THE INFLUENCE OF STORMWATER IMPAIRMENT ON WHOLE-ECOSYSTEM METABOLISM OF SUBURBAN VERMONT STREAMS

A Thesis Presented

by

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Abstract

The "urban stream syndrome" (Meyer *et al*. 2005, Walsh et al. 2005a) describes a well-studied and consistent pattern of biological, chemical, and physical degradation to lotic systems. However, the impact of urbanization on key ecosystem-scale ecological processes (e.g. rates of primary production, respiration, nutrient uptake) is still unclear, despite increasing calls to include these integrated measures in holistic assessments of stream health (Bunn *et al*, 1999; Walsh *et al*, 2005). Our ability to understand, diagnose, and mitigate the impacts of urbanization – and restore ecosystem services linked to these processes – is thus limited.

To better understand how watershed development has impacted ecological processes in northwestern Vermont, we measured whole-ecosystem metabolism in 7 streams in over two years. Study streams were selected based upon *a prior* classification by the Vermont Department of Environmental Conservation (VT DEC) as either "impaired" for urban stormwater runoff (303d listed) or in "attainment" of state standards according to prior monitoring of biotic indicators (macroinvertebrates and fish). We confirmed and augmented these classifications by conducting additional assessments of biological community structure, stream geomorphic and habitat conditions, and stream water chemistry.

We used the open-channel, single-station approach (Odum 1956, Bott 1996) with several modifications to conduct nearly continuous monitoring of whole-stream metabolism. We modeled relationships between discharge and stream dimension, and incorporated these as dynamic variables in the metabolism calculations. We estimated 271 daily rates of gross ecosystem production (GEP), ecosystem respiration (ER), net daily metabolism (NDM), as well as the ratio of production to respiration (P/R) split almost evenly between the impaired and attainment condition stream groups.

GEP was significantly higher in the stormwater-impaired streams, particularly during the spring and summer months; ER was closely linked to the production of autochthonous resources. The attainment condition streams, on the other hand, were characterized by more consistent and less vigorous in-stream primary production. Attainment condition streams were more heterotrophic, and processed organic matter from a more diverse resource base throughout the year. At the individual stream level, we also found significant correlations between P/R ratio and benthic macroinvertebrate community metrics, geomorphic and habitat scores, mean PO_4 concentration, and specific conductivity.

We propose that the altered 'metabolic regime' observed in our stormwater-impaired study streams may represent another aspect of the urban stream syndrome associated with this particular level of watershed development. We suggest that measures to limit the drivers of in-stream primary production (i.e. sunlight, temperature, nutrients) may help encourage a more 'natural' metabolic regime in urban stormwater-impaired streams in some areas.

Dedication

This thesis is dedicated to my parents, Lawrence and Sandra. Their eternal support and encouragement propel and guide me to work for a better world. For them, I am truly lucky, thankful, and appreciative.

This work is also dedicated to Dr. Keri-Nicole Dillman. I will be always grateful for her love and support. She taught me what it means to be a true environmentalist.

Acknowledgements

I must first acknowledge and thank my mentor and friend, Dr. William 'Breck' Bowden. Very few graduate students are given the responsibility, budget, and latitude entrusted to me, and I hope my hard work over the past many years has repaid a portion of my debt.

Spending hundreds of tough days together in the field can strain some relationships, but quite the opposite occurred with my great friend and colleague Joe Bartlett. I am grateful for Joe's outstanding spirit, knowledge, and companionship throughout our very challenging and tiring field research experiences. Nat Morse also provided critical fieldwork assistance (and great camaraderie) in 2004.

This project would not have been possible without significant financial support from the United State Environmental Protection Agency as part of the *Redesigning the American Neighborhood* Project. Financial support was also generously provided by the City of South Burlington and the National Science Foundation's Vermont EPSCoR program. I sincerely thank these organizations for recognizing the importance of protecting and rehabilitating urban streams, and promise to do my part in this important mission.

Table of Contents

A. Field data (stage, discharge, dissolved oxygen, temperature, conductivity, PAR)

B. Whole-stream metabolism calculations (performed in my EXCEL-based models)

C. Hydrologic rating curves

D. Dynamic variable construction and rating curves (width, depth, velocity)

E. Benthic macroinvertebrate community assessment results

F. Water quality sampling results

G. Rapid stream geomorphic and habitat assessment results

H. Solute injection experiment (SIE) results – nutrient uptake dynamics of impaired

and attainment condition streams

List of Tables

List of Figures

Comprehensive Literature Review

This review begins with a brief introduction to the impacts of watershed urbanization on the biological, chemical, physical/hydrological condition of stream and rivers. Next, it shows that despite increased attention to urban streams in recent decades, very little is know about how watershed urbanization affects key ecosystem processes (including rates of nutrient uptake, decomposition, primary production, and respiration). This gap in scientific understanding has been highlighted in recent years by prominent stream ecologists, continues substantively unaddressed, and is the primary motivation for my research.

Whole-ecosystem metabolism is a technique used to estimate rates of two key ecosystem functions - primary production and respiration - in aquatic systems. My research employs this methodology to evaluate differences between suburban stormwater-impaired and 'attainment' condition streams near Burlington, Vermont. Thus, substantial consideration is given here to the theoretical underpinnings of the technique, different methodological options for its performance, and the various factors thought to influence possible outcomes.

I. Watershed Urbanization and Stream Condition

 "Urbanization" refers to the anthropogenic process of modifying land cover from a natural state (i.e. forest and meadow) through urban development (Coles *et al*. 2004). The clearing of natural vegetation, compaction of soils, construction of roads, buildings, and other infrastructure, and settlement by human populations all constitute aspects of

urbanization. Urbanization has been recognized as a major source of stream impairment in the United States (U.S. Environmental Protection Agency 2000) and around the world, and it is now widely accepted that watershed urbanization results in fundamental changes to stream ecosystems (Paul and Meyer 2001, Center for Watershed Protection 2003).

Rivers and streams are drainage pathways of the landscape, and are formed and maintained in response to a combination of climatic, geologic, and land cover conditions (Leopold *et al.* 1964, Booth 1991). Streams are open-systems, and the continuous movement of water, energy, and materials creates an ever-changing, dynamic condition. The biological, chemical, and physical properties of any stream are all complexly inter-related and dependent upon processes occurring within the surrounding landscape. For example, seasonal trends in precipitation, surface runoff and groundwater flow, water temperature, canopy cover and shading, and biological activity, all influence water chemistry (e.g. the concentrations of inorganic material, dissolved ions, nutrients, and organic matter), which will vary from time to time and from place (Allan 1995). Human-induced changes in a watershed (e.g. conversion to agricultural or urban development) will thus set in motion a cascade of potential changes to physical form of a stream channel, the chemical composition of the stream water, and ultimately the resident biota.

Urbanization results in fundamental changes to the landscape and the associated rainfall-runoff dynamics that historically formed and maintained the structure and function of streams and rivers. As vegetation and pervious soil is replaced with impervious surfaces (e.g. roads, buildings) and compacted soils, a greater percentage of rainfall is converted into overland flow (Booth 1991). Urban development often includes efficient routing of rainfall via drainage infrastructure networks, further accelerating the rapid transport of

rainfall to a stream network (Walsh *et al.* 2004). These factors combine to fundamentally

alter the way in which rainfall is transported to the natural drainage network during storm

events. Streams receive stormwater runoff faster, with greater intensity, and more

frequently then under natural conditions. In addition, less rainfall is able to infiltrate to

the subsurface, thus reducing groundwater inputs to streams and reducing base flows.

These hydrologic consequences of urbanization are well studied (e.g. Leopold 1968,

Booth and Jackson 1997), and are summarized in the typically pre- and post-development

hydrograph below.

Figure 1: Hydrologic Impacts of Urbanization

(Center for Watershed Protection, 2003 [from Scheuler, 1987])
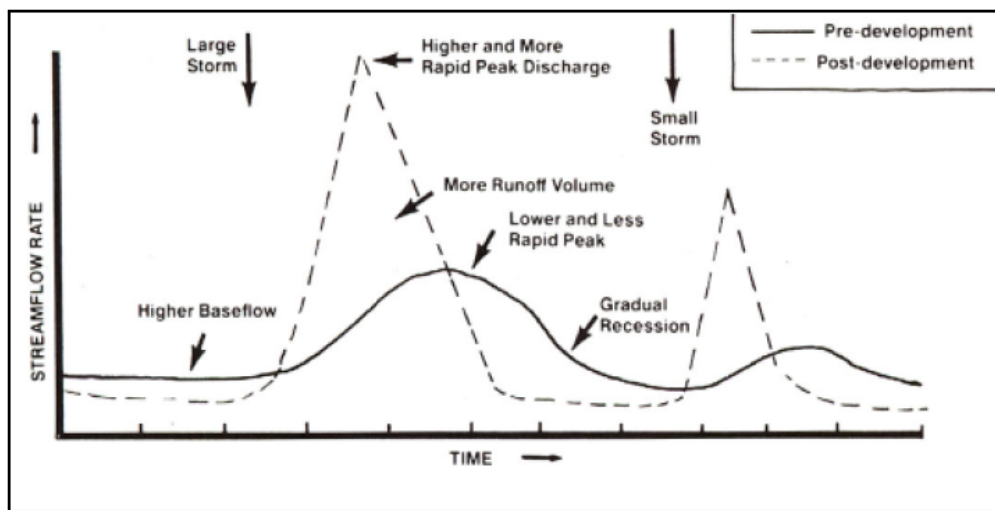
Increased storm flows and decreased base flows in urban areas lead to geomorphic

instability in stream systems (Dunne and Leopold 1978). Streams adjust to the modified

conditions in a variety of ways, but typically involve a predictable sequence of down-

cutting, incision, bank erosion, and widening (Booth 1991, Center for Watershed

3

Protection 2003). These changes in the physical geometry of streams leads to a

cascading set of impacts that includes loss of riparian vegetation, increase in water

temperatures, loss of habitat and habitat simplification, and modified sediment regimes,

to name only a few (Finkenbine *et al.* 2000, Booth and Jackson 1997).

In addition to these fundamental changes in watershed hydrology, impervious areas also

accumulate pollutants for rapid transport to surface water (Burton and Pitt 2001, Hatt *et

al.* 2004). When compared to streams in undeveloped watersheds, streams in urban

developed watershed are typically characterized by higher concentrations of suspended

sediment, nutrients, heavy metals, coliform bacteria, petroleum constituents, and

pesticides (Center for Watershed Protection 2003, Paul and Meyer 2001). Gresens *et al.*

(2007) suggest that urban stormwater runoff, and its effect on water quality, deserves

primary consideration (along with altered hydrology) as a main driver of biological

impairment, particularly in watersheds with lower levels of imperviousness. In the

Northeastern United States (and likely elsewhere), streams in urban and suburban areas

are also becoming increasingly saline as a result of winter de-icing operations (Kaushal *et

al.* 2005).

With the stress urbanization places on the natural physical form and water chemistry of

streams, it is not surprising that watershed development has been consistently linked to

altered biological community structure. The Center for Watershed Protection (2003)

summarizes or refers to 33 studies linking decreased aquatic insect diversity with

increased levels of urbanization, as well as another 19 that found a related decline in fish

diversity. More recently, in a study of 30 streams in Georgia, Roy *et al.* (2003) found

increases in urban land cover to be positively correlated with nutrient concentrations,

specific conductance, turbidity, and total suspended solids. In addition to reduced water quality, the Georgia streams with urban land cover also were characterized by less diverse and more pollution tolerant benthic macroinvertebrates communities. Taylor *et al.* (2004) established a link between increased benthic algal biomass (chlorophyll *a*) and urbanization in 16 streams studied near Melbourne, Australia, and cited stormwater infrastructure delivery of a phosphorus subsidy as a likely cause. Walker and Pan (2006) evaluated diatom assemblages in 47 streams near Portland, OR, and found consistent differences in the urban and rural study streams. In 2004, the U.S. Geological Survey issued a comprehensive report on the biological, chemical, and physical condition of coastal New England streams (Coles *et al.* 2004), which found similar correlations with urbanization as noted above in terms of the benthic macroinvertebrate, fish, and algae communities.

The overall relationship between watershed development and stream condition is well-summarized in a simple conceptual model entitled the "Impervious Cover Model," shown below in Figure 2. The y-axis is generic (given as "stream quality") because regardless of the measure of stream health, the result is the same when watershed urbanization increases. Here, and in many studies, the extent of watershed urbanization is measured by the percentage of the watershed covered by impervious surfaces (Center for Watershed Protection 2003). At even modest levels of watershed urbanization (~10%), there is a consistent drop in stream quality from biological, chemical, or physical perspective.

Figure 2: The Impervious Cover Model (Center for Watershed Protection, 2003)
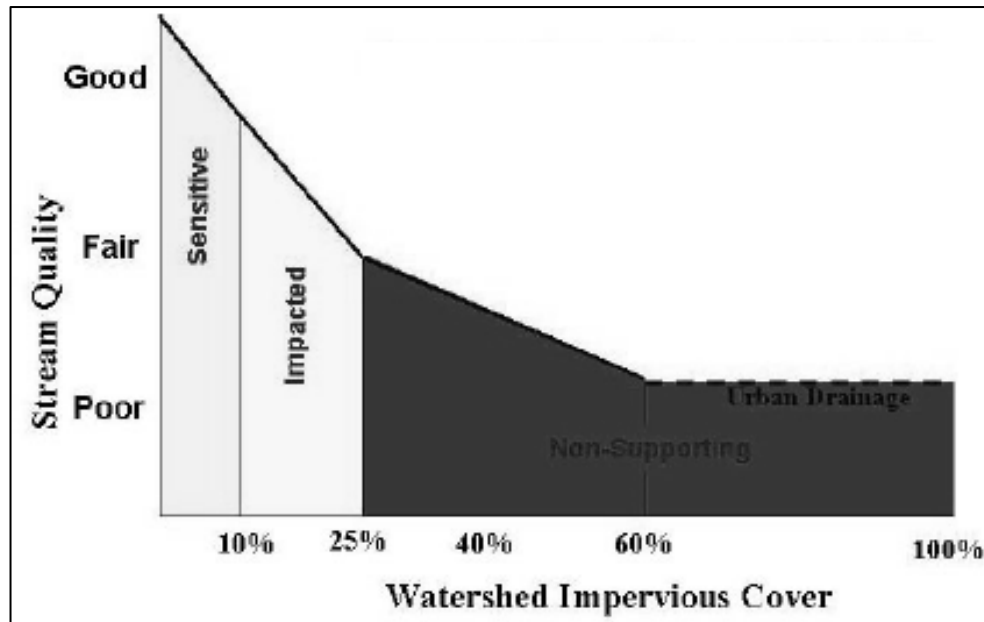
Increased attention has been given to the study of urban streams in recent decades, and several outstanding works have been published summarizing prior findings (i.e. Paul and Meyer 2001, Center for Watershed Protection 2003). The patterns of stream degradation associated with watershed urbanization have recently been synthesized into a more unified theory, termed the "urban stream syndrome" (Meyer *et al.* 2005, Walsh et al. 2005a). Watershed urbanization is now believed to be strongly associated with an entire suite of modifications and impairments, which occur in a predictably pattern, and with predictable consequences to the biological communities of streams and rivers. In general, these changes include an altered flow regime (e.g. flashier hydrographs), simplified stream network (particularly the elimination of low order streams), increased nutrient and pollutant concentrations, altered channel geometry and stability, simplified in-stream habitat, and reduced biological diversity with an increased percentage of pollution tolerant species (Paul and Meyer 2001, Walsh et al. 2005a). Table 1 below (from Walsh

et al. 2005a) provides an excellent summary of these issues. The cascade of changes that

stem from landscape urbanization begins with watershed hydrology, shifts to the abiotic

template, and results in biotic alteration from the natural state.

Table 1.   Symptoms associated with the "urban stream syndrome" from Walsh *et al* 2005. Arrows indicate the direction of consistent response observed in multiple studies. Limited research indicates that additional study is required before determining the consistency of response.

Feature	Consistent response	Inconsistent response	Limited research
Hydrology	↑ Frequency of overland flow ↑ Frequency of erosive flow ↑ Magnitude of high flow ↓ Lag time to peak flow ↑ Rise and fall of storm hydrograph	Baseflow magnitude	
Water chemistry	↑ Nutrients (N, P) ↑ Toxicants ↑ Temperature	Suspended sediments	
Channel morphology	↑ Channel width ↑ Pool depth ↑ Scour ↓ Channel complexity	Sedimentation	
Organic matter	↓ Retention	Standing stock/inputs	
Fishes	↓ Sensitive fishes	Tolerant fishes Fish abundance/biomass	
Invertebrates	↑ Tolerant invertebrates ↓ Sensitive invertebrates		Secondary production
Algae	↑ Eutrophic diatoms ↓ Oligotrophic diatoms	Algal biomass	
Ecosystem processes	↓ Nutrient uptake	Leaf breakdown	Net ecosystem metabolism Nutrient retention P:R ratio

II. Ecosystem Processes in Urban Streams

While considerable research has been conducted to examine the effects of urbanization

on the hydrological, biological, physical, and chemical condition of lotic systems,

relatively little is know about how urbanization affects rates of ecosystem-level *processes*

in streams and rivers. Measurements of ecosystem function or process offer a

fundamentally different lens through which to view stream condition. Bunn and Davies

(2000) describe these different approaches in terms of 'pattern' and 'process.' Other ecologists commonly refer to the 'structure' and 'function' of a stream ecosystem (e.g. Allen 1995).

Stream ecosystem functions have been typically described in terms of the ecosystem services provided (Meyer 1997, Meyer *et al.* 2005). Fish production (for consumptive purposes) and water purification (through nutrient sequestration and organic matter breakdown) are examples of such services. These in particular are linked to primary production and heterotrophic activity (respiration) which occur at the base of the food web in a stream ecosystem (Bott *et al.* 2006a).

Human societies depend upon the ecosystem services provided by streams and rivers (e.g. freshwater for drinking and irrigation, waste purification). Yet according to Meyer *et al.* (2005), "less is known about ecosystem function than any other aspect of urban streams but it is likely that the altered physical, chemical, and biotic conditions will impact ecosystem function." Furthermore, despite the availability of a number of widely-used and refined field techniques, "ecosystem processes such as primary production, leaf decomposition, or nutrient cycling have been overlooked in urban streams" (Paul and Meyer 2001). According to Fellows *et al.* (2006), "there is a growing concern that measures of ecosystem health should include not only aspects of their organization (e.g. biodiversity, species composition, food web structure), but also their vigor (e.g. rates of production, nutrient cycling) and resilience (ability to recover from disturbance)." In recognition of the lack of understanding of urban stream ecosystem function, there has been an increasing call to include an understanding of fundamental ecosystem processes in holistic assessments of stream health (Bunn *et al.* 1999, Walsh et al. 2005a).

8

The few studies that have evaluated ecosystem functions in urban streams are summarized below. These include measures of nutrient uptake, leaf litter decomposition, and stream metabolism (primary productivity and respiration). My research focuses on stream metabolism, and thus only a brief review of studies of other ecological processes is provided here.

Using the framework of 'nutrient spiraling' and solute injection field techniques (Stream Solute Workshop 1990), nutrient uptake rates have been evaluated in a few urban streams. In two recent studies, urban streams in the southwestern (Grimm *et al.* 2005) and the southeastern (Meyer *et al.* 2005) United States were shown to have longer uptake lengths (and reduced nutrient uptake rates) than the more rural counterpart streams. Possible reasons for the diminished nutrient uptake include simplified channel structure and reduce hydrologic retentiveness, increased storm flows, and a reduced amount of fine benthic organic matter (FBOM). Urban streams are often characterized by elevated background nutrient levels, and it is likely that saturation kinetics contributes to reduced uptake as reported in other studies in non-urban areas (Dodds *et al.* 2002). Long nutrient uptake lengths have also been reported in rivers downstream of wastewater treatment plants, also suggesting that nutrient loading and saturation affect the ability of an ecosystem to remove pollutants (Marti *et al.* 2001, Pollock and Meyer 2001; both from Paul and Meyer 2001). Gibson (2004) reported similar uptake rates (lengths and velocities) for ammonium and soluble reactive phosphorus for a set of small headwater forested and suburban streams near Atlanta, GA; however, the suburban streams also exhibited longer retention times, which may have contributed to the similarity of the results.

9

Rates of organic matter decomposition have been measured in several urban streams using leaf-packs. Paul *et al.* (2006) measured breakdown rates of chalk maple leaves in 12 streams near Atlanta, GA, which included forested, agricultural, suburban, and urban settings. Breakdown rates were fastest in the urban and agricultural streams, followed by the suburban and forested sites. In the urban streams, low levels of fungal biomass and shredder-type macroinvertebrates were found associated with the leaf packs, and physical fragmentation (mechanical breakdown) from storm flows was hypothesized as the primary cause. Fast rates of willow leaf breakdown were reported in 2 suburban New Zealand streams (Collier and Winterbourne 1986; from Paul *et al.* 2006). In a study of 18 headwater streams in Florida, Chadwick *et al.* (2006) evaluated leaf litter breakdown along with other biological, chemical, and physical attributes typically impacted by urbanization. Like Paul *et al.* (2006), this study found the rates of litter mass loss increased with catchment impervious cover. However, Chadwick also identified a threshold-type response, whereby breakdown decreased after watershed impervious cover exceeded 40%. Flow regime, snail and invertebrate communities, and water chemistry were identified as likely factors influencing breakdown rates.

In a limited number of studies, ecosystem level measures of respiration and primary production have been evaluated in urban streams using whole-ecosystem metabolism techniques. At this time, these studies include only one recently published article in a peer-reviewed journal (Meyer *et al.* 2005), and several doctoral dissertations (Paul 1999, Gibson 2004, Aldridge 2005). Several 'suburban' streams were also included in the study of Catskill region streams by Bott *et al.* (2006a).

Meyer *et al.* (2005) evaluated the ecosystem processes of six streams near Atlanta, GA.

Four of the streams were considered urban (25-40% watershed impervious cover) and

two were considered non-urban and forested (1% watershed impervious cover). While

urbanization was found to affect both nutrient uptake and leaf breakdown rates, no trend

was evident for stream metabolism on the study dates. The authors indicated that stream

metabolism "seems less altered in these urbanizing landscapes than are nutrient v_f [uptake

velocity) values" and "metabolism in our streams did not respond to urbanization."

However, there are several weaknesses in the paper that undermine these generalizations

concerning the metabolism findings. For example, there is no description of the

methodology used in the metabolism (nor leaf breakdown) experiments and conclusions

are based on only 1 to 4 days worth of evaluation. For additional details, it is necessary

to refer to the actual source document and dissertation of co-author M.J. Paul (1999).

As part of his doctoral dissertation at the University of Georgia, Paul (1999) measured

whole-stream metabolism (using a two-station, open channel method with propane

evasion to estimate reaeration) in eight (8) streams in Georgia along a land-use gradient

including (2 of each) forested, suburban, urban, and agricultural watersheds. Metabolism

was measured once at each site in the spring and fall over 2 years. Analysis of Variance

(ANOVA) was used to compare metabolism between different land-use categories on an

annual and seasonal basis. Potentially confounding factors to land-use that might explain

variation in metabolism rates were assessed using principle component and correlation

analyses (to identify explanatory factors) and multiple regression (to determine which

factors best explained variance). No significant relationship was found between gross

primary production (GPP), community respiration (CR), or net ecosystem metabolism

(NEM) and human population density. Metabolism in the urban streams was similar to

that of the forested streams, "suggesting that these measures of ecosystem function are not effective for detecting urban impacts in Piedmont streams. (Paul 1999)" However, Paul states elsewhere that while measures of CR were similar between forested and urban sites, GPP was generally higher at the urban sites. The urban and forested sites showed no difference in terms of season (spring versus fall) for GEP, CR, and NEM.

It is also important to note that key metabolism values were different between the Paul (1999) dissertation and Meyer *et al.* (2005) paper for the same streams, as shown below in Table 1. One explanation is that Meyer *et al.* (2005) reported only metabolism values for days of solute injection experiments. However, the findings are substantively different from those reported by Paul (1999) even though the number of days used in the analyses was similar. Thus, it is difficult to draw conclusions or even inferences from this information given these discrepancies as shown in Table 2 below.

Table 2: Comparison of Meyers *et al.* (2005) and Paul (1999) Metabolism Findings

Study	Stream	n (days)	Status	GPP	ER	NEM	P/R (calculated)
Meyer et al. 2005	Snake Creek, GA	3	F - Catchment mostly forested	1.19	5.23	-4.03	0.23
Meyer et al. 2005	Flat Shoals, GA	4	F - Catchment mostly forested	0.43	7.60	-7.18	0.06
Meyer et al. 2005	Nickjack Creek, GA	2	U - Catchment mostly urban	0.76	8.72	-7.96	0.09
Meyer et al. 2005	Sope Creek, GA	1	U - Catchment mostly urban	2.38	2.77	-0.39	0.86
Meyer et al. 2005	Rottenwood Creek, GA	3	U - Catchment mostly urban	0.89	1.31	-0.41	0.68
Meyer et al. 2005	Peachtree Creek, CA	3	U - Catchment mostly urban	1.82	8.28	-6.46	0.22
Paul 1999	Snake Creek, GA	5	Forest	0.30	1.73	-1.43	0.17
Paul 1999	Flat Shoals, GA	5	Forest	0.10	2.01	-1.91	0.05
Paul 1999	Nickjack Creek, GA	5	Suburban	0.37	2.32	-1.94	0.16
Paul 1999	Sope Creek, GA	5	Suburban	0.21	0.40	-0.19	0.53
Paul 1999	Rottenwood Creek, GA	5	Urban	0.20	1.43	-1.23	0.14
Paul 1999	Peachtree Creek, GA	5	Urban	0.38	2.28	-1.91	0.17

*Gross primary production (GPP), community respiration (CR), and net ecosystem metabolism (NEM) are in units g O_2 m$^-$^{2} day $^{-1}$. The status is presented as it appears in the original study.

A few other studies have been published on urban stream metabolism, but are dated or use alternative methods. Ball *et al.* (1973, from Paul and Meyer 2001) reported higher

rates of respiration and productivity in an urban river compared to a forested river. Wang *et al.* (2003) proposed and used the "extreme value method (EVM)," which is similar to the "Delta Method" of Chapra and DiToro (1991), to estimate photosynthesis and respiration in an agricultural and urban stream in Indiana. The urban stream was found to have lower rates of respiration and photosynthesis, but the use of a novel method to estimate metabolism – based upon mathematical modeling – makes use of the findings for comparison purposes difficult.

As part of her doctoral dissertation at the University of Georgia, Gibson (2004) estimated metabolism rates in a large regulated river with substantial wastewater inputs below Atlanta, GA. Metabolism was measured on 14 dates using the upstream-downstream diurnal dissolved oxygen change technique, and reaeration was estimated using the energy dissipation method (Tsivoglou and Neal 1976). The floating orange technique was used to estimate water velocity and a build a relationship to discharge from a nearby U.S. Geological Survey stream-gaging station. A variety of chemical, physical, and biological data was also collected to explore possible relationships to metabolism, including solar radiation and barometric pressure from a state monitoring site (25km away), water chemistry the day before the metabolism measurements, and algae sampled from snags within the study reach. She found that hydropeaking (flow increase from dam releases) reduced gross primary production, while increased FPOM and phosphorus (P) loading increased community respiration. The study river is too large (average daily discharge was ~50 m3/s) for useful comparison with any of the streams in our study, although findings related to disturbance and nutrient loading may be relevant.

Gibson (2004) also estimated metabolism rates in 8 small headwater streams near Atlanta, GA (catchment areas of 0.3 to 1.8 km^2); 4 of the streams were located in forested conservation land, and 4 were located in suburban developed areas (with intact riparian canopy cover). Metabolism was measured once in an 80-m reach of each stream using either the upstream-downstream or single-station approach [more discussion of methodology is found later in this review] and propane evasion techniques to estimate reaeration. All streams were found to be highly heterotrophic with very low rates of primary production. For the forested and suburban streams, respectively, GPP ranged from 0.06 to 0.59 g O_2 m^{-2} day $^{-1}$ and 0.06 to 0.16 g O_2 m^{-2} day $^{-1}$, and CR ranged from 0.79 to 5.15 g O_2 m^{-2} day $^{-1}$ and 0.44 to 2.86 g O_2 m^{-2} day $^{-1}$. No meaningful differences in metabolism were found between the study reaches, but the degree of development in the 'suburban' catchments does not appear to have been significant (e.g. intact riparian corridor, natural channel form, high hydrologic retentiveness).

In another recent doctoral dissertation at the University of Adelaide (Australia), Aldridge (2005) evaluated metabolism rates in 3 sections (un-modified, impacted, and engineered) of 2 streams in southern Australia. These sections represented a gradient of land use change from rural to heavily urban (with concrete lined channels). Metabolism was measured 4 times in each reach using re-circulating benthic chambers. Metabolic rates varied seasonally for the impacted reaches, but less so for one of the un-modified reaches, which was characterized by low GPP, CR, and NEM. The actual values are not provided, but are available in the following figures:

14

Figure 3: CR and GPP Findings from Aldridge (2005)
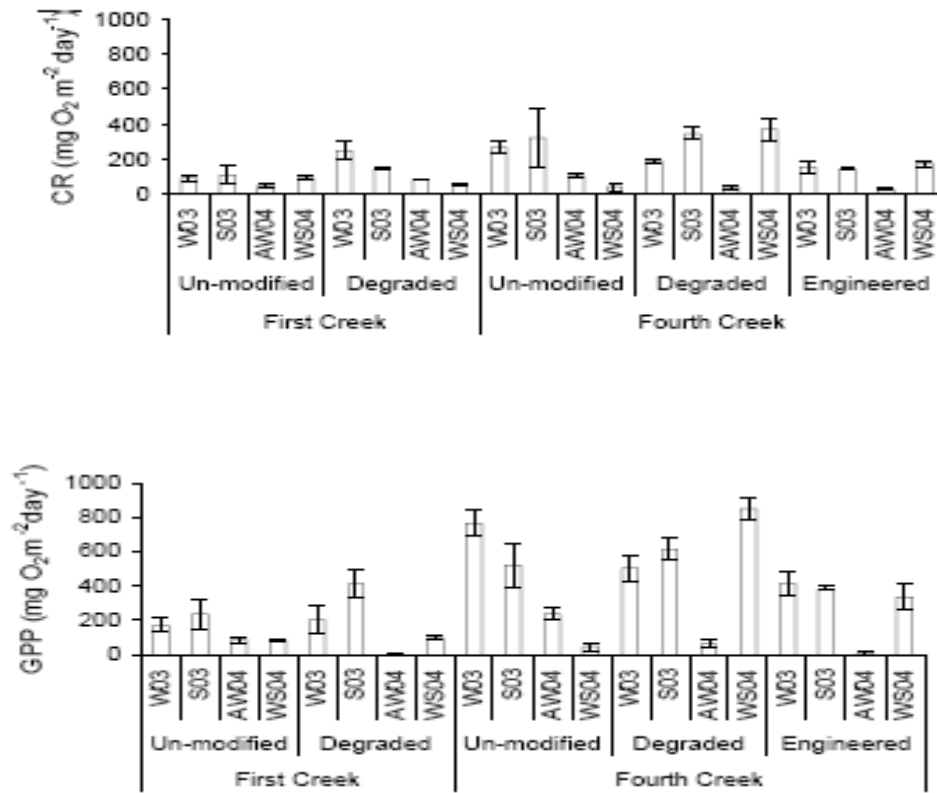
Aldridge noted that these values are low compared to other studies. In addition, he indicated that while heterotrophic conditions are typically found elsewhere in un-impacted streams, conditions in Australia such as sparse canopy cover and limited terrestrial inputs favor autotrophy (GPP>CR). For the most pristine of all his study reaches (First Creek, unmodified), Aldridge noted that the consistently low metabolic rates may represent the stability of the stream ecosystem against disturbance (Uehlinger 2000 cited). Rates of GPP and NEM were highest in the impacted reaches where organic matter was dominated by filamentous algae, with removal of riparian vegetation, increased light, and possibly reduced grazing (although no insect survey was performed) cited as likely factors. Despite these findings about the most pristine and most impacted

reaches, the overall extent of variation led Aldridge to conclude that 'generalizations about differences between pristine and impacted reaches are difficult."

Recently, Bott *et al*. (2006a) evaluated the metabolism of 10 streams in the Catskill and Upper Hudson Valley Regions which flow into the New York City drinking water reservoirs. Four (4) of the streams included in this study were located in modestly urbanized watersheds (11-26% residential), and considered 'suburban' by the authors. Using numerous days of metabolism values across several years, they found a negative correlation between GEP and ER to percent residential land use. Streams in these areas were small (compared to others in the study), characterized by closed tree canopies, and associated with higher concentrations of toxins (e.g. PAHs) and nutrients. Areas dominated by forests and agriculture had larger streams with greater light exposure. Thus, a variety of potentially confounding factors may have limited the ability to detect the influence of land use on metabolism, as noted by the authors. They also note that the observed negative correlation between GEP and percent urbanization differ from the results of Meyer *et al*. (2005), who are noted to have found "no correlations between metabolism variables and indicators of urbanization." (Bott *et al*. 2006a) In addition, Bott *et* al. (2006a) also cite two other studies relating landscape disturbance with reduced GPP (conversion to pasture in Young and Huryn 1999, and clearing and soil compaction in Houser *et al*. 2005).

It is important to note that most of the studies of metabolism in urban streams noted above – with the exception of Bott *et al*. (2006a) - involved only a few days worth of field data collection and analysis, which may account for the unclear findings. As Aldridge (2005) notes, "to accurately predict changes in stream metabolism across broad

spatial or temporal scales, extensive measurements may be required." While Bott *et al.*

(2006a) included more days of evaluation, they found a "dizzying array" of "near-stream

and in-stream factors" potentially confounded the effect of land use on metabolism

findings.

Indeed, it is no surprise then that the limited evaluation to date prevents any conclusions

concerning the effect of urbanization on stream metabolism (Walsh et al. 2005a). That

gap in scientific understanding concerning urban stream metabolism is a primary reason

for my study of streams in Vermont.

III. Whole-Ecosystem Metabolism – Theory and Methods

In aquatic ecosystems, the concept of "metabolism" is comprised of two component

ecological processes - primary production (photosynthesis) and respiration (Fellows *et al.*

2006). These are fundamental ecological process describing how much organic carbon is

produced and consumed within the system (Bunn and Davies 2000, Young *et al.* 2004),

and are important drivers of nutrient cycling and other ecological processes (Mulholland

et al. 2001). For decades, stream ecologists have considered the ratio of photosynthesis

to respiration within a stream to be of critical importance (Odum 1956, Fisher and Likens

1973). It is a basic description of the energy budget for a stream community and has

implications for the percentage of organic matter that is processes or exported to

downstream receiving waters (Cummins 1974). Whole-system methods for evaluating

stream metabolism have been used for decades for a wide range of purposes, including

(for example) to provide evidence of the River Continuum Concept (Bott *et al.* 1985,

McTammany *et al.* 2003), to relate chemical, physical, and biological variation across

biomes to ecological function (e.g. Lamberti and Steinman 1997, Mulholland *et al.*

2001), and to better understand the role of the hyporheic zone in stream ecosystems

(Naegli and Uehlinger 1997, Fellows *et al.* 2001).

Primary production is the conversion of inorganic carbon to organic matter by

photosynthesizing organisms. It is a biological *rate* involving the conversion of solar

energy to reduced chemical energy (carbohydrates). During this process, carbon dioxide

is consumed and oxygen is produced. In aquatic ecosystems, photosynthesis is

performed by algae, cyanobacteria, bryophytes, and macrophytes (Bott 1996). In-stream

production (autochthonous resources) in many streams accounts for only a small

percentage of the overall energy budget. For example, in the heavily shaded, cool, stream

studied by Fisher and Likens (1973) in New Hampshire, only 1% of the annual energy

flux was estimated to be from in-stream production. In most areas, terrestrial sources of

organic matter (allochthonous resources; e.g. leaf litter, dissolved organic matter) are the

major energetic resource for the streams ecosystem (Cummins 1974, Allan 1995).

However, in warmer, less-shaded areas (e.g. grassland and desert area) the percentage of

organic carbon supplied by in-stream production has been shown to be much higher

(Young and Huryn 1996, Mulholland *et al.* 2001).

Respiration is essentially the reverse of photosynthesis, with oxygen consumed and

carbon dioxide produced during the breakdown of carbohydrates. The fixed energy

stored in plant biomass is referred to as net primary production (NPP) and a portion of

that is consumed through autotrophic respiration (R_a). For primary producers, the total

amount of energy produced is gross primary production (GPP):

18

$$GPP = NPP + R_a \qquad \text{(Bott 1996)}$$

Both plant and animal life within aquatic systems – including fish, invertebrates, macrophytes, algae, and microbes – perform respiration to sustain life. Ecosystem level measures of respiration provide an indication of total consumption of organic matter supplied by sources both within (autochthonous) and outside (allochthonous) the ecosystem (Mulholland *et al.* 2001).

The theory behind measurements of ecosystem metabolism is thus grounded in the basic equation for photosynthesis:

$$6\ CO_2 + 12 H_2O \rightarrow 6\ O_2 + C_6H_{12}O_6 + 6\ H_2O \qquad \text{(from Bott 1996)}$$
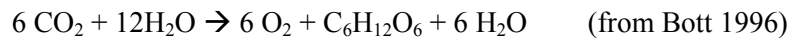
It is possible to estimate rates of photosynthesis and respiration by evaluating changes in either oxygen (dissolved in aquatic systems) or carbon dioxide concentrations, although former is more commonly used given the relative ease of measurement and large diurnal changes (Young *et al.* 2004). Stream metabolism can be estimated by measuring dissolved gas change directly in a stream or river (known as the 'open system' or 'open channel' method), or by enclosing a portion of the ecosystem (e.g. a substrate sample) within a chamber ('closed' system or 'chamber' method) and measuring dissolved oxygen change in the chamber (Bott *et al.* 1978). Both methods involve monitoring dissolved oxygen concentrations at regular intervals. The observed changes in concentration are related to biotic factors influencing the dissolved oxygen budget; namely, input from photosynthesis and removal from (aerobic) respiration. The

challenge of the method is to separate the biotic from the abiotic influences (e.g.

temperature, reaeration) on the dissolved oxygen budget.

Methods for measuring metabolism *in-situ* based upon diurnal changes in dissolved

oxygen concentrations were first introduced by Odum (1956). This seminal paper

provided the fundamental mass-balance relationship that constitutes the foundation for all

measurements of metabolism in open systems; specifically:

$$Q \text{ (dissolved } O_2) = P - R +/- E,$$

where Q is the concentration of dissolved oxygen, P is photosynthesis, R is respiration,

and E is gas exchange between the atmosphere and the water column. As shown in the

following conceptual model, it is simply the construction is a dissolved oxygen budget

for a stream reach.

Figure 4: Conceptual Model for Dissolved Oxygen Budget
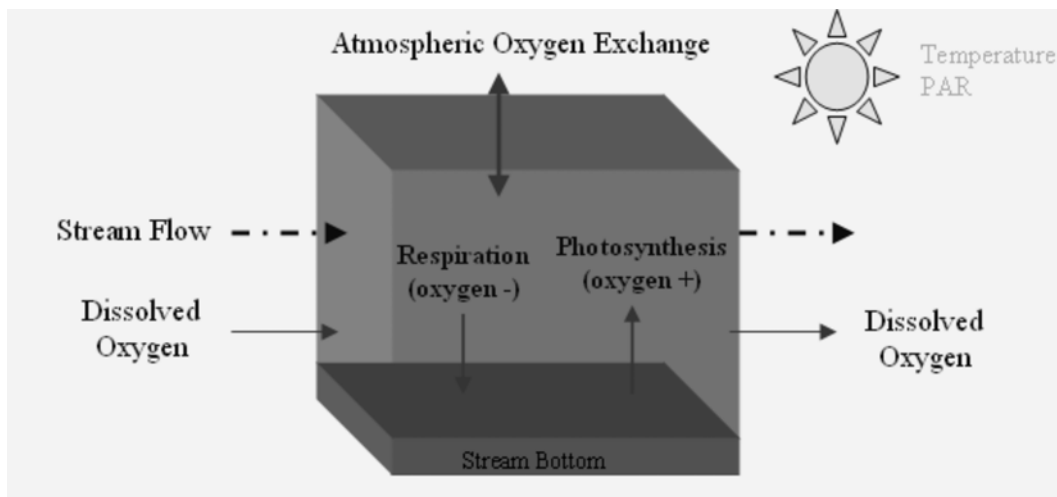
The flux of groundwater must also be considered in the mass-balance equation, particularly where the effect may be large relative to the rates of biological processes or reaeration (McCutchan *et al.* 2002). Odum (1956) considered this potential effect, and suggested that only reaches without tributaries or obvious groundwater seeps were appropriate for the open-channel method. Recently, mathematical corrections for groundwater inputs have been provided (Hall and Tank 2005), along with suggested thresholds for incorporation into metabolism calculations, when groundwater oxygen content and rate of gain/loss within a reach are known.

Open system measurement techniques may involve the use of a single monitoring station (single station method) or two stations placed at either end of a study reach (upstream-downstream method). If the single station method is used, it is assumed that changes in dissolved oxygen concentrations are uniform throughout the entire reach (Bott 1996). To calculate metabolic metrics, single-station methods use the changes in dissolved oxygen at one site over time, where two-station methods use the changes in dissolved oxygen concentrations between two stations set at ends of a specified reach (Young and Huryn 1999). The primary advantage of the open-system method is the inclusion of the whole ecosystem under natural conditions (Huryn *et al*. 2004).

An alternative to open-system measurement techniques is the use of chambers to enclose portion of the stream bottom to create a microcosm. Chamber methods have the distinct advantage over the open-system methods in that no estimate of reaeration is required (Young *et al.* 2004). Chamber methods have been successfully used to isolate the relative contribution to overall metabolism from various ecosystem compartments such as the benthos versus the water column (Naegeli and Uehlinger 1997). However, the use of

chamber has numerous disadvantages as well, most of which relate to the artificialities of the enclosed system (Young and Huryn 1999). For example, water velocity, temperature, and light within the chamber will differ from natural conditions, and nutrients can become depleted (Young *et al.* 2004). Many researchers have attempted to modify chamber designs to overcome some of these disadvantages. Bunn *et al.* (1999), for example, maintained water velocities similar to natural conditions and regularly flushed the chamber with stream water to address nutrient depletion. However, as Young *et al.* (2004) note, many of these problems cannot be solved simply through adjustments to chamber design and maintenance. Respiration rates also have been found to be underestimated by the chamber method (Marzolf *et al.* 1994), likely as a result of exclusion of the hyporheic zone. Given the limitations of the chamber method, I elected to employ the open-system method for our study.

Perhaps the main challenge associated with the open-system method is estimating the rate (and direction) of dissolved oxygen exchange between the atmosphere and the water column (known as reaeration). There are a variety of methods that can be used to estimate reaeration, including engineering equations based on stream hydraulic characteristics (e.g. Tsivoglou and Neal 1976) and analysis of the dissolved oxygen record itself (i.e. Westlake and Owens 1974, Young and Huryn 1996, McBride and Chapra 2005, Young *et al.*, 2004). A variety of methods to empirically measure reaeration have also been attempted, including the use of floating domes (Copeland and Duffy 1964) and the injection of volatile tracers (Rathbun 1978). Field measurement of reaeration for small, turbulent streams with low-productivity has been improved dramatically in the past several decades. Marzolf *et al.* (1994) presented a field-based measurement technique that involves the simultaneous injection of conservative (non-

reactive) and volatile (reactive) tracers to estimate a reaeration coefficient. This

coefficient is used to calculate the reaeration flux, which is used to mathematically

correct field measurements of dissolved oxygen. Young and Huryn (1998) identified a

mathematical error in the equation presented by Marzolf *et al.* (1994) and their corrected

equation is now widely accepted and used in the construction of key interim variables

during metabolism analyses:

$$\text{Reaeration flux} = DO_{deficit} \times k_{O2} \times T,$$

where the dissolved oxygen deficit ($DO_{deficit}$) is multiplied by the reaeration coefficient

(k_{O2}) and travel time (T). This is the formula we used in the spreadsheet model

developed to calculate metabolic rates from the raw field data, except that the travel time

is a fixed interval of one hour following Bott (1996).

Many contemporary studies of stream metabolism use propane evasion techniques to

estimate reaeration (e.g. Houser *et al.* 2005, Mulholland *et al.* 2001, Hall and Tank

2003). However, propane evasion methods are also considered complicated, costly, and

time consuming, and alternate methods to estimate reaeration are also commonly used.

For example, Bott *et al*. (2006b), Gibson (2004), and McTammany *et al.* (2003)

employed the energy dissipation model (EDM) of Tsivoglou and Neal (1976) to estimate

reaeration as follows:

$$k_{20} = K' \text{ x } (\Delta H / \Delta X) \text{ x } V$$

where k_{20} is the reaeration rate at 20 ºC, K' is an empirical constant based upon discharge, $\Delta H/\Delta X$ is channel slope, and V is water velocity. An adjustment for water temperature at the time of measurement is typically made following the correction suggested by Elmore and West (1961). Mulholland *et al.* (2001) compared measured reaeration rates (derived from propane evasion) with calculated values (using the EDM), and concluded that the EDM may provide suitable estimates of reaeration for streams with depths > 6cm. After a review of these considerations, we elected to use the EDM for estimating reaeration in our study[1].

The importance of accurately estimating reaeration rates, as well as maintaining high quality control during field measurements, is highlighted by McCutchan *et al.* (1998). This paper provides an excellent review of the uncertainties associated with the open-system measurement techniques, and how those uncertainties affect confidence that should be associated with metabolism findings. In particular, McCutchan *et al.* (1998) showed that estimates of respiration are more likely subject to error than estimates of productivity, particularly in streams with high reaeration coefficients ($k_{20} > 100$/day).

For both open-system and chamber techniques, measuring changes in dissolved oxygen (and other important variables such as temperature) over at least 24-hours allows for the computation of 2 basic parameters: Net oxygen change in the light (the combination of photosynthesis and respiration); and, (2) respiration in the dark (Bott 1996). During the night, respiration is the only biological influence on the dissolved oxygen budget, as

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[1] It should be noted here that we spent considerable time and effort pioneering a new method for estimating reaeration in our study streams based upon measurement of sound pressure with a relationship to stream flow. The results of those efforts were recently published in the Journal of the North American Benthological Society (Morse *et al.*, 2007), and I am a co-author on that paper. However, that work is beyond the scope of my thesis, and further discussion is not included in this literature review or elsewhere in this thesis.

photosynthesis is sunlight dependent. Daily estimates for respiration are developed by

extrapolating the nighttime values throughout the daylight hours (Bott 1996). The

method for estimating daytime respiration is subject to potential error from

photorespiration by plants (Parkhill *et al*. 1998). Furthermore, the technique does not

allow for the separation of heterotrophic versus autotrophic respiration (R_a), and thus the

term "community" (CR) or "ecosystem" (ER) respiration is used to account for the

collective effect on the dissolved oxygen budget.

By analyzing diurnal profiles of dissolved oxygen, and extending nighttime respiration

through the daylight hours, it is possible to develop daily estimates for GPP[2] (Mulholland

et al. 2001). The net daily metabolism (NDM), or total amount of organic matter

produced *and* consumed within a stream, is calculated as:

$$NDM = GPP - CR \qquad \text{(Bott 1996)}$$

If GPP > CR for a given day, there is a net addition of energy to the system, NDM is

positive and the ratio of GPP/CR is > 1. If CR > GPP, NDM is negative, the GPP/CR

ratio is < 1, and there is a net loss of energy from the system (Bott 1996). The ratio of

GPP to CR is commonly described as the "P/R" (production/respiration) ratio.

Studies of stream metabolism often explore the relationship between the key components

– GEP and ER. Some studies have identified a positive relationship, in which increases

in GEP are associated with increases in ER (e.g. Bunn *et al.* 1999). Other studies have

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[2] We elected to use the term "gross ecosystem productivity" or GEP and "ecosystem respiration" or ER, in lieu of GPP and CR, to further emphasize that our measurements constitute the entire stream ecosystem rather than individual compartments.

shown weak or non-existent relationships (Mulholland *et al.* 2001, Houser *et al.* 2005).

The relationship between the two is likely influenced by a variety of factors (see below)

which differ between stream systems, making generalizations difficult or impossible.

The final variables (GPP, CR, NDM) produced during whole-stream metabolism

evaluations are typically expressed in terms of a rate of dissolved oxygen production or

consumption per unit area; for example, mg O_2 m^{-2} day^{-1}. These units are sometimes

converted to g or mg of carbon per stream area (Bott 1996). Recently, Bott *et al.* (2006b)

and Sweeney *et al.* (2004) make the case that area-based units may not allow for the best

comparison of streams of different size. Two streams may have similar metabolic rates,

but because of width differences, may have very different overall rates of ecosystem

function. Bott *et* al (2006b) suggest multiplying metabolic rate estimates in area-based

units by *width* to provide estimates per unit stream length (mg O_2 m^{-1} day^{-1}). Our study

recognizes the logic of this concept, and provides metabolism estimates in both area- and

length-based units.

IV. Factors that influence stream metabolism

Stream metabolism has been described as a "particularly important indicator" (Fellows *et*

al. 2006) of stream health because its two component processes – primary production and

respiration – both respond to environmental variables that are affected by landscape

disturbance (Bunn *et al.* 1999). Urbanization results in fundamental changes to the

landscape that have direct impacts on conditions within and around stream systems. As

discussed below, many of those conditions have been shown to be important

determinants of stream metabolism, including light, temperature, nutrient concentration,

discharge regime, and stream morphology. It is important to cover these factors here, as they influenced the selection of our study sites (we attempted to minimize differences in terms of canopy cover, size, slope, etc.), and shape the interpretation of our results as possible covariates.

The removal of vegetation from the riparian corridor commonly occurs during urbanization, resulting in an increased amount of sunlight reaching the water surface and benthos. It is logical that increased amounts of sunlight should translate into higher rates of primary productivity, and GPP has been found to be strongly correlated with PAR (photosynthetically active radiation) (Mulholland *et al.* 2001), related to percent canopy cover (Bunn *et al.*1999, Fellows *et al.* 2006), and subject to light saturation kinetics (Young and Huryn 1996). However, in some cases, the effect of increased light may also be mediated by high turbidity (Young and Huryn 1999). Increased sunlight reaching the water surface may also result in increased water temperature, which has been shown to be a significant factor regulating stream metabolism (e.g. Bott *et al.* 1985).

Time of year strongly influences both temperature and available sunlight, and seasonal changes in stream metabolism have been evaluated in numerous studies. In an inter-biome study of streams in the United States (and along the river continuum in each stream), Bott *et al.* (1985) evaluated stream metabolism using chamber techniques across seasons. While considerable variation was observed, respiration was highest in the fall for most reaches (likely as a result of leaf litter inputs), and primary production was highest in the spring (likely from increase light prior to leaf out). Uehlinger *et al.* (2006) found distinct seasonal patterns of GEP and ER over 15-years in the River Thur in Switzerland. Both GEP and ER were highest around May, with declines observed for

each until a winter low point. In evaluating the effects of a disturbance gradient in a

military reservation, Houser *et al.* (2005) observed seasonal patterns in metabolism, but

no covariance with temperature, indicating the temperature was not the primary driver of

seasonal differences. High ER was found in the winter and spring, and lower ER was

found in the summer and autumn months. Significant seasonal differences in mean GEP

values were not observed, but the highest GEP occurred in the spring. All of these

findings highlight how many factors are involved in governing stream metabolism,

including light, nutrients, and temperature, which vary considerably between season, for

streams in different biomes, and of different sizes.

Nutrients are also a key factor controlling periphyton biomass, and this relationship has

received considerable attention in studies of stream metabolism. In their study of streams

across different biomes in the United States, Mulholland *et al.* (2001) found strong

relationships between soluble reactive phosphorus (SRP) concentrations and ER. They

also found a strong relationship between SRP and GPP when available sunlight was

included in a multiple regression model. In a review of GPP findings for 30 streams in

the northern hemisphere, Lamberti and Steinman (1997) found a significant positive

correlation with SRP concentrations. In their study of streams draining agricultural

catchments in the Midwest, Bernot *et al.* (2006) found a significant positive correlation

between GPP and nutrient concentrations (NH_4, NO_3, and SRP); no significant

relationship was found between ER and nutrient concentrations. Fellows *et al.* (2006)

found that total nitrogen concentrations in stream water explained 59% of variation for

GEP and ER at 47 study sites in southeastern Australia. Because elevated nutrient

concentrations are a common aspect of the 'urban stream syndrome' (Meyer *et al.* 2005,

Walsh et al. 2005a), we might expect nitrogen and/or phosphorus subsidies in our urban streams to contribute to elevated rates of GPP (and possibly ER).

Ecosystem metabolism has been linked with nutrient uptake (Hall and Tank 2003), another important ecosystem function in lotic systems. Information on ecosystem metabolism thus may provide an indication of the capability of the stream to remove, store, and process nutrients from the water (Young *et al*. 2004).

The relationship between nutrient uptake and ecosystem metabolism has been less clear in other studies. Bernot *et* al (2006) found no significant relationship between stream metabolism (GEP or ER) and nutrient uptake parameters in their study of agricultural streams in the Midwestern United States. The multiple controls on stream metabolism (e.g. light, temperature) are noted as potentially confounding factors that may obscure the relationship between metabolism and nutrient uptake rates. In addition, all of these study streams were characterized by very high nutrient concentrations, and saturation dynamics were believed to limit uptake parameters.

Urbanization and the associated conversion of pervious to impervious surfaces have dramatic effects on the hydrologic regime of a watershed, as discussed above. Streams in urbanized watershed typically are characterized by 'flashier' storm hydrographs (Walsh et al. 2005a). High flow periods may substantially reduce both GEP and ER, followed by recovery during inter-storm periods (Huryn *et al*. 2004). However, GEP has been shown to be more sensitive to flow fluctuation than ER, particularly during bed-moving spates (Uehlinger and Naegli 1998). This makes sense given that high flows and associated sheer stress may be sufficient to scour benthic algae communities (Peterson 1996 from

29

Huryn *et al*. 2004). The reduction in GEP cause by high flow periods also has been

shown to reduce the P/R ratio (Young and Huryn 1996).

The effect of storm flows on stream metabolism is also a function of the substrate

composition, which may provide more or less stable conditions for algae colonization,

depending on size and resistance to bed-moving spates. Large substrate material may be

more resistant to disturbance, and provide a more stable surface for algal biomass

accumulation and associated primary production (Biggs *et al.* 2001).

Young and Huryn (1996) found that temporal variation in discharge affected the

longitudinal patterns of metabolism in their study of the Taeri River in New Zealand.

The first study year was characterized by frequent floods and variable flow conditions,

with heterotrophic conditions (P/R<1) present in most locations; autotrophic conditions

(P/R >1) found only in the upper reaches. In contrast, the second study year was

characterized by an unusually prolonged period of stable flow, and the entire river was

found to be autotrophic. In a long-term (1986-2000) study of a 7th order European river,

Uehlinger (2006) also found that disturbance by bed-moving spates had a major influence

on GEP and ER. These findings indicate that hydrologic variability may play an

important role in determining patterns of metabolism.

Modified hydrologic regimes in urban watersheds also often leads to habitat

simplification in stream systems (Walsh et al. 2005a). As noted above, unnatural flow

patterns may reduce natural meander patterns, straighten stream segments, flush in-

stream habitat structures (e.g. large woody debris), and via sediment transportation and

deposition smoother areas of stream substrate (Booth and Jackson 1997). Habitat

simplification (reduced substrate heterogeneity) has been shown to be related to reduced

rates algal productivity and respiration (Cardinale *et al.* 2002).

Sedimentation may influence stream metabolism through several mechanisms – first by

reducing the amount of available light reaching the benthos (turbidity), second through

accumulation on the stream bottom and smothering of primary producers (Young *et al.*

2004), and third by increasing the abrasive properties of stream flow thereby increasing

the potential for scouring (Peterson 1996, from Young *et al*. 2004). Sedimentation has

the potential to smoother aquatic organisms, but also may block the connection between

surface and groundwater in the hyporheic zone (Boulton *et al.* 1997), with potential

implications for community respiration (Young *et al.* 2004). The hyporheic zone of a

stream is thought to strongly influence metabolism, and has been estimated to account for

a large proportion (50-85%) of ecosystem respiration (Naegli and Uehlinger 1997,

Fellows *et al.* 2001). At the same time, other studies suggest a positive relationship

between the amount of fine sediment on the streambed and respiration rates (Hedin 1990,

Hill *et al.* 1998; both from Young *et al*. 2004). Potential explanations are unclear, but

may be related to increased organic matter contained in the sediments, or an increased

surface area for colonization by microbes (Young *et al.* 2004).

V. Comparison with prior findings

As noted above, Meyer *et al.* (2005) - and to some extent Bott *et al*. (2006a) - provide the

only peer-reviewed contemporary study of metabolism in urban streams. However,

numerous studies of streams in non-urban watersheds have been performed, and are

useful for comparison purposes to our findings. This data allows us to determine the

reasonableness of our results. In order to narrow the universe of potential studies, I attempted to identify only those streams of similar size (based upon stream order and drainage area) that employed open-system methods. The results of this review are summarized on the following page; all values for GEP and ER are in units g O_2 m^{-2} day^{-1}.

Table 3: Summary of prior metabolism findings at comparable streams

Study	Description	Location	Catchment area	Order	n (days)	GEP	ER	Purpose	Findings
Houser et al. 2005	10 low-gradient, sandy bottom streams in forested catchments with intact riparian canopies	Georgia, U.S.A.	0.3 - 3.7	2 and 3	unclear (>40 possibly per site)	<0.01 - 1.75	0.3 – 16.3	To evaluate the effect of a disturbance (roads, soil clearing) gradient on stream metabolism	Upland disturbance negatively affected both GEP and ER
Mulholland et al. 2001	8 streams from a range of climates and locations in North America, all relatively undisturbed by human influence	North America		1 to 3	1 per site	<0.1 - 15	2.4 - 11	To identify controls on the stream metabolism rates across a wide geographic range	PAR and SRP explained 90% of variation in (log) GPP, and SRP and transient storage zone size explained 73% variation in ER
Bott et al. 2006b	13 pairs of stream reaches (forest and meadow) in 3 watersheds	Pennsylvania and Maryland, U.S.A.	0.7 – 123.3	1 to 5	~20 per site (over 2 years)	0.02 - 5.3	1.22 - 13.45	To evaluate the effect of riparian vegetation and geomorphology on stream metabolism	Differences identified between forest and meadow reaches and between seasons. Also, the expression of units in terms of length compared with area.
Bott et al. 2006a	10 streams draining to NYC drinking water supply reservoirs with a range of land uses (forested, agricultural, and suburban).	New York, U.S.A.	"mid to large" sized streams	n/a	~8-10 per site over 3 years.	0.23 - 4.32	1.39 – 8.3	To evaluate ecosystem processes in stream draining to NYC drinking water supply reservoirs, and relate findings to potentially influential variable at multiple scales.	Baseline values established for future comparison; Metabolism findings related to instream environmental and water-chemistry variables, and shading. Land use impacts were confounded by stream size and canopy cover.

Study	Description	Location	Catchment area	Order	n (days)	GEP	ER	Purpose	Findings
Meyer et al. 2005	6 streams in urban and forests catchments	Georgia, U.S.A.	48 - 221	3 to 4	1-4 per site	0.43 - 2.38	1.31 - 8.72	To evaluate ecosystem processes in urban streams.	No significant differences in metabolism identified, although slightly higher GPP found in urban streams.
Gibson 2004	8 headwater streams in forested and suburban developed catchments, all with natural channel form and canopy cover	Georgia, U.S.A.	0.3 - 1.8	1	1 per site	0.06 - 0.59	0.79 - 5.15	To evaluate uptake length and metabolism in small suburban streams	No differences identified in metabolism.
Wilcock et al. 1998	23 lowland streams in primarily agriculture catchments	New Zealand	12 - 357	n/a	3-4 per site	0.5 - 29.2	1.6 - 37.5	To characterize streams in intensively grazed areas according to productivity, respiration, and reaeration.	Using the DOFLO model to analyze diurnal DO curves, identified 5 groupings of streams
Fellows et al. 2001	2 headwater streams at high elevation (>2000m)	New Mexico, U.S.A.	n/a	1	1 per site	0.2 - 1.7	2.3 - 14.7	To determine the contribution of the hyporheic zone to ER in streams with different surface-subsurface exchange characteristics.	The hyporheic zone contributed significantly to ecosystem function in the 4 study reaches

Study	Description	Location	Catchment area	Order	n (days)	GEP	ER	Purpose	Findings
Hall and Tank 2003	11 streams in Grand Teton National Park at high elevation (>2000m) and with very low nutrient concentration	Wyoming, U.S.A.	n/a	n/a	1 per site	0.13 - 3.11	0.97 - 13.30	To evaluate the relationship between biological demand (primary production) and nutrient uptake	Nitrogen uptake velocity was strongly related to rate of GPP.

V. References

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Article

This article is prepared pursuant to the submission guidelines of the journal <u>Freshwater Biology</u>, which specifies the following arrangement:

(a) *Title page.*

(b) *Summary.*

(c) *Introduction.*

(d) *Methods.*

(e) *Results.*

(f) *Discussion.*

 (g) *Acknowledgments.*

(h) *References.*

(i) *Tables.*

(j) *Figure legends.*

(k) *Illustrations.*

Title Page

The influence of stormwater impairment on whole-ecosystem metabolism of suburban streams in Vermont (U.S.A.)

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Running header: A. Hackman et *al*.

Summary

1. To evaluate how watershed development has impacted in-stream ecological
   processes in northwestern Vermont (U.S.A.), we measured whole-ecosystem
   metabolism in 7 study streams over 2 years. Streams were selected based upon *a
   prior* classification by the Vermont Department of Environmental Conservation
   (VT DEC) as either "impaired" for urban stormwater runoff (303d listed) or in
   "attainment" of state bio-monitoring standards. We confirmed and augmented
   these classifications by conducting additional assessments of biological
   community structure, stream geomorphic and habitat conditions, and stream
   water chemistry.

2. We used the open-channel, single-station approach (Odum 1956, Bott 1996) and
   estimated 271 daily rates of gross ecosystem production (GEP), ecosystem
   respiration (ER), net daily metabolism (NDM), as well as the ratio of production
   to respiration (P/R) split almost evenly between the impaired and attainment
   condition stream groups. We modeled relationships between discharge and
   stream dimension, and incorporated these as dynamic variables in the metabolism
   calculations.

3. Over the entire study period, GEP was significantly ($p < 0.01$) higher in the
   impaired streams (median 2.98 g O_2 m^{-2} day^{-1}) compared to the attainment
   condition streams (median 1.16 g O_2 m^{-2} day^{-1}). Both stream groups, however,
   exhibited similar rates of ER (median -4.97 and -4.84 g O_2 m^{-2} day^{-1} for the
   impaired and attainment condition groups, respectively). The attainment

condition streams were more heterotrophic than the impaired streams (median P/R of 0.27 versus 0.57). NDM was significantly ($p < 0.05$) lower in the impaired streams; however, this finding does not imply reduced overall processing of organic matter. Rather, it implies that the distribution of processing is different, with impaired streams more dependent on stimulated autochthonous resources, and the attainment condition streams supported by a more diverse resource base.

4. The two groups of streams exhibited significantly different seasonal patterns of ecosystem metabolism. Relative stability characterized the metabolic regime of the attainment condition streams; rates GEP and ER were generally consistent across seasons. In contrast, relative instability driven by seasonally-stimulated GEP characterized the impaired streams. Mean impaired stream GEP in the spring , summer, and fall months was 4.57, 5.55, and 1.65 g O_2 m^{-2} day^{-1}, respectively; seasonal changes in ER mirrored the changes in primary production.

5. Our findings provide a holistic description of the structure and function of streams in rapidly developing suburban areas in northwestern Vermont. These stormwater-impaired streams were characterized by physical deterioration, habitat loss, nutrient enrichment, simplified biological community structure, and stimulated in-stream primary production.

6. We propose that the altered 'metabolic regime' observed in our impaired study streams may represent another aspect of the urban stream syndrome associated

with this particular level of watershed development. We suggest that measures to limit the drivers of in-stream primary production (i.e. sunlight, temperature, nutrients) may help encourage a more 'natural' metabolic regime in urban stormwater-impaired streams in some areas.

Introduction

The 'urban stream syndrome' (Meyer *et* al. 2005, Walsh et al. 2005a) describes a well-studied and consistent pattern of stream degradation associated with watershed development. In recent decades, much attention has been paid to the plight of urban streams (e.g., Paul and Meyer 2001, Center for Watershed Protection 2003). Urbanization is responsible for fundamentally altering watershed hydrology (Dunne and Leopold 1978, Walsh *et* al. 2004), causing physical instability of the stream channel (Booth 1991), habitat loss (Finkenbine *et* al. 2000), nutrient loading and water quality deterioration (Hatt *et* al. 2004), and biological community change (Roy *et* al. 2003, Taylor *et* al. 2004). In the Northeastern United States, a similar link between urbanization and widespread stream degradation has been established (Coles *et* al. 2004).

While considerable research has been conducted to examine the effects of urbanization on the hydrological, biological, physical, and chemical characteristics of lotic systems, relatively little is know about how urbanization affects rates of basic ecological *processes* in these streams and rivers (Walsh et al. 2005a). Measurements of ecosystem function or process offer a fundamentally different and integrative approach to assess stream condition. Bunn and Davies (2000) describe these different approaches in terms of 'pattern' and 'process.' Increasingly, these measurements of ecological processes are

being included in holistic assessments of stream condition (Bunn *et* al. 1999, Bott *et* al. 2006a, Fellows *et* al. 2006), though they have not been widely used to evaluate urban streams (Paul and Meyer 2001, Walsh et al. 2005a). Relevant examples include studies of nutrient uptake rates in the southeastern (Meyer *et* al. 2005) and southwestern (Grimm *et* al. 2005) United States that indicate diminished capability on the part of urban streams to remove nutrients from the water column. Other recent studies using leaf litter packs show increased breakdown rates in urban streams (Paul *et* al. 2006, Chadwick *et* al. 2006). There have been a few attempts to evaluate stream metabolism in urban and suburban watersheds (Gibson 2004, Aldridge 2005, Meyer *et*. al 2005, Bott *et* al. 2006a). However, to date no clear trends have emerged from these studies.

The concept of stream "metabolism" involves of two components – primary production and respiration – both of which are fundamental ecological processes that help to describe the energy cycle of any ecosystem. Primary production is the conversion of inorganic carbon to organic matter by photosynthesizing organisms using solar energy. As a biological rate, it describes the contribution to the overall stream resource budget from in-stream sources (versus terrestrial sources). Respiration (also a biological rate) is the conversion of food resources into the energy necessary to sustain life. Ecosystem-scale measures of respiration provide an indication of total consumption of organic matter supplied by sources both within (autochthonous) and outside (allochthonous) the ecosystem (Mulholland *et al.* 2001). Measures of metabolism thus estimate of the amount of organic matter produced *and* consumed within a stream ecosystem (Bunn and Davies 2000).

Primary production and respiration directly influence key ecosystem services provided by streams. For example, water purification is accomplished in part via organic matter breakdown (respiration) and nutrient sequestration (Bott *et* al. 2006a), which has been linked to primary production (Hall and Tank 2003). Energy resources at the base of the food web are integral to the success of upper trophic levels, including fish production, which is a consumable protein source for humans and other organisms (Meyer *et* al. 2005). Rates of photosynthesis and aerobic respiration contribute to dissolved oxygen regulation in streams (Bott et *al*. 2006a). The relative balance between primary production and respiration helps determine the percentage of organic matter that is processed or exported to downstream receiving waters, and has been considered indicative of overall stream water quality for decades (Cummins 1974).

Despite the importance of primary production and respiration in the maintenance of healthy streams, very little is known about how urbanization impacts these processes. Methods to evaluate stream metabolism have existed for decades (Odum 1956, Owens and Westlake 1974, Bott 1996) and have undergone considerable refinement with advances in technology and technique (Marzolf *et* al. 1994, Young and Huryn 1998, Hall and Tank 2005). These methods have been used in numerous studies of rural streams and rivers (e.g. Naegli and Uehlinger 1997, Fellows *et al.* 2001, McTammany *et al.* 2003), are quickly gaining acceptance around the world in routine assessments of stream and river health (e.g. Young *et* al. 2004), and are becoming recognized as integrative measures that are responsive to multiple factors associated with landscape change (Fellows *et* al. 2006). Yet only a handful of studies have utilized this powerful approach to assess urban streams (Gibson 2004, Aldridge 2005, Meyer *et* al. 2005, Bott *et* al. 2006a).

The purpose of this study was to investigate how ecosystem level measures of primary productivity and respiration have responded to rapid watershed development in northwestern Vermont, USA. In these streams, we expected that altered stream water chemistry (nutrient enrichment) and physical degradation (leading to increased temperature and available sunlight) would stimulate both primary production and respiration even if the biotic structure of these steams was simplified by the overall development impact.

Methods

Site descriptions

In Vermont, watershed urbanization and associated stormwater runoff have degraded the condition of a number of streams and receiving waters (VT DEC 2006). For this study, we selected a set of seven (7) 3rd and 4th order streams in northwestern Vermont (U.S.A.) that drain directly or indirectly into Lake Champlain. Initial selections were based upon regulatory classification by the Vermont Department of Environmental Conservation (VT DEC), consultation with agency staff, and extensive field reconnaissance. Three (3) of the streams were located in watersheds with widespread suburban development and were identified as being 'impaired' by urban stormwater runoff in required reports (Section 303.d of the Clean Water Act) to the U.S. Environmental Protection Agency (EPA).   The other 4 streams were located in nearby watersheds with more limited development, and were in attainment of the state's assessment criteria, based upon macroinvertebrate and fish community indices (i.e., biocriteria). We will refer to these streams that met the

49

state's criteria as "attainment" condition streams to emphasize that they were not pristine "reference" streams. We assumed *a priori* that the classifications by VT DEC accurately described the biological (as well as chemical and physical) condition of the study reaches. However, as described below, we confirmed and augmented these classifications by conducting additional assessments of biological community structure, stream geomorphic and habitat conditions, and stream water chemistry.

Study reaches (100-200m) were identified within these streams at points near historic VT DEC monitoring locations. Final selections were based upon upstream catchment area, substrate type (gravel/cobble), stream form (riffle-pool), absence of surface water tributaries, and canopy cover (generally open), with accessibility and safety concerns as factors as well. Further description of the watershed characteristics of the study streams is provided in Table 1 and Figure 1. The physical and chemical characteristics of the study reaches are provided in Table 2.

Ecosystem Metabolism

We measured gross ecosystem productivity (GEP) and ecosystem respiration (ER) using the single-station, open-system approach (Odum 1956, Bott 1996). Diel changes in dissolved oxygen (DO), temperature, and specific conductivity were recorded at each site using a YSI model 600 XLM sonde equipped with a YSI model 6562 DO sensor (YSI Environmental, Inc., Yellow Springs, OH). Sondes were placed in the thalweg at the bottom of each study reach at approximately one-half depth, in an area of well-mixed water. Prior to deployment, the sondes were calibrated in water-saturated air. Throughout deployment, calibration was verified (1-3 times per week) in the field using a

WTW model Oxi 340i handheld DO meter (WTW GmbH & Co., Germany), which was calibrated in water-saturated air prior to each use. If the YSI and WTW readings were within 0.5 mg L^{-1} DO, then no re-calibration was performed. If probe disagreement was greater than 0.5 mg L^{-1} DO, then the YSI probe was recalibrated *in-situ* to the value of the roving WTW probe. We measured photosynthetically active radiation (PAR) or solar radiation (SR) at the stream bank of each site using an ONSET model M003 or S003 sensor and HOBO Micro Station data logger (Onset Computer Corporation, Pocasset, MA). To allow comparison between sites, we converted SR to PAR units using the simple equation from Simms *et al*. (2005).

Monitoring probes were deployed at each site between approximately July 2004 to November 2005. We did not perform monitoring during the winter months (December through March) due to ice hazards. Monitoring was terminated at Indian Brook and Johnnie Brook in July 2005 due to beaver-related impacts and equipment loss due to a large storm event, respectively. We monitored Patrick Brook in 2004 and Lewis Creek in 2005 (both attainment condition streams); all other streams were studied for 2 consecutive years. We found it necessary to move from Patrick Brook to Lewis Creek because of concerns about the effects on our measurements of an upstream impoundment identified after the 2004 field season.

All DO, temperature, conductivity, and PAR, data were recorded in the field at 5-minute intervals. We removed clearly erroneous values from the uncorrected DO record, aggregated all data to hourly mean values, and merged data from different sensors under a common date and time stamp. Corrections to the DO data were required because of errors caused by a variety of sources, including biofilm buildup or macroinvertebrate

colonization on the DO sensor membrane or accumulated debris on the sondes. For the

metabolism calculations, we only utilized data sets where drift was less than 0.5 mg L^{-1}

DO between field calibrations. Prior to input into the metabolism calculations model, the

minor (<0.5 mg L^{-1} DO) drift within these sets was corrected using linear regression and

interpolation between calibration points.

We estimated the reaeration coefficient using the energy dissipation method (Tsivoglou

and Neal 1976), which is based upon stream depth, slope, and velocity. We chose this

method given its use in other recent studies (e.g. Bott *et al*. 2006b, McTammany *et al.*

2003), suitable water depth of greater than 6cm (Mulholland *et al* 2001), and our interest

in constructing simple reaeration rating curves. We used the scaling for the empirical

constant (K) suggested by Bott (1996) to provide an adjustment to the Tsivoglou and

Neal (1976) equation based upon discharge. While sacrificing some accuracy associated

with more complex gas evasion techniques, we thought this simple and cost-effective

method would adequately estimate reaeration for comparison purposes. Moreover, we

were interested in exploring whether our methods and findings could assist in

establishing monitoring protocols and benchmarks for stream health assessments that

might be used economically by regulatory agencies.

Stream discharge

At each site, we used pressure transducers (Model WL-15, Global Water Instrumentation,

Inc., Gold River, CA) to measure and record water level in 5-minute intervals. Recording

stations were located in laterally constrained sections (to maximize stage height

amplitude) with stable cross-sections and in areas of calm surface water. We performed

discharge surveys using a Marsh McBirney Flomate 2000 (Marsh McBirney, Inc.,

Frederick, MD) electromagnetic velocity meter and top setting wading rod and

constructed rating curves with 5 to 9 data points, over a range of discharges, for each year

at each site.   A large storm event destroyed our gage on Potash Brook on August 28,

2004 and we used USGS data from a stream gaging station located approximately 150m

upstream for the remainder of that year for this study; we reconstructed the Potash Brook

stream gage in 2005.

Structural Assessments (Biological, Physical, and Chemical Characterization)

To confirm the *a prior* classification of either 'impaired' or 'attainment' condition based

on the state's long-term data, we performed a survey of the benthic macroinvertebrate

community structure at 6 of the study sites in October 2004 during the late-fall index

period following the same methods used by the VT DEC (VT DEC 2003a). We used VT

DEC data for Lewis Creek (VT DEC 2001). Briefly, we collected benthic

macroinvertebrates from 3 representative riffles (1 sample, 2 replicates) within each study

reach. We placed a 500-µm D-net on the stream bottom and used upstream disturbance

(by hand for 30 seconds) to thoroughly dislodge attached organisms in approximately 1

m^2 of substrate. Moving upstream, we repeated this process at 4 different locations

within the selected riffle that represented the range of velocities and substrate

characteristics present. The samples were partially elutriated in the field then the

remaining organic matter and invertebrates were washed into 250 ml Nalgene

polypropylene bottles and preserved with 75% ethanol. At the Rubenstein Ecosystems

Science Laboratory (Burlington, VT), we washed the samples through a #30 sieve, spread

contents on a tray divided into 24 equal squares, selected six random squares, and

removed organisms (by hand and using a dissecting microscope) until at least 300 were

counted. Macroinvertebrates were identified to genus when possible (except

Chironomidae, which were identified to Family), and non-insects were identified to

Order using standard keys (Merritt and Cummings 1996, Peckarsky *et al*. 1990). For

each site, we developed standard metrics used by VT DEC to describe the benthic

macroinvertebrate community including density (the relative abundance of organisms in a

sample), richness (the number of distinct taxa in a sample), EPT Richness (the number of

taxa in a sample from the orders Ephemeroptera, Plecoptera, and Tricoptera), Hilsenhoff

Biotic Index (a measure of the macroinvertebrate assemblage tolerance to nutrient

enrichment [Hilsenhoff 1987]), and Percent Model Affinity of Orders (PMA-O; a

measure of order level similarity to a reference stream model [Novak and Bode 1992])

(VT DEC 2003a).

We also used the rapid geomorphic and habitat assessment components of the Vermont

Stream Geomorphic Assessment Protocols (VT DEC 2003b) to assess 6 of the study

streams; we used VT DEC data for Lewis Creek (VT DEC 2004)   These assessments

involved scoring stream reaches based upon observed conditions such as bank stability,

embeddedness, pool variability, channel alteration, vegetation, and degree of incision, to

name only a few. Additional cross-sectional characterization surveys were performed at

least once per year at all sites to perform more detailed measurements of stream and

channel geometry. At 5 m intervals along the entire reach, we measured average width

and depth (wetted and channel), substrate type, planar morphology (e.g. pool, chute,

riffle), and percent embeddedness. In addition, during the cross-sectional

characterization survey we visually estimated by percent cover the general types of

benthic micro and macro algae (e.g. biofilm, filamentous) every 5 m. We measured

stream channel slope in the field using a laser range finder (Laser Technology, Inc.,

Englewood, CO) and staff with an optical sighting lens, and recorded GPS and elevation

using a handheld Garmin GPSmap 76 (Garmin International, Inc., Olathe, KS).

To estimate background nutrient concentrations, stream water samples were collected

from each study reach during the cross-sectional characterization surveys, filtered in the

field, and preserved on ice. All samples were analyzed for nitrate (NO_3) and

orthophosphate (PO_4) using standard methods (EPA 300.0 and 365.1, respectively) at

EPA-certified commercial laboratories in Vermont.

Metabolism Calculations

Daily rates of gross ecosystem productivity (GEP) and ecosystem respiration (ER) were

calculated using a spreadsheet-style model based primarily on Bott (1996). A term to

model groundwater inputs (Hall and Tank, 2005) was included initially, but we

concluded that only extreme levels of groundwater inputs and dissolved oxygen levels

would substantively affect our values. In addition, we did not sample groundwater to

determine DO concentrations and could not locate prior groundwater sampling results for

our 7 sites. On that basis, we decided not to include a groundwater correction term and

acknowledge this exclusion as a potential source of error. Hourly mean values for DO,

temperature, stage/discharge, and PAR were inputs into the spreadsheet, and then a series

of calculations were performed to construct a suite of interim variables for each hourly

time step. Included in these calculations were a series of rating curves that we developed

for each site that adjusted stream width, depth, cross-sectional area, and average velocity

estimates at each time step based upon discharge (Hackman, 2008).

We calculated the rate of DO change as the difference between consecutive hourly mean

values. We determined the DO saturation concentration using a 3rd order polynomial

regression of temperature versus DO (YSI, Inc. 2006) and then subtracted it from the

stream water DO concentration to provide the saturation deficit. We adjusted our

dynamic value for the reaeration coefficient (kO_2) at each time-step for the actual water

temperature per Elmore and West (1961). Next, we calculated the gas exchange rate (or

'reaeration flux' per Young and Huryn 1998) between the atmosphere and water column

by multiplying the adjusted kO_2 by the saturation deficit. We then calculated a

reaeration-adjusted rate of DO change by adding together the DO change rate and

reaeration flux. This final interim variable has been described as the net rate of oxygen

change due to metabolism (Fellows *et al*. 2001) or net ecosystem production (NEP)

(Mulholland *et al*. 2001).

Daily rates of ER were calculated by summing NEP values during night hours plus

daytime ER, which was estimated by linearly interpolating between the ER values from

the pre-dawn and post-dust hours (set by using a PAR threshold of 1.3 *u*mol m^{-2} sec^{-1}). In

our calculations and throughout this paper, ER is given a negative sign (-) to indicate DO

consumption. The daytime sum of NEP plus daytime ER was used to estimate a daily

rate of gross ecosystem production (GEP). These calculations produced ER and GEP

estimates in volumetric units (g O$_2$ m^{-3} day^{-1}), which were converted to streambed area-

based units (g O$_2$ m^{-2} day^{-1}) by multiplying by water depth (m). We further multiplied by

stream water width (m) to provide estimates in units per stream length (g O$_2$ m day^{-1}) per

Bott *et al*. (2006b). Daily estimates for GEP and ER were summed to calculate net daily

metabolism (NDM) is both area and length-based units. The unit-less ratio of GEP to ER (P/R) was also calculated for each day.

Data Analysis

Prior to data analysis, we evaluated potential outliers in the daily metabolic values (GEP, ER, NDM, and P/R) for each study stream. This was accomplished by examining the data for each site using a variety of data plots and a general cutoff of +/- 3 standard deviations from the mean. When potential outliers were identified, we evaluated environmental conditions (e.g. discharge level, rapid change in discharge, temperature, sunlight) for the day in question. Nearly all of the outlier data were related to rapid discharge changes during the day in question. Similar errors in metabolism calculations related to rapid flow changes have been identified in other studies (Uehlinger 2000, Fellows *et al*. 2006). This process resulted in the exclusion of 16 of 287 total days worth of our metabolism data.

All data with daily observations (e.g. metabolism values, temperature, PAR) were evaluated for normality (Kolmogorov-Smirnov and Shapiro-Wilk tests, histograms, and normal probability plots) and homogeneity of variances (Levene's test). We observed that some data were non-normal and had unequal variances (transformations were unsuccessful) and thus elected to use non-parametric tests in these cases. To evaluate overall differences between the impaired and attainment condition groups of streams, we used the Mann-Whitney U two-independent sample test. To evaluate the group differences by season, we first split the data by season and then used the same non-parametric test. Daily metabolism data were grouped into seasons defined as spring

57

(April to June), summer (July to September), and fall (October to November). We used

scatterplots and the non-parametric Spearman Rank correlation analyses to compare

metabolism (e.g. GEP vs. ER) and driving variables (e.g. PAR, temperature, and

discharge) for the impaired and attainment condition streams.

We used scatterplots and simple linear correlation to assess the relationships between our

structural measures of stream condition (benthic macroinvertebrates, stream

geomorphology/habitat, and water quality) and median metabolic rates (GEP, ER, NDM,

P/R) for each of the study streams. These small data sets were normally distributed. To

confirm the a *priori* classification of streams as either impaired or in attainment

condition, t-tests were used to evaluate differences in the measures for biological,

chemical, and physical conditions for each group of study streams. Benthic

macroinvertebrate metrics for Lewis Creek (LEWI) involving counts per unit area

(density, richness, and EPT index) were not included in the correlations due to the higher

level of identification performed by VT DEC staff; non-dimensional metrics for this

stream were included (Hilsenhoff Biotic Index and PMA-O). All statistical analyses

were performed using SPSS v.13.0 (SPSS, Inc., Chicago, IL).

Results

Ecosystem metabolism – General comparison of impaired and attainment condition
streams

Values for GEP, ER, NDM, and P/R varied considerably within each stream and between

the different study streams (Table 3). For the impaired group of streams, GEP ranged

from 0.14 to 17.10 g O_2 m^{-2} day^{-1}, and ER ranged from -0.25 to -40.95 g O_2 m^{-2} day^{-1}.

For the attainment condition group of streams GEP and ER also varied considerably, but over a much narrower range than the impaired streams. GEP and ER for the attainment condition streams ranged between 0.09 and 4.39 g O_2 m^{-2} day^{-1}, and -0.48 and -15.47 g O_2 m^{-2} day^{-1}, respectively. When converted to length-based units, GEP for the impaired and attainment condition streams ranged from 0.63 to 43.88 g O_2 m^{-1} day^{-1}, and 0.30 to 17.06g O_2 m^{-1} day^{-1}, respectively. Ranges of ER in length-based units for impaired and attainment condition streams were similar at -0.93 to -124.28 g O_2 m^{-1} day^{-1}, and -1.36 to -109.50 g O_2 m^{-1} day^{-1}, respectively.

A comparison of median metabolism values for the pooled data for the two groups of study streams is presented in Figure 2, with significance from Mann-Whitney U tests indicated. Pooling the data resulted in 133 days of data for the impaired streams, and 138 days for the attainment condition streams. Rates of GEP were significantly higher at the impaired sites in both area ($p < 0.001$) and length-based ($p < 0.001$) units. In area-based units, median GEP for the impaired and attainment condition streams was 2.98 and 1.16 g O_2 m^{-2} day^{-1}, respectively. In length-based units, the difference in median value between groups was more pronounced at 12.26 and 3.70 g O_2 m^{-1} day^{-1}, respectively.

Median ER values for impaired and attainment condition streams were -4.97 and -4.84 g O_2 m^{-2} day^{-1} in area-based units, and -18.08 and -16.45 g O_2 m^{-1} day^{-1} in length-based units. Compared to GEP, the difference in ER was thus less pronounced, and only statistically significant ($p = 0.046$) in the length-based units. The difference in ER was not significant in area-based units ($p = 0.269$).

The difference in NDM between the two groups was significant in area-based units, with impaired and attainment condition stream median values of **-**1.98 and –3.30 g O_2 m^{-2} day^{-1}, respectively (p = 0.007). In length-based units, NDM for impaired and attainment condition streams was also significantly different, with median values of -7.51 and -10.07 g O_2 m^{-1} day^{-1} (p = 0.011), respectively. The ratio of production to respiration was significantly (p<0.001) higher at impaired streams (median = 0.57) compared to the attainment condition streams (median = 0.27).

Ecosystem metabolism – Seasonal differences between impaired and attainment condition streams

A comparison of the median metabolism values separated by season for the impaired and attainment condition stream groups is presented in Figure 3, with significance from Mann-Whitney U tests indicated. Separating the results by season resulted in similar sample sizes - spring (n = 23 and 26), summer (n=73 and 72 days), and fall (n=37 and 40 days) - for the impaired and attainment condition streams, respectively.

In the spring, impaired stream GEP was significantly higher than the attainment condition streams in area (median 2.03 versus 0.57 g O_2 m^{-2} day^{-1}; p = 0.002) and length-based units (median 8.39 versus 3.92 g O_2 m^{-1} day^{-1}; p = 0.002). ER was also significantly higher in the impaired streams during this season in area (median -6.64 versus -4.09 g O_2 m^{-2} day^{-1}; p = 0.014) and length-based units (median -28.09 versus -13.56 g O_2 m^{-1} day^{-1}; p = 0.018). In area-based units, NDM was greater for the impaired streams compared to the attainment condition group (median -3.55 versus -1.24 g O_2 m^{-2} day^{-1}; p = 0.094). This marginally significant difference in NDM between impaired and attainment

condition streams disappeared, however, in length based units (median -11.77 versus -6.36 g O_2 m^{-1} day^{-1}; p = 0.214). In the spring, impaired streams were characterized by slightly higher P/R (median 0.33 versus 0.29) at a level of marginal significance (p = 0.081).

In the summer months, median GEP at the impaired streams was 4.55 g O_2 m^{-2} day^{-1} (area units) and 14.28 g O_2 m^{-1} day^{-1} (length units). These rates of in-stream primary production were significantly higher (p < 0.001 for both units of measure) than the attainment condition streams, which had median GEP rates of 1.19 g O_2 m^{-1} day^{-1} and 4.96 g O_2 m^{-1} day^{-1} in area and length-based units, respectively. Median ER rates for the impaired and attainment condition streams was similar in both area-based (-6.12 versus -6.04 g O_2 m^{-2} day^{-1}; p = 0.143) and length-based units (-22.03 versus -22.22 g O_2 m^{-1} day^{-1}; p = 0.341). However, median rates of NDM were significantly lower in the impaired streams (-1.94 g O_2 m^{-2} day^{-1} and -7.69 g O_2 m^{-1} day^{-1}) compared to the attainment condition streams (-4.60 g O_2 m^{-2} day^{-1}; p = 0.015, and -16.62 g O_2 m^{-1} day^{-1}; p = 0.002). Impaired streams had significantly higher (p < 0.001) P/R (median = 0.64) compared to the attainment condition streams (median = 0.24).

In the fall months, median GEP rates were similar at the impaired and attainment condition streams in area (1.00 versus 1.13 g O_2 m^{-2} day^{-1}; p = 0.729) and length-based units (2.37 versus 2.09 g O_2 m^{-1} day^{-1}; p = 0.014). Median ER rates were lower at the impaired versus attainment condition streams in area-based units (-2.65 versus -3.91 g O_2 m^{-2} day^{-1}; p = 0.018), but slighter greater when converted to length-based units (-8.40 versus -7.53 g O_2 m^{-1} day^{-1}; p = 0.895). Median NDM was significantly lower (p = 0.002) at the impaired streams in area-based units (-1.35 versus -2.97 g O_2 m^{-2} day^{-1}), and

marginally lower (p = 0.078) in length-based units (-3.38 versus -5.77 g O_2 m^{-1} day^{-1}). P/R was significantly higher (p = 0.003) at the impaired streams (median = 0.47) compared to the attainment condition streams (median = 0.26).

Relationship between metabolism and environmental variables

For each group of streams, the correlation between GEP and ER was significant, but the relationship was stronger for the impaired sites. In area-based units, impaired stream GEP to ER was highly correlated (rho = 0.82, p < 0.001), as was the relation for the attainment condition streams (rho = 0.53, p < 0.001). Similar significance was observed in the comparison of GEP to ER in length-based units for the impaired (rho = 0.78, p < 0.001) and attainment condition (rho = 0.55, p < 0.001) stream groups (Figure 4).

In the comparison of GEP and ER to key environmental variables thought to influence metabolism (PAR, temperature, discharge), we elected to use the length-based units for the metabolism variables. These units normalize values for width differences, and thus provide a better comparison of the groups.

Temperature was significantly correlated to GEP (rho = 0.36, p < 0.001) and ER (rho = 0.37, p = 0.001) at the impaired streams. However for the attainment condition streams, temperature was only marginally correlated to GEP (rho = 0.13, p = 0.065) and not significantly correlated to ER (rho = 0.03, p = 0.360). A similar set of relationships was found for PAR. At the impaired streams, PAR was significantly correlated to GEP (rho = 0.50, p < 0.001) and ER (rho = 0.30, p = 0.001). For the attainment condition streams, PAR was significantly correlated to GEP (rho = 0.17, p = 0.027) but not to ER (rho =

62

0.09, p = 0.140). Discharge was significantly correlated to both GEP and ER for both the

impaired (rho = .041, p < 0.001; and, rho = 0.60, p < 0.001) and attainment condition (rho

= 0.35, p < 0.001; and, rho = 0.36, p < 0.001) stream groups, respectively.

Stream status confirmation - Biological, physical, and chemical conditions

The biological, physical, and chemical conditions of the two stream groups differed

significantly, confirming the *a priori* classification of streams as either 'impaired' or

'attainment' condition. In general, the impaired streams were characterized by lower

biological diversity (benthic macroinvertebrates), less stable physical form, less available

in-stream habitat, and higher stream water conductivity and nutrient concentrations.

Table 4 provides the results of our structural assessments by individual study stream.

Benthic macroinvertebrate community structure differed significantly between the

impaired and attainment condition stream groups, respectively, in terms of mean richness

(12.2 versus 30.3, p = 0.001), EPT richness (4.4 versus 18.3; p = 0.002), Hilsenhoff

Biotic Index (5.8 versus 3.0; p = 0.002), and PMA-O (45.1 versus 76.3; p = 0.002).

However, the impaired and attainment condition streams did not differ significantly in

terms of benthic macroinvertebrate density (737.1 versus 622.8; p = 0.680).

The rapid geomorphic (RGA) and habitat (RHA) assessment results indicate significant

differences between the groups of study streams. In terms of habitat, the mean impaired

stream score was significantly lower (p = 0.007) than the attainment condition streams

(0.49 versus 0.79, respectively). Mean geomorphic condition score was also lower at the

impaired streams (0.47 versus 0.70 for the attainment condition streams), but the

difference was statically significant at a very marginal level (p = 0.106). The Vermont Stream Geomorphic Assessment Protocols (VT ANR 2003b) provide the following criteria for RGA and RHA scoring: Reference condition (0.85 to 1.00); good condition (0.65 to 0.84); fair condition (0.35 to 0.64); and poor condition (0.00 to 0.34).

In terms of stream water chemistry, mean NO_3 concentration of the impaired streams (0.736 mg L^{-1}) was greater than the attainment condition streams (0.212 mg L^{-1}) at a marginal level of significance (p = 0.073). Mean PO4 concentration were also higher at the impaired streams (0.019 versus 0.012 mg L^{-1} for attainment condition streams), but the difference was not significant (p = 0.173). The difference in mean specific conductance between the impaired and attainment condition streams was highly significant (812 versus 168 uS cm^{-1}; p < 0.001).

Relationship between metabolism and structural measures of stream conditions

We performed simple linear regressions of median metabolism values against the results of our structural assessments of stream condition (metrics describing benthic macroinvertebrate community structure, geomorphology, habitat, and water chemistry) for each individual study stream. Length-based units were again used for the median metabolism values to normalize for differences in stream width. The results are presented in Table 5, and several of the most interesting relationships are presented in Figure 5. These results should be viewed as suggestive, given the small number of streams compared (n = 6 or 7), but nevertheless indicate association between several measures of structure and function. The ratio of primary production to respiration (P/R)

64

was highly correlated to several descriptors of biological, physical, and chemical condition of the study streams.

Discussion

Stimulated metabolism and the implications for stormwater- impaired streams

The suburban stormwater-impaired streams we evaluated over two years in Vermont were characterized by significantly different rates, as well as altered timing, of fundamental ecological processes when compared to nearby counterpart attainment condition streams. The streams in our study that were classified by the state environmental agency as impaired for stormwater runoff were characterized by many of the same biological, physical, and chemical conditions commonly associated with the "urban stream syndrome" (Meyer *et al*. 2005, Walsh et al. 2005a). The study streams in less-developed watersheds, on the other hand, were considered by the state to be in 'attainment' condition. The results of our structural assessments confirmed these classifications by several common measures of stream health. The ecological processes evaluated in our study streams – rates of primary production and respiration at the ecosystem level – were also clearly impacted by factors associated with watershed development.

Rates of GEP were significantly different between the impaired and attainment condition stream groups over the 271 days included in our study. In both area- and length-based units of measurement, the highest rates of GEP observed in the impaired streams were approximately 3 times that of the attainment condition streams. However, both stream

65

groups had similar GEP at the low end of the range observed over the study period. Median GEP of the impaired stream group was also approximately 3 times that of the attainment condition streams in area- (2.98 versus 1.16 g O_2 m^{-2} day^{-1}) and length-based (12.26 and 3.70 g O_2 m^{-1} day^{-1}) units, respectively.

Temperature (Bott *et al.* 1985), sunlight (Mulholland *et al.* 2001), and nutrient concentrations (Lamberti and Steinman 1997, Bernot *et al.* 2006) are known to be important drivers of in-stream primary production. Watershed urbanization has been associated with increases in all three of these factors (Center for Watershed Protection 2003, Paul and Meyer 2001). The impaired streams in our study were also characterized by higher phosphorus and nitrogen stream water concentrations, and both were well correlated, respectively, to GEP and P/R at the individual stream level. The observed higher rate of GEP in our impaired streams is consistent with other aspects of the urban stream syndrome, such as increased algal biomass (Taylor et *al*. 2004).

We would not expect, however, for rates of GEP to continue to increase indefinitely with watershed development. For example, increases in stream water toxicity have been associated with watershed urbanization (Hatt et *al*. 2004 and others), and GEP will be limited in some urban watershed by the presence of herbicides, heavy metals, and other toxins. Davies and Jackson (2006) put forth such an idea in their description of a highly impacted tier of watershed development, at which poor water quality reduces algal production from an expected high point found at more intermediate tiers (driven by increased temperature and nutrient enrichment). Such a situation was apparently detected by Bott et *al*. (2006a) in a subset of urban-impacted streams in New York (U.S.A), where stream water toxicity appeared to suppress stream metabolism. The nature of watershed

development surrounding our impaired suburban streams in Vermont was not yet
sufficient to result in this type of decreased metabolism associated with more extensive
urbanization. The condition of the stormwater-impaired streams in our study were more
consistent with symptoms found at more intermediate tiers of watershed development
described by Davies and Jackson (2006), including elevated P/R, changes in benthic
macroinvertebrate community composition, and increased algal abundance.

The implications for the type of accelerated biomass production rate that we observed in
our impaired study streams are unclear. However, there are a number of potential
consequences worth noting. It has been suggested that rapid growth of macro-algae may
reduce the abundance of other types of micro-algae, some of which may provide more
favorable food sources (Bunn and Davies 2002, U.S. EPA 1995). The stimulated macro-
algae observed in our impaired streams may simply create infrastructure for trapping
sediment and altering benthic habitat, rather than serving as a nutrient-rich primary food
resource. Stream nutrient enrichment may result in dramatic daily fluctuations in
dissolved oxygen concentrations, and ultimately lead (particularly in stagnant areas) to
dangerously low levels as plant material decomposes (Center for Watershed Protection
2003). Biofilms have been described as playing a critical role in the ability of lotic
systems to purify stream water (Sabater *et al*. 2002), and thus the replacement of biofilms
with macro-algae may effect uptake of substances from the water column.

Unlike the dramatic differences observed in GEP, we did not observe such contrast in ER
between the impaired and attainment condition streams. Both stream groups exhibited
similar median rates of ER over the entire study period. As a result, the ratio of
production to respiration (P/R) was significantly higher at the impaired streams, which

were thus characterized as more autotrophic than the attainment condition streams. Similarly, the balance of GEP and ER was significantly different between the study groups. The significantly lower rate of NDM observed at the impaired streams, however, does not necessarily imply reduced overall processing of organic matter. Rather, it implies that the distribution of that processing is very different, with the impaired streams more dependent upon stimulated autochthonous sources, and the attainment condition streams supported by a more diverse resource base.

Seasonal metabolism dynamics

While the two groups of study streams were characterized by significant differences in overall metabolism (Figure 4), they also differed significantly by season (Figure 5). Accordingly, a closer examination of the seasonal differences and patterns helps to explain the overall differences, potential environmental drivers, and ecological implications.

The ecosystem metabolism of the attainment condition group of streams in our study maintained relative stability between seasons. GEP of the attainment condition streams was slightly elevated in the spring months (mean 1.46 g O_2 m^{-2} day^{-1}; summer and fall mean rates were 1.35 and 1.18 g O_2 m^{-2} day^{-1}) which is consistent with findings from other studies of stream metabolism in forested watersheds with limited development (e.g. Bott 1985, Robert et al. 2007). We found ER, NDM, and P/R to be relatively consistent between seasons in the attainment condition streams. For example, mean P/R for the spring, summer, and fall periods was 0.35, 0.34, and 0.35, respectively.

68

In contrast, the impaired stream group was characterized by much more pronounced

seasonal shifts in ecosystem metabolism. Mean GEP values from the spring, summer,

and fall were 4.57, 5.55, and 1.65 g O_2 m^{-2} day^{-1}, respectively. The spring rate of GEP in

the impaired streams was approximately 4 times greater than in the attainment condition

streams. Seasonal changes in ER mirrored the seasonal changes in primary production,

with higher rates in the spring and summer, and much lower rates in the fall. The fall

months were thus characterized by substantially reduced metabolism compared to earlier

months. Using enclosed chamber methods in several Australian streams, Aldridge (2005)

also found that metabolic rates varied seasonally for urban-impacted reaches, but less so

for an un-modified reach. If relative consistency characterized the metabolic regimes of

our attainment condition study streams, then relative instability driven by seasonally-

stimulated GEP characterized our impaired study streams.

Given the seasonal findings, it is not surprising that we found different relationships

between GEP and ER to environmental variables closely related to season at the impaired

and attainment condition streams. In the impaired streams, GEP and ER were both

highly correlated to both temperature and PAR. In contrast, there was a more limited

relationship at the attainment condition streams. Measures to limit both of these

environmental factors – such as increased riparian canopy cover – are thus logical in

stormwater-impaired streams to help achieve a more "natural" metabolic regime. Such

measures would ideally be combined with efforts to reduce stormwater infrastructure

connectivity and associated nutrient subsidies (Walsh et *al*. 2005b), which, as noted

earlier, have been related to increased algal biomass in some urban settings (Taylor et *al*.

2004).

Comparison to other studies

The attainment condition streams in our study were characterized by values of GEP and ER that are consistent with other studies of similar sized streams in watersheds with limited human impact. The mean values for GEP and ER for the 4 attainment condition streams in our study (1.32 and -8.16 g O_2 m^{-2} day^{-1}, respectively) fall within the range values found recently in Piedmont (Maryland and Pennsylvania, U.S.A) streams (GEP 0.02 to 5.30 g O_2 m^{-2} day^{-1}; and, ER -1.22 to -13.45 g O_2 m^{-2} day^{-1}) by Bott *et al*. (2006b). In upstate New York streams (U.S.A) with negligible urban development, Bott et al. (2006a) found mean GEP ranging from 2.02 to 4.32 g O_2 m^{-2} day^{-1}, and mean ER ranging from -3.94 to -8.30 g O_2 m^{-2} day^{-1}. In their study of streams in different biomes across North America, Mulholland *et al*. (2001) found GEP and ER that ranged from <0.1 to 15 g O_2 m^{-2} day^{-1}, and -2.4 to -11 g O_2 m^{-2} day^{-1}, respectively. Note that we have assigned a negative (-) sign to the ER results from these studies, which the authors reported as positive, for comparison purposes.

Only a few studies have evaluated metabolism in suburban or urban settings using open-system methods. Meyer *et al*. (2005) found mean GEP and ER ranging from 0.76 to 2.38 g O_2 m^{-2} day^{-1} and -1.31 to -8.72 g O_2 m^{-2} day^{-1}, respectively in 4 "mostly urban" 3rd and 4th order urban streams in Georgia (U.S.A). Gibson (2004) found relatively low rates of GEP and ER (0.06 to 0.59 g O_2 m^{-2} day^{-1} and -0.79 to -5.15 g O_2 m^{-2} day^{-1}, respectively) in an evaluation of 4 suburban streams also in Georgia. However, these streams were in much smaller catchments (0.3 to 1.8 km^2) and described as having natural channel form and canopy cover. Neither of these studies reported statistically significant differences in metabolism between the groups of (sub)urban and more rural study streams. However,

70

we suspect that the small number of days evaluated (1 to 4 days total at all of these sites) may have contributed to the lack ability to detect of statistically significant differences. As noted above, Bott et *al*. (2006a) evaluated several streams in urbanized areas (11-26% urban) in New York (U.S.A.) in their study of New York City drinking water supply watersheds. Mean GEP and ER for those streams was 0.65 and -3.11 g O_2 m^{-2} day^{-1}, respectively, and the authors indicated that stream water toxicity may have contributed to lower metabolic rates than found elsewhere in their study.

Many studies of stream metabolism have reported significant variation in observed daily values (e.g. Fellow et al. 2006). This variation is related to the many factors that influence stream metabolism and vary from day to day, including discharge, PAR, turbidity, temperature, turbidity, and nutrient availability. Thus, it is not surprising that clear differences in metabolism have not been identified in prior studies urban streams; not enough days were include in those studies. The importance of using more extensive periods of monitoring to accurately demonstrate differences in stream metabolism has recently been noted by Aldridge (2005) and Roberts et *al*. (2007). By including hundreds of days of data in our metabolism study, we were able to demonstrate clear differences in the metabolic regimes of impaired and attainment condition streams in northwestern Vermont.

Conclusions

In Northwestern Vermont, we have identified significant differences in the ecosystem metabolism of suburban stormwater-impaired and counterpart attainment condition streams by evaluating hundreds of days across multiple streams and seasons. This study

thus provides a yardstick for comparison and future use when examining ecological processes in urbanizing watersheds. In our study, these processed-based measures were well-correlated to other more traditionally used biological, physical, and chemical measures of stream health. Together, the combination of structural and functional measures provides a holistic understanding of stream condition.

As Constanza (1992) noted in his discussion of ecosystem health, the benefit of increased ecosystem vigor may, in some cases, be outweighed by negative consequences to biological diversity and system resilience. This dynamic is supported by our findings at suburban stormwater-impaired streams in Vermont. In these streams, rates of in-stream primary production were substantially higher (more vigorous) than counterpart attainment condition streams, and biological diversity (measured by benthic macroinvertebrate community structure) was significantly lower. We suggest that in such settings, steps to limit the known drivers of primary production may help to achieve a more natural metabolic regime and improve the inherently linked ecosystems services. We further suggest that an altered metabolic regime (including intensity and timing) represents another aspect of the urban stream syndrome in some watersheds.

Ecosystem processes have been called key indicators of river health and integrity (Bunn and Davies, 2000). Assessments of two ecological processes – primary productivity and respiration – are rapidly gaining acceptance as integral components of holistic evaluations of stream health in the United States (Bott *et al*. 2006a and 2006b) and abroad (Fellows *et al*. 2006, Huryn *et al*. 2004). Given the relationship of these processes to key ecosystem services such as C cycling, water purification services, and dissolved

oxygen regulation in stream systems (Bott et al, 2006a), we encourage greater use of ecosystem metabolism monitoring in routine assessments of stream health.

Acknowledgements

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Table 1. Watershed characteristics for the study streams. Stream order and drainage area were determined using geographic information system (GIS) tools. Watershed land cover percentages obtained from VT DEC and (for Potash Brook) from the City of South Burlington (Nelson and Nealon 2003). Elevation and slope were measured in the field. Fields with – indicates data not available from VT DEC. Status is impaired (I) or attainment (A) condition.

	Study Streams						
	Indian Brook	Munroe Brook	Potash Brook	Johnnie Brook	Lewis Creek	Mill Creek	Patrick Brook
Abbreviation	INDI	MUNR	POTA	JOHN	LEWI	MILL	PATR
Status	I	I	I	A	A	A	A
Order	3	3	3	3	3	4	3
Drainage area (km^2)	19.5	13.9	18.1	9.5	18.3	41.9	16.2
% residential	18.3	24.4	35.0	8.0	3.6	8.4	14.2
% forested	43.1	25.7	8.6	77.5	78.8	76.3	27
% commercial and industrial	--	2.5	25	0	0	0	4.0
% crop and field	--	39.7	30	11.2	12.6	9.9	49.2
Elevation (m)	75	52	76	182	137	98	117
Slope (%)	0.8	1.8	1.2	1.7	0.3	1.2	1.8

Table 2. Physical and chemical characteristics of the study streams. Stream dimensions, discharge, stream water characteristics, and PAR are mean seasonal values from days of metabolism calculations included in this study. Fields with -- indicates no values from the season. Status is impaired (I) or attainment (A) condition

	Study Streams						
	INDI	MUNR	POTA	JOHN	LEWI	MILL	PATR
Status	I	I	I	A	A	A	A
Width (m)							
Spring	5.1	2.9	4.2	3.4	6.7	6.9	--
Summer	3.8	2.5	4.7	2.5	7.0	6.1	2.2
Fall	3.7	2.2	4.9	1.8	--	--	2.0
Depth (m)							
Spring	0.26	0.23	0.19	0.17	0.24	0.47	--
Summer	0.17	0.20	0.23	0.15	0.27	0.26	0.18
Fall	0.17	0.14	0.25	0.12	--	--	0.13
Discharge (L s^{-1})							
Spring	428	125	72	112	454	1437	--
Summer	45	92	208	82	550	239	187
Fall	31	14	282	32	--	--	30
Temperature (^{o}C)							
Spring	13.2	11.1	20.7	11.3	19.2	7.5	--
Summer	15.9	19.8	20.1	16.8	20.1	15.9	20
Fall	11.9	9.9	11.4	8.8	--	--	9.9
Dissolved O$_2$ (mg L^{-1})							
Spring	10.4	10.8	7.7	10.7	8.9	11.6	--
Summer	9.8	8.7	8.9	9.1	8.9	9.6	9.0
Fall	10.8	10.6	10.8	10.9	--	--	11.0
PAR (uE)							
Spring	335	393	337	215	325	250	--
Summer	221	273	334	299	372	238	229
Fall	190	134	108	175	--	--	158

Table 3. Whole-ecosystem metabolism results for the 7 study streams included in this study provided in both area and length-based units. Outliers have been removed. Negative values for ER and NDM indicate oxygen consumption, while positive values for GEP indicate oxygen production. Status is impaired (I) or attainment condition (A). P/R is the same regardless of unit of measurement, and is only displayed once.

|	Study Sites						
	INDI	MUNR	POTA	JOHN	LEWI	MILL	PATR
Status	I	I	I	A	A	A	A
N (days)	18	62	53	56	21	36	25
Area Units							
GEP (g O_2 m^{-2} d^{-1})							
Mean	0.84	6.43	2.98	2.06	0.37	1.04	0.86
Median	0.76	5.99	2.78	1.77	0.34	1.05	0.83
IQR	1.07	8.56	2.29	1.04	0.31	0.27	0.48
ER (g O_2 m^{-2} d^{-1})							
Mean	-1.72	-12.81	-4.90	-8.49	-1.01	-5.80	-3.87
Median	-0.96	-8.98	-4.23	-8.52	-1.01	-4.92	-3.21
IQR	2.68	12.68	3.00	5.95	0.57	4.09	4.02
NDM (g O_2 m^{-2} d^{-1})							
Mean	-0.88	-6.38	-1.92	-6.43	-0.65	-4.77	-3.01
Median	-0.14	-3.45	-1.63	-6.37	-0.54	-3.79	-2.34
IQR	2.21	7.29	3.11	6.36	0.46	4.46	3.09
P/R							
Mean	0.92	0.55	0.66	0.32	0.36	0.32	0.38
Median	0.83	0.53	0.60	0.24	0.31	0.21	0.31
IQR	0.94	0.24	0.58	0.37	0.22	0.22	0.35
Length Units							
GEP (g O_2 m^{-1} d^{-1})							
Mean	3.89	16.61	13.82	5.19	2.51	6.39	1.74
Median	3.24	14.26	12.73	3.68	2.44	6.53	1.62
IQR	4.58	23.90	10.03	4.36	2.02	1.62	0.94
ER (g O_2 m^{-1} d^{-1})							
Mean	-8.43	-33.43	-23.09	-19.79	-6.88	-37.08	-7.89
Median	-4.51	-21.96	-20.33	-19.88	-6.72	-30.54	-6.34
IQR	12.62	34.34	16.43	12.13	3.92	27.03	8.29
NDM (g O_2 m^{-1} d^{-1})							
Mean	-4.54	-16.81	-9.27	-14.60	-4.37	-30.68	-6.15
Median	-0.49	-8.04	-7.69	-14.53	-3.97	-23.49	-4.62
IQR	10.21	19.03	15.30	13.93	2.99	26.55	6.57

Table 4. Results of the biological, physical, and chemical assessments performed to evaluate the *a priori* classification as "impaired" or "attainment condition" for our study sites. Data for Lewis Creek are from VT DEC assessments (VT DEC 2001 and 2004); some benthic macroinvertebrate metrics are considerably different (i.e. density) due to higher resolution sample identification by VT DEC staff. RGA and RHA scores correspond to the following VT DEC categories (VT DEC 2003b): Reference Condition (0.85 to 1.00); good condition (0.65 to 0.84); fair condition (0.35 to 0.64); and, poor condition (0.00 to 0.34). Specific conductance is the median values from days of metabolism calculations included in this study. Nitrate (NO_3) and orthophosphate (PO_4) are mean values from all sampling events. Status is impaired (I) or attainment condition (A).

|	Study Sites						
	INDI	MUNR	POTA	JOHN	LEWI	MILL	PATR
Status	I	I	I	A	A	A	A
Biological							
Benthic macroinvertebrates							
Density (# m^{-2})	297	1065	849	650	5136	405	814
Richness (# diff organism m^{-2})	15.0	11.3	10.3	29.0	60.0	33.0	29.0
EPT Richness (# diff organism m^{-2})	6.0	3.7	3.7	18.7	27.5	21.3	15.0
Hilsenhoff Biotic Index	5.7	6.1	5.7	2.4	3.5	2.2	3.8
PMA-O	37.3	53.3	44.5	73.7	82.0	80.3	69.3
Physical							
Rapid geomorphic assessment (RGA)	0.35	0.58	0.49	0.74	0.79	0.80	0.45
Rapid habitat assessment (RHA)	0.46	0.51	0.49	0.87	0.62	0.85	0.82
Composite score	0.81	1.09	0.98	1.61	1.41	1.65	1.27
Chemical							
Specific conductance (*u*S/cm)	578	651	1175	156	168	147	243
NO_3 concentration (*u*g L^{-1})	1045	296	867	154	539	131	24
PO_4 concentration (*u*g L^{-1})	15	24	17	7	8	21	11

Table 5. Correlations between median metabolism rates and structural assessment results for individual study streams. Values are Pearson correlation coefficient (R) and statistical significance (p-value). Bold values indicate p <= 0.05. Values used for benthic macroinvertebrates are means of all replicates collected per site. Rapid assessment scores are single values from the discrete survey performed at each study reach. Specific conductance values are median values from monitoring days with corresponding metabolism values. Nutrient concentrations are mean values from all sampling events.

|	Median metabolism rate (g O_2 m^{-1} day^{-1}) or ratio			
	GEP	ER	NDM	P/R
Biological				
Benthic macroinvertebrates				
Density	0.62 (p=0.193)	0.14 (p=0.792)	-0.18 (p=0.738)	-0.10 (p=0.853)
Richness	-0.69 (p=0.133)	0.18 (p=0.732)	0.62 (p=0.189)	**-0.84 (p=0.035)**
EPT Richness	-0.61 (p=0.195)	0.31 (p=0.556)	0.72 (p=0.106)	**-0.86 (p=0.028)**
Hilsenhoff Biotic Index	0.58 (p=0.175)	-0.26 (p=0.571)	-0.67 (p=0.103)	**0.88 (p=0.010)**
PMA-O	-0.45 (p=0.317)	0.20 (p=0.666)	0.53 (p=0.222)	**-0.95 (p=0.001)**
Physical				
Rapid assessment scores				
Geomorphic condition (RGA)	-0.08 (p=0.861)	0.51 (p=0.246)	0.68 (p=0.093)	**-0.79 (p=0.034)**
Habitat condition (RHA)	-0.49 (p=0.261)	0.28 (p=0.536)	0.65 (p=0.115)	**-0.89 (p=0.007)**
Composite score	-0.33 (p=0.472)	0.45 (p=0.313)	**0.75 (p=0.050)**	**-0.96 (p=0.001)**
Chemical				
Daily monitoring or discrete sampling				
Specific conductance (*u*S/cm)	0.73 (p=0.062)	0.08 (p=0.857)	-0.33 (p=0.467)	0.72 (p=0.070)
NO_3 concentration (*u*g L^{-1})	0.17 (p=0.723)	-0.36 (p=0.427)	-0.56 (p=0.188)	**0.86 (p=0.012)**
PO_4 concentration (*u*g L^{-1})	**0.77 (p=0.044)**	0.57 (p=0.181)	0.27 (p=0.552)	0.31 (p=0.502)

**Figure 1.** Study watershed locations in the Champlain Valley of Northwestern Vermont (U.S.A)
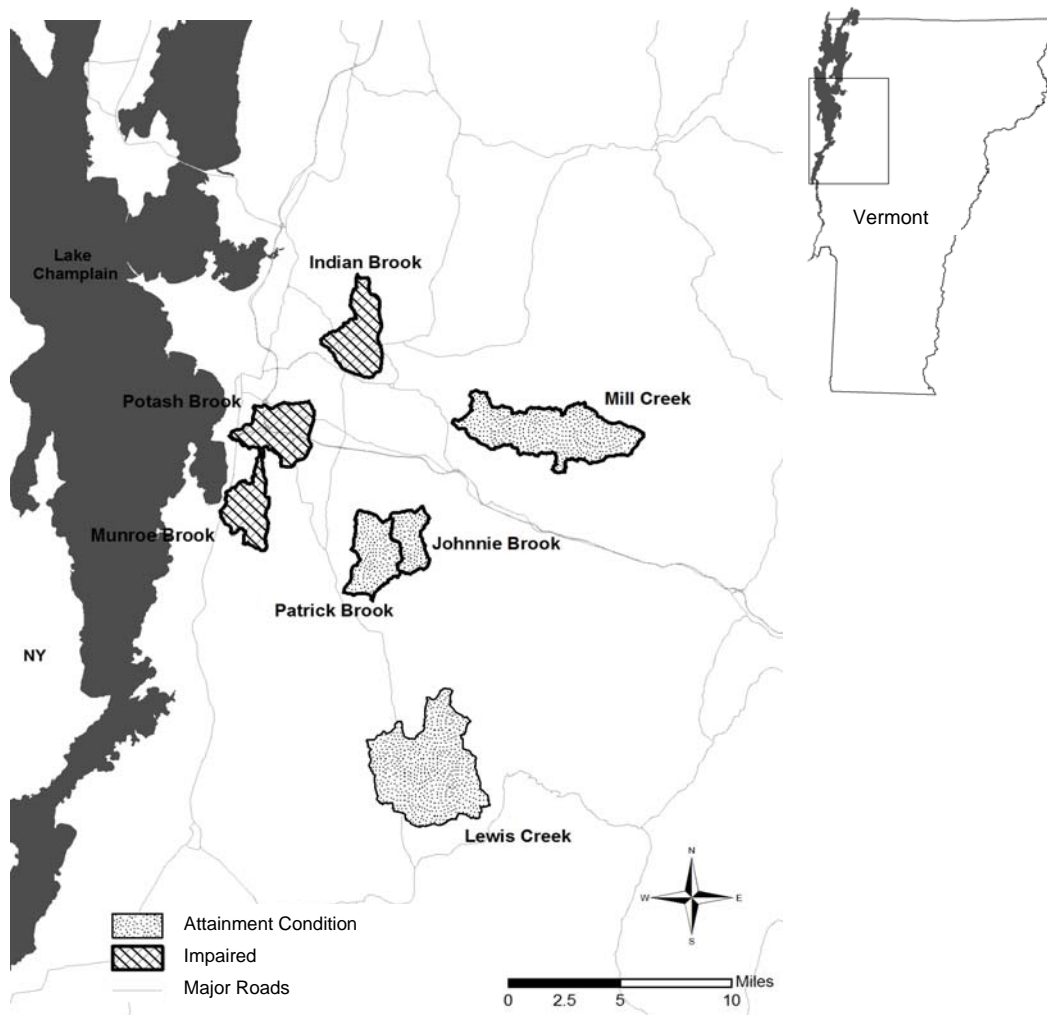
Figure. 2: Whole-ecosystem metabolism results pooled for impaired (n=133 days) and attainment condition (n=138 days) streams in area and length-based units. Boxes are 25th and 75th percentiles with the median value indicated by the interior line; error bars are the 10th and 90th percentiles. Statistical significance (Mann-Whitney U tests) indicated as: *p <= 0.1; **p<=0.05; ***p<=0.01. Panel A. values are in area-based units, and Panel B. values are in length-based units.
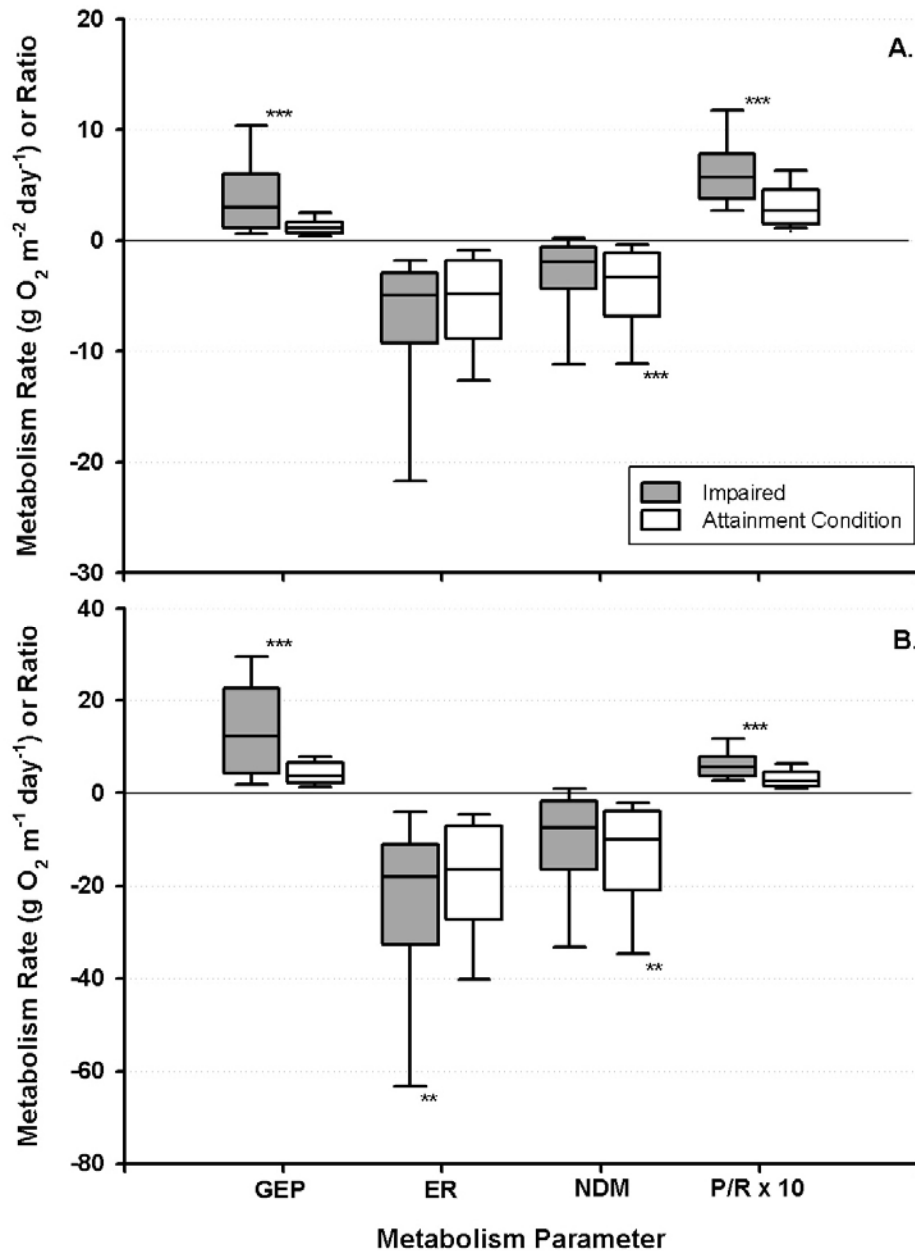
Figure 3. Whole-ecosystem metabolism results pooled for impaired and attainment condition streams by season in area and length-based units. Boxes are 25th and 75th percentiles with the median value indicated by the interior line; error bars are the 10th and 90th percentiles. Statistical significance (Mann-Whitney U tests) indicated as: *p <= 0.1; **p<=0.05; ***p<=0.01. Panels A and B are spring values (n = 23 and 26 days for impaired and attainment condition streams), panels C and D are summer values (n = 73 and 72 days for impaired and attainment condition streams), and panels E and F are fall values (n = 37 and 40 days for impaired and attainment condition streams).
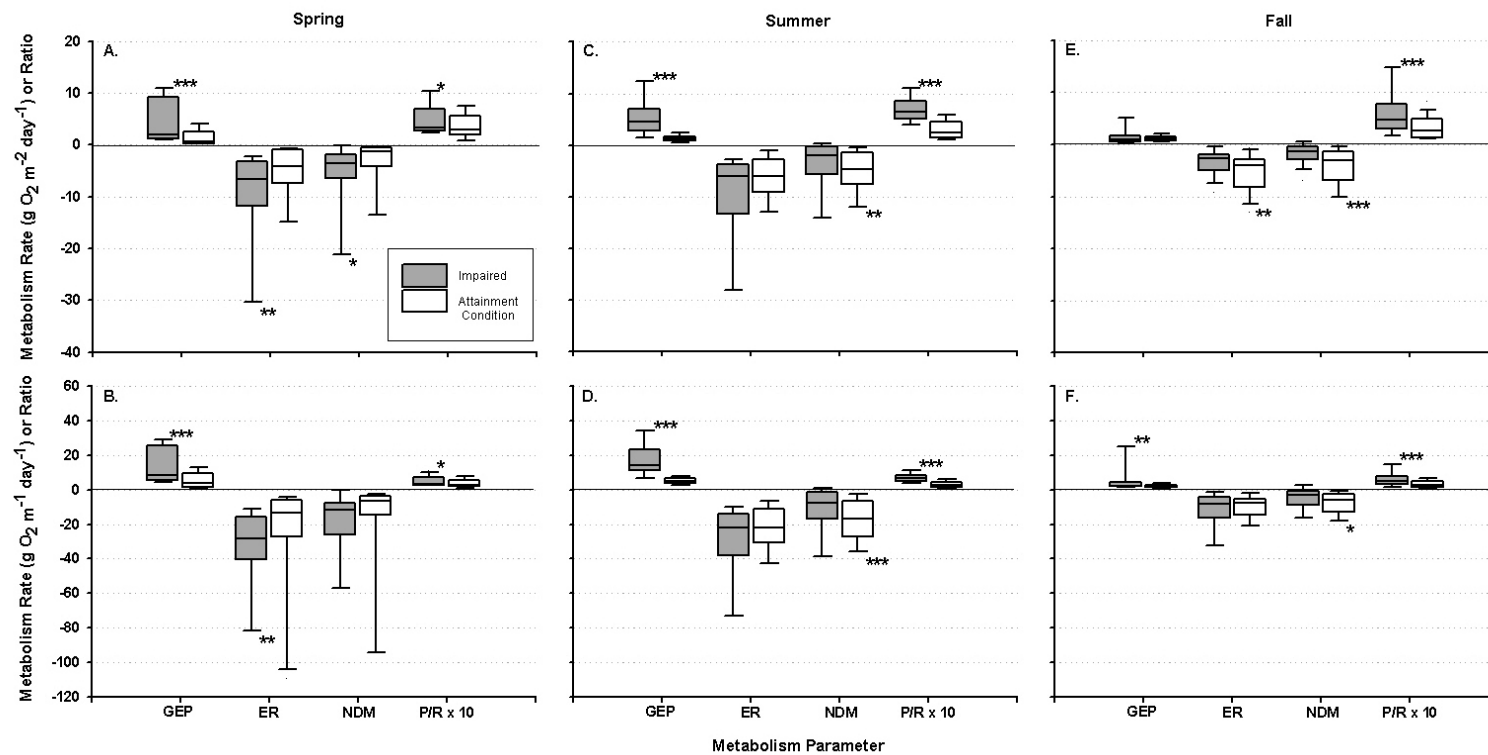
Figure 4. GEP versus ER in length units (g O_2 m^{-1} day^{-1}) for impaired (n = 133 days) and attainment condition (n = 138 days) study streams. Spearman's correlation coefficient (rho) and statistical significance indicated for both groups of streams.
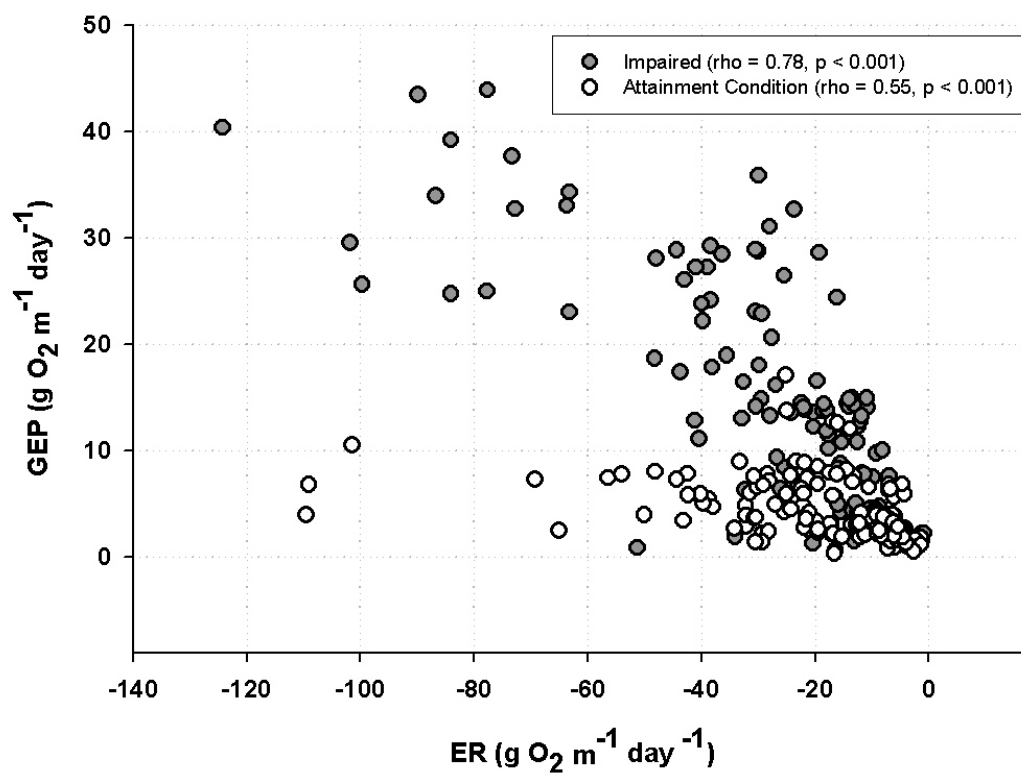
Figure 5. Scatter plots comparing median metabolism values and structural assessment results for the individual study streams. Plots indicate P/R versus (A) Hilsenhoff biotic index, (B) benthic macroinvertebrate density and (C) richness, rapid geomorphic (D) and habitat (E) scores, and (F) mean specific conductivity.
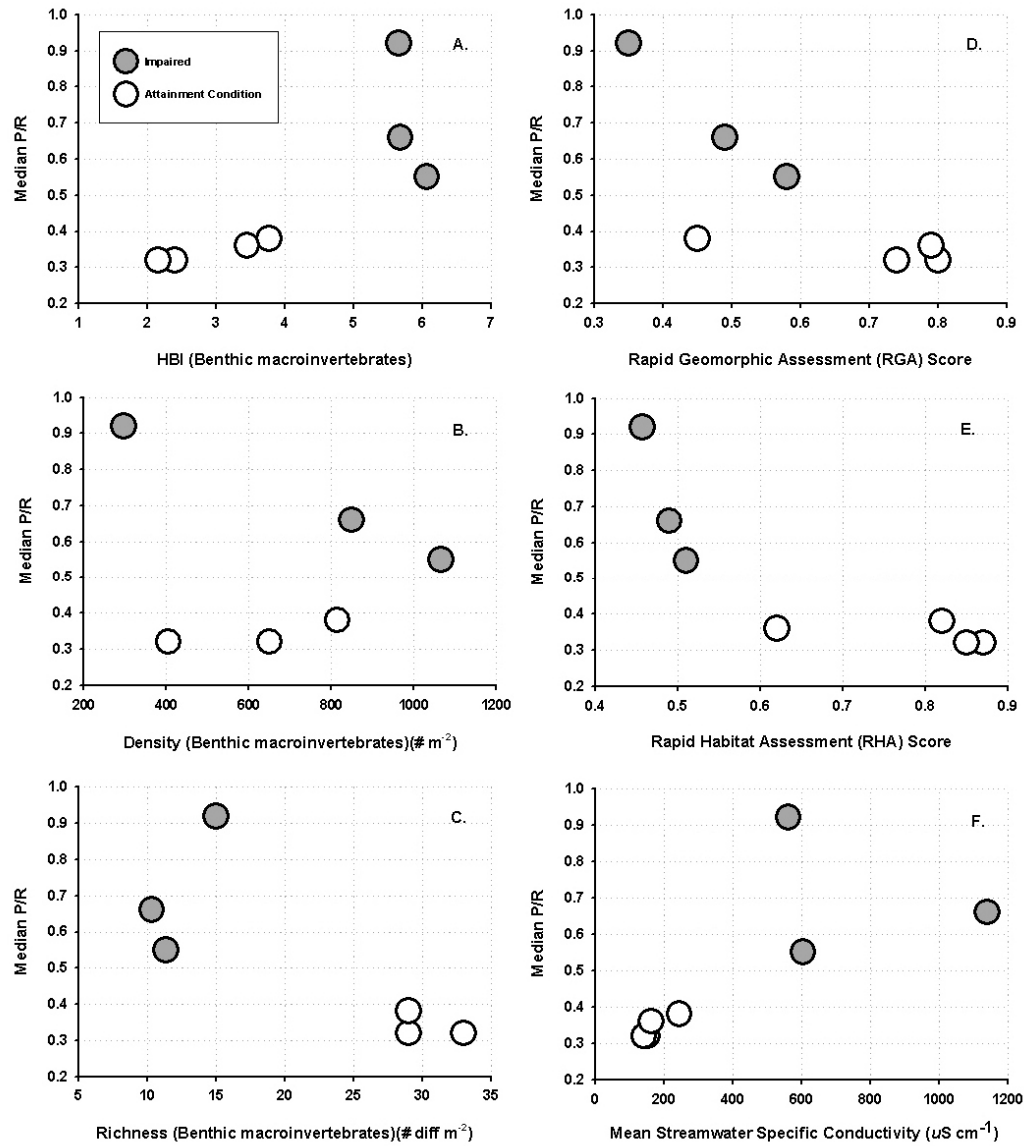
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Appendices (*On CD)*

A. Field data (stage, discharge, dissolved oxygen, temperature, conductivity, PAR)

B. Whole-stream metabolism calculations (performed in my EXCEL-based models)

C. Hydrologic rating curves

D. Dynamic variable construction and rating curves (width, depth, velocity)

E. Benthic macroinvertebrate community assessment results

F. Water quality sampling results

G. Rapid stream geomorphic and habitat assessment results

H. Solute injection experiment (SIE) results – nutrient uptake dynamics of impaired

and attainment condition streams