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# Effects of Nitrogen Deposition and Flow Permanence on Stream Organic Matter Dynamics

Michael Andrew Joseph Chadwick

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**EFFECTS OF NITROGEN DEPOSITION AND FLOW PERMANENCE ON  
STREAM ORGANIC MATTER DYNAMICS**

By

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B.S. Rutgers, The State University of New Jersey, Cook College, 1993

M.S. Auburn University, 1997

A THESIS

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Requirements for the Degree of

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(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

August, 2003

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# **EFFECTS OF NITROGEN DEPOSITION AND FLOW PERMANENCE ON STREAM ORGANIC MATTER DYNAMICS**

By Michael Andrew Joseph Chadwick

Thesis Advisor: Dr. Alexander D. Huryn

An Abstract of the Thesis Presented  
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The objective of this study was to investigate the effects of N enrichment and flow permanence on stream organic matter dynamics at the Bear Brook Watershed in Maine (BBWM). BBWM is a paired-catchment manipulation of atmospheric  $(\text{NH}_4)_2\text{SO}_4$  deposition, and the goal of the experiment is to understand how increased N affects forested catchments. The treatment has increased stream nitrate and foliar N concentrations in the treatment watershed. Because streams draining BBWM are intermittent, this investigation provided an opportunity to investigate the combined effects of stream flow permanence and human alteration of N cycling in a forested watershed.

Several lines of evidence suggested that stream drying affects streams more than N deposition. For leaf-litter processing, elevated dissolved N concentrations played a minimal role in regulating stream leaf-litter processing. Increased foliar N, however, did influence detritus processing by increasing microbial activity, and possibly increasing detritivore biomass. Based on these findings, I concluded that physical similarities between streams regulated leaf-litter loss rates. For stream organic matter dynamics, BBWM did not have different inputs or storage, and only modest differences in export of coarse organic matter. These results support the conclusion that N additions at BBWM do not affect these streams, and that physical characteristics regulate what happens to organic matter. Utilization of organic matter, measured as invertebrate secondary production, was also the same between streams, but varied temporally. Increased production in the second year was attributed to increased stream permanence and organic matter biomass. These results again suggest that N deposition at BBWM has little effect on organic matter dynamics, specifically utilization. Differences in drying for streams did affect production and invertebrate assemblage structure. To further assess stream drying effects, secondary production was quantified in 6 reaches with differing drying regimes. Production ranged from 1.7 to 2.9 g AFDM m<sup>-2</sup> yr<sup>-1</sup> among all reaches, and flow permanence and organic matter biomass appeared to influence these patterns. This work suggests that chemical changes in streams because of atmospheric N deposition are less important than gradients in flow permanence in regulating organic matter in intermittent streams.

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## **Chapter 1:**

### **GENERAL INTRODUCTION**

The effects of acid deposition and watershed N-saturation are currently being studied in two adjacent catchments at the Bear Brook Watershed in Maine (BBWM). Following the “small-watershed technique” of Likens et al. (1977), dry ammonium sulfate ( $[(\text{NH}_4)_2\text{SO}_4]$ ) has been applied by air to the treatment watershed (West Bear Brook) every other month since November 1989, while an adjacent watershed (East Bear Brook) has served as an untreated reference. This experiment was designed to mimic the atmospheric deposition levels of the Adirondack region in a watershed that has historically received much lower N and S deposition. Annual loading of N (total of wet plus dry) to West Bear Brook has been increased by 300% and the watershed is now approaching chronic acidification and N-saturation (Galloway et al. 1983, Kahl et al. 1993, Cosby et al. 1996, Norton et al. 1999). Along with the experimental manipulation of acid deposition at BBWM, the streams are uniquely suited for an investigation of stream permanence, because they naturally differ in degrees of drying. Currently, stream water chemistry is being used to monitor catchment responses, but treatment effects on stream processes have not been examined. Both the ongoing N deposition manipulation and the natural gradient of stream permanence at BBWM provide a unique opportunity to study the combined effects of these factors on organic matter dynamics. The goals of this research were 1) to evaluate the effects of catchment N deposition on leaf-litter processing, organic matter dynamics, and macroinvertebrate community

structure and secondary production, and 2) to investigate the effects of stream permanence and detritus availability on macroinvertebrate community structure and secondary production.

### **Organic Matter Dynamics**

Organic matter dynamics of stream ecosystems are affected by changes in physical and chemical parameters (e.g., N deposition and channel drying at BBWM). Understanding these changes requires defining and quantifying amounts and types of inputs, storage, and transport of organic fractions present in stream ecosystems (Fisher and Likens 1973, Mulholland 1981, Cummins et al. 1983, Webster and Meyer 1997). An accounting of organic matter also allows for estimations of ecosystem efficiencies and degrees of non-utilization of organic resources (Fisher and Likens 1972, Webster et al. 1990, Richardson 1991, Webster and Meyers 1997). This holistic approach integrates vital ecological processes (e.g., decomposition, primary and secondary production,) and should provide insight into the dynamic ecosystem responses of physical, chemical, and biological variables to changes within stream systems.

#### Inputs and retention of organic matter

Aquatic ecosystems can be classified in terms of the origins of organic matter input. Autochthonous ecosystems (i.e., where gross primary production (P) exceeds system respiration (R)) receive the bulk of their organic matter through autotrophic C fixation. Conversely, allochthonous ecosystems (i.e.,

where  $P < R$ ) gain organic matter from outside the system and are heterotrophic. For lotic systems, Vannote et al. (1980) proposed a model (River Continuum Concept - RCC) that relates stream-size to energy inputs and ecosystem function. As a stream flows away from its headwaters, the RCC makes predictions about the relationships between primary production and respiration. In headwater reaches, where primary production can be light-limited by the presence of a dense canopy cover (e.g., Feminella et al. 1989, Hill et al. 1995), organic matter is supplied by terrestrial inputs. In temperate climates, these terrestrial inputs come mainly as autumn-shed leaves (Wallace et al. 1995, Benfield 1997). This direct dependence on allochthonous carbon input by the biotic communities of headwater streams has been well demonstrated by Wallace et al. (1997, 1999), who showed that secondary production of benthic invertebrates in a litter-excluded stream decreased over a three year period and was significantly less than a reference stream.

Other inputs of organic carbon to include dissolved forms (as through-fall and in groundwater) and autochthonous sources (Fisher and Likens 1973, Cummins et al. 1983), although in headwater streams these other sources tend to contribute much less than coarse particulate organic matter (CPOM, e.g., leaves and woody debris). For example, Satellite Branch (a small forested catchment located at the Coweeta Hydrologic Laboratory, North Carolina) had annual leaf litter inputs of  $\sim 635 \text{ g AFDM m}^2$ , which is an order of magnitude higher than the  $\sim 80 \text{ g AFDM m}^2$  that came from gross primary production, throughfall and groundwater sources combined (Wallace et al. 1997). Similarly,

Bilby and Bisson (1992) showed that allochthonous inputs for a forested headwater stream were 5 times higher and autochthonous inputs were 0.5 times lower than a similar clear-cut stream. Finally in a system similar to BBWM (e.g., northern, forested headwater streams), Fisher and Likens (1972) showed that allochthonous sources contributed > 90% of all organic matter.

For these types of streams, it is clear that CPOM is the major source of organic carbon, but there are several factors that control the amounts of material. Benfield (1997) showed that a significant, positive correlation exists between litter fall and amounts of precipitation and latitude, which suggests that differences in quantities of leaf litter inputs between streams can be controlled by climatic variables. High stream flow can alter amounts of CPOM present within stream reaches by increasing transport to downstream reaches. Further, elevated discharge can also compromise retentive structures like debris dams, causing increased transport (Bilby 1981, Boulton and Lake 1992). Loss of organic matter from streams can also occur via movement of material to riparian habitats (Jones and Smock 1991, Maridet et al. 1995, Wallace et al. 1995).

The type and degree of storage within a stream channel is attributable to both riparian conditions and channel geomorphology (Bilby 1981, Maridet et al. 1995, Wallace et al. 1995, Angradi 1996, Lamberti and Gregory 1996). Upstream reaches tend to be more efficient in the retention of organic matter because higher inputs of wood debris result in the formation of debris dams (Bilby and Likens 1980, Webster et al. 1994, Jones 1997). In fact, Trotter (1990) found that the addition of wood increased the amounts of organic matter stored

within stream channels. Other retentive features such as boulders and pools can also serve to increase the retention of organic matter (Huryn and Wallace 1987, Webster et al. 1994, Jones 1997). Increased retention induces greater storage and can lead to more physical and biological processing of organic matter. With elevated processing rates there can be increased conversions of CPOM to fine particulate organic matter (FPOM). This reduction in particle size leads to more efficient exports of organic matter (Wallace et al. 1982, Golladay et al. 1987, Cuffney et al. 1990, Jones and Smock 1991).

#### Processing of leaf-litter

There are three stages in the processing of leaves in streams: 1) leaves enter aquatic systems and soluble compounds are leached directly from the material (loss of mass by physical and chemical processes), 2) fungi and bacteria colonize surfaces and then degrade and macerate the leaves (i.e., leaf conditioning; loss of mass by biological processes), and 3) leaves are fragmented by both hydraulic action and shredder macroinvertebrates (loss of mass by physical and biological processes). Both fungi [i.e., aquatic hyphomycetes; see Ingold (1975) and Bärlocher (1992) for a brief description of this group] and bacteria play important roles in the second stage of leaf litter processing. For leaves that enter streams, decomposition of carbon sources by microbial communities (fungi and bacteria, sensu Superkropp and Klug 1976), involves the digestion of structural plant polysaccharides. This digestion also aids in the conversion of entire leaves to FPOM (Superkropp et al. 1976, Findlay

and Arsuffi 1989, Bärlocher 1992). Aquatic hyphomycetes tend to appear first on leaves due to their ability to mobilize extracellular enzymes (e.g., pectinases and ligases) that can digest structural carbon compounds (Superkropp et al. 1976). Bacteria generally lack the ability to digest structural carbon compounds, and thus colonize detrital organic matter after fungi (Superkropp and Klug 1976, Findlay and Arsuffi 1989). Further, fungi have higher biomass on leaf surfaces when compared to bacteria (Superkropp and Klug 1976). Bacteria may be more significant in the processing of leaf-litter than previously thought, because of high turnover rates on leaf surfaces. Although bacteria maintain lower biomass on organic matter compared to fungi, they can be highly productive. Given this, net bacterial activity may play a large role in organic matter processing (Findlay and Arsuffi 1989). Further, bacterial production of carbon rich exopolymers may be important in overall organic matter dynamics in streams (Hall and Meyer 1998).

Interaction between aquatic fungi, bacteria (both responsible for leaf conditioning) and shredder organisms (that further fragment leaves) can influence litter breakdown rates (Cummins 1973, Anderson and Sedel 1979, Superkropp 1992). Shredder feeding activities have been shown to inhibit aquatic hyphomycetes (Bärlocher 1980). Shredders can also reduce fungal diversity by selectively feeding on certain fungal species (Superkropp 1992, Arsuffi and Superkropp 1985). This was demonstrated in a headwater stream treated with insecticide, where Superkropp and Wallace (1992) found increased aquatic hyphomycete conidia in transport and related this change to the concomitant decrease in shredders. Decreases in leaf conditioning rates by

fungi and bacteria can be caused by shredders. Besides their minor role in moderating aquatic hyphomycete abundance and diversity, shredders play an important role in organic matter dynamics because of their feeding activities.

Feeding activities of shredder organisms partition CPOM into FPOM (Cummins et al. 1973, Anderson and Sedell 1979). This reduction in particle size can be through ingestion and excretion (Shepard and Minshall 1984) and simple fragmentation (Cummins et al. 1973). This processing of CPOM to FPOM contributes to the fate of organic matter in two basic ways. First, smaller size fractions are more readily exported from stream reaches and second, the partitioning of CPOM to FPOM creates food resources for collector-gather organisms (Fisher and Likens 1973, Wallace et al. 1982, Cuffney et al. 1990, Cushing et al. 1993). This has been demonstrated by Cuffney et al. (1990), where reductions in shredder abundance by an insecticide treatment resulted in both decreases in leaf litter decomposition rates and decreases in FPOM export.

The RCC (Vannote et al. 1980) predicts that shredders and collectors should dominate headwater reaches due to both direct (e.g., feeding directly on detritus) and indirect (e.g., feeding on detritivores) links to CPOM resources. For example, Huryn and Wallace (1988) found that trichopteran shredders accounted for ~30% total secondary production, while trichopterans feeding on FPOM accounted for ~40% of total annual secondary production in a forested headwater stream. Similarly, Dieterich et al. (1997) showed that in a forested intermittent stream, ~70% of the emerging insects by biomass were shredders and collectors and that in this system shredders emerged before collectors. To

further elucidate this pattern, laboratory experiments showed that shredder presence could increase collector growth rates (Dieterich et al. 1997). This linking of shredder activities to collector-gather feeding has major implications for the overall importance of CPOM processing. In a whole stream litter exclusion experiment, Wallace et al. (1997) showed a direct link between CPOM availability and shredders and FPOM feeding organisms. In this experiment, less retentive habitats in the treatment stream had low detritivore (both CPOM and FPOM feeders) production.

## **N Deposition**

Pollutant emissions to the atmosphere, especially from the burning of fossil fuels, and the subsequent deposition of acidic S and N compounds have been in the forefront of applied and basic research for decades. Atmospheric deposition of S has been decreasing since at least 1970 (Sisterson et al. 1990), and research has increasingly focused on the recovery of ecosystems from acidification (e.g., Likens et al. 1996). Ecosystem recovery, as indicated by increasing pH of surface waters, has not followed declines in S deposition as expected (Driscoll et al. 1989, 1995, Norton et al. 1994, Likens et al. 1996). One of several explanations for this observed trend is continued atmospheric deposition of N. The effect of N-deposition was dismissed as irrelevant until the late 1980's (e.g., Aber et al. 1989). In the United States, N deposition, and the related phenomenon of watershed acidification and N saturation are of greatest concern in the northeast, where nitrate concentrations in streams draining

forested watersheds are higher than in other forested regions elsewhere in the country.

Effects of catchment acidification and N-deposition on organic matter processing in aquatic ecosystems can be manifested in a multitude of ways including slowing leaf decomposition and decreasing aquatic fungi diversity (Mulholland et al. 1987, Dubey et al. 1994), altering macroinvertebrate community structure (Smith et al. 1990, Guérol et al. 1995, Griffith et al. 1995, Smock and Gazzera 1996), and increasing invertebrate drift (Hall et al. 1982, Weatherley et al. 1988, Kratz et al. 1994, Smock and Gazzera 1996).

Evidence suggests that leaf decomposition in aquatic systems may be modified by atmospheric deposition of N. For example, rates of decomposition tend to increase in nutrient-rich hard-water streams where neither N nor phosphorus seems limiting (Chamier 1992, Superkropp and Chauvet 1995). Increases in N concentrations alone have also been shown to increase leaf decomposition. Meyer and Johnson (1983) found the leaf litter decomposed 2.8 times more quickly in a nitrate enriched stream. Similarly, Superkropp and Chauvet (1995) showed that leaf decomposition rates were positively correlated with nitrate concentrations for both hard-water and soft-water systems. Conversely, Newbold et al. (1983) did not find increased decomposition when additional ammonium was added to the stream. From these examples, it is reasonable to assume that N additions to N-limited streams may elevate leaf processing rates, whereas N additions should not result in changes to leaf processing rates in P and N/P-limited streams.

Catchment acidification may also affect organic matter dynamics. Low ambient pH has been shown to slow the rate of decomposition by inhibiting fungi, bacteria, and shredding invertebrates. In four acidic streams (pH 4.5–6.4), Mulholland et al. (1987) found that rate of leaf loss slowed significantly in streams with pH < 5.7. In the same study, microbial respiration rates and bacterial production decreased with decreasing pH, and shredder biomass was highest in the highest pH stream. These findings indicate that inhibition of the second stage of leaf decomposition is responsible for observed decreases in leaf decomposition with decreases in pH. A possible mechanism for decreased leaf decomposition suggested by Mulholland et al. (1987) was that accumulation of toxic aluminum slowed bacterial metabolism in streams with low pH. Chamier's (1992) review of aquatic hyphomycetes and water quality also comments on the potential toxic effects of aluminum on aquatic fungi. Another explanation for the inhibitory effects of low pH on leaf decomposition is related to the different pH optima of enzymes used by aquatic hyphomycetes for decomposition (Jenkins and Superkropp 1995). In two Alabama streams (6.3 and 8.2 pH), pectin-lyase, an enzyme responsible for degrading structural carbon compounds in leaves, was found to have higher activities in the high pH stream, and consequently was responsible for increased decomposition rates (Jenkins and Superkropp 1995). Other hydrolytic enzymes (with increased affinities for low pH waters) had decreased activities in the high pH stream. However, the fastest rates of leaf decay were in the low pH stream, and this indicates that pectin-lyase was more important in leaf decomposition (Jenkins and Superkropp 1995).

## **Stream Permanence**

Streamflow permanence is generally described by three conditions: perennial streams with year-round flow (i.e., complete flow permanence), intermittent streams that cycle from flowing to non-flowing on predictable, climate-induced phases, and ephemeral streams that only flow following rain (Gordon et al. 1992). Within intermittent streams, there are widely ranging degrees of permanence, from streams that completely dry at the surface for some period (e.g., Sycamore Creek, Arizona-Fisher et al. 1982, East and West Bear Brooks, Maine-personal observations) to streams that lose flowing water in only certain parts of the stream channel (e.g., Boulton and Lake 1992, Closs and Lake 1994, Feminella 1996).

Physico-chemical and biological responses associated with both the drying and rewetting of stream channels have only recently gained more attention (Williams 1996). Most studies to date only deal with the changes in biological community structure (Delucchi 1988, Closs and Lake 1994, Feminella 1996, Dieterich et al. 1997, Paltridge et al. 1997) or species-specific responses to changes in stream flow (Williams et al. 1995, Jacobi and Cary 1996, Zamora-muñoz and Svensson 1996). Some heuristic models suggest that a continuum of drying periodicity can act to filter communities in temporary aquatic systems based on lengths of taxa generation times (Stearns 1976, Williams 1996). In systems with non-seasonal and unpredictable drying, aquatic invertebrates would tend to be short-lived, whereas in systems with predictable drying periodicities, taxa with longer life histories could be present. These models further suggest

that taxa associated with temporary aquatic systems would have high dispersal, rapid growth rates, and tend to be competitively inferior to taxa from perennial systems (Stearns 1976, Williams 1996). If populations of taxa can be removed from intermittent streams because of drying, these systems should tend to have fewer taxa than perennial systems, and this has been shown (Delucchi 1988, Shivoga 2001). However, decreased richness has not been observed in all systems (Feminella 1996, Dieterich and Anderson 2000, Pires et al. 2000, del Rosario and Resh 2001). Several factors may explain why some intermittent systems retain taxa richness, including: predictable drying periodicity, release from competitively dominate taxa, or proximity to colonists (Williams 1996). Understanding ecological functions that occur in intermittent streams could facilitate better understanding of the processes that regulate populations and communities.

Few studies have looked at functional responses in intermittent streams. Boulton and Lake (1992) showed that storage of benthic organic matter within intermittent stream channels increased during decreased flow periods and that there was a corresponding increase in benthic detritivores during these times. Similarly, Mollá et al. (1996) found that fine sestonic organic matter ( $< 1\text{mm}$ ) and coarse sestonic organic matter increased during a pooling phase (i.e., stream flows ceased increasing the number of disjunct pool habitats) when the streams became autotrophic. Finally, the timing of drying and rewetting were shown to influence the timing of life-cycles of resident fauna and consequently, food-web structure can vary due to environmental constraints of drying (e.g., changes in

proportions of predators [Closs and Lake 1994]). Intermittent forested headwater reaches have seasonally large inputs of metabolic resources (e.g., leaf fall) and direct connectivity to both upper watersheds and to the rest of the stream corridor. Investigating organic matter dynamics in these sites may allow for a more complete grasp of catchment-level processes.

Stream flow permanence in colder climates can also be affected by snow and ice. Snow pack can regulate both daily and seasonal stream hydrographs (Caine 1992, Prowse 1994). In small streams, a complete freeze can result in anchor ice and a lack of flow. Alternatively, ice break-up and snow pack melting are known to increase water temperature, flow and suspended sediment concentrations (Prowse 1994, Scrimgeour et al. 1994). These changes in stream characteristics are also suggested as possible mechanisms for transport of organic matter, both within stream channels and from riparian habitats (Scrimgeour et al. 1994) for streams.

### **Study Site**

Two first-order streams that drain two contiguous forested catchments (~10 ha) in Hancock County, southwestern Maine (42° 52' N, 68° 06' W) served as the main area of concentration. The two catchments (Bear Brook Watersheds, Maine – BBWM) are part of a long term study investigating the effects of acid deposition on forested catchments (Kahl et al. 1993, Norton et al. 1994, Uddameri et al. 1995). West Bear Brook has received bimonthly treatments of dry  $(\text{NH}_4)_2\text{SO}_4$  ( $1800 \text{ eq ha}^{-1} \text{ y}^{-1}$ ) since 1989. Nitrate concentrations have

steadily risen in West Bear Brook to ~5x ambient (as measured in East Bear Brook).

Both catchments are in the upper 210 m of Lead Mountain (elevation 475 m) and have areas of 10.2 ha (East Bear Brook) and 10.9 (West Bear Brook). The upper elevation of each catchment is dominated by red spruce (*Picea rubens*) and lower elevations are a mix of American beech (*Fagus grandiflora*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghenensis*), and red spruce (White 1996). Descriptions of parent geology and the overlying soil types have been described and mapped (Norton et al. 1994).

Six separate reaches are present as the streams flow from their origins to Bear Pond. Reaches are defined by the unique habitats present. The reaches present are: 1) East Bear Brook above the weir, 2) West Bear Brook above the weir, 3) East Bear Brook below the weir, 4) West Bear Brook below the weir, 5) Bear Brook (second order confluence of East and West Bear Brooks), and 6) a low gradient swamp reach, ~200m upstream of Bear Pond. Among the six reaches, three distinct combinations of habitat features (e.g., pools, debris dams, riffles, bedrock outcrops) exist. These include intermittent, high gradient headwaters, a medium gradient second order reach, and a low gradient cedar swamp reach. Differences in reach properties have been shown to affect biological processes, such as macroinvertebrate community structure (Carter et al. 1996, Richards et al. 1997), secondary production (Huryn and Wallace 1987, Wohl et al. 1995), and metabolism (Young and Huryn 1996)

Weirs are located on both of the headwater reaches and are equipped to record stage height at 5 min intervals. Stage data are sent to USGS, Reston, Virginia via satellite. Stream hydrology data are reduced and validated by the USGS, Augusta, Maine. Approximately 300 m of stream are located above each weir and both streams flow for another ~300 m below each weir before they join. Discharge for both streams ranges seasonally from 0–575 L/s. The streams are ice-covered from approximately January through March. The upper reaches (i.e., above each weir) of both streams flow from November to May (i.e.,  $Q > 0.2$  L/s). Based on ~10 years of discharge data, East Bear Brook has ~60% probability of having no flow and West Bear Brook has a 25% probability of having no flow during the driest times of the year (June to October). Clearly, West Bear Brook has a higher degree of stream permanence. Surveys of East and West Bear Brooks and the confluence show that retentive structures (e.g., debris dams and lateral boulders) are abundant. The habitats created by these structures may play an important role in ecosystem responses to N deposition (e.g., nutrient uptake- Newbold et al 1983, Triska et al. 1990) and provide refugia from drying. The lower reaches of West Bear Brook and the confluence of the two streams appear to be perennial. The habitat structure of all reaches, excluding the cedar swamp reach, are composed of regular combinations of plunging riffles and debris-dam pools interspersed by bedrock-outcrop runs. The habitat in the cedar swamp reach is an irregular combination of debris dams, deep pools, and slow flowing runs. In East Bear Brook the gradient eases and the channel becomes braided below the weir.

## **Dissertation Format**

This dissertation is organized as a series of 4 separate manuscripts and a final summary. Chapters 2-4 investigate the stream ecosystem response to the ongoing ecosystem manipulation at BBWM (i.e., West Bear Brook relative to East Bear Brook). Chapter 5 examines the 6 reaches that drain Lead Mountain to investigate effects that stream permanence has on aquatic macroinvertebrates.

In Chapter 2, I report the findings of an investigation on how increases in stream and foliar N concentrations affect leaf litter processing rates. This work was conducted from 1997–1999 and includes processing rates of the dominant deciduous leaves found at BBWM (e.g., red maple, sugar maple, and American Beech). In Chapter 3, coarse organic matter input, storage, and export potential are examined. The main goal for this chapter was to assess the extent to which organic matter dynamics differ between West and East Bear Brooks. Chapter 4 deals with aquatic macroinvertebrate responses to the ecosystem N and S treatment. Both secondary production and community structure are discussed. Finally, Chapter 5 looks at how a continuum of stream permanence can effect aquatic macroinvertebrate production. References cited for all chapters follow the summary found in Chapter 6.

## Chapter 2:

### EFFECT OF A WHOLE-CATCHMENT N ADDITION ON STREAM DETRITUS PROCESSING



## Introduction

Human activities, such as burning of fossil fuels, fertilizer production, and the agricultural production of N fixing crops, have resulted in measurable changes to the global N cycle, including increased atmospheric N deposition (Vitousek et al. 1997). Atmospheric N deposition is known to have detrimental effects on forested ecosystems (Aber et al. 1989). These effects include leaching of important nutrient cations, acidification of soils and streams, and alterations to soil and stream N retention and transport in soils and streams (Aber et al. 1989, Vitousek et al. 1997, Peterson et al. 2001).

Numerous studies of stream ecosystem responses to atmospheric deposition have focused on acidification (e.g., Griffith et al. 1994, Likens et al. 1996). The effect of atmospheric deposition of N in streams, however, remains obscure (Burns 1998). Studies of the effects of N inputs to streams from riparian and catchment-level sources, although numerous, are often confounded by factors such as canopy clearing and sedimentation, because these studies are typically designed in the context of landuse practices (Sallenave and Day 1991, Johnson et. al 1997, Carpenter et al. 1998, Miltner and Rankin 1998, Sponseller and Benfield 2001). In comparison, atmospheric N deposition is relatively free from such confounding factors and may thus elicit different, and perhaps more subtle, responses from stream ecosystems. In addition, atmospheric N deposition not only increases N concentrations in stream water, it is also predicted to alter the N dynamics for entire catchments (i.e., N saturation; Aber et al. 1989, Peterjohn et. al 1996). A conceptual model of the effects of chronic

atmospheric N deposition on forested ecosystems (Aber et al 1989) suggests that increased deposition will not only result in elevated concentrations of inorganic N, but will also cause forest vegetation to sequester higher levels of foliar N. As a consequence, streams draining these catchments may also have N-enriched detritus. Increased N availability from both water and detrital sources may thus alter detritus processing.

Rates of detritus processing in streams can increase with elevated concentrations of dissolved  $\text{NO}_3^-$  and  $\text{NH}_4^+$  because of changes in microbial and/or shredder activity (Meyer and Johnson 1983, Chamier 1992, Suberkropp and Chauvet 1995, Robinson and Gessner 2000, Grattan and Suberkropp 2001). Increased N concentrations do not always accelerate processing rates. For example, when N is not limiting, faster processing rates would not be expected. In these cases, other nutrients or factors (e.g., shredder activity) regulate detritus processing (Newbold et al. 1983, Sponseller and Benfield 2001). In contrast with factors that accelerate processing, increased acidity slows processing rates by inhibiting the activity of fungi, bacteria, and shredding invertebrates (Hildrew et. al 1984, Mulholland et al. 1987, Osgood and Boylen 1992, Chamier 1992, Jenkins and Suberkropp 1995, Dangles and Guérolde 1998). Changes in leaf tissue quality can also affect processing rates. Leaf-litter with high N and low lignin concentrations has faster rates of processing than detritus with lower N and high lignin concentrations (Webster and Benfield 1986, Royer and Minshall 2001). Thus, N deposition may potentially increase rates of detritus processing because

of the corresponding increases in N availability, whereas the corresponding acidification may reduce processing rates.

A long-term N deposition experiment at the Bear Brook Watershed in Maine (BBWM) provides a unique opportunity to study the interrelated effects of changes in stream water chemistry and foliar N content on detritus processing. Following the “small-watershed technique” of Likens et al. (1977), dry  $(\text{NH}_4)_2\text{SO}_4$  has been applied to the treatment catchment every other month since November 1989, whereas an adjacent catchment serves as a reference. Annual deposition of N (wet + dry) has been increased by 300% and the treatment catchment is approaching chronic acidification and N saturation (Kahl et al. 1993, Cosby et al. 1996, Norton and Fernandez 1999). For this study, I compared rates of leaf-litter processing between the streams draining the N-amended catchment and the reference catchment. I also assessed if changes in foliar chemistry (i.e., N-enriched leaves from the treatment catchment) resulted in alterations in detritus processing. I hypothesized that my results would reflect the conditions predicted for terrestrial systems by a conceptual N saturation model (Aber et al. 1989), with higher rates of processing occurring in the stream draining the treated catchment and for N-enriched leaves.

## **Methods**

### Study site

This study was conducted in 1st -order streams that drain 2 contiguous catchments (~10 ha each) in Hancock County, Maine (lat 42° 52' N, long 68° 06' W). Both catchments are above 265 m on Lead Mountain (475 m asl). A mix of

American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), and red spruce (*Picea rubens*) cover both catchments (White 1996). Soils are coarse-loamy Spodosols developed on till; the soils average 1 meter in depth (David et al. 1990). The bedrock is quartzite and calc-silicate with granite intrusions. Both streams are equipped with weirs and stage height is recorded at 5-min intervals (<http://water.usgs.gov/me/nwis/rt>). Temperature loggers (Onset Computer Corporation, Pocasset, Massachusetts) placed ~150 m above each weir recorded stream temperatures at 5-min intervals. Approximately 300 m of stream channel is located above each weir. The wetted width of each stream channel averages ~1 m and mean annual discharge varies from 2.3 to 4.3 L/s. Channel form is similar in each stream and retentive structures (e.g., debris dams and boulders) are abundant (MAC, unpublished data). Both streams dry during the summer and are often ice-covered in winter. A summary of physical and chemical parameters for each stream appears in Table 2.1.

#### Experimental design and field methods

Leaf-litter processing was quantified in the autumn of 1997, 1998, and 1999. Red maple processing was quantified in all years, whereas sugar maple and American beech processing were quantified in 1999. Freshly fallen leaves were collected from each catchment to provide 2 different leaf litter sources: N-enriched (WBB+N) and reference (EBB). All leaves were air dried to constant.

**Table 2.1.** Physical and chemical data for the study streams. Values (ranges) represent averages of regular samples during the period leaf bags were deployed, except for annual temperature. Discharge is from the US Geological Survey Water Resources of Maine (<http://water.usgs.gov/me/nwis/rt>). All other values are from the Senator George J. Mitchell Center for Environmental and Watershed Research, Orono, Maine. WBB+N = treatment catchment. EBB = reference catchment. dd = degree days (0oC threshold). ANC = acid neutralizing capacity. DOC = dissolved organic carbon. DL = detection limits (5 µg/L for NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>; 1 µg/ L for total P).

Parameter	WBB+N	EBB
Location (lat x long)	44°51'34"N x 68°06'23"W	44°51'35"N x 68°06'20"W
Drainage area (ha)	10.2	10.7
Discharge (L/s)	3.50 (26.30–0.25)	3.60 (30.00–0.00)
Annual temperature (°C)	5.09 (16.00–0.00)	5.16 (16.00–0.00)
dd for 1997, 1998, 1999	279, 224, 258	279, 224, 263
Specific conductance (µS/cm)	45.00 (48.00–36.00)	24.80 (30.00–22.00)
pH	4.90 (5.20–4.60)	5.56 (6.00–5.12)
ANC (µeq/L)	-8.40 (0.00–15.00)	1.10 (12.00–9.00)
SO <sub>4</sub> <sup>2-</sup> (mg/L)	8.90 (10.40–8.20)	4.40 (5.30–3.70)
NO <sub>3</sub> <sup>-</sup> (mg/L)	2.40 (5.80–1.10)	< DL (0.10–<DL)
NH <sub>4</sub> <sup>+</sup> (mg/L)	0.02 (0.20–<DL)	0.02 (0.05–<DL)
Total Al (mg/L)	0.45 (0.81–0.24)	0.12 (0.24–0.06)
Total P (µg/L)	2.28 (8.20–<DL)	1.36 (6.70–<DL)
DOC (mg/L)	1.82 (3.70 - 1.09)	2.53 (4.40 - 1.50)

mass before being used. Litter bags (35 X 14 cm with 5 mm polypropylene mesh) were packed with pre-massed, dry leaves. To prevent fragmentation, leaves were moistened before being packed. Bags were paired (N-enriched and reference leaves) and anchored to each stream bottom. Handling losses were measured from 4 to 6 bags per leaf source, which were carried into the field and then returned for laboratory processing. When retrieved from each stream, litter bags were placed directly into plastic bags and returned to the laboratory in coolers. Locating and retrieving some bags after ~30 days was hampered by ice cover. Dry bags or those encased in ice were not used.

The 1997 study assessed differences in processing rates between WBB+N and EBB for N-enriched and reference red maple leaves, and longitudinal differences in processing caused by the effects of a potential N availability gradient. Litter bags were filled with ~6 g of air-dried red maple leaves of either leaf litter source (N-enriched or reference leaves). Bags were deployed in each stream at 30-m intervals along a reach that extended 90 m below each weir to 180 m above each weir. All bags (10 per treatment combination) were retrieved after 45 d. The 1998 study used a similar design. Bags containing ~8 g of air-dried red maple of either leaf litter source were placed in similar habitats in a ~200 m reach above each weir. Ten bags per treatment combination were retrieved after 14, 28, 42, and 56 d. The 1999 study expanded the 1998 study by including red maple, sugar maple, and American beech. Ten bags per treatment combination were retrieved after 7, 28, and 56 d.

### Laboratory methods

All litter bags were processed within 3-d of retrieval. Their contents were poured into a plastic basin containing water. Whole leaves and fragments were removed by hand. Ten leaves per bag were chosen for measurement of leaf softness, an index of microbial activity (Suberkropp and Klug 1980). Leaf softness was measured as the mass required to push a standard metal rod through leaf tissue (i.e., penetrance as in Hury et al. 2002). After leaf softness measurements, leaf litter was placed in a paper bag and dried to constant mass in a forced-air oven (60°C). Ash mass was determined after igniting (550°C) a subsample (1–3 g) of oven-dried leaf litter for at least 1 h. Ash-free dry mass (AFDM) remaining was calculated from these measurements and then corrected for handling losses quantified using breakage bags (see above). In 1997 and 1998, initial % N and % C of leaf tissue were measured for each leaf source (i.e., N-enriched and reference). In 1999, % N and % C of leaf tissue were measured for each leaf species and source collected at 0, 7, and 56 d of processing. In 1999, % lignin of leaf tissue was also measured for each leaf species and source after 7 d of processing. Leaf tissue analyses (% N and % C - dry combustion, % lignin - gravimetry after acid extraction [Chapman and Pratt 1961]) were performed by the Maine Agricultural and Forestry Experiment Station Analytical Laboratory/Maine Soil Testing Service Laboratory. In 1998 and 1999, macroinvertebrates retained on a 500- $\mu$ m mesh sieve from the 56-d samples were identified to lowest practical taxonomic level and then measured to the

nearest 1 mm. Individual and total biomass was estimated using taxon-specific, length mass relationships (Benke et al. 1999).

### Data analysis

The treatments were assessed for differences in leaf loss, leaf softness, and C:N ratios using factorial analysis and the general linear model (SAS Institute. 1989. SAS/STAT user's guide, version 6, 4th edition, Cary, North Carolina). In 1997, statistical differences for leaf loss and leaf softness were assessed using a 2-factor, nonparametric ANOVA (Zar 1984). Rates of litter loss ( $k$ ) and softening ( $k_s$ ) were estimated as  $\ln(\text{final}/\text{initial})/\text{time}$ . In 1998 and 1999, ANCOVA (with time as the covariate) was used to analyze differences in leaf loss and litter softening. Orthogonal contrasts were used to assess stream and leaf nutrient effects (i.e., WBB+N vs EBB, N-enriched leaves vs. reference leaves; Freund, R.J. and R.C. Littell. 1981. SAS for linear models. SAS Institute, Cary, North Carolina). Rates of processing ( $k$  and  $k_s$ ) were estimated by fitting patterns of time specific-leaf loss or softening to a negative exponential decay curve. Carbon to N ratios (C:N) for 1999 were also analyzed with ANCOVA. Percent lignin for each leaf species in 1999 was arcsine-square-root transformed and then analyzed with 2 sample  $t$ -tests (e.g., N-enriched vs reference leaves). Differences in shredder biomass in both 1998 and 1999 were assessed by ANOVA using the same 2-factor model used to analyze the 1997 data for litter processing. Sample sizes reflect the channel area available to ensure bags were submerged. Because sample sizes were maximized, further control of type II

error was achieved by considering differences statistically significant at  $p < 0.10$ . This level was set prior to beginning any fieldwork.

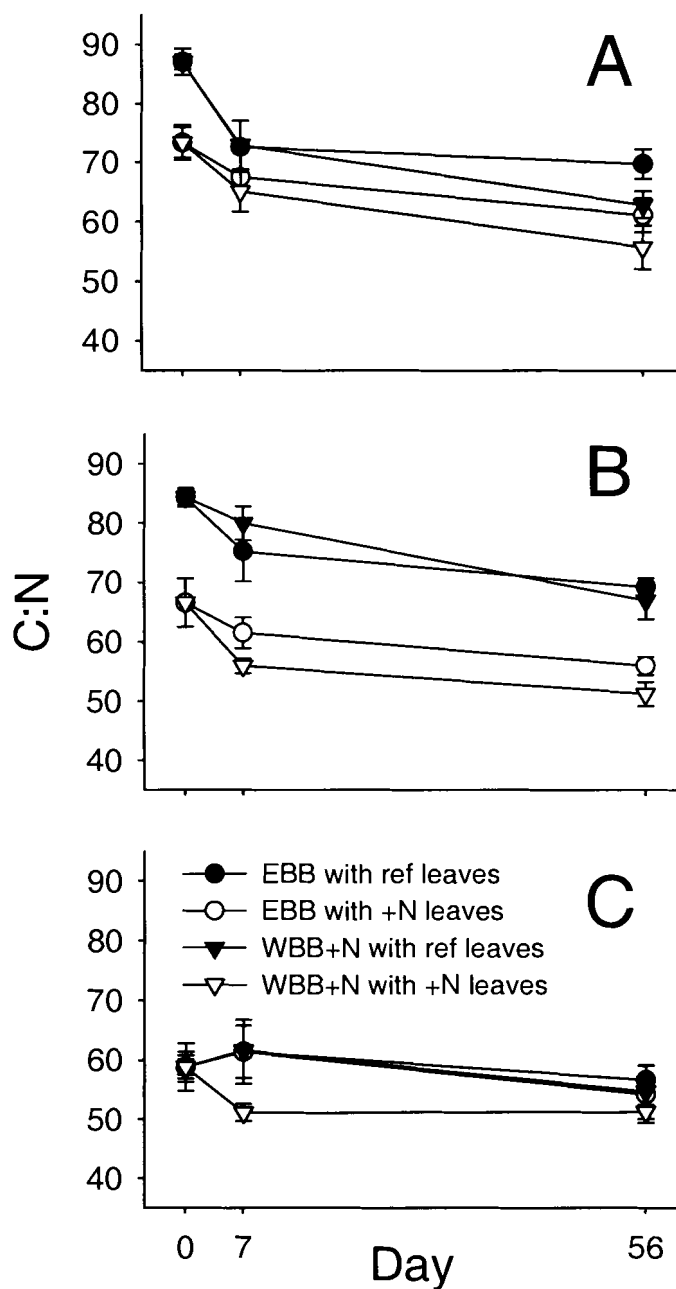
## Results

### Foliar chemistry

Initial C:N for red maple varied from 71 to 84 for N-enriched leaves and 85 to 98 for reference leaves for all 3 sample years. In 1999, N-enriched leaf C:N ratios for red maple were lower than reference leaf ratios ( $F = 88.4$ ,  $p < 0.001$ ; Fig. 2.1A). Both leaf sources followed the same pattern through time (Fig. 2.1A). The differences between leaf sources were driven primarily by increased % N, although decreased % C also contributed. Percent lignin (17.8–23.3%) did not differ between leaf sources ( $t_{(2),5} = 1.57$ ,  $p = 0.150$ ).

Initial C:N for sugar maple, ranged from 76 to 95 and were higher for reference leaves than for N-enriched leaves ( $F = 96.5$ ,  $p < 0.001$ ; Fig 2.1B.) Changes of % C and % N as a result of processing were similar to red maple. Percent lignin was significantly lower for N-enriched sugar maple (15.5%) compared to reference sugar maple (19.2%;  $t_{(2),5} = 4.73$ ,  $p < 0.01$ ).

Initial C:N for American beech in 1999 were the same for both leaf sources (58; Fig. 2.1C). Changes in C:N through time showed a slightly different pattern than red or sugar maple. Only N-enriched leaves in WBB+N exhibited significant decreases ( $F = 8.1$ ,  $p < 0.01$ ) as a result of increased % N. Percent lignin (20.2–28.1%) did not differ between leaf sources ( $t_{(2),5} = 0.204$ ,  $p = 0.843$ ).



**Figure 2.1.** Initial, 7-d and 56-d C:N ratios (mean  $\pm$  2 SE) for red maple (A), sugar maple (B), and American beech (C) litter placed in each stream in 1999. Reference leaves were collected in the reference catchment (EBB); N-enriched leaves were collected in the treatment catchment (WBB+N).

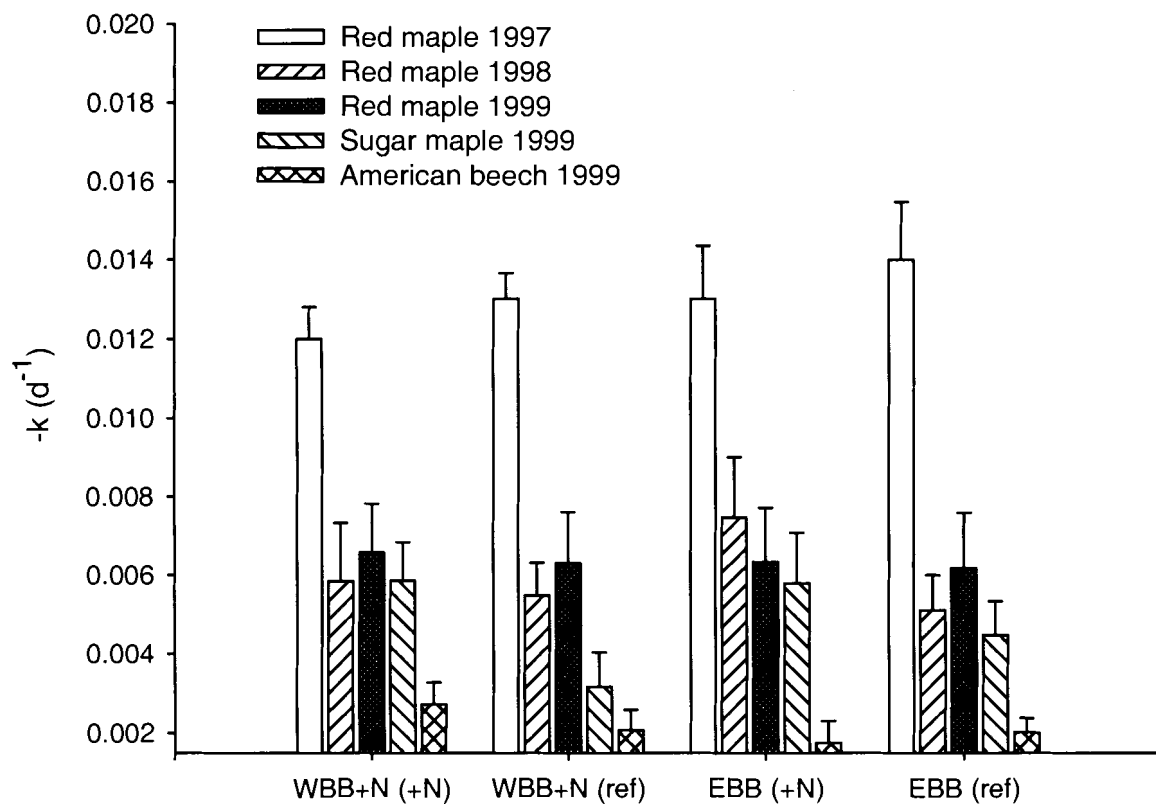
### Litter processing: mass loss

*Red maple 1997*—Longitudinal differences in % AFDM remaining in EBB and WBB+N were not observed. Based on this finding, samples for each stream were pooled for further analysis. Mean rates of AFDM loss varied from 0.012 to 0.014/d (~ 0.0020– 0.0023/dd; Fig. 2.2). Percent AFDM remaining after 45 d ranged from 55% to 60%. There were no statistical differences among treatment combinations ( $F = 1.74$ ,  $p = 0.177$ ).

*Red maple 1998*—Mean rates of leaf loss were 0.005 to 0.007/d (~0.0013– 0.0018/dd; Fig. 2.2) which were lower than mean rates from 1997. Percent AFDM remaining after 56 d ranged from 58% for N-enriched leaves in EBB to ~70% for reference leaves in both streams. There were significant differences between leaf sources ( $F = 29.10$ ,  $p < 0.001$ ), with N-enriched leaves having higher leaf loss than reference leaves (Table 2.2). However, there were no statistical differences between streams (Table 2.2).

*Red maple 1999*—Mean rates of leaf loss (0.006/d, ~0.0013/dd; Fig. 2.2) did not vary among the treatments and there was no difference in leaf loss for either leaf source or between streams ( $F = 1.64$ ,  $p = 0.184$ ). Percent AFDM remaining after the 56-d exposure was ~65% for all treatments.

*Sugar maple 1999*—Of all leaf species used in my study, sugar maple showed the most dramatic differences in leaf loss for both stream (WBB+N > EBB) and leaf source ( $F = 20.12$ ,  $p < 0.001$ ; Table 2.2). Rates of loss where



**Figure 2.2.** Mean ( $\pm 2$  SE) rates of leaf loss ( $-k$ ) for each stream and leaf type. Reference leaves (ref) were collected in the reference catchment (EBB); N-enriched leaves (+N) were collected in the treatment catchment (WBB+N).

**Table 2.2.** Summary of the orthogonal contrast for ANCOVA treatment results for leaf loss. Reference leaves (ref) were collected in the reference catchment (EBB); N-enriched leaves (+N) were collected in the treatment catchment (WBB+N).

Year	Leaf species	Parameter	p	Leaf-loss assessment
1998	Red maple	Stream Leaf	0.31 <0.001	WBB+N = EBB +N > ref
1999	Sugar maple	Stream Leaf	0.003 <0.001	WBB+N > EBB +N > ref
1999	American beech	Stream Leaf	0.13 <0.001	WBB+N = EBB +N > ref

highest for N-enriched leaves in both streams (0.006/d, ~ 0.0013/dd) and lowest for reference leaves in WBB+N (0.003/d, ~ 0.0007/dd; Fig. 2.2). Percent AFDM remaining after the 56-d exposure was highest for reference leaves in WBB+N (80%) and lowest for N-enriched leaves in WBB+N (60%).

*American beech 1999*—Rates of leaf loss (~0.002/d, 0.0004/dd; Fig. 2.2) were the slowest of all leaf species used in this study. All treatments indicated that < 20% of leaf tissue was lost, but the difference in loss between leaf sources was significant (N-enriched > reference;  $F = 7.00$ ,  $p < 0.001$ ; Table 2.2)

#### Litter processing: leaf softening

*Red maple 1997*—After 45 d, penetrance ranged from 442 g for N-enriched leaves in EBB to 374 g for reference leaves in WBB+N. Rates of litter softening differed between N-enriched leaves (~0.008/d, 0.0013/dd) and reference leaves (~0.010/d, 0.0016/dd;  $F = 5.77$ ,  $p = 0.022$ ; Table 2.3; Fig. 2.3). However, no difference was detected between streams ( $F = 0.85$ ,  $p = 0.364$ ). Reference leaves showed higher rates of softening than N-enriched leaves, indicating higher microbial activity (i.e., increased leaf softness and rates of softening are as a result of higher degrees of tissue maceration by fungi, see Suberkropp and Klug 1980).

*Red maple 1998*—Penetrance decreased in a similar pattern for both leaf sources. The most dramatic decreases occurred in the first 2-w exposure, and this pattern was more pronounced for N-enriched leaves. Leaf softness after 56 d (~300 g) was similar among all leaves. Rates of softening were higher than the previous year (N-enriched leaves = ~0.012/d, 0.003/dd, reference leaves =

~0.011/d, 0.0027/dd; Fig. 2.3), and N-enriched leaves were significantly softer (Table 2.3). As in 1997, there were no differences in leaf softness between streams (Table 2.3).

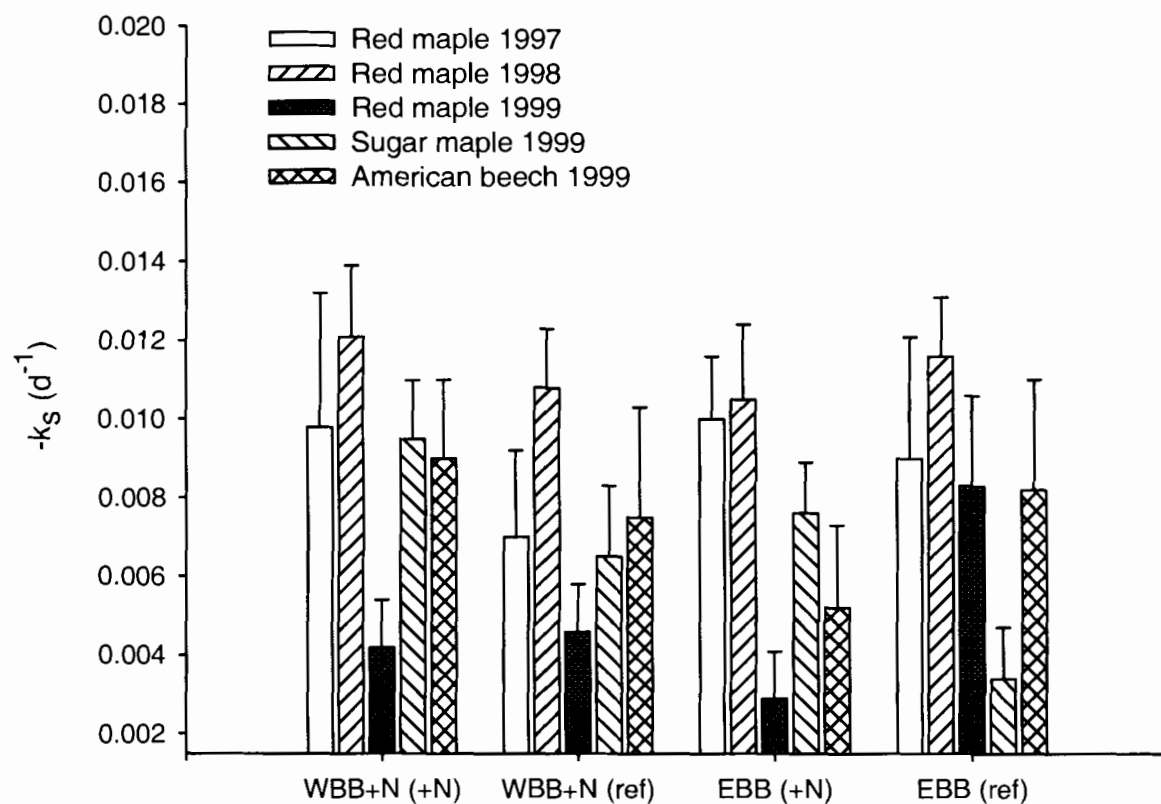
*Red maple 1999*—Penetrance after 56 d (~300 g) was similar among all leaves. Litter softening showed no difference among any treatment combinations. Measurements of softening rates were affected by the considerably lower initial softness (e.g., ~425 g all red maple, 1999 vs ~600 g all red maple, 1997) and by more variable softness among all leaves collected for each exposure. Although no significance among treatments was found for leaf softness, rates of softening were highest in reference leaves in EBB (0.008/d, 0.0016/dd) and lowest for N-enriched leaves in EBB (0.003/d, 0.0006/dd; Fig. 2.3).

*Sugar maple 1999*—Penetrance after 56 d ranged from ~350 g (EBB with reference leaves) to ~225 g (WBB+N with N-enriched leaves). Rates of litter softening ranged from 0.0034/d (0.0007/dd) for reference leaves in EBB to 0.0095/d (0.0019/dd) for N-enriched leaves in WBB+N (Fig. 2.3). Leaf softness was significantly different for leaf sources, with N-enriched leaves being consistently softer (Table 2.3). The significance of this latter result was equivocal, however, because N-enriched leaves were initially softer.

*American beech 1999*—Penetrance after 56 d for N-enriched leaves in WBB+N (~350 g) was 50 g less than in the other treatments, and these leaves were significantly softer than reference leaves (Table 2.3). Softening rates for N-enriched leaves were ~0.008/d (0.0016/dd) and for reference were ~0.007/d (0.0014/dd; Fig. 2.3).

**Table 2.3.** Summary of the a posteriori test (1997) and orthogonal contrasts (1998, 1999) for leaf softness. Reference leaves (ref) were collected in the reference catchment (EBB); N-enriched leaves (+N) were collected in the treatment catchment (WBB+N).

<b>Year</b>	<b>Leaf species</b>	<b>Parameter</b>	<b>p</b>	<b>Leaf-softness assessment</b>
1997	Red maple	Stream Leaf	>0.10 <0.10	WBB+N = EBB +N < ref
1998	Red maple	Stream Leaf	0.41 0.04	WBB+N = EBB +N > ref
1999	Sugar maple	Stream Leaf	0.13 <0.001	WBB+N = EBB +N > ref
1999	American beech	Stream Leaf	0.51 0.01	WBB+N = EBB +N > ref



**Figure 2.3.** Mean ( $\pm 2$  SE) rates of leaf softening ( $-k_s$ ) for each stream and leaf type. Reference leaves (ref) were collected in the reference catchment (EBB); N-enriched leaves (+N) were collected in the treatment catchment (WBB+N).

## Macroinvertebrates

Average macroinvertebrate taxonomic richness across all treatment combinations in each year ranged from 7 to 12 taxa per litter bag, whereas total richness ranged from 20 to 32 taxa (Table 2.4). For taxa that feed on coarse detritus (i.e., shredders), average richness ranged from 3 to 7 taxa per litter bag and total richness from 7 to 10 taxa (Table 2.4). No pattern in the distribution of taxa either among leaf species and leaf sources or between streams was discernable (Table 2.4). The most common shredders among all treatments were *Ostrocerca* (Plecoptera:Nemouridae) and *Lepidostoma* (Trichoptera: Lepidostomatidae). Other common taxa included: Orthoclaadiinae (Diptera: Chironomidae), *Rhyacophila* (Trichoptera: Rhyacophilidae), and terrestrial centipedes (Chilopoda). Average total biomass for 1998, ranged from 10 to 23 mg AFDM/bag (Table 2.4). Average shredder biomass was lowest in EBB with reference leaves (3 mg AFDM/bag) and highest in WBB+N with N-enriched leaves (12 mg AFDM/bag; Table 2.4) and was statistically different both for leaf source ( $F = 3.43$ ,  $p = 0.074$ ) and stream ( $F=3.55$ ,  $p = 0.069$ ). Average total biomass for all treatment combinations in 1999 ranged from 12 to 22 mg AFDM/bag (Table 2.4) and there was no difference in either total biomass or shredder biomass.

## **Discussion**

### Stream effects

It was expected that the continuing N additions to the WBB+N catchment would alter litter processing because of three factors: increased stream  $\text{NO}_3^-$

**Table 2.4.** Average biomass (mg AFDM/litter bag) and percent biomass (in parentheses) for 1998 and 1999 taxa composing  $\geq 1\%$  of biomass. A summary of total richness, average richness, and average taxa biomass (mg AFDM/litter bag) for all invertebrates and shredders (SHR) appears at the bottom of each column. Numbers in parentheses following average biomass are 2 SE. Reference leaves (ref) were collected in the reference catchment (EBB); N-enriched leaves (+N) were collected in the treatment catchment (WBB+N). – = not present.

Taxon	Red maple (1998)		WBB+N (ref)	WBB+N (+N)	Red maple (1999)		WBB+N (ref)	WBB+N (+N)
	EBB (ref)	EBB (+N)			EBB (ref)	EBB (+N)		
Isotomidae	0.3 (2.4)	0.3 (2.8)	0.2 (1.7)	0.3 (1.2)	–	–	–	–
<i>Allocapnia</i>	–	–	–	–	–	0.2 (1.6)	–	–
<i>Amphinemura</i>	–	0.9 (8.2)	–	1.2 (5.3)	–	–	–	–
<i>Leuctra</i>	–	0.3 (2.6)	0.1 (1.2)	1.7 (7.2)	0.4 (3.0)	0.5 (3.2)	1.4 (10.9)	1.2 (11.1)
<i>Ostrocerca</i>	1.9 (17.4)	1.8 (15.6)	1.9 (19.5)	3.9 (16.9)	3.9 (22.7)	1.5 (10.2)	1.6 (11.9)	1.8 (17.1)
<i>Paranemoura</i>	–	–	–	–	0.2 (1.2)	–	–	0.1 (1.4)
<i>Soyedina</i>	1.2 (10.4)	0.7 (6.2)	1.0 (10.0)	1.0 (4.4)	0.2 (1.2)	–	0.2 (1.6)	0.3 (3.2)
<i>Sweltsa</i>	–	–	0.5 (4.8)	–	–	–	–	–
<i>Homoplectra</i>	–	0.3 (2.5)	–	0.3 (1.3)	–	–	0.5 (3.6)	–
<i>Hydatophylax</i>	–	–	0.1 (1.0)	–	–	–	0.2 (1.4)	–
<i>Lepidostoma</i>	0.2 (1.4)	1.6 (14.2)	1.2 (12.1)	3.3 (14.4)	1.2 (8.2)	1.7 (8.2)	2.1 (16.1)	1.7 (15.7)
<i>Parapsyche</i>	0.3 (2.6)	0.9 (8.0)	–	1.3 (5.6)	–	–	–	0.1 (1.2)
<i>Pseudostenophylax</i>	–	0.6 (5.3)	–	–	–	–	–	–
<i>Rhyacophila</i>	0.9 (8.1)	0.6 (5.1)	0.6 (6.2)	3.1 (13.5)	0.4 (2.5)	1.0 (7.0)	1.0 (7.3)	0.4 (3.8)
<i>Wormaldia</i>	0.7 (6.3)	–	0.1 (1.2)	–	0.7 (4.6)	0.6 (4.0)	0.2 (1.7)	0.1 (1.2)
<i>Prosimulium</i>	0.4 (3.4)	–	0.4 (3.6)	–	0.3 (1.9)	3.1 (21.3)	0.2 (1.1)	0.2 (1.5)
Tanypodinae	–	–	0.2 (1.5)	0.5 (2.1)	0.2 (1.1)	0.2 (1.3)	0.3 (2.1)	0.4 (3.5)
Orthoclaadiinae A	–	–	–	–	1.5 (10.2)	1.3 (8.6)	0.2 (1.7)	–
<i>Brillia</i>	–	0.2 (1.3)	0.2 (1.9)	1.8 (5.1)	0.6 (4.3)	0.6 (4.0)	0.3 (1.7)	0.2 (2.1)
<i>Corynoneura</i>	0.2 (1.8)	–	0.4 (4.3)	–	–	0.3 (2.2)	–	–

Table 2.4. continued:

Taxon	Red maple (1998)		WBB+N (ref)	WBB+N (+N)	Red maple (1999)		WBB+N (ref)	WBB+N (+N)
	EBB (ref)	EBB (+N)			EBB (ref)	EBB (+N)		
<i>Tvetenia</i>	2.1 (19.1)	1.5 (14.2)	2.7 (27.3)	3.3 (14.4)	1.9 (12.8)	2.1 (14.5)	3.0 (23.3)	2.2 (20.9)
Tanytarsini	–	–	0.2 (1.5)	–	–	0.4 (2.4)	0.3 (2.2)	0.3 (2.5)
Oligochaeta	0.3 (2.3)	0.3 (3.0)	0.1 (1.3)	–	0.3 (2.1)	0.4 (2.4)	0.8 (5.8)	0.1 (1.1)
Chilopoda	2.2 (19.5)	0.6 (5.1)	–	0.8 (3.4)	2.4 (16.6)	–	0.4 (3.4)	1.1 (10.8)
Total richness	26	28	20	29	28	27	29	27
SHR total richness	8	9	8	9	8	7	8	7
Avg. richness	9	9	7	12	11	10	10	9
SHR avg. richness	3	3	3	7	4	4	4	3
Avg. total biomass	10 (5.1)	11 (5.8)	9 (6.4)	23 (14.3)	15 (5.5)	15 (9.7)	14 (5.8)	12 (5.1)
Avg. SHR biomass	3 (2.2)	6 (4.9)	5 (2.6)	12 (8.0)	6 (3.4)	5 (1.7)	6 (3.7)	6 (3.6)

37	Taxon	Sugar maple 1999		WBB+N (ref)	WBB+N (+N)	American beech 1999		WBB+N (ref)	WBB+N (+N)
		EBB (ref)	EBB (+N)			EBB (ref)	EBB (+N)		
	<i>Allocapnia</i>	–	0.2 (2.0)	1.4 (9.1)	–	0.2 (1.3)	–	–	–
	<i>Leuctra</i>	–	0.8 (7.2)	1.1 (7.0)	1.3 (11.0)	0.5 (3.6)	1.3 (6.0)	1.3 (8.1)	1.8 (12.0)
	<i>Ostrocera</i>	1.4 (12.9)	1.9 (17.3)	1.9 (19.0)	1.7 (14.0)	1.8 (12.7)	1.9 (9.0)	1.2 (7.7)	2.0 (12.9)
	<i>Paranemoura</i>	–	–	0.7 (1.0)	0.2 (1.6)	–	–	–	–
	<i>Soyedina</i>	0.5 (4.5)	–	–	0.4 (3.6)	–	–	–	0.3 (1.6)
	<i>Sweltsa</i>	–	–	–	–	–	0.2 (1.1)	–	–
	<i>Homoplectra</i>	–	–	–	0.3 (3.0)	–	–	1.2 (7.8)	1.8 (11.6)
	<i>Hydatophylax</i>	1.2 (11.1)	0.1 (1.0)	–	–	–	–	0.2 (1.1)	–
	<i>Lepidostoma</i>	0.5 (4.5)	0.7 (6.6)	0.3 (1.9)	1.1 (9.4)	2.0 (14.4)	3.7 (17.2)	1.9 (12.3)	0.9 (5.7)
	<i>Parapsyche</i>	–	–	0.3 (2.0)	–	–	–	0.3 (1.7)	–
	<i>Pseudostenophylax</i>	–	–	–	0.5 (3.9)	–	0.3 (1.5)	–	–
	<i>Rhyacophila</i>	0.7 (6.5)	0.4 (3.4)	0.9 (5.5)	–	0.6 (3.9)	0.8 (4.0)	1.6 (10.0)	0.6 (4.0)
	<i>Wormaldia</i>	0.2 (1.6)	0.5 (4.2)	–	0.9 (6.1)	1.8 (8.3)	0.2 (1.1)	–	–

Table 2.4. continued:

Taxon	Sugar maple 1999				American beech 1999			
	EBB (ref)	EBB (+N)	WBB+N (ref)	WBB+N (+N)	EBB (ref)	EBB (+N)	WBB+N (ref)	WBB+N (+N)
<i>Prosimulium</i>	0.2 (1.5)	0.2 (1.7)	0.4 (2.2)	0.2 (1.5)	0.4 (3.1)	0.6 (2.6)	0.4 (2.5)	0.3 (1.6)
<i>Hemerodromia</i>	0.1 (1.2)	—	—	—	—	—	—	—
<i>Pedicia</i>	—	—	1.3 (8.0)	—	—	—	1.3 (8.1)	—
Tipula	—	—	0.5 (3.2)	—	—	—	—	—
Tanypodinae	0.5 (4.5)	0.3 (2.9)	0.3 (1.7)	0.2 (1.7)	0.4 (2.6)	0.4 (1.9)	0.5 (3.0)	0.3 (1.9)
Chironomidae A	—	—	0.3 (3.0)	1.7 (12.0)	3.2 (15.0)	—	—	—
Orthoclaadiinae A	0.6 (8.3)	1.8 (16.1)	—	0.2 (1.8)	1.7 (12.0)	—	—	—
Orthoclaadiinae B	0.1 (1.3)	—	—	0.2 (1.6)	—	—	—	—
<i>Brillia</i>	0.2 (2.0)	0.6 (5.3)	—	1.0 (8.3)	0.4 (2.9)	0.6 (2.7)	0.4 (2.3)	0.3 (1.8)
<i>Corynoneura</i>	—	0.1 (1.0)	—	—	—	—	—	—
<i>Tvetenia</i>	3.0 (27.5)	1.8 (16.0)	3.7 (23.7)	2.4 (20.3)	3.6 (25.8)	4.4 (20.8)	3.3 (21.5)	4.5 (29.6)
Tanytarsini	0.6 (5.9)	0.2 (1.8)	0.5 (3.2)	0.2 (1.9)	0.3 (2.1)	0.6 (2.6)	0.3 (2.0)	1.2 (8.1)
Oligochaeta	0.4 (3.4)	0.3 (2.5)	2.1 (13.0)	0.3 (2.8)	0.6 (4.1)	0.7 (3.1)	0.2 (1.2)	—
Chilopoda	—	0.9 (7.8)	—	—	—	—	1.1 (6.8)	0.5 (3.4)
Total richness	25	25	32	26	28	30	29	27
SHR total richness	7	8	10	7	6	7	9	8
Avg. richness	9	10	11	10	10	11	10	10
SHR avg. richness	3	4	4	4	3	4	4	4
Avg. total biomass	12 (6.3)	11 (4.5)	16 (5.0)	12 (2.9)	14 (7.4)	21 (11.2)	16 (7.2)	15 (4.6)
Avg. SHR biomass	4 (2.3)	5 (2.2)	6 (2.7)	6 (2.1)	5 (3.0)	8 (5.4)	5 (2.3)	5 (1.5)

concentrations, increased acidity, and increased leaching of cations to the stream, including Al, which is potentially toxic to aquatic organisms. All of these factors have been independently shown to alter litter processing rates (Meyer and Johnson 1983, Mulholland et al. 1987, Palumbo et al. 1987, Groom and Hildrew 1989, Maltby and Booth 1991, Suberkropp and Chauvet 1995, Chamier and Tipping 1997, Dangles and Guerold 1998, Suberkropp 1998). Nevertheless, my study has revealed no instances where leaf softness, and only one instance where leaf loss, differed between streams (Table 2.5). Similarities in both physical and biological mechanisms that drive litter processing in streams may explain these results.

Physical factors (e.g., habitat, temperature, and current) can affect detritus processing in streams (Webster and Benfield 1986). At BBWM, both streams have comparable habitat composition. Temperature and discharge patterns in autumn are also almost identical. These similarities may contribute to the lack of difference either in mass loss or softening. Nonetheless, biological mechanisms, such as microbial activity and shredder feeding, are also involved in stream detritus processing.

Microbial decomposition of leaf tissue is affected by both internal and external nutrient sources (e.g, N and P; Suberkropp 1998). Lack of differences in litter processing between streams may be a result of oligotrophic concentrations of P. Rates of litter processing can be P limited (Elwood et al. 1981, Newbold et al. 1983, Suberkropp and Chauvet 1995, Robinson and Gessner 2000, Grattan and Suberkropp 2001), and the extremely low levels of this nutrient could explain

**Table 2.5.** Summaries of statistical results for litter processing at Bear Brook Watershed in Maine (1997-1999). Statistically significant results are bolded.

AFDM = Ash-free dry mass.

<b>year</b>	<b>Leaf species</b>	<b>Stream effects</b>	<b>Leaf effects</b>
1997	Red maple	AFDM remaining Leaf softness	AFDM remaining <b>Leaf softness</b>
1998	Red maple	AFDM remaining Leaf softness	<b>AFDM remaining</b> <b>Leaf softness</b>
1999	Red maple	AFDM remaining Leaf softness	AFDM remaining Leaf softness
	Sugar maple	<b>AFDM remaining</b> Leaf softness	<b>AFDM remaining</b> <b>Leaf softness</b>
	American beech	AFDM remaining Leaf softness	<b>AFDM remaining</b> <b>Leaf softness</b>

why increased stream N availability did not alter rates of processing in either stream. Increased total P exports from WBB+N have been reported (Roy et al. 1999). Despite this increase, bioavailable phosphate is undetectable in both streams ( $<1 \mu\text{g/L}$ ; MAC, unpublished data), which suggests that  $\text{PO}_4^{=}$  may be limiting. Lastly, rates of litter softening respond to changes in nutrient levels only when increases are below saturating levels (i.e.,  $0.2 \text{ mg/L NO}_3^-$  and  $5 \mu\text{g/L PO}_4^{=}$  for selected headwater streams in Maine; Hurn et al. 2002). Increases in available nutrients above these thresholds, as seen for  $\text{NO}_3^-$  in WBB+N, may not result in faster litter processing.

Another potential explanation for the lack of stream effects on litter processing is stream acidity (for WBB+N and EBB respectively: mean pH 4.90 vs 5.4; mean ANC  $-8$  vs  $1$ ). Both streams are acidic, and several studies have shown that rates of detritus processing are reduced in acidic systems. For example, in 4 acidic streams (pH 4.5–6.4), Mulholland et al. (1987) found that rate of leaf loss slowed significantly in streams with pH  $< 5.7$ . Similarly, beech leaves incubated in an acidic stream (pH = 4.5) had breakdown rates 9 times slower than in a circumneutral stream (Dangles and Guerold 1998). Reduced microbial activity because of elevated Al is a mechanism to explain observed reductions in litter processing in acidic streams (Mulholland et al. 1987, Jenkins and Suberkropp 1995, Chamier and Tipping 1997). The pH of both streams at BBWM was either below or near 5.7, so there is potential for Al toxicity that can alter leaf processing (Mulholland et al. 1987, Palumbo et al. 1987, Groom and

Hildrew 1989, Maltby and Booth 1991, Chamier and Tipping 1997, Suberkropp 1998).

Last, shredder biomass and taxonomic richness alter rates of litter loss in streams (Jonsson and Malmquist 2000), so attributes of shredder assemblages in a stream may override effects of N deposition. The streams at BBWM tend to have low shredder biomass compared to forested headwater streams elsewhere in Maine (Huryn et al. 2002), suggesting that shredder activity is not the dominant force for leaf loss in either stream. This contention is further supported by the 1998 results. Shredder biomass in 1998 differed between leaf source and stream but, despite these differences, the highest shredder biomass was associated with the treatment with the lowest leaf loss.

#### Leaf effects

Unlike stream effects, there were measurable differences in litter processing as a result of leaf source. For red maple (1998) and sugar maple and American beech (1999), litter processing (both tissue loss and softening) was significantly greater for N-enriched than reference leaves. It is possible the N-enriched leaves provide higher substrate quality for colonizing microbial communities. Foliar sources can provide sufficient nutrients for aquatic hyphomycete production (Suberkropp 1998) and, in oligotrophic systems such as BBWM, foliar nutrients may become more important sources than stream water. Foliar sources of nutrients may not be sufficient for all leaf species because of varying concentrations of other foliar compounds, especially lignin (Webster and Benfield 1986, Gessner and Chauvet 1994, Royer and Minshall 2001).

When N-enriched leaves had high rates of leaf softness they also had high rates of leaf loss. This increased processing also tended to be paired with greater shredder biomass, although these observations were only statistically significant for red maple in 1998. Fungal conditioning of leaves increases palatability to shredders (Suberkropp 1992, Arsuffi and Suberkropp 1985), which could lead to increased feeding activity and subsequently higher rates of litter loss. Results from this study suggest that elevated foliar N content can affect litter processing by increasing microbial and shredder activity (as seen in leaf softness and loss, respectively).

In conclusion, study results suggest that chemical changes in WBB+N (i.e., decreased pH and increased stream N concentrations) caused by the long-term, catchment-scale N treatments were too weak to elicit a response in stream litter processing. The lack of consistency of these results (Table 2.5) suggests that detritus processing in streams draining N saturated catchments does not respond to cumulative processes that may drive detritus breakdown on forest floors (Wagner et al.1999). Effects of N deposition on stream-litter processing are subtle and apparently caused by alterations in foliar chemistry and subsequent differences in microbial conditioning, with possible changes in shredder activity. Based on consider observations from three years of study, conclusions about how N deposition alters stream-litter processing would vary from negative to positive (Table 2.5). This implies that annually fluctuating factors, such as stream water acidity or foliar chemistry, are more important than N amendments for determining rates of litter processing. Further, results suggest

that elevated N in stream water at BBWM plays a minimal role in moderating stream-detritus processing. It is likely that the stream ecosystem function of detritus processing is limited because of naturally occurring acidic or oligotrophic conditions.

**Chapter 3:**

**EFFECTS OF ATMOSPHERIC N DEPOSITION ON COARSE  
ORGANIC MATTER IN A HEADWATER STREAM**



The Whale's Back by C.L. Chadwick

## Introduction

The deposition of N to forests results in predictable changes to ecosystem structure and function (Aber 1989, Peterjohn et al. 1996, Fenn et al. 1998). Initial increases in N availability reduce nutrient limitation stimulate increased forest productivity, and increase N concentrations in plant tissue (Gilliam et al. 1996, White et al. 1999). Leaching of nitrate, nutrient cations, and aluminum from forest soils may also occur simultaneously (Aber et al. 1989, Kahl et al. 1993, Peterjohn 1996, Norton et al. 1999). As the entire forest ecosystem becomes increasingly altered by excess N, productivity may begin to decline (Aber et al. 1989). Predictions about alterations to streams because of catchment N saturation have been limited to water chemistry (i.e., nitrate and cation concentrations). However, changes in water chemistry and forest productivity may also result in changes in ecosystem structure and function, due to the direct dependence streams have on their catchments for both organic matter and nutrients (Hynes 1975, Vannote et al. 1980, Wallace et al. 1999).

Food webs of forested, headwater streams are largely supported by coarse particulate organic matter (CPOM; Fisher and Likens 1973, Wallace et al. 1999). Consequently, there are numerous studies of stream CPOM dynamics (Fisher and Likens 1973, Fisher 1977, Cummins et al. 1983, Webster and Meyer 1997, Webster et al. 1999). Biological, chemical and physical processes regulate the amounts and types of input, storage, and transport of CPOM within stream ecosystems. These processes include movement of material to stream channels, processing, consumption, storage, and downstream transport (Fisher

and Likens 1973, Anderson and Sedell 1979, Cummins et al. 1983, Speaker et al. 1984, Webster and Benfield 1986, Webster and Meyer 1997 and references within, Webster et al. 1999). The effects of catchment-level N deposition and subsequent increases in N availability on these processes are unknown.

An ongoing paired-catchment experiment at the Bear Brook Watershed in Maine (BBWM; Norton et al. 1999) provides a unique opportunity to investigate how stream CPOM dynamics are affected by N deposition. Since 1989, ammonium sulfate has been applied to an entire forested catchment with loading rates similar to the Adirondack region of New York State (~6 Kg/ha N and ~20 kg/ha S deposition; National Atmospheric Deposition Program (NRSP-3)/National Trends Network 2003). The treatment catchment is West Bear Brook (WBB+N) and the adjacent catchment, East Bear Brook (EBB), is the reference. Several lines of evidence suggest that WBB+N is proceeding towards N saturation. Nitrogen saturation occurs when N is present in concentrations that exceed those needed to sustain forest productivity. Symptoms of N-saturation documented from WBB+N include catchment acidification, elevated nitrate concentrations in stream water, and increased foliar N content (Kahl et al. 1999, Norton et al. 1999, White et al. 1999, Chapter 2). Nevertheless, processing rates of stream detritus have been shown to be minimally affected by the treatment, potentially because of pre-existing acidic and oligotrophic conditions (Chapter 2). Increased foliar N levels in the WBB+N catchment have elevated microbial activity, increased shredder biomass, and altered rates of stream detritus processing (Chapter 2). These results suggest that streams that drain catchments with elevated N

deposition may respond more strongly to alteration in the quality and supply of organic matter (due to effects on forest productivity) than to changes in stream water quality.

Because of the close relationships between forest and stream (Wallace et al. 1999), changes predicted for forested ecosystems due to N deposition should translate into changes in stream organic matter dynamics. The main objective of this study was to quantify and to contrast organic CPOM inputs, storage, and export between the streams at BBWM. If N saturation increases forest productivity, CPOM inputs increase and benthic organic matter could increase. CPOM inputs and benthic organic matter could diminish if N saturation leads to declines in forest productivity.

### **Study Site**

The Bear Brook Watershed in Maine (BBWM) is in eastern Maine, USA (44° N, 68°06 W). Each catchment is ~10 ha and has similar soils, topography, aspect, gradient, and hydrology (see Norton et al. 1999 for a complete description of each catchment). Intermittent streams drain each catchment and both have similar physical structure (Table 3.1). The entire WBB+N catchment has been treated bimonthly with ammonium sulfate to increase annual loadings of N by 300%. The adjacent catchment (EBB) serves as the reference. The ongoing N manipulation at WBB+N has decreased stream water pH, ANC and

**Table 3.1.** Physical characteristics for the streams at the Bear Brook Watershed in Maine. WBB+N = treatment stream, EBB = reference stream.

=====			
Variable	WBB+N	EBB	References and notes
-----			
Latitude	44° 52'	44° 52'	
Order	1 (intermittent)	1 (intermittent)	
Catchment area (ha)	10.2	10.7	
Streambed area (m <sup>2</sup> )	410	403	
Gradient (%)	31	31	
Mean annual water temperature (°C)	5.1	5.2	
Mean annual discharge (L/sec)	3.0	3.1	(1997-2000)
Mean annual precipitation (cm)	140	140	(1987-1996; Norton et. al. 1999)
Annual range of precipitation (cm)	70 –190	70 –190	(1987-1996; Norton et. al. 1999)
Percent stream habitat:			
bedrock	11.7	8.5	
debris dam	21.7	18.3	
riffle/run	43.3	46.6	
pool	23.3	26.6	
=====			

dissolved organic carbon. Further, nitrate, calcium, magnesium, aluminum, and specific conductance have all increased (Norton et al. 1999).

## **Methods**

### Input

Sixteen vertical liter traps ( $0.25 \text{ m}^2$ ) located directly over the streambed and sixteen lateral traps located adjacent to the streambed ( $0.5 \text{ m}$  long x  $0.2 \text{ m}$  high x  $0.3 \text{ m}$  deep) were placed randomly along each stream to collect CPOM entering their channels. Traps were deployed in August (1998, 1999) and emptied ~ every six weeks in autumn and again after spring snowmelt. Collections were not made in summer, when there was no surface water, or in winter when traps were snow covered. All material was sorted into CPOM types (American beech leaves, maple leaves, wood, or miscellaneous), dried to constant mass ( $60^\circ \text{C}$ ), and then weighed. A portion from each sample was ashed ( $550^\circ \text{C}$ ) and weighed to calculate ash free dry mass (AFDM). Total lateral inputs were doubled to arrive at a final estimate because traps only sampled one side of each stream. Total annual input was calculated by adding input during leaf abscission to input estimated using the spring collections. Differences in input from both vertical and lateral traps between streams and years were assessed independently using two sample *t*-tests. Control of type II error was achieved by designating an  $\alpha$  level of 0.10 prior to the study.

### Storage

Benthic organic matter (BOM) was sampled approximately monthly from November 1998 - May 1999 and October 1999 - July 2000 in each stream using a Surber sampler ( $0.9 \text{ m}^2$  -  $250\mu\text{m}$  mesh). Three samples were taken from each of the dominant habitat types (bedrock, debris dams, riffle/runs, and pools). Bedrock was sampled only in the first year. All samples were preserved in ~5% formaldehyde. BOM was processed in the same manner as catchment input (see above), but the miscellaneous category was split into two size fractions (i.e.,  $>2\text{mm}$  and  $< 2\text{mm}$ ). Average biomass for each BOM type was calculated from 1,000 monthly, habitat-weighted estimates generated by resampling with replacement. Total BOM was then calculated by summing across BOM types to create 1,000 estimates for each stream. Statistical comparisons between streams for BOM types and total BOM were made by comparing 90% confidence intervals. Nonoverlapping confidence intervals indicated a significant difference. Control of type II error was achieved by designating an  $\alpha$  level of 0.10 prior to this study.

### Export

Export potential for coarse particulate organic matter was measured using leaf and stick analogs. Leaf analogs were equilateral triangles (~8 cm edge) cut from blue tarp. Stick analogs were 0.5 m long dowels (1 cm diameter). Five hundred, individually labeled leaf analogs and 30 labeled dowels were released into each stream ~250 meters above each weir in September 1999. After the

initial release, monthly surveys for analogs were conducted until May 2000. Analogs were “recovered” by visual inspection of the stream channel and riparian areas. When an analog was recovered, its location (i.e., distance moved from release point) and position were measured. Analog positions were categorized as debris dams, channel (riffle/runs and pools), or lateral to the channel. No analogs were removed from the stream channels. Seasonal differences in the distribution of analogs among position types between streams were assessed using a  $\chi^2$  test. Export coefficients for each sample period were quantified as the slope of the negative exponential decay of percent analogs in transport versus distance from the release point (Lamberti and Gregory 1996). Movement rates (m/day) were calculated for all analogs between sample periods. The relationship between movement rates and maximum discharge, and the difference between streams were analyzed using linear regression.

#### Leaf litter loss

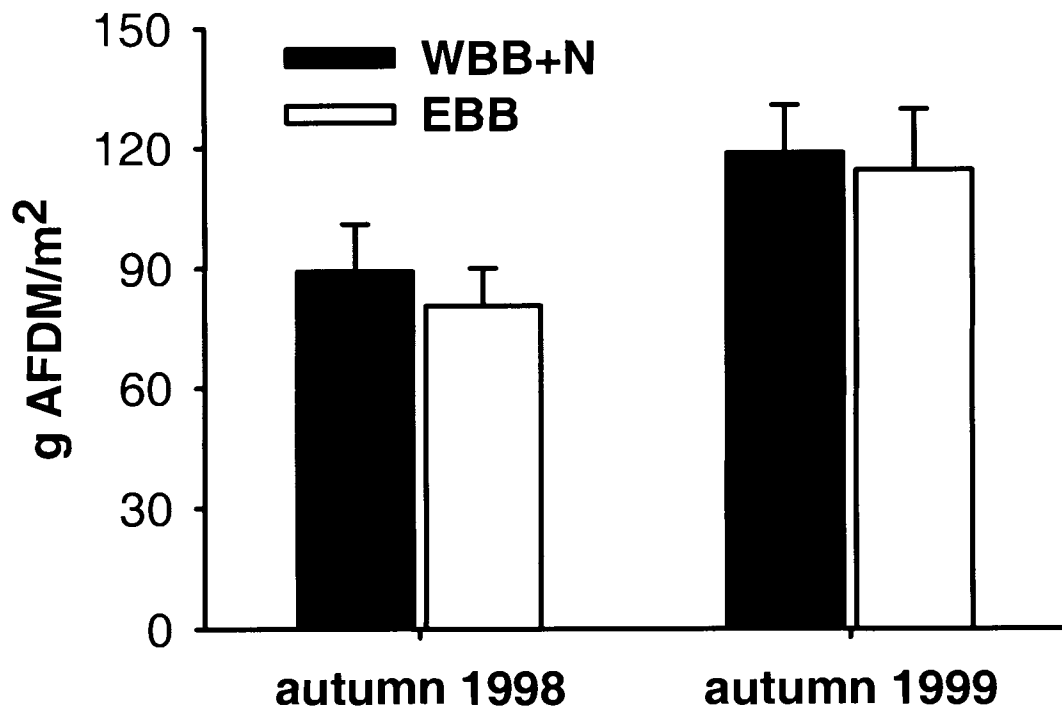
Loss rates ( $\text{d}^{-1}$ ) for both American beech (*Fagus grandifolia*) and maple (*Acer* spp.) were derived using the ratio of total input ( $\text{g AFDM m}^{-2} \text{d}^{-1}$ ) to average biomass ( $\text{g AFDM/m}^2$ ). These values were then compared to rates quantified using litter bag techniques (see Chapter 2).

## Results

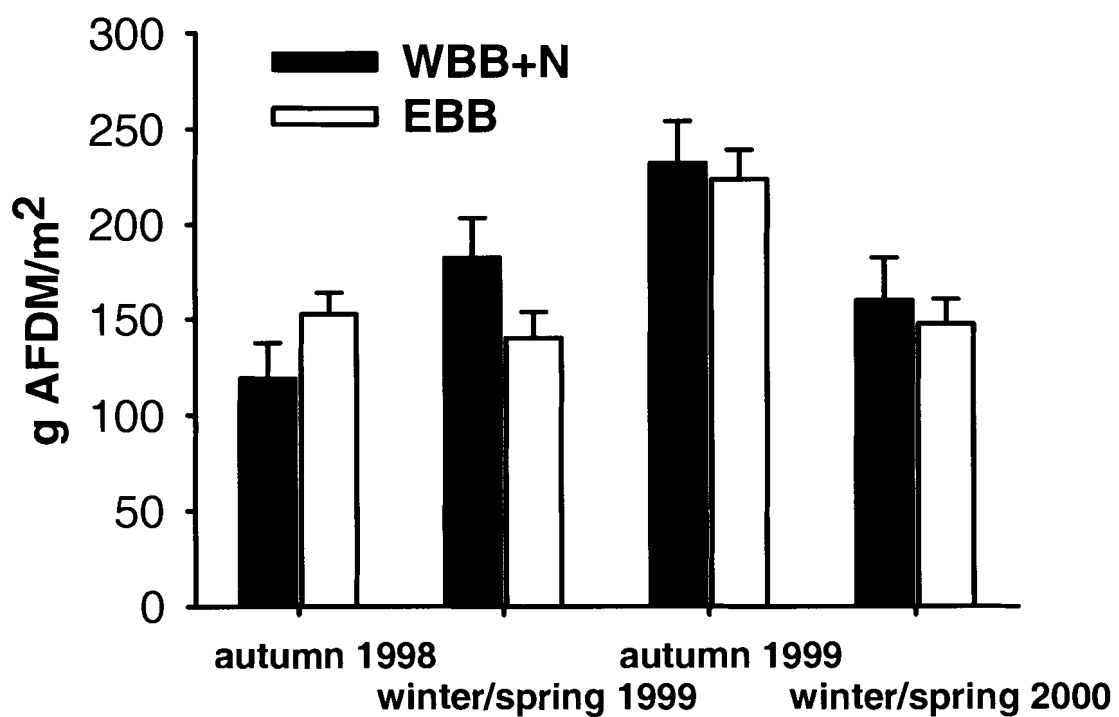
### Input

Vertical input of coarse organic matter in autumn ranged from 60–125 g AFDM/m<sup>2</sup> in each stream. Average vertical litter input did not differ between streams in either year (1998:  $t = 1.16$ ,  $p = 0.265$ ; 1999:  $t = 0.43$ ,  $p = 0.67$ ; Fig. 3.1), however there was significantly more input to each stream during 1999/2000 (1998/1999 vs. 1999/2000:  $t = 5.00$ ,  $p < 0.001$ ). For the 1998/1999 winter/spring collection, vertical inputs did not differ between streams ( $t = 0.53$ ,  $p = 0.62$ , range = 84–144 g AFDM/m<sup>2</sup>). Due to the damage caused to traps during winter, collections for winter/spring 1999/2000 were not made. Mean monthly vertical inputs (17 g AFDM/m<sup>2</sup>), for all months other than during leaf abscission, were estimated using the 1998/1999 winter/spring collections. Total annual vertical inputs were 282 and 273 g AFDM/m<sup>2</sup> in 1998/1999 and 311 and 307 g AFDM/m<sup>2</sup> in 1999/2000 (WBB+N and EBB, respectively).

Lateral inputs of coarse organic matter in autumn ranged from 125–225 g AFDM/m<sup>2</sup> for both streams. Average lateral inputs for the autumn collection did not differ between streams in either year (1998  $t = 0.95$ ,  $p = 0.36$ , 1999  $t = 0.18$ ,  $p = 0.86$ ; Fig. 3.2). Similar to vertical inputs, there was significantly more input in autumn during 1999/2000 (1998/1999 vs. 1999/2000  $t = 3.03$ ,  $p < 0.006$ ). For the winter/spring collection, lateral inputs for both streams ranged from 140–170 g AFDM/m<sup>2</sup> and no differences were observed between streams in 1999 (WBB+N vs. EBB  $t = 0.9$ ,  $p = 0.37$ ). Many traps failed in WBB+N in 2000.



**Figure 3.1.** Autumn mean ( $\pm 2$  standard errors) direct coarse particulate organic matter inputs for WBB+N and EBB for 1998 and 1999. WBB+N = treatment stream, EBB = reference stream.



**Figure 3.2.** Seasonal mean ( $\pm 2$  standard errors) lateral inputs for WBB+N and EBB from 1998 -2000. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass.

Lateral inputs to WBB+N in 2000 were estimated from collections made in EBB for the same year because of the similarities between streams in 1999.

Estimated monthly lateral inputs were 23 g AFDM/m<sup>2</sup>. Total annual lateral inputs were 454 g AFDM/m<sup>2</sup> and 406 g AFDM/m<sup>2</sup> in 1998/1999 and 525 g AFDM/m<sup>2</sup> and 477 g AFDM/m<sup>2</sup> in 1999/2000 (WBB+N and EBB, respectively).

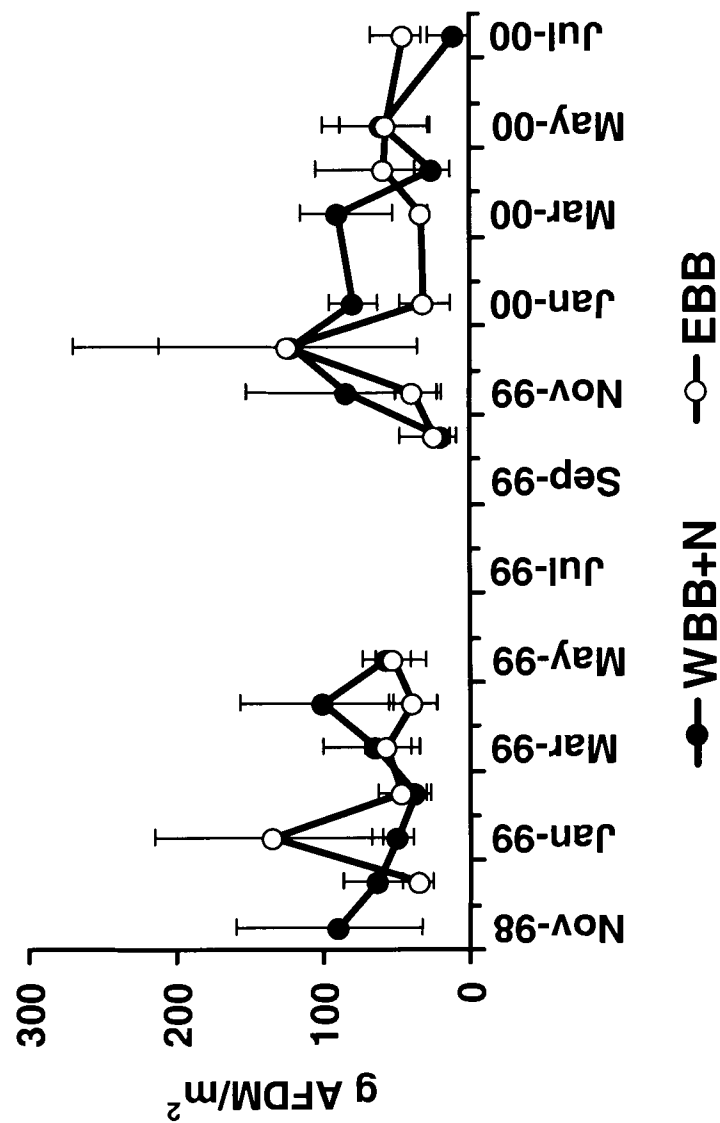
Total input of CPOM was 736–835 g AFDM/m<sup>2</sup> for WBB+N and 679–784 g AFDM/m<sup>2</sup> for EBB (1998/1999 and 1999/2000, for each stream respectively; Table 3.2). Vertical inputs accounted for ~40% of total inputs for each stream. CPOM composition was similar between streams. American beech leaves were the dominant CPOM type (~66–68%), followed by miscellaneous non-woody material (e.g., birch, cherry, moss, unidentifiable leaf fragments; ~18%), maple leaves (~7–8%), and small woody material (~5–8%).

### Storage

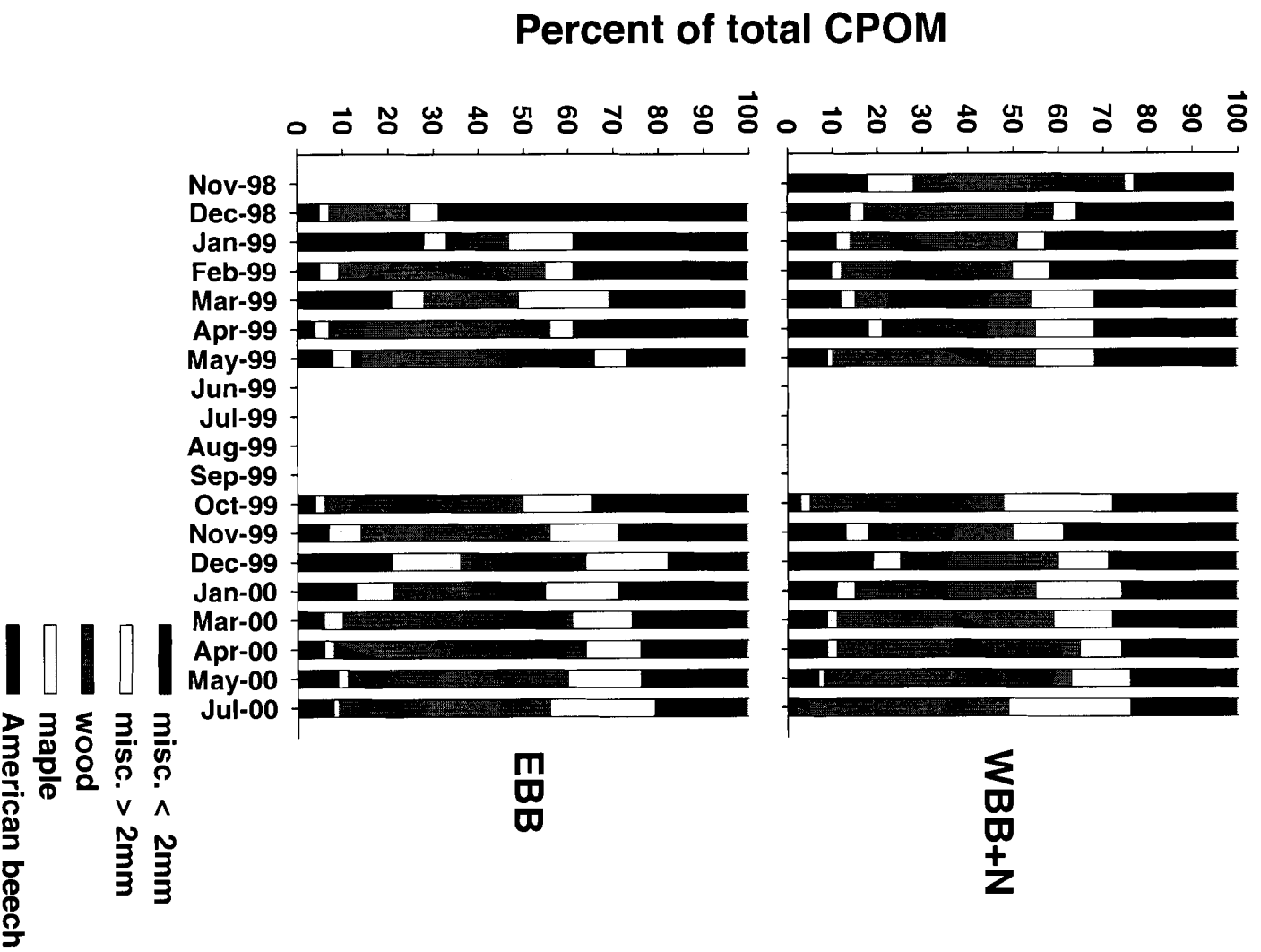
Over the entire sampling period, habitat-weighted CPOM biomass varied from 243 g AFDM/m<sup>2</sup> (EBB: Jan 2000) to 979 g AFDM/m<sup>2</sup> (WBB+N: March 2000; Fig. 3.3). However, no differences in total CPOM biomass were observed between streams (i.e., 90% C.I. always overlapped; Fig. 3.3). The distribution of CPOM among litter types varied monthly, but was similar between streams (Fig. 3.4). Wood and miscellaneous material < 2mm accounted for 50–85% of all CPOM (wood ~40% and misc. < 2mm ~30%; Fig. 3.4). Coarse leaf material, comprised of American beech, maple and miscellaneous material > 2mm, accounted for 15–50% of CPOM (Fig. 3.4). Leaf biomass increased after

**Table 3.2.** Organic matter parameters for the streams at the Bear Brook Watershed in Maine. All parameters are reported as ash-free dry mass. WBB+N = treatment stream, EBB = reference stream, DOM = dissolved organic matter, CPOM = coarse particulate organic matter, FBOM = fine benthic organic matter, GPP = gross primary production.

Variable	WBB+N	EBB	References and notes
Inputs ( $\text{g m}^{-2} \text{y}^{-1}$ )			
Gross primary production	0.30–1.14	0.34–1.15	Morin et al. 1999 and Lamberti & Steinman 1997
Direct	300	285	this study (average for both study years)
Lateral	490	441	this study (average for both study years)
Groundwater DOM	516	492	based on annual average DOC and discharged from 1990 to 1995 (data provided by Senator George J. Mitchell Center for Environmental & Watershed Research)
§ Biomass ( $\text{g/m}^2$ )			
CPOM	689	607	this study (average for both study years)
Small woody debris	246	243	this study (average for both study years)
Large wood	NA	NA	
Outputs			
Autotrophic respiration ( $\text{g m}^{-2} \text{y}^{-1}$ )	0.15–0.57	0.17–0.58	estimated as 50% GPP
Heterotrophic respiration ( $\text{g m}^{-2} \text{y}^{-1}$ )	~50	~50	estimated from Sinsabaugh 1997
FBOM transport ( $\text{kg/y}$ )	NA	NA	
DOM transport ( $\text{kg/y}$ )	367	385	based on data from 1988-1996 (David et. al 1999)



**Figure 3.3.** Monthly mean ( $\pm$  90 confidence limit) habitat-weighted CPOM for WBB+N and EBB. No samples were taken from June –September 1999 because the streams lacked surface water. WBB+N = treatment stream, EBB = reference stream, CPOM = coarse particulate organic matter, AFDM = ash-free dry mass.



**Figure 3.4.** Percent of average CPOM biomass for WBB+N and EBB by CPOM type. WBB+N = treatment stream, EBB = reference stream, CPOM = coarse particulate organic matter, AFDM = ash-free dry mass

**Table 3.3.** Percent of average habitat-weighted CPOM biomass by A) CPOM type, and B) habitat. WBB+N = treatment stream, EBB = reference stream, CPOM = coarse particulate organic matter, WBB+N = treatment stream, EBB = reference stream.

A.	CPOM type	Stream	
		WBB+N	EBB
-----			
	American Beech	11.0	10.5
	maple	3.1	4.8
	wood	42.5	39.4
	miscellaneous > 2mm	12.4	13.2
	miscellaneous <2mm	31.0	32.0
-----			
B.	Habitat	Stream	
		WBB+N	EBB
-----			
	bedrock	2.1	1.2
	debris dam	64.4	65.5
	riffle/run	21.5	22.6
	pool	12.0	11.2
=====			

leaf abscission in autumn and after winter snow melt (Fig. 3.4). Similarities in monthly CPOM biomass can be accounted for by similarity in CPOM storage among habitat types, particularly debris dams (Table 3.3). Debris dam storage accounted for ~65 % of all CPOM present, followed by riffle/runs (~22%), pools (12%), and bedrock (~2%; Table 3.3).

### Export

The average recovery of leaf analogs was 34% in WBB+N and 29% in EBB. In both streams, recovery ranged from 14–73% (Table 3.4), with the lowest recovery occurring during snow cover. Rates of dowel recovery were also similar between streams with 79 and 82% average recovery for WBB+N and EBB, respectively. Dowel recovery ranged from 63–100%, and showed no seasonal pattern (Table 3.4). Neither leaf analogs nor dowels were ever recovered downstream of the either study reach.

Leaf analogs and dowels traveled further in WBB+N (Table 3.4, Fig. 3.5). Consequently, instantaneous retention rates were lower in WBB+N than EBB (Table 3.4). Linear regression of analog movement versus maximum discharge showed significant, positive relationships (Fig. 3.6). At similar discharge, leaf analogs moved significantly farther in WBB+N than in EBB, supporting the conclusion that WBB+N had higher CPOM export potential. However, no difference in dowel movement relative to discharge was observed.

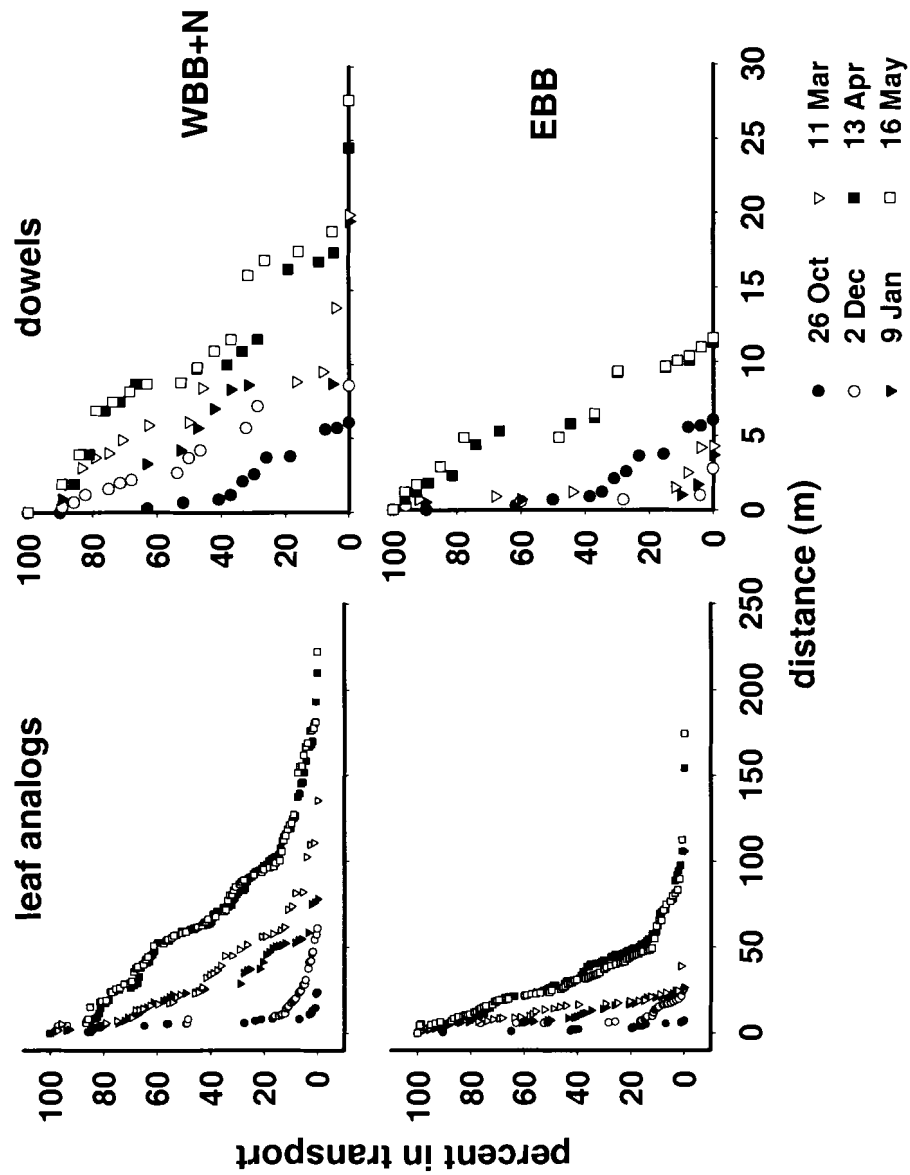
The spatial distribution of leaf analog retention differed significantly between streams

**Table 3.4.** Summary of leaf and wood analog export for the streams at Bear Brook Watershed in Maine. Values are reported for each stream as WBB+N / EBB. k is slope of the negative exponential decay of percent analogs in transport versus distance from the release point. All analogs were released on 22 September 1999. WBB+N = treatment stream, EBB = reference stream, SE = 1 standard error, movement = m/day Q = discharge (l/sec).

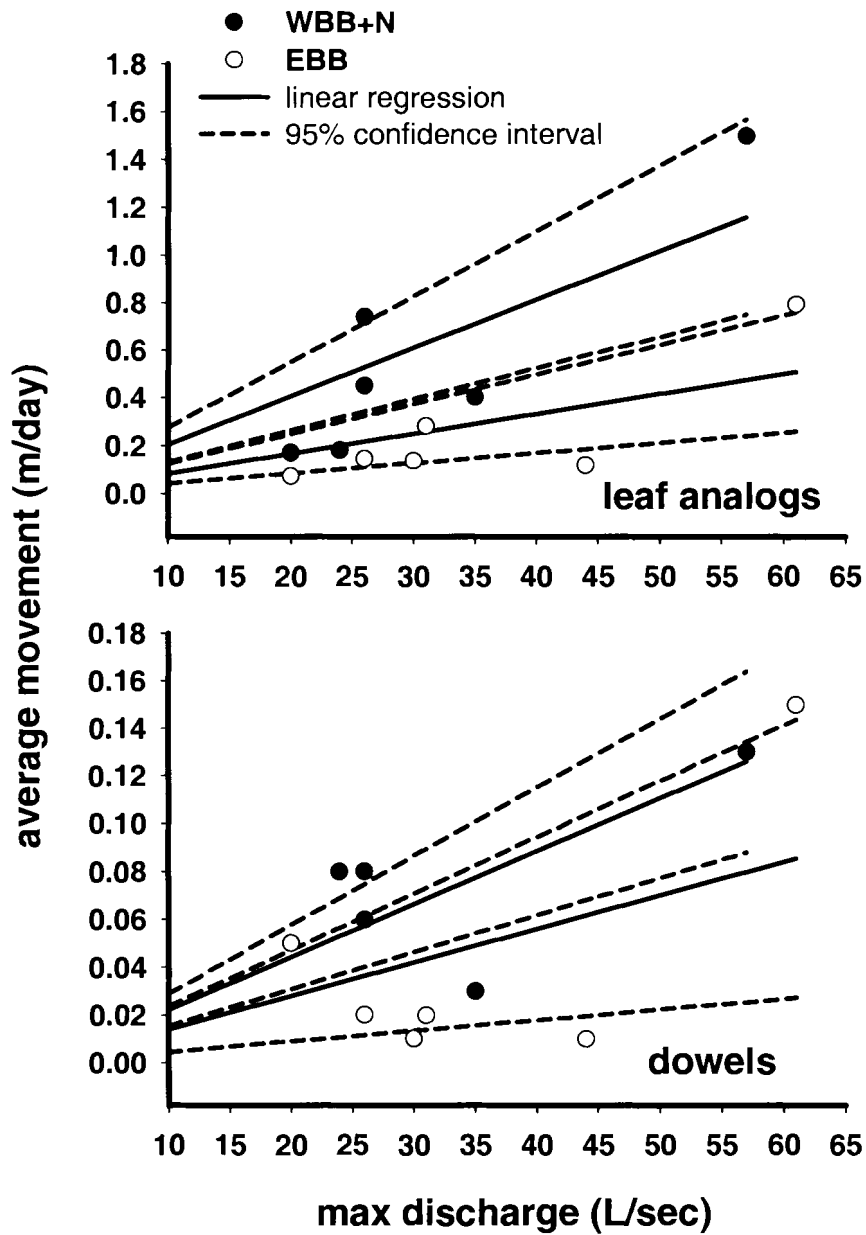
date	leaf analogs % recovery	-k (r <sup>2</sup> )	movement (SE)	wood analogs % recovery
26 Oct 1999	53 / 73	0.163 (0.86) / 0.451 (0.97)	0.17 (0.006) / 0.07 (0.003)	100 / 97
2 Dec 1999	60 / 34	0.151 (0.88) / 0.162 (0.83)	0.18 (0.016) / 0.14 (0.009)	93 / 83
9 Jan 2000	17 / 14	0.035 (0.97) / 0.102 (0.96)	0.45 (0.052) / 0.14 (0.019)	63 / 70
11 Mar 2000	14 / 14	0.029 (0.98) / 0.074 (0.92)	0.40 (0.058) / 0.12 (0.021)	80 / 83
13 Apr 2000	32 / 20	0.016 (0.96) / 0.032 (0.97)	1.50 (0.102) / 0.79 (0.060)	73 / 90
16 May 2000	27 / 16	0.016 (0.96) / 0.036 (0.98)	0.74 (0.107) / 0.04 (0.051)	63 / 90

Table 3.4 continued

date	-k (r <sup>2</sup> )	movement/day (SE)	max Q (avg. Q)
26 Oct 1999	0.446 (0.92) / 0.492 (0.92)	0.05 (0.011) / 0.05 (0.011)	20 (4) / 20 (4)
2 Dec 1999	0.205 (0.96) / 1.47 (0.84)	0.08 (0.016) / 0.02 (0.002)	24 (4) / 26 (4)
9 Jan 2000	0.152 (0.93) / 1.13 (0.83)	0.06 (0.026) / 0.01 (0.002)	26 (5) / 30 (6)
11 Mar 2000	0.138 (0.87) / 0.760 (0.86)	0.03 (0.008) / 0.01 (0.002)	35 (3) / 44 (4)
13 Apr 2000	0.094 (0.87) / 0.157 (0.90)	0.13 (0.039) / 0.15 (0.020)	57 (9) / 61 (10)
16 May 2000	0.082 (0.90) / 0.175 (0.89)	0.08 (0.039) / 0.02 (0.008)	26 (5) / 31 (5)



**Figure 3.5.** Percent analogs (leaf and wood) for each sample period in WBB+N and EBB. WBB+N = treatment stream, EBB = reference stream

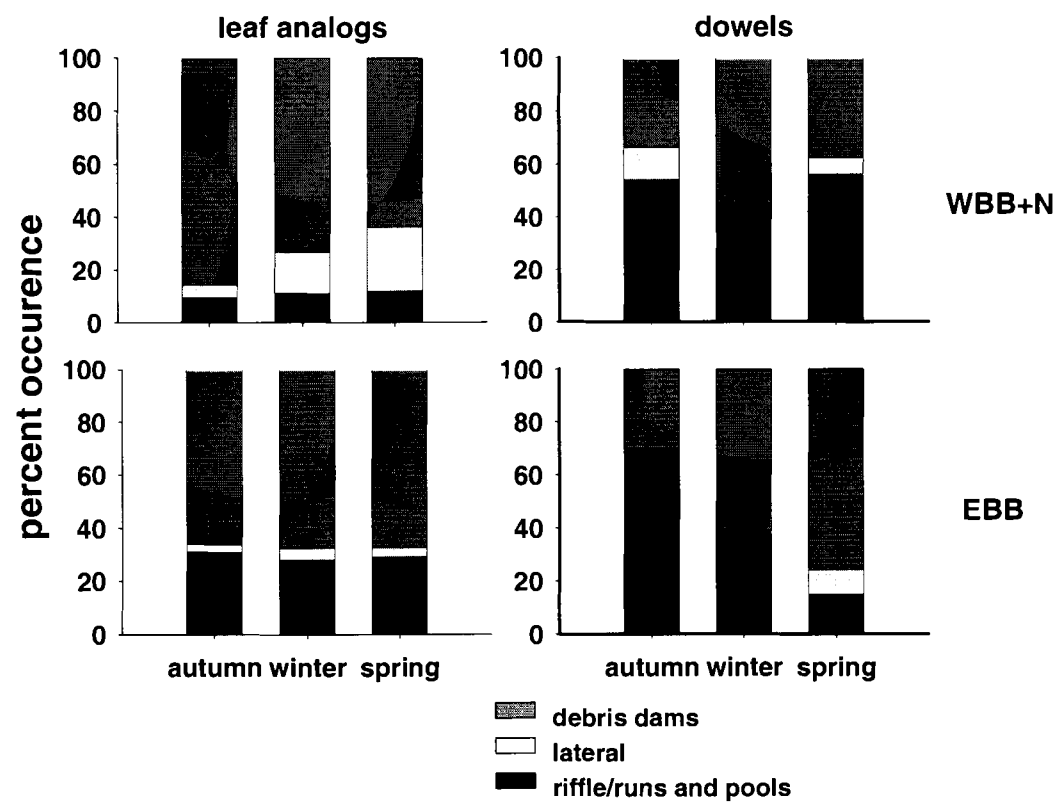


**Figure 3.6.** Linear regression analog movement versus maximum discharge (leaf analogs: WBB+N: movement =  $0.026 \times \text{max discharge}$ ,  $R^2 = 0.78$ ,  $F_{1,6} = 17.9$ ,  $p = 0.008$ ; EBB = N movement =  $0.011 \times \text{max discharge}$ ,  $R^2 = 0.66$ ,  $F_{1,6} = 9.9$ ,  $p = 0.002$ ; dowels: WBB+N: movement =  $0.00198 \times \text{max discharge}$ ,  $R^2 = 0.67$ ,  $F_{1,6} = 10.1$ ,  $p = 0.03$ ; EBB movement =  $0.00191 \times \text{max discharge}$ ,  $R^2 = 0.49$ ,  $F_{1,6} = 4.7$ ,  $p = 0.08$ ). WBB+N = treatment stream, EBB = reference stream.

(overall:  $\chi^2_8 = 220$ ,  $p < 0.001$ ; autumn:  $\chi^2_2 = 22$ ,  $p < 0.001$ ; winter:  $\chi^2_2 = 40$ ,  $p < 0.001$ ; spring:  $\chi^2_2 = 140$ ,  $p < 0.001$ ). In both streams, leaf analogs were retained mostly in debris dams (Fig. 3.7). In WBB+N, lateral retention of leaf analogs (i.e., along the stream bank) increased from 5% in autumn to 25% in spring, while lateral retention in EBB was consistently ~4% (Fig. 3.7). Retention of leaf analogs in riffle/runs and pools was greater in EBB (~30%) than WBB+N (~10%; Fig. 3.7). For dowels, overall retention differed between streams ( $\chi^2_8 = 259$ ,  $p < 0.001$ ) and seasonal differences were found in autumn and spring (autumn:  $\chi^2_2 = 125$ ,  $p < 0.001$ ; winter:  $\chi^2_2 = 3$ ,  $p = 0.27$ ; spring:  $\chi^2_2 = 132$ ,  $p < 0.001$ ). Initially most dowels were retained in riffles/runs or pools (Fig. 3.7). In winter, dowels in both streams were evenly distributed between riffle/runs and pool and debris dams (Fig. 3.7). After snow melt, most dowels in EBB were found in debris dams and pools (~75%), but dowels in WBB+N increased in riffle/runs (Fig. 3.7). Lateral retention of dowels was typically < 10% in both streams.

### Leaf litter loss

For American beech, processing rates derived from inputs and mean biomass ranged from 0.015–0.021/d and were similar between both years and streams (Table 3.5). However, these processing rates were an order of magnitude faster than rates obtained using litter bags (~0.002/d; Chapter 2). Processing rates for maple leaves derived from inputs and standing biomass



**Figure 3.7.** Percent occurrence of analogs (leaf and wood) in different retentive features for WBB+N and EBB. WBB+N = treatment stream, EBB = reference stream, lateral = not found in a stream channel.

**Table 3.5.** Leaf litter processing rates based on organic matter parameters. Values are reported for each stream as WBB+N / EBB. System-level processing rates are calculated as inputs/standing biomass. Processing rates from litterbags are from Chapter 2. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass.

		<b>American Beech</b>		<b>maple</b>	
		<b>1998 – 1999</b>	<b>1999 – 2000</b>	<b>1998 – 1999</b>	<b>1999 - 2000</b>
67	average biomass (g AFDM/m <sup>2</sup> )	66 / 60	61 / 51	18 / 25	17 / 28
	estimated input (g AFDM m <sup>-2</sup> d <sup>-1</sup> )	0.96 / 1.19	1.21 / 1.09	0.11 / 0.14	0.14 / 0.13
	system-level rates (d <sup>-1</sup> )	0.015 / 0.020	0.020 / 0.021	0.006 / 0.006	0.009 / 0.005
	processing rates from litterbags	N/A	0.002 / 0.002	0.006 / 0.006	0.006 / 0.006

ranged from 0.005–0.009/d (Table 3.5) and were similar to processing rates derived from litterbags (~0.006/d; Chapter 2).

## **Discussion**

### Inputs, storage, and exports

It was predicted that stream organic matter dynamics would be altered due to the catchment wide increase in N availability. However, I found that the streams draining BBWM did not have statistically different inputs or coarse organic matter biomass, and I found only modest differences in export potential. Organic matter inputs to stream ecosystems can be both spatially and temporally variable (Cummins et al. 1983, Weigelhofer and Waringer 1994, Benfield 1997, Webster and Meyer 1997). Suggested reasons for this include variability in channel-scale factors (e.g., bank inclination, stream width, density of riparian vegetation and wind patterns) and catchment-scale factors (e.g., precipitation, forest vegetation type, and latitude; Weigelhofer and Waringer 1994, Benfield 1997). The similarities in CPOM inputs between WBB+N and EBB are most likely driven by the similarities between the two catchments (Table 3.1) and provide evidence that the N deposition treatment (e.g., increased  $\text{NO}_3^-$  and decreased pH in streams) is not affecting stream CPOM inputs.

Like CPOM inputs, similarities in CPOM storage between WBB+N and EBB are likely due to similar channel structure and geomorphology. The type and degree of storage in streams has been attributed to riparian conditions and channel geomorphology (Bilby 1981, Maridet et al. 1995, Raikow et al. 1995,

Wallace et al. 1995, Angradi 1996, Lamberti and Gregory 1996). Upstream reaches retain more organic matter due to higher inputs of wood debris which results in the formation of debris dams (Bilby and Likens 1980, Webster et al. 1994, Jones 1997). Further, wood additions to streams have been shown to increase CPOM storage (Trotter 1990). Other retentive features, such as boulders and pools, also serve to increase CPOM storage (Huryn and Wallace 1987, Webster et al. 1994, Jones 1997). Similarities in CPOM storage between WBB+N and EBB are most attributable to debris dam habitats that comprise ~20% of both streams and store ~65% of CPOM occurring in each stream.

Export potential of leaf analogs was the only difference detected between streams during the study (Fig. 3.6). This finding is particularly interesting, given that the greatest analog movement occurred in WBB+N which consistently had lower mean and maximum discharge (Table 3.4). High discharge has been shown to alter amounts of CPOM in streams by reducing leaf retention (Bilby 1981, Boulton and Lake 1992, Webster et al. 1994, Wallace et al 1995). Further, these events can move material to riparian habitats (Jones and Smock 1991, Maridet et al. 1995, Wallace et al. 1995). WBB+N and EBB both had reduced leaf retention and storage in riparian habitats due to elevated discharge (Figs. 3.6 & 3.7). However, EBB had a less dramatic response. Two explanations for these observations in export are possible: 1) channel gradient in the middle reaches of EBB are slightly less than WBB+N, and 2) EBB tends to be a more intermittent stream with dry reaches occurring more frequently (M.A. Chadwick,

personal observations). The lack of difference found in wood analog movements is perhaps more important than differences in leaf analog movements to overall organic matter export in these streams, because wood creates and maintains retentive habitats (Bilby 1981). With increased retention, more CPOM processing can occur (Wallace et al. 1982, Golladay et al. 1987, Cuffney et al. 1990, Jones and Smock 1991).

### Litter processing

Increased N availability in WBB+N did not alter system-level processing rates or benthic organic matter standing biomass relative to EBB, which supports previous findings of no difference between detritus processing in litterbags (Chapter 2). N availability, as both a stream solute and in foliar tissue, has been shown to alter detritus processing rates (Meyer and Johnson 1983, Webster and Benfield 1986, Chamier 1992, Suberkropp and Chauvet 1995, Suberkropp 1998, Robinson and Gessner 2000, Grattan and Suberkropp 2001, Royer and Minshall 2001). The lack of a measurable N-treatment effect on CPOM processing may be driven by a combination of factors including limitations by nutrients other than N (e.g., phosphorus), intermittent stream flow, or low pH.

Based on the ratios of inputs to standing biomass, American beech and maple litter processing rates were similar for both the treatment and reference stream. For maple leaves, processing rates using both the whole-system and litterbag methods gave similar results ( $\sim 0.006/\text{d}$ ). American beech processing rates based on input and biomass were an order of magnitude faster than rates based on litterbags. An explanation for the discrepancy between leaf types may

be due to underestimates of storage in debris dams or differences in the patterns of leaf loss and movement.

In order to understand the discrepancies between the whole-system and litter bag methods for estimating processing rates, I employed a simple heuristic model. Assuming that habitats are evenly spaced along each stream, the distance between debris dams would be ~10 m (i.e. ~300 m of stream with 20% of channel as debris dam with each debris dam 2 m long = 30 debris dams/stream spaced 10 m apart). Based on this estimate, movements of leaf analogs indicated that an average leaf would require < 45 days to encounter a debris dam. At a processing rate of 0.018/d (Table 3.5), American beech leaves would lose > 75% of their mass in 45 days. Clearly, American beech biomass is not lost from these streams that quickly (Fig. 3.4). This rapid loss rate is apparently an overestimate due to the use of habitat-weighted rather than habitat specific estimates of litter biomass. Further, the loss rate derived for American beech using habitat-weighted values (Table 3.6) reflects net movement of leaves into debris dams rather than loss due to processing. Estimates of leaf inputs and biomass in debris dams (i.e., where most leaves are stored) for American beech yield system-level processing rate of 0.002/d, which is similar to processing rates obtained from litter bags. In contrast to American beech, processing rates for maple litter estimated using both litter bags and the habitat-weighted whole system approach were comparable (~0.006/d), whereas rates for debris dams yielded rates that were too low (Table 3.6). The discrepancy between results for

**Table 3.6.** Leaf litter processing rates for American beech and maple in debris dams based on organic matter parameters. Catchment inputs are estimated as ((total daily stream inputs x % debris dam habitat)/10 debris dam per stream) x probability of retention in a debris dam (see Fig. 3.8). Stream inputs are estimated as (((total daily stream inputs) x (% non-debris dam habitat) x (% remaining after travel time to a debris dam))/10 debris dam per stream) x probability of retention in a debris dam (see Fig. 3.8). Total inputs are the sum of catchment inputs and stream inputs. System-level processing rates are calculated as inputs/standing biomass. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass.

	American beech		maple	
	WBB+N	EBB	WBB+N	EBB
average biomass (g AFDM/m <sup>2</sup> )	52	44	14	22
catchment inputs (g AFDM m <sup>-2</sup> d <sup>-1</sup> )	0.024	0.016	0.003	0.003
stream inputs (g AFDM m <sup>-2</sup> d <sup>-1</sup> )	0.075	0.068	0.008	0.009
estimated total inputs	0.099	0.084	0.011	0.012
input / biomass (d <sup>-1</sup> )	0.002	0.002	0.0008	0.0005

maple are likely due to faster processing in all habitats for this litter. The comparison of the results of these different approaches suggests that the slow processing rates for American beech result in significant breakdown after storage in debris dams, whereas the more rapid processing rates for maple result in significant breakdown prior to storage in debris dams. These results clearly show that information describing litter breakdown, transport, and storage must be integrated to better understand the processing dynamics of different litter species.

#### Organic matter dynamics

Organic matter inputs, export, and processing in WBB+N and EBB were not only similar to each other, but they are also similar to other forested, headwater streams (see Webster and Meyer 1997; Table 3.7). Total litter input showed similar patterns among these streams. WBB+N and EBB tended to have higher lateral and lower vertical input than the other sites. Turnover rates of coarse organic matter were intermediate at BBWM (~215 days) compared to other streams. However, turnover rates for all of these streams were the same order of magnitude (113 -375 days). The shortest turnover (113 days) occurred in Walker Branch, Tennessee which had the highest mean annual discharge and temperature. The longest turnover (375 days) occurred in the Bear Brook, New Hampshire where temperature and discharge were lower. It appears based on this small data set, that the N-deposition treatment at BBWM does not strongly alter overall organic matter dynamics and that physical factors (e.g., temperature

**Table 3.7.** Site characteristics and organic matter parameters for selected forested, headwater streams. WBB+N = treatment stream, EBB = reference stream, lat=latitude, temp=average annual stream temperature, ws=watershed area, prcp=annual precipitation, GPP=gross primary production, CBOM=coarse benthic organic matter, FBOM=fine benthic organic matter, turnover=CBOM/total coarse input. This table is modified from Webster and Meyer (1997).

=====									
site characteristics									
site	lat	order	temp (°C)	ws (ha)	prcp (cm)	slope (m/m)	flow (l/s)	width (m)	bed area (m <sup>2</sup> )
Satellite Branch, NC	35	1	12	8	172	0.200	2	1.34	375
EBB, ME	45	1	5	11	140	0.310	3	1.2	403
WBB+N, ME	45	1	5	10	140	0.300	3	1.2	410
Walker Branch, TN	36	1	13	38	140	0.035	12	3.5	1260
Bear Brook, NH	44	2	6	13	123	0.280	4	2.2	6377
Hugh White Creek, NC	35	2	12	61	188	0.150	19	2.76	8085
-----									

Table 3.7. continued.

site	inputs				standing biomass			coarse turnover
	GPP	direct	lateral	total litter	wood	CBOM	FBOM	turnover
		(g m <sup>-2</sup> y <sup>-1</sup> )			(g/m <sup>2</sup> )		(days)	
Satellite Branch, NC	3.8	492	137	629	6000	320	526	186
EBB, ME	0.8	285	441	726	243	420	187	211
WBB+N, ME	0.7	300	490	790	246	512	177	237
Walker Branch, TN	71.0	459	106	565	50	175	330	113
Bear Brook, NH	3.5	594	0	594	530	610	53	375
Hugh White Creek, NC	5.8	506	71	578	5446	213	166	135

and mean annual discharge) and geomorphology may have the greatest ability to explain differences in organic matter dynamics among these streams.

**Chapter 4:**

**RESPONSE OF STREAM INVERTEBRATE PRODUCTION TO**

**ATMOSPHERIC N DEPOSITION AND CHANNEL DRYING**



Above the weirs by C.L. Chadwick

## **Introduction**

The importance of first-order, intermittent streams has often been underestimated due to their small size. Recent studies, however, have shown that these streams can collectively comprise a majority of both total stream length and catchment area (Meyer and Wallace 2001). These systems are critical sources of water, organic matter, and nutrients to downstream reaches (Vannote et al. 1980, Takashi, Sidle, and Richardson 2002), and can support taxonomically unique and rich biological communities (Dieterich and Anderson 2000). First-order streams have also been shown to play an important role in N cycling (Peterson et al. 2001). Greater than 50% of inorganic N received by such streams can be retained or transformed. These processes can occur quickly (hours to minutes) and over small distances (10–100 meters of stream; Peterson et al. 2001). Elevated concentrations of dissolved N can lead to reduced storage and increased transport of N, potentially leading to eutrophication downstream (Peterson et al. 2001). This is of great concern in the northeastern United States where nitrate concentrations in streams draining forested catchments are typically higher than in other forested regions in the country due to atmospheric N deposition (see Aber et al. 1989).

N deposition and subsequent catchment acidification can alter stream ecosystem structure and function in many ways. These include altering detritus quantity and quality (Gilliam 1996, White 1999, Chapter 2), decreasing litter processing rates (Mulholland et al. 1987, Dubey et al. 1994), changing macroinvertebrate community structure (Smith et al. 1990, Guérol et al. 1995,

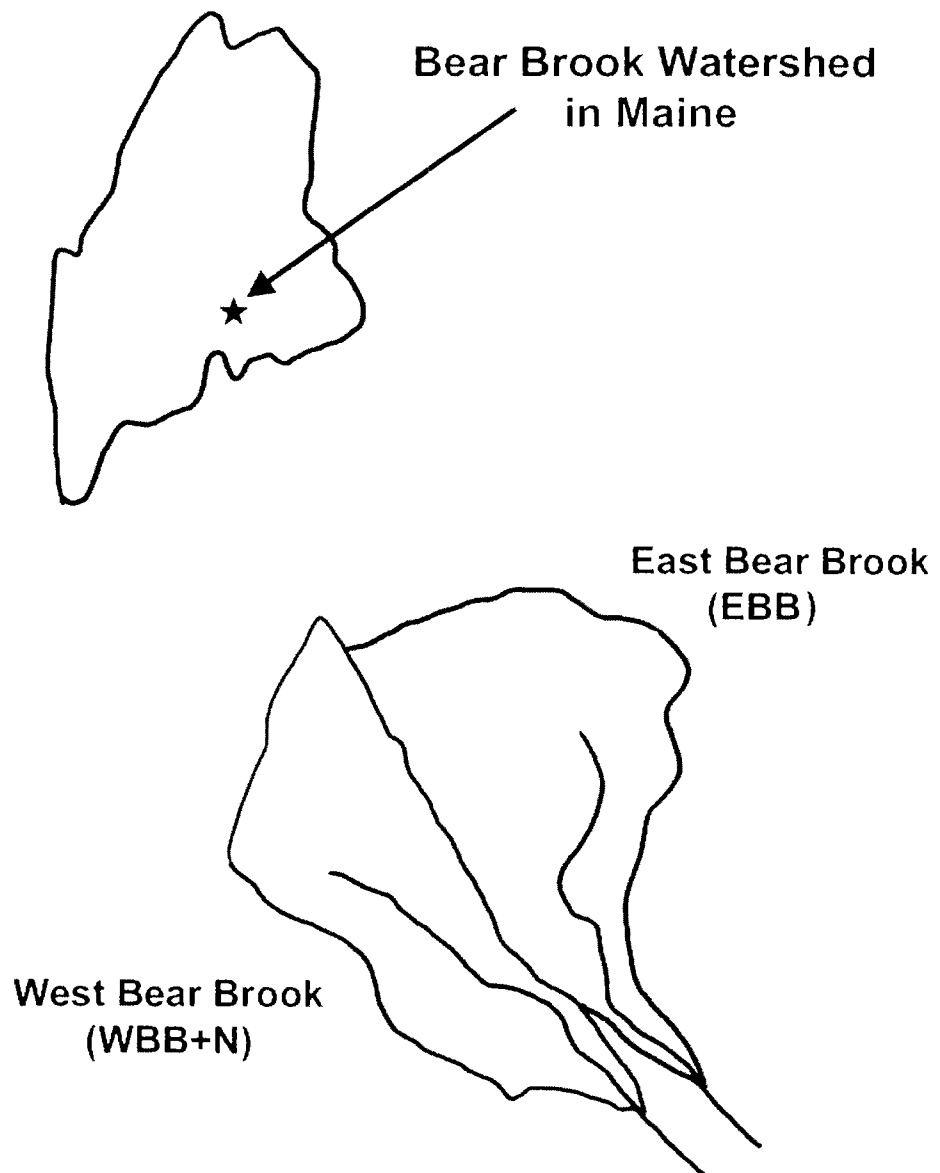
Griffith et al. 1995, Smock and Gazzera 1996) and secondary production (Hall et al. 1982, Weatherley et al. 1988, Kratz et al. 1994, Smock and Gazzera 1996). The effects of N-deposition on these processes can be further complicated by the diverse flow regimes found in first-order streams.

Headwater streams can be categorized based on their flow regimes. Perennial streams have year-round flow (i.e., complete flow permanence), intermittent streams cycle from flowing to non-flowing in predictable, climate-induced phases, and ephemeral streams only flow immediately following precipitation (Gordon et al. 1992). Intermittent streams show a wide range of permanence, from streams that completely dry at the surface for some period (e.g., Sycamore Creek, Arizona-Fisher et al. 1982, East and West Bear Brooks, Maine-personal observations) to streams that lose flowing water in only certain parts of the channel (e.g., Boulton and Lake 1992, Closs and Lake 1994, Feminella 1996). Physico-chemical and biological responses associated with both the drying and rewetting of stream channels only recently have gained more attention (Delucchi and Peckarsky 1989, Feminella 1996, Williams 1996, Dieterich et al. 1997, Paltridge et al. 1997).

Most studies of intermittent streams have dealt with the changes in biological community structure (Delucchi 1988, Closs and Lake 1994, Feminella 1996, Mollá et al. 1996, Dieterich et al. 1997, Paltridge et al. 1997) or species-specific responses to changes in stream flow (Williams et al. 1995, Jacobi and Cary 1996, Zamora-muñoz and Svensson 1996). A few studies have looked at functional responses in intermittent streams. For example, Richardson (1990)

found that intermittent streams can have reduced detritus processing rates compared to perennial streams due to a reduction in shredder richness and biomass. Bolton and Lake (1992) showed that storage of benthic organic matter increased during decreased flow periods and was associated with an increase in benthic detritivores. The timing of drying and rewetting can also “filter” resident fauna based on life histories (Delucchi and Peckarsky 1989, Dieterich and Anderson 1995). Consequently, food-web structure can vary due to the environmental constraints of drying (e.g., changes in proportions of predators [Closs and Lake 1994]). Drying can therefore affect stream secondary production by altering both community structure and resource availability.

A whole-catchment manipulation of N and S deposition was established at the Bear Brook Watershed in Maine (BBWM) to investigate the effects of atmospheric deposition on forest ecosystem function (Church 1999). BBWM consists of two forested catchments that are each drained by an intermittent stream (Fig. 4.1). East Bear Brook (EBB) is the reference catchment and West Bear Brook (WBB+N) is the treated catchment, which has received bimonthly additions of ammonium sulfate ( $\sim 1,800 \text{ eq ha}^{-1} \text{ y}^{-1}$ ; a 300% increase in N deposition) since November 1989. One of the early goals of this experiment was to evaluate existing catchment acidification models, and to evaluate N retention and transformations associated with the observed increased export of nitrate (see Norton et al. 1999 for more details). However, assessment of the effects on stream structure and function was not included in the early objectives of this project.

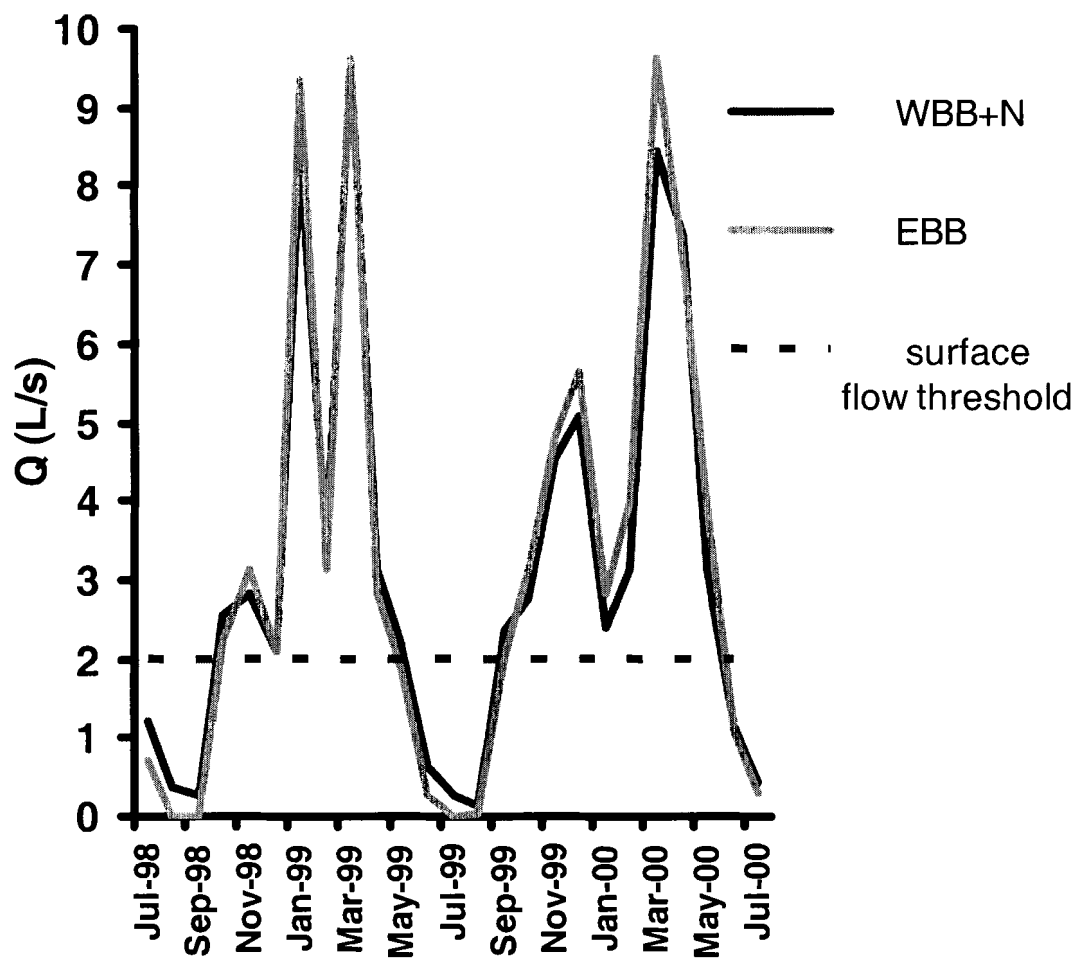


**Figure 4.1.** Map of Maine indicating the location the Bear Brook Watershed in Maine, and the contiguous study catchments. West Bear Brook is the treatment catchment (10.2 ha) and East Bear Brook is the reference catchment (10.7 ha).

The ongoing paired-catchment experiment at BBWM provides a unique opportunity to examine how atmospheric N depositions can affect invertebrates in an intermittent, headwater stream. The objective for this study was to determine: 1) if increased whole-catchment N deposition alters invertebrate secondary production in the intermittent streams at the Bear Brook Watershed in Maine, and 2) if stream permanence influences secondary production by altering community structure and resource availability

### **Study Site**

BBWM contains two first-order, intermittent streams that drain contiguous forested catchments (~10 ha) in Hancock County, southwestern Maine (Fig. 4.1). The catchments have similar soils, topography, aspect, gradient, and hydrology (see Norton et al. 1999 for a description of each catchment). American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), and red spruce (*Picea rubens*) are common in each catchment (White 1996). The ongoing N manipulation in the treated catchment (WBB+N) has decreased stream water pH, ANC and concentrations of dissolved organic carbon. At the same time, specific conductance and concentrations of nitrate, calcium, magnesium, and aluminum have increased (Norton et al. 1999). Both streams have comparable physical structure and similar inputs, standing stocks, and processing rates of organic matter (Chapter 3). Surface flow usually occurs from November to May. Streams are ice covered in winter (personal observations). During this study (November 1998–July 2000), the streams showed similar patterns in discharge (Fig. 4.2) and both lost surface flow for



**Figure 4.2.** Mean monthly discharge for West and East Bear Brook. The flow necessary for surface water flow (i.e., flow threshold - the gray dotted line) is based on observations of each stream channel above the v-notch weir used to measure discharge. WBB+N = treatment stream, EBB = reference stream, Q = discharge.

extended time periods. In 1999, both streams lost surface flow by the middle of May. In 2000, both streams continued to flow until July. WBB+N had a total of 95 dry days with the longest consecutive dry period lasting for 22 days, while EBB was dry for a total of 174 days with the longest consecutive dry period lasting for 60 days. Based on these observations and the continuous record of stage height, the threshold discharge to maintain surface flow is ~2 L/s (Fig. 4.2).

## **Methods**

Benthic macroinvