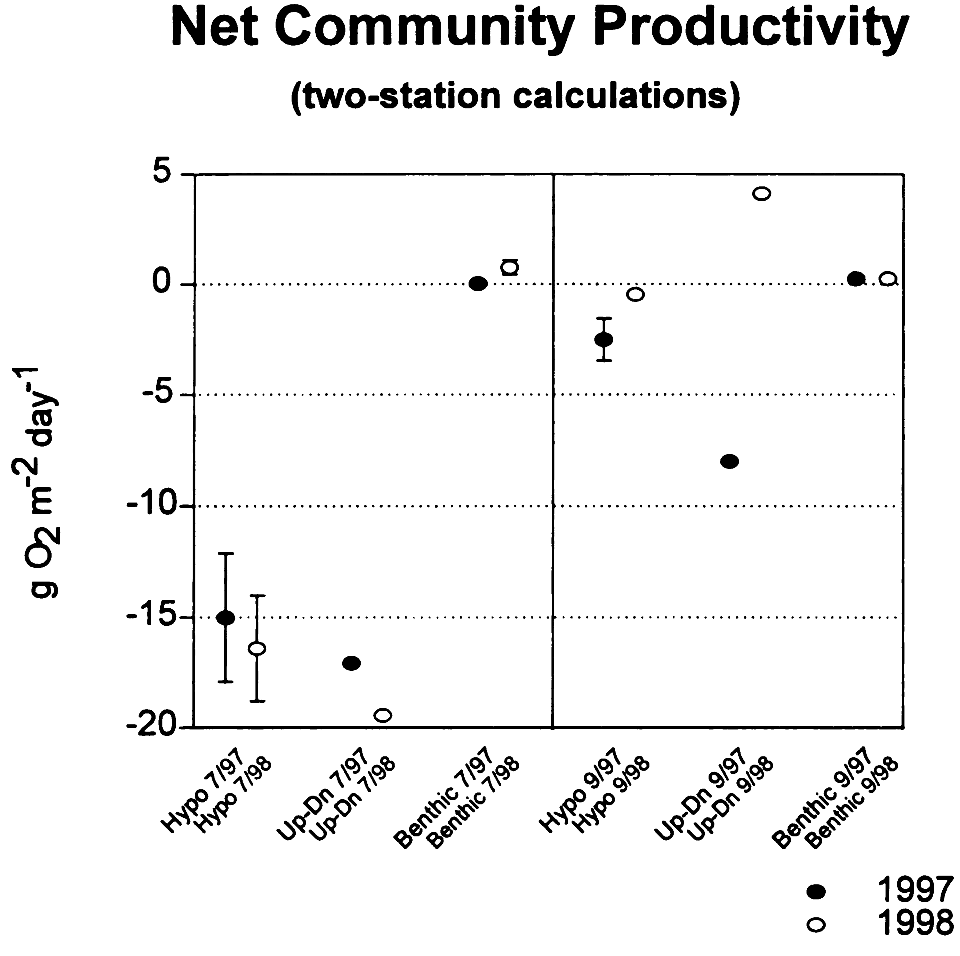

Figure 6. Net community productivity was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. Both the July Augusta Creek site and the September Kellogg Forest Augusta Creek site were monitored in 1997 and 1998. The upstream-downstream estimates were made using two-station calculations.

that the standard error around these means increased (Figure 7). Calculating both 1997 and 1998 September data sets using the single-station equations instead of one calculated as a two-station and the other as a single-station reduced the difference between these two dates. This reduction is likely an artifact of using identical equations. The July comparison suggests that standard error around the September mean may have been reduced if two-station calculations were possible for both data sets.

I combined the replicates from both years for each method to statistically explore differences in methodology. I justified this because the 1997 and 1998 measurements within methods were very similar at both sites (Figure 8). Measurements from one year to the next were so similar that within-method variance was actually reduced when the years were combined. Caution should be used when analyzing results concerning the upstream-downstream method because the upstream-downstream method has an n value of only two. Unfortunately statistical analysis is not otherwise possible since the method cannot be replicated and the Monte Carlo approach of McCutchan et al. (1998) was not used.

The NCP values obtained using the upstream-downstream and hyporheic chamber techniques were not significantly different during the July (1997 and 1998 combined) experiment. Both methods produced significantly lower NCP values than the closed benthic chambers. The benthic chambers suggested that NCP was slightly greater than zero while the other two methods provided negative values. This is not surprising because the latter two methods include hyporheic respiration.

The lack of a significant difference between hyporheic chambers and the upstream-downstream techniques suggests that the mean depth of the hyporheic zone at the July

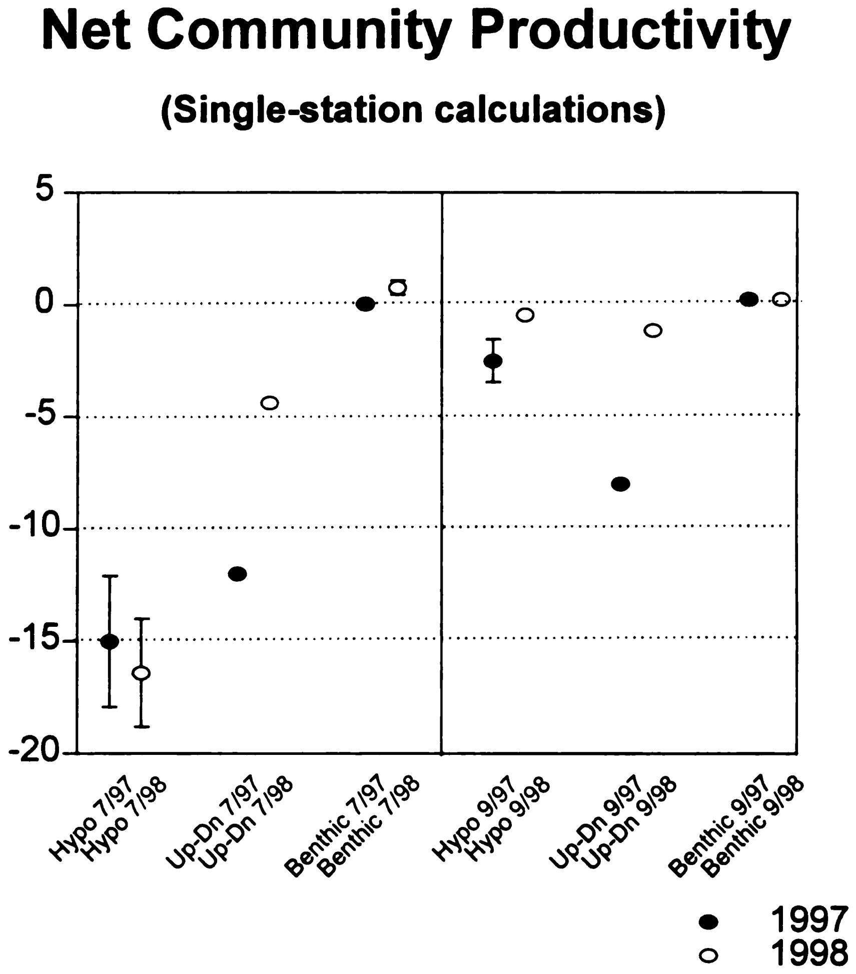

Figure 7. Net community productivity was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. The upstream-downstream estimates were made using single-station calculations. The July upstream-downstream estimates become more variable from 1997 to 1998 when single-station calculations were used.

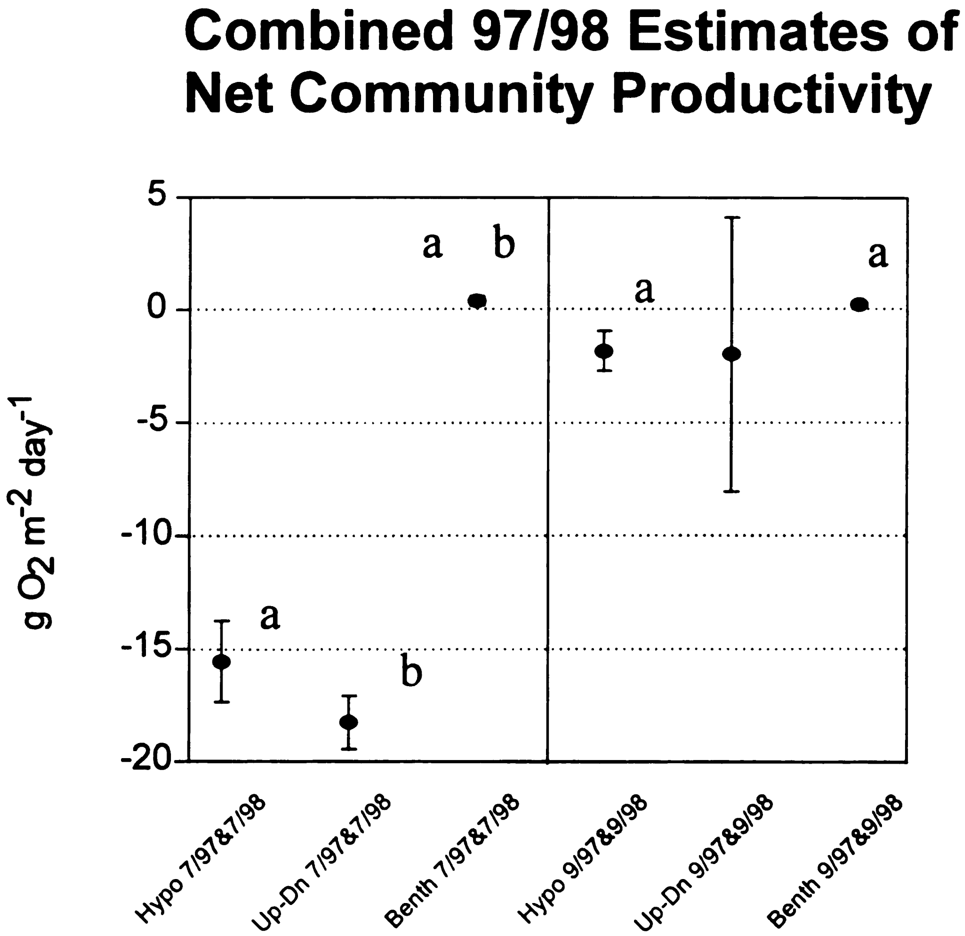

Figure 8. The replicates from 1997 and 1998 for each method were combined and compared statistically using a Mann-Whitney U test ($p < 0.05$). Since the upstream-downstream technique can not be replicated, n equals two for both sites. Alike letters indicate significant ($p < 0.05$) differences.

(1997 and 1998 combined) Augusta Creek site within the 36 m riffle section was approximately the same or slightly greater than the depth of the hyporheic chamber, or that the majority of the respiration took place in the top 20 cm of the hyporheic zone and a small percentage took place at depths greater than 20 cm. The large difference between the benthic chamber and the other two methods suggests that inclusion of hyporheic respiration significantly reduces NCP at this site. The benthic chamber measured approximately equal amounts of primary production and respiration at the streambed during the daylight hours. The inclusion of hyporheic respiration revealed an oxygen consumption rate during the daylight hours of approximately 15 to 20 grams per square meter per day.

Similar results were expected at the Kellogg Forest site in September (1997 and 1998 combined), but this was not the case. Similar to the combined July experiments, there was no significant difference between the upstream-downstream and hyporheic chamber techniques, and the hyporheic chamber produced significantly lower NCP values than the benthic chamber, but this time the upstream-downstream and benthic chamber techniques were not significantly different. All three of the methods produced NCP values very near zero at this site.

Between-method NCP values were very similar, and therefore, these data suggest that the mean depth of the hyporheic zone at Kellogg Forest was very small, likely only a few centimeters. Previous studies showed that water does not circulate through the sediments inside benthic chambers, so measurements of oxygen flux in the chambers reflect little or no hyporheic respiration. Particle size data supports the idea that the hyporheic zone was very small at this site. Fine surficial sediments in this 30 m run likely created anaerobic conditions just below the streambed.

Net Daily Metabolism

Net daily metabolism (NDM) is defined as gross community productivity (GCP) minus 24-hour community respiration (CR_{24}). Estimates of both GCP and CR_{24} involves extrapolating night-time respiration through daylight hours and therefore both include error associated with this extrapolation. Algal respiration in the light is not the same as it is in the dark, and photorespiration, or the enzymatic consumption of oxygen during the synthesis of glycolate, cannot be accounted for (Bott 1996). When CR_{24} is subtracted from GCP, the extrapolated respiration is removed. NDM is therefore free from errors associated with extrapolating respiration during the day and only expresses direct measures of NCP and night-time respiration.

NDM results followed similar patterns as NCP. Like NCP, within method measurements were very similar between 1997 and 1998. This indicates that not only were within method measurements made during the daytime similar, as shown by NCP values, but also nighttime measurements were similar between 1997 and 1998 (Figure 9). Again the greatest difference between years was observed using the upstream-downstream technique at Kellogg Forest and can likely be attributed to the differences in single-station and two-station calculations. The difference between years at Kellogg Forest using the upstream-downstream method is reduced when both measurements are calculated as single-station methods (Figure 10), but the two-station method is considered to be more reliable and should be used when possible. When the replicates from both years at the July August Creek site were combined, the hyporheic chamber and upstream-

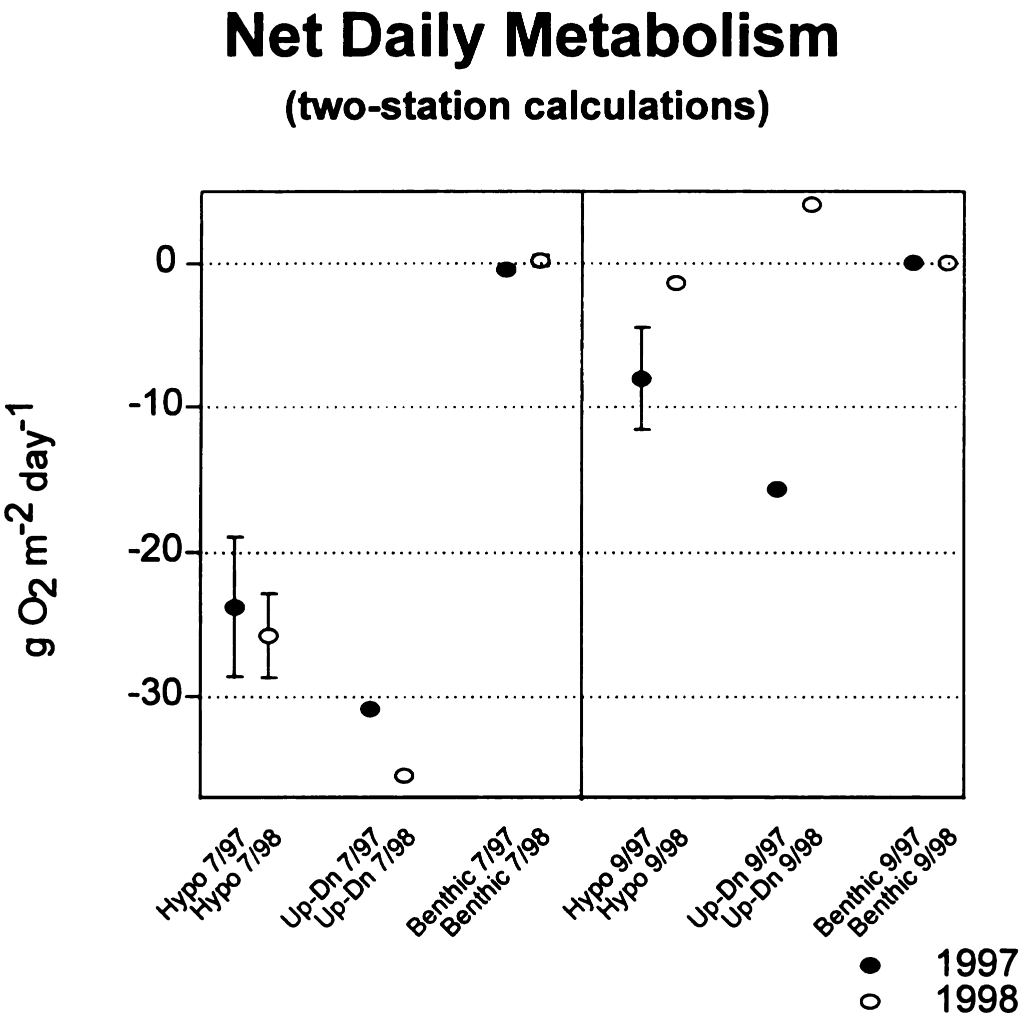

Figure 9. Net daily metabolism was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. Both the July Augusta Creek site and the September Kellogg Forest Augusta Creek site were monitored in 1997 and 1998. The upstream-downstream estimates were made using two-station calculations.

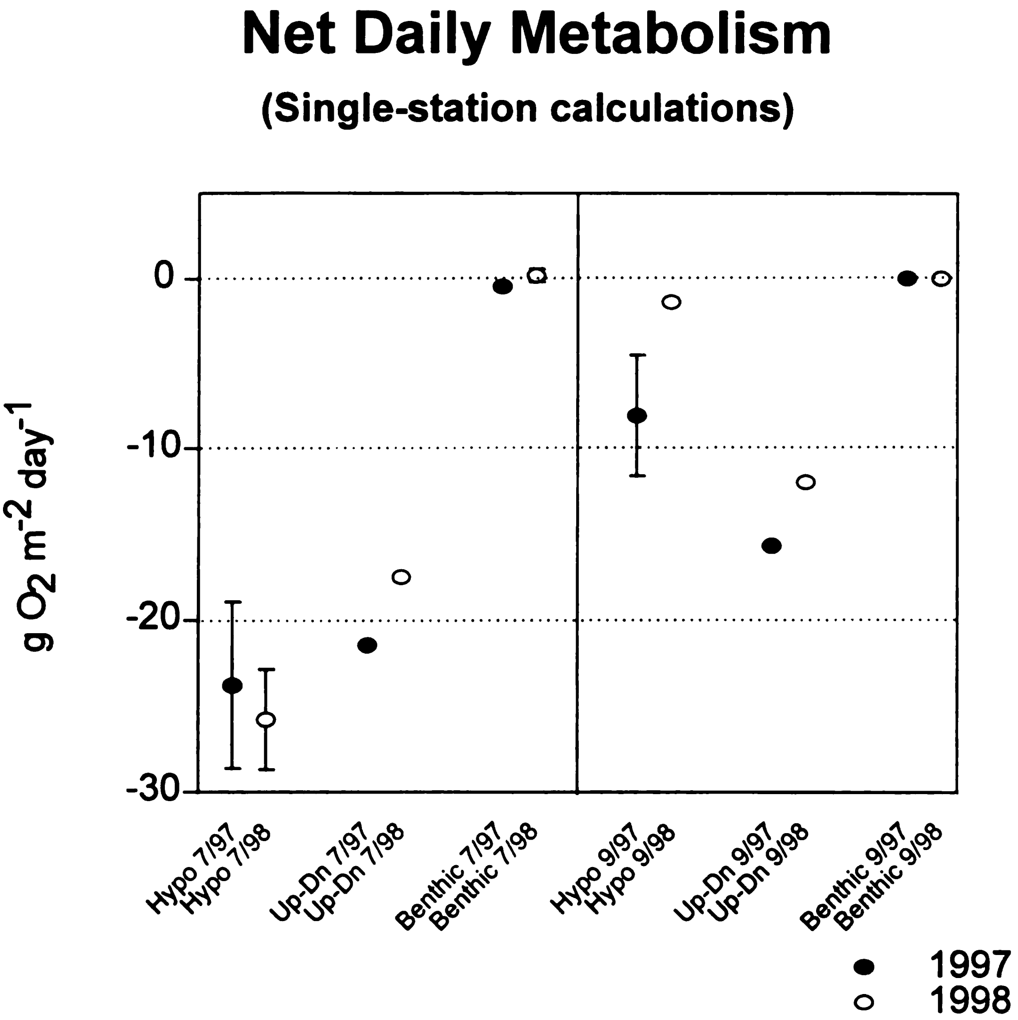

Figure 10. Net daily metabolism was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. The upstream-downstream estimates were made using single-station calculations.

downstream methods produced results that were not significantly different from each other. Both were significantly less than benthic chamber estimates (Figure 11).

Neither the hyporheic nor the benthic chambers produced significantly different NDM values from the upstream-downstream method at the September Kellogg Forest site, but they were significantly different from each other. The hyporheic chamber showed significant but only slightly lower NDM than benthic chambers at this site. The relationship between measures of NDM among techniques was nearly identical to the relationship between measures of NCP, except the difference, although not significant, between the hyporheic and the upstream-downstream methods appears slightly larger. Since NDM can be reduced algebraically to NCP minus Cr_{night}, it appears as if the upstream-downstream method measured slightly more respiration than the hyporheic chamber. Based on these un-extrapolated parameters, we can assume that the differences between methods were only due to differences in measured respiration, or that differences in respiration far outweighed any differences in measured productivity. These conclusions are based on the fact that primary productivity is only measured during the day while respiration is measured both day and night. Very similar patterns were observed between NCP measured only during daylight and NDM measured both day and night. Also, the most pronounced differences in NCP and NDM are between the benthic chamber and the other two techniques at the July Augusta Creek site. This difference is almost certainly due to difference in measured respiration. By design these methods measure different amounts of CR.

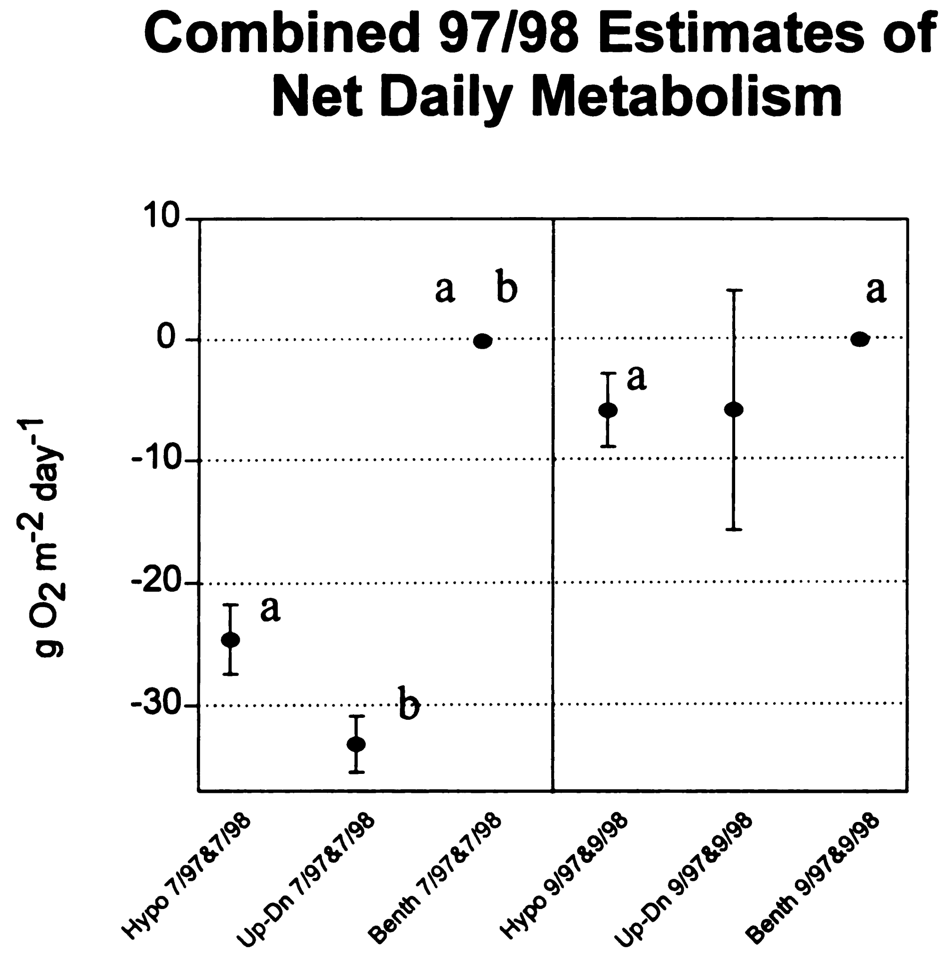

Figure 11. The replicates from 1997 and 1998 for each method were combined and compared statistically using a Mann-Whitney U test ($p < 0.05$). Since the upstream-downstream technique can not be replicated, n equals two for both sites. Alike letters indicate significant ($p < 0.05$) differences.

Community Respiration

Community Respiration (CR_{24}) is defined as the amount of respiration measured at night plus nighttime respiration extrapolated through the daylight hours. CR_{24} does not account for differences in algal respiration in the light versus the dark.

Measures of CR_{24} made in 1998 using each method compared well to the previous year (Figure 12). Again I combined replicates from each year for comparison. At the July Augusta Creek site, the relationship of CR_{24} results between methods was the inverse of the trend observed with NCP and NDM. This supports the idea that respiration was the major factor controlling differences between methods. The upstream-downstream method measured the highest CR_{24} at 38.0 mg O_2 m^{-2} day^{-1} , the hyporheic chamber followed with 24.6 mg O_2 m^{-2} day^{-1} and finally the benthic chamber CR_{24} was 1.3 mg O_2 m^{-2} day^{-1} (Figure 13). All three methods produce results significantly different from each other.

The three methods used simultaneously can estimate the mean depth of the hyporheic zone within the 35 m reach. CR_{24} associated with surface sediments was 1.3 mg O_2 m^{-2} day^{-1} therefore, hyporheic respiration down to 20 cm of depth was 23.7 mg O_2 m^{-2} day^{-1}, or 24.6 mg O_2 m^{-2} day^{-1} minus 1.3 mg O_2 m^{-2} day^{-1}. I recommend subtracting surface respiration because respiration associated with combined heterotrophs and autotrophs is not likely comparable to heterotrophic respiration of the hyporheic zone. While Fuss and Smock (1996) found that 70% of whole stream respiration occurred in the hyporheic zone, the metabolic rate per surface area of substrate was lower than other compartments. Other studies have found similar respiration rates at the streambed and in the hyporheic zone on an aerial basis (Grimm and Fisher 1984; Pusch and Schwoerbel

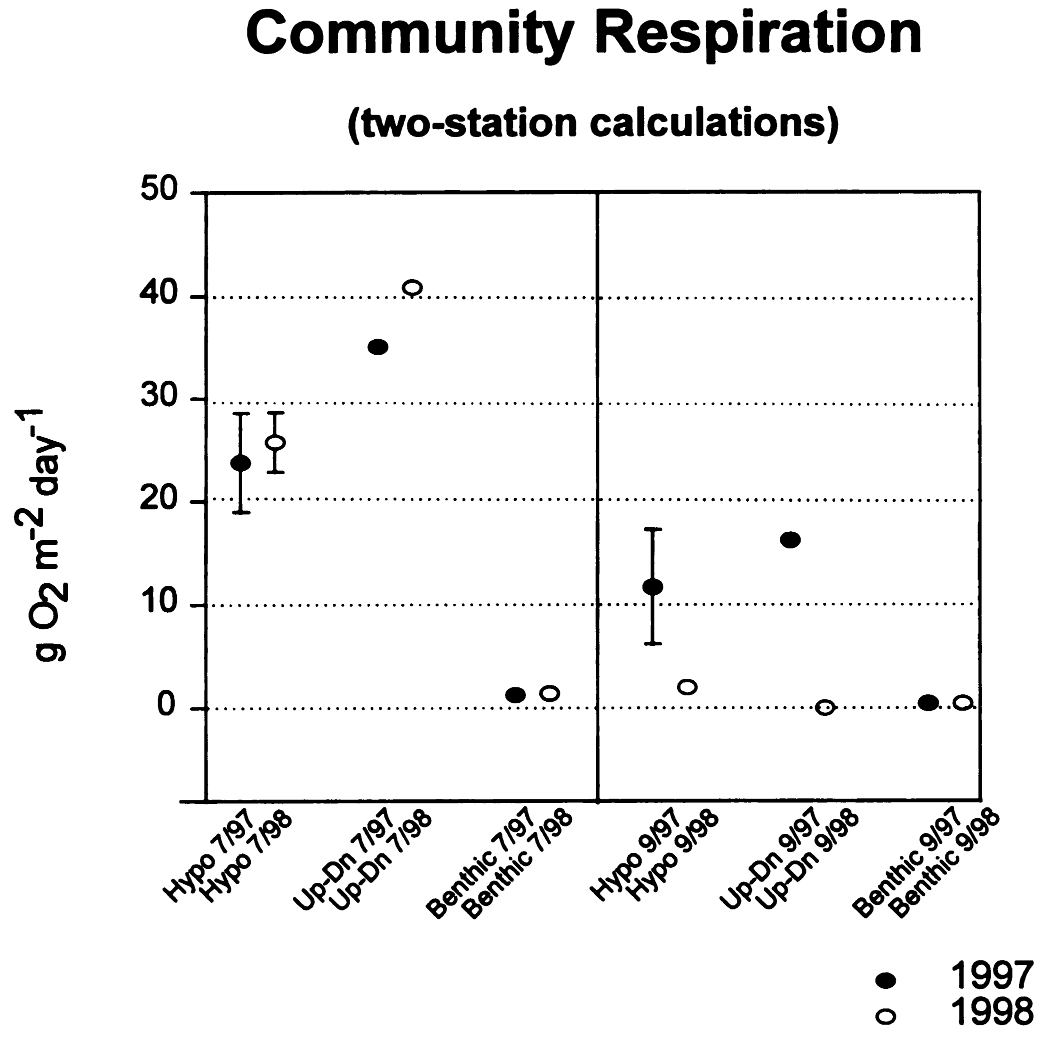

Figure 12. Community Respiration was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. Both the July Augusta Creek site and the September Kellogg Forest Augusta Creek site were monitored in 1997 and 1998. The upstream-downstream estimates were made using two-station calculations.

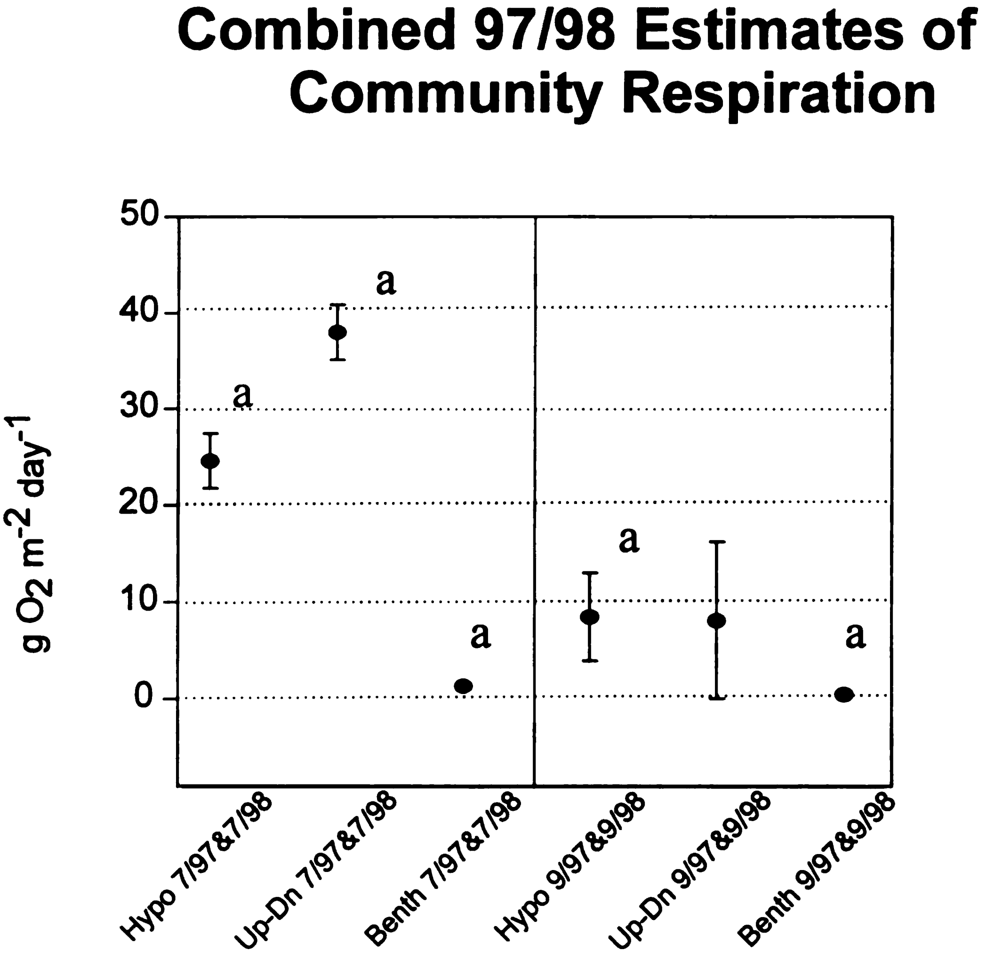

Figure 13. The replicates from 1997 and 1998 for each method were combined and compared statistically using a Mann-Whitney U test ($p < 0.05$). Since the upstream-downstream technique can not be replicated, n equals two for both sites. Alike letters indicate significant ($p < 0.05$) differences.

1994; Naegeli et al. 1995; Jones et al. 1995). I assumed that hyporheic respiration is relatively constant with depth and that the upstream-downstream method does account for all of the hyporheic respiration. The mean depth of the hyporheic zone was approximately 32 cm or 20 cm multiplied by 38.0 mg O_2 m^{-2} day^{-1} divided by 23.7 mg O_2 m^{-2} day^{-1}. The similarity of community respiration between years suggests that the depth of the hyporheic zone remained relatively constant at the July Augusta Creek site from 1997 to 1998.

The between-method CR_{24} values measured at Kellogg Forest in September also showed a pattern inverse of NCP and NDM when replicates were combined. There was no significant difference between the upstream-downstream method and the other two methods. The hyporheic and benthic chambers did, however, produce small but significantly different results.

Benthic chambers produced nearly identical results from 1997 to 1998. CR_{24} measurements made with the upstream-downstream method and hyporheic chamber in 1998 were quite lower than they were in 1997. It appears as if the depth of the hyporheic zone decreased from 1997 to 1998, and in fact, these data suggest that the hyporheic zone was nearly non-existent in 1998. Possible explanation for the decrease would include decreased stream water velocity through the reach increasing sedimentation, or an increase in ground water upwelling. The latter is very unlikely since the entire reach would have had to have an increase in upwelling and an increase of great enough magnitude to nearly eliminate oxygenated water from entering the sediments. This would not likely occur in one year, if at all. The reach was dominated by sandy sediments both years suggesting that the reach was likely a depositional area with low permeability.

Dole-Oliver (1998) suggested that exchange processes where distinct pool-riffle sequences are not present are controlled by channel bed porosity. Sediment data suggested that mean sediment size did not change. However, stream discharge and stream water velocity was lower during the 1998 experiment than it was during the 1997 experiment. On 13 September 1997 stream discharge was 0.82 m3/s and mean stream water velocity was 0.20 m/s. On 3 September 1998 stream discharge was 0.59 m3/s and stream water velocity was 0.15 m/s. The 3 September 1998 discharge and velocity was much lower than it was on 13 September 1997 but I have no evidence showing that the mean annual discharge or velocity at this site was actually lower in 1998. Another possible explanation involves construction of a span bridge only five meters downstream of the downstream station. Again, I have no evidence or reason to believe that construction of the bridge impacted the study area. There is also the possibility that the depth of the hyporheic zone in this reach varies with discharge to the extent that a decrease of 0.23 m^3/s nearly eliminated the hyporheic zone. It is difficult to say how realistic this explanation may be. It is not only realistic but probable that a change in discharge of this magnitude could reduce the depth of the hyporheic zone several centimeters. Unfortunately I can not be sure how deep the hyporheic zone was in 1997 because the upstream-downstream CR_{24} fell within the standard error of the mean hyporheic CR_{24}. Therefore, the depth of the hyporheic zone in 1997 was 20 cm or less. In 1998 the depth of the hyporheic zone must have decreased anywhere from a few to 20 cm from 1997.

An alternative explanation for the reduction in upstream-downstream CR_{24} is that the hyporheic zone did not decrease in size, but the microbial community within the zone was reduced. Young and Huryn (1996) found that discharge within a year can dramatically impact metabolism. Uehlinger and Naegeli (1998) observed bed-moving spates reducing both GCP and CR_{24}. GCP was much more impacted by the spate but recovered faster than CR_{24}. It is possible that a spate occurred prior to the run reducing GCP and CR_{24}, only GCP already recovered and CR_{24} had not. This explanation is unlikely since the run took place following a month of very limited rainfall.

Gross Community Productivity

Measures of GCP were also very similar from 1997 to 1998 at the July Augusta Creek site (Figure 14). In 1997 and 1998 GCP was non-detectable using the hyporheic chamber. This was actually determined a-priori with preliminary interstitial water velocity measurements. These measurements showed that the combination of chamber length and high velocity of interstitial water flow would demand D.O. probes that could detect changes at the 0.01 mg/l level. My probes did not have that capability. The chamber length was arbitrarily chosen for easy transport and handling and could easily be made longer when sensitive probes are not available. The upstream-downstream technique measured slightly but significantly higher GCP than the closed benthic chambers. The mean for the two years using the upstream-downstream method was 4.8 mg O_2 m^{-2} day^{-1} and the mean using the benthic chamber was 1.3 mg O_2 m^{-2} day^{-1}. There are several possible explanations for the inconsistency between methods. First, the upstream-downstream method may have included macrophyte primary production, but this is unlikely because no macrophytes were observed in that reach. Next, there may have been patches of high algal productivity with the reach caused by reduced flow

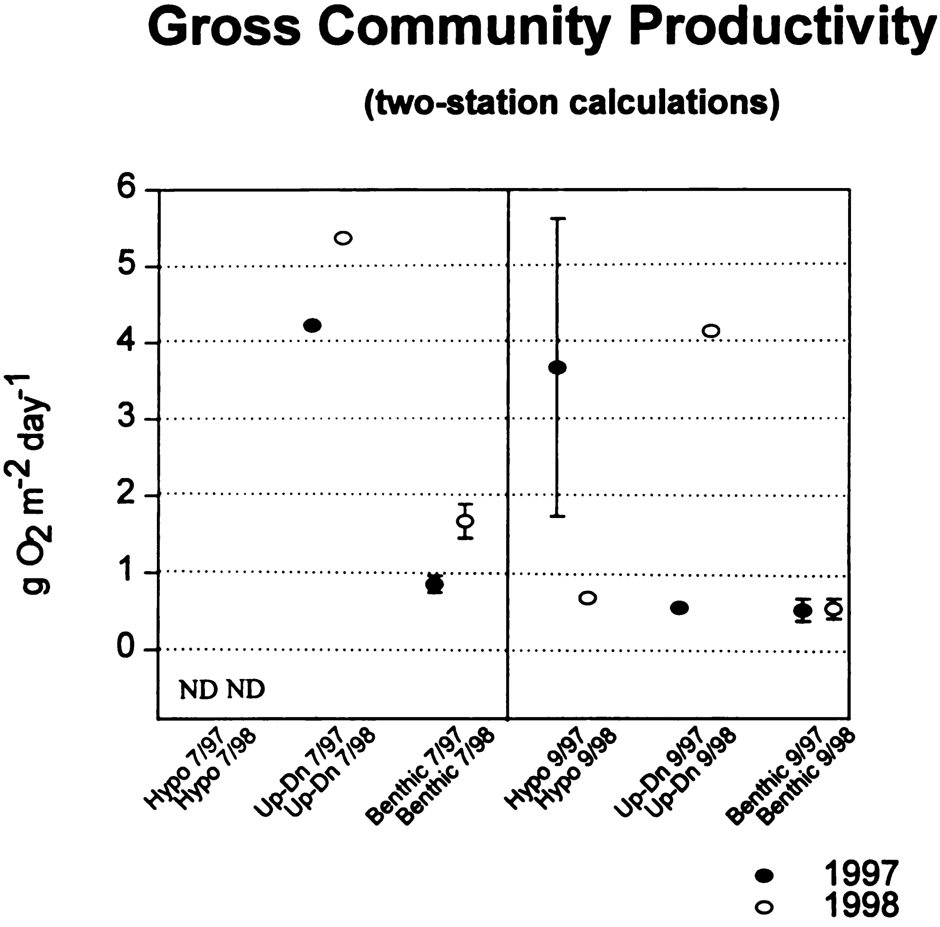

Figure 14. Gross community productivity was estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. Both the July Augusta Creek site and the September Kellogg Forest Augusta Creek site were monitored in 1997 and 1998. The upstream-downstream estimates were made using two-station calculations.

velocities or groundwater upwelling. However, there was no visible heterogeneity of primary production. Finally, a nutrient may have been periodically limiting primary productivity in the closed benthic chamber. The chambers were flushed when dissolved oxygen concentrations dropped below 5.0 mg O_2 m^{-2} day^{-1} or rose above 11.0 mg O_2 m^{-2} day^{-1}. While flushing will decrease the chance of a nutrient becoming limiting, I cannot be sure that a nutrient never became limiting during the experiment.

GCP measurements made at the September Kellogg Forest site were variable from 1997 to 1998 using the upstream-downstream and hyporheic chamber methods. Closed benthic chambers produced nearly identical GCP values in 1997 and 1998. When replicates from the two years were combined, there was no significant difference between the upstream-downstream method and the other two techniques (Figure 15). There was a small but significant difference between the hyporheic and benthic chambers with the hyporheic measurement slightly greater. The upstream-downstream technique produced a mean from both years of 2.3 mg O_2 m^{-2} day^{-1}, the hyporheic chamber produced a GCP of 2.6 mg O_2 m^{-2} day^{-1} and the benthic chambers measured 0.5 mg O_2 m^{-2} day^{-1}. Again, nutrient limitation occasionally occurring in the closed chambers seems to be the most likely explanation for the difference between techniques. One may argue that since benthic chambers produced the most repeatable results, as indicated by low standard error, that these results are the most accurate. In actuality, the relatively small standard error is a result of GCP being so near zero.

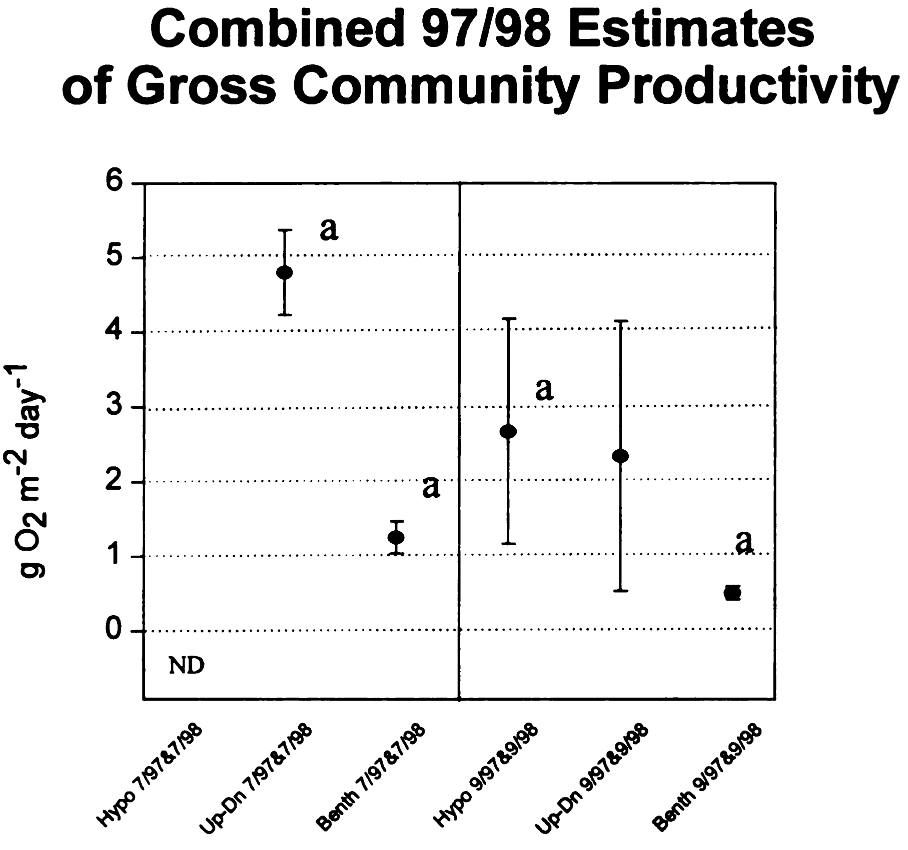

Figure 15. The replicates from 1997 and 1998 for each method were combined and compared statistically using a Mann-Whitney U test ($p < 0.05$). Since the upstream-downstream technique can not be replicated, n equals two for both sites. Alike letters indicate significant ($p < 0.05$) differences.

P/R values

P/R values are the ratio of GCP to CR_{24}. Within-method P/R values were similar between the 1997 and 1998 experiments with the exception of the upstream-downstream method in September at Kellogg Forest (Figure 16). I combined the replicates from each year keeping in mind that the extremely large variance associated with the upstream-downstream method in September was due to the 1998 experiment (Figure 17).

P/R did not apply to the hyporheic chamber at the July Augusta Creek site because GCP was non-detectable. However, NCP and NDM measurements using the hyporheic chamber suggested that P/R would have been very similar to upstream-downstream P/R. The mean P/R value using the upstream-downstream technique was 0.13, extremely heterotrophic, the mean benthic chamber value was 0.94, nearly autotrophic.

Upstream-downstream P/R was not significantly different from the other two methods at the Kellogg Forest site due to the extremely large variance associated with this mean. The 1997 upstream-downstream P/R value was 0.03 while the 1998 value was 108. The latter value is extremely high and obviously unrealistic. The value was probably the result of a combination of factors. The upstream-downstream method measured GCP higher than the other two methods in 1998. The technique may have measured macrophyte production missed by the other two methods. Small patches of *Nasturtium officinale* (watercress) were observed along the margins of the reach. On the other hand, the upstream-downstream method measured the lowest CR_{24} at this site in 1998. Fine sediment found in this reach resulted in a lower hydraulic conductivity. One chamber designated for just this purpose was used to measure velocity through the interstitial spaces. In 1998 interstitial velocity was 0.0004 m/s, a value identical to the

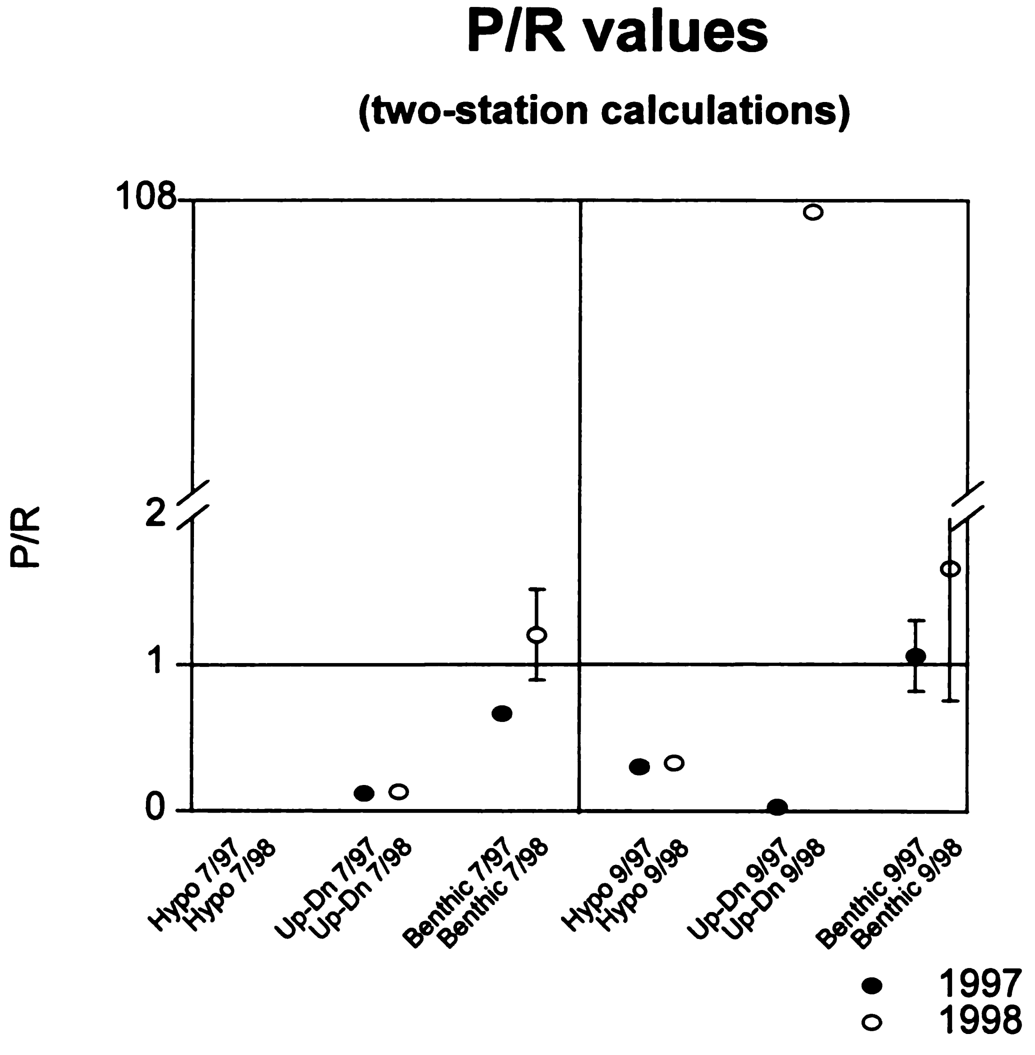

Figure 16. P/R values were estimated using the hyporheic chamber, benthic chamber, and the upstream-downstream technique. Both the July Augusta Creek site and the September Kellogg Forest Augusta Creek site were monitored in 1997 and 1998. The upstream-downstream estimates were made using two-station calculations.

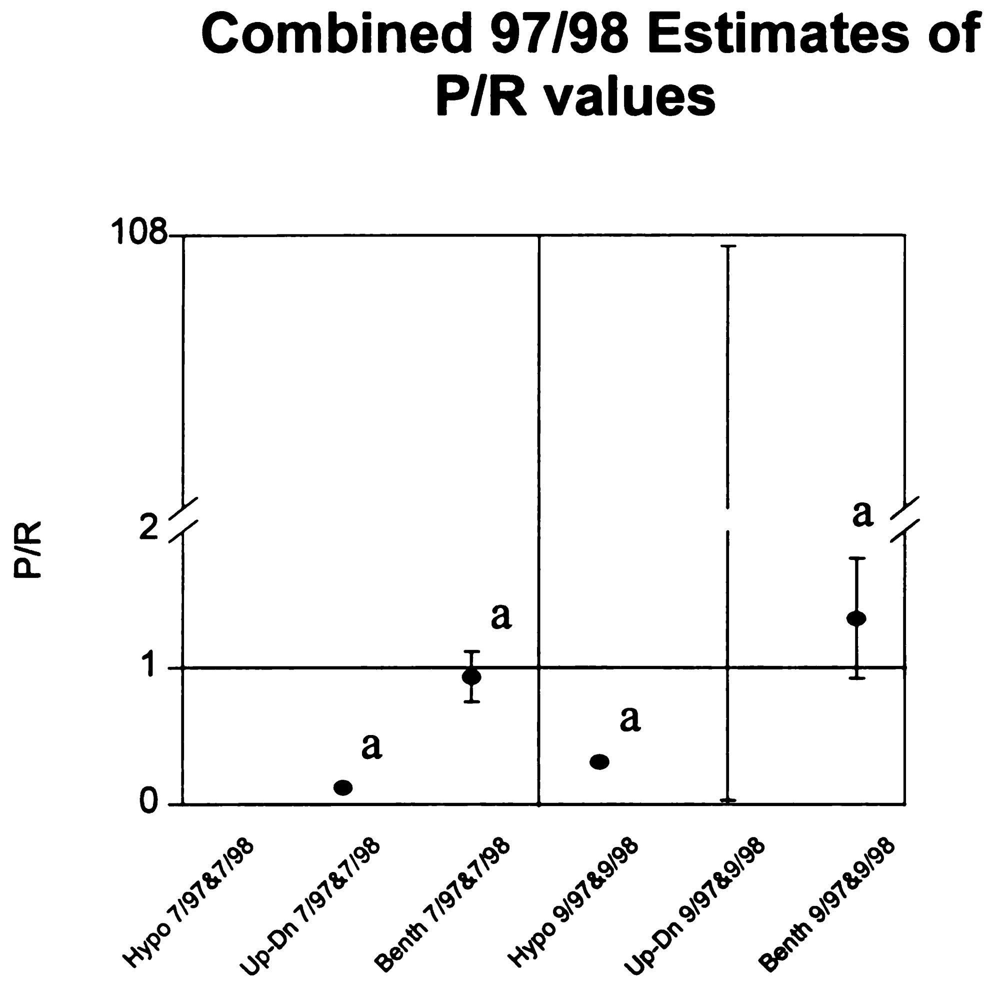

Figure 17. The replicates from 1997 and 1998 for each method were combined and compared statistically using a Mann-Whitney U test. Since the upstream-downstream technique can not be replicated, n equals two for both sites. Alike letters indicate significant ($p < 0.05$) differences.

velocity measured in 1997. Although exchange was not measured, a combination of lower discharge and low hydraulic conductivity at this site may have reduced exchange between surface and hyporheic water within the reach. This does not explain why the upstream-downstream method produced a CR_{24} value lower than the closed benthic chamber. CR_{24} measured with the benthic chamber was 0.48 O_2 m^{-2} day^{-1} and the upstream-downstream method yielded an estimate of only 0.04 O_2 m^{-2} day^{-1}. Perhaps this difference was due to sampling error. McCutchan et al. (1998) estimated that respiration values obtained using the upstream-downstream method in a low gradient stream with a low metabolic rate would be plus or minus 34% of the actual rate. They also pointed out that the precision and resolution of measurement used in their simulations would rarely be achieved in the field. Unfortunately, solid conclusions can not be drawn without replication.

The hyporheic chamber produced a significantly lower P/R estimate than the benthic chamber. The benthic chamber predicted autotrophy with a P/R value of 1.36 while the hyporheic chamber predicted heterotrophy with a P/R value of 0.31.

These data compare very well to previous metabolism measurements made at Augusta Creek. In 1973 through 1975, King and Cummins (1989) measured metabolism using closed benthic chambers at two sites, one approximately one kilometer upstream of the July Augusta Creek site and the other approximately one kilometer downstream of the Kellogg Forest site. Their CR_{24} estimates ranged from 0.24 to 0.94 mg O_2 m^{-2} day^{-1} near the July Augusta Creek site and 0.32 to 1.41 mg O_2 m^{-2} day^{-1} near the Kellogg Forest site. GCP ranged from -0.01 to 0.59 mg O_2 m^{-2} day^{-1} near the July Augusta Creek site and 0.53 to 2.16 mg O_2 m^{-2} day^{-1} near the Kellogg Forest site. Bott et al. (1985) also made seasonal metabolism measurements on Augusta creek using closed benthic chambers in 1976. Their CR_{24} values ranged from 1.53 to 2.66 mg O_2 m^{-2} day^{-1} approximately one kilometer downstream of the July Augusta Creek site and 1.55 to 2.97 mg O_2 m^{-2} day^{-1} approximately one kilometer downstream of the Kellogg Forest site. GCP ranged from 0.50 to 2.80 mg O_2 m^{-2} day^{-1} and from 0.72 to 3.40 mg O_2 m^{-2} day^{-1} at the two sites respectively. My measurements made using the closed benthic chambers fall very near if not within these ranges.

CONCLUSIONS

It is difficult to predict the amount of error associated with the upstream-downstream method since it cannot be replicated. However, the method produced comparable results at the two sites from 1997 to 1998. The methods used for these experiments involving conservative and volatile tracers to estimate oxygen diffusion are quite involved. Experience with these techniques could reduce sampling error. Very specialized equipment along with a trained operator are necessary to conduct these measurements. With experience, the technique can give reliable results. Unfortunately, the upstream-downstream technique without the conservative and volatile tracers is often considered suspect due to the uncertainty associated with reaeration estimates derived from empirical relations in the literature. When parameters from the two-station experiments were calculated using a single station technique, they gave very different results in an unpredictable direction. For example, CR_{24} values calculated using a single station were lower at the July Augusta Creek site for both years and higher at the Kellogg Forest. GCP was lower than the two-station technique in 1997 at the July Augusta Creek site, and the single-station was much higher than the two-station technique at the same site in 1998. Finally, variance between years tended to increase when the single-station calculations were used in place of the two-station calculation for all of the parameters.

The simple design of the hyporheic chambers should reduce sampling error. However, the variance associated with these chamber measurements was often higher than that associated with closed benthic chambers. This error might have been reduced substantially if interstitial water velocity had been measured in individual replicates and applied to those specific data. Velocity measurements involved spiking a randomly chosen chamber with concentrated sodium chloride. This was not done in each chamber because sediments from the replicates were taken to the lab and analyzed for chlorophyll a and organic content. Concentrated sodium chloride could have had deleterious effects on these data and metabolism measurements. Ideally, velocity measurements should be made after metabolism measurement in each replicate chamber. Preliminary studies suggested that using one chamber for velocity would provide a good estimate of velocity for all of the chambers, perhaps because measurements were made at a small scale in a single riffle. However, the hyporheic zone has been shown to be extremely variable and the magnitude of variability is likely stream and even riffle dependent.

Closed benthic chambers maintained low variability between replicates for the entire study, making them extremely good candidates for comparative studies of surface sediment metabolism. Even so, special attention should be given to factors limiting primary productivity, especially if comparisons are carried out between streams, as the time involved for a nutrient to become limiting would be expected to vary widely from stream to stream.

The three methods used simultaneously can reveal error otherwise overlooked while compartmentalizing metabolism and therefore provide much more information about the system. Bott et al. (1997) cautioned that one should not collect metabolism data in a routine manner without assessing potential sources of error. Use of the benthic chamber provides estimates of surface sediment metabolism. Combining these estimates with estimates from hyporheic chambers would allow surficial sediment respiration associated with autotrophs and heterotrophs to be subtracted from hyporheic chamber measurements, providing estimates of hyporheic metabolism to a known depth. This value in turn could be used in conjunction with the whole system estimate of the upstream-downstream method to provide an estimate of mean hyporheic depth for a given reach of stream.

APPENDICES

APPENDIX A

Substrate data based on three cores taken from hyporheic chambers.

Sample	Date	Chlorophyll a (Phaeophytin corrected mg m^{-2})	Percent organic content to 20 cm depth
AuSable R.	6/96	----	0.9 ±0.1
N.B. AuSable	6/96	105.3 ± 24.5	2.9 ± 1.2
N.B. AuSable	6/97	145.1 ± 47.3	2.6 ± 1.7
Jordan	9/96	736.6 ± 161.2	1.8 ±1.3
Red Cedar	6/97	55.4 ± 9.7	1.0 ± 0.0
Augusta Cr.	7/97	85.4 ± 7.4	2.9 ± 1.0
Augusta Cr.	7/98	102.8 ± 26.7	1.1 ± 0.4
Augusta Cr. (Kellogg Forest)	9/97	169.5 ± 21.9	1.2 ± 0.2
Augusta Cr. (Kellogg Forest)	9/98	49.5 ± 21.9	0.9 ± 0.1

Percent inorganic > 8 mm	Percent inorganic 2.0 - 8.0 mm	Percent inorganic 0.250 - 2.0 mm	Percent inorganic 0.125 -0.250 mm	Percent inorganic < 0.125 mm
----	----	----	----	----
----	----	----	----	----
42.2 ± 8.1	18.2 ± 1.2	38.8 ± 7.8	0.5 ± 0.3	0.2 ± 0.1
0.4 ± 0.1	2.5 ± 0.1	94.6 ± 0.2	2.4 ± 0.1	0.1 ± 0.0
<10*	<10*	<10*	<10*	>90*
61.8 ± 6.1	19.2 ± 2.8	17.7 ± 3.4	0.5 ± 0.1	0.7 ± 0.0
75.8 ± 9.9	11.4 ± 4.5	12.0 ± 5.1	0.4 ± 0.2	0.3 ± 0.2
19.4 ± 3.2	21.5 ± 3.3	57.4 ± 2.9	1.4 ± 0.3	0.2 ± 0.0
12.0 ± 3.5	29.0 ± 0.4	50.3 ± 3.3	7.4 ± 0.6	1.2 ± 0.2

* Estimated value-the sample would not pass through a sieve due to consolidated clay.

APPENDIX B

Example of calculations for each method using data from Augusta Creek on 29 July 1997.

Hyporheic Chamber
Discharge: 1.224 $m^3\ hr^{-1}$ **Area**: 0.153 m^3 **Interstitial-water/sediment area**: 0.35
Interstitial discharge: 0.4284 $m^3\ hr^{-1}$

	DO change from upstream to downstream port (mg/l)			Rate of change (g $O_2\ m^{-2}\ hr^{-1}$)		
Time	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3
00:00	-0.4	-0.3	-0.1	-1.12	-0.84	-0.28
01:00						
02:00	-0.5	-0.1	-0.55	-1.40	-0.28	-1.54
03:00						
04:00	-0.5	0	-0.5	-1.40	0.00	-1.40
05:00						
06:00	-0.6	-0.1	-0.35	-1.68	-0.28	-0.98
07:00	-0.4	-0.3	-0.3	-1.12	-0.84	-0.84
08:00	-0.5	-0.2	-0.3	-1.40	-0.56	-0.84
09:00	-0.4	-0.2	-0.3	-1.12	-0.56	-0.84
10:00	-0.5	-0.4	-0.25	-1.40	-1.12	-0.70
11:00	-0.6	-0.3	-0.25	-1.68	-0.84	-0.70
12:00	-0.55	-0.2	-0.4	-1.54	-0.56	-1.12
13:00	-0.55	-0.2	-0.4	-1.54	-0.56	-1.12
14:00	-0.55	-0.3	-0.4	-1.54	-0.84	-1.12
15:00	-0.65	-0.3	-0.4	-1.82	-0.84	-1.12
16:00	-0.65	-0.2	-0.3	-1.82	-0.56	-0.84
17:00	-0.65	-0.4	-0.3	-1.82	-1.12	-0.84
18:00	-0.45	-0.3	-0.1	-1.26	-0.84	-0.28
19:00	-0.4	-0.5	-0.1	-1.12	-1.40	-0.28
20:00	-0.4	-0.4	-0.25	-1.12	-1.12	-0.70
21:00	-0.4	-0.4	-0.25	-1.12	-1.12	-0.70
22:00	-0.4	-0.3	-0.15	-1.12	-0.84	-0.42
23:00	-0.4	-0.4	-0.1	-1.12	-1.12	-0.28

# of light hours	14.58
# of night hours	9.42

	Rep 1	**Rep 2**	**Rep 3**
# of light readings	15	15	15
# of night readings	6	6	6

NCP (g O_2/m^2*day)	-20.82	-12.52	-11.70
CR (g O_2/m^2*hr)	1.39	0.77	0.81
GCP (g O_2/m^2*day)	ND	ND	ND
NDM (g O_2/m^2*day)	-33.44	-18.56	-19.36
P/R	0.00	0.00	0.00

Benthic Chamber
Chamber volume (l): 9.5, 9.5, 9.5 **Sediment conversion to m^2**: 15

	DO change from previous reading (mg/l)			**Rate of change (g O_2 m^{-2} hr^{-1})**		
Time	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3
00:00	-0.2	-0.3	-0.4	-0.03	-0.04	-0.06
01:00	-0.25	-0.3	-0.45	-0.04	-0.04	-0.06
02:00	-0.25	-0.3	-0.45	-0.04	-0.04	-0.06
03:00	-0.3	-0.25	-0.35	-0.04	-0.04	-0.05
04:00	-0.3	-0.25	-0.35	-0.04	-0.04	-0.05
05:00	-0.4	-0.45	-0.7	-0.06	-0.06	-0.10
06:00	-0.4	-0.45	-0.7	-0.06	-0.06	-0.10
07:00	-0.2	-0.2	-0.4	-0.03	-0.03	-0.06
08:00	-0.1	-0.1	-0.1	-0.01	-0.01	-0.01
09:00	-0.1	0	-0.1	-0.01	0.00	-0.01
10:00	0.3	0.3	0	0.04	0.04	0.00
11:00	0.5	1	0.3	0.07	0.14	0.04
12:00	1.1	0.5	1.9	0.16	0.07	0.27
13:00	0.5	0.5	0.4	0.07	0.07	0.06
14:00	-0.1	0.2	0.2	-0.01	0.03	0.03
15:00	0.1	0	0	0.01	0.00	0.00
16:00	-0.2	-0.2	-0.3	-0.03	-0.03	-0.04
17:00	-0.2	-0.1	-0.3	-0.03	-0.01	-0.04
18:00	-0.3	-0.4	-0.3	-0.04	-0.06	-0.04
19:00	-0.2	-0.3	-0.3	-0.03	-0.04	-0.04
20:00	-0.3	-0.3	-0.4	-0.04	-0.04	-0.06
21:00	-0.4	-0.4	-0.5	-0.06	-0.06	-0.07
22:00	-0.3	-0.3	-0.6	-0.04	-0.04	-0.09
23:00	-0.3	-0.4	-0.4	-0.04	-0.06	-0.06

# of light hours	14.58		
# of night hours	9.42		
	Rep 1	**Rep 2**	**Rep 3**
# of light readings	15	15	15
# of night readings	9	9	9

NCP (g O_2/m^2*day)	0.06	0.07	0.01
CR (g O_2/m^2*hr)	0.04	0.05	0.07
GCP (g O_2/m^2*day)	0.70	0.78	1.06
NDM (g O_2/m^2*day)	-0.33	-0.36	-0.61
P/R	0.68	0.69	0.63

Upstream-downstream

k_{oxygen} * travel time = 0.1140*1.625 = 0.18525

							(two station)	(one station)
	Time	**Temp 1**	**Temp 2**	**Temp**	**upstream**	**downstream**	**Change DO**	**Mean DO**
AM	11:00	19.00	19.00	19.00	7.70	7.60	-0.10	7.65
PM	12:00	19.50	19.50	19.50	7.80	7.60	-0.20	7.70
	1:00	20.00	20.20	20.10	7.90	7.70	-0.20	7.80
	2:00	21.20	21.30	21.25	7.90	7.90	0.00	7.90
	3:00	21.50	21.50	21.50	7.70	7.60	-0.10	7.65
	4:00	22.20	22.50	22.35	7.70	7.60	-0.10	7.65
	5:00	22.50	22.70	22.60	7.50	7.40	-0.10	7.45
	6:00	22.50	22.80	22.65	7.30	7.20	-0.10	7.25
	7:00	22.20	22.50	22.35	7.00	7.00	0.00	7.00
	8:00	22.00	22.20	22.10	6.80	6.70	-0.10	6.75
	9:00	21.50	22.00	21.75	6.60	6.50	-0.10	6.55
	10:00	21.20	21.50	21.35	6.60	6.60	0.00	6.60
	11:00	20.50	21.00	20.75	6.60	6.50	-0.10	6.55
AM	12:00	20.00	20.50	20.25	6.70	6.60	-0.10	6.65
	1:00							
	2:00	19.00	19.20	19.10	6.80	6.70	-0.10	6.75
	3:00							
	4:00	18.20	18.70	18.45	7.00	6.90	-0.10	6.95
	5:00							
	6:00	17.00	17.50	17.25	7.30	7.20	-0.10	7.25

7:00	16.50	16.90	16.70	7.60	7.40	-0.20	7.50
8:00	16.20	16.50	16.35	7.70	7.60	-0.10	7.65
9:00	16.20	16.50	16.35	7.90	7.70	-0.20	7.80
10:00	16.50	16.80	16.65	8.00	7.80	-0.20	7.90
11:00	17.00	17.00	17.00	8.20	7.90	-0.30	8.05

(at 841 ft)	(100%-mean)	(instantaneous)	(Flux into water)	(two station)	(one station)
				(diff. between stn's)	(difference per hr)
100 % sat	**DO deficit**	**Reaeration Flux**	**-Reaeration Flux**	**Corr. rate of chg**	**Corr. rate of chg**
9.00	1.35	0.25	-0.25	-0.35	0.10
8.91	1.21	0.22	-0.22	-0.42	-0.17
8.80	1.00	0.18	-0.18	-0.38	-0.08
8.60	0.70	0.13	-0.13	-0.13	-0.03
8.57	0.92	0.17	-0.17	-0.27	-0.42
8.40	0.75	0.14	-0.14	-0.24	-0.14
8.38	0.93	0.17	-0.17	-0.27	-0.37
8.38	1.13	0.21	-0.21	-0.31	-0.41
8.40	1.40	0.26	-0.26	-0.26	-0.51
8.46	1.71	0.32	-0.32	-0.42	-0.57
8.53	1.98	0.37	-0.37	-0.47	-0.57
8.59	1.99	0.37	-0.37	-0.37	-0.32
8.69	2.14	0.40	-0.40	-0.50	-0.45
8.78	2.13	0.39	-0.39	-0.49	-0.29
8.98	2.23	0.41	-0.41	-0.51	-0.36
9.10	2.15	0.40	-0.40	-0.50	-0.30
9.33	2.08	0.39	-0.39	-0.49	-0.24
9.44	1.94	0.36	-0.36	-0.56	-0.11
9.51	1.86	0.34	-0.34	-0.44	-0.19
9.51	1.71	0.32	-0.32	-0.52	-0.17
9.45	1.55	0.29	-0.29	-0.49	-0.19
9.38	1.33	0.25	-0.25	-0.55	-0.10

Single-station calculations

# of light hours	14.58
# of night hours	9.42
# of light readings	15
# of night readings	6
	Rep 1
NCP (g O_2/m^2*day)	-12.01
CR (g O_2/m^2*hr)	1.00
GCP (g O_2/m^2*day)	2.59
NDM (g O_2/m^2*day)	-21.44
P/R	0.11

Two-station calculations

# of light hours	14.58
# of night hours	9.42
# of light readings	15
# of night readings	6
	Rep 1
NCP (g O_2/m^2*day)	-17.08
CR (g O_2/m^2*hr)	1.46
GCP (g O_2/m^2*day)	4.23
NDM (g O_2/m^2*day)	-30.85
P/R	0.12

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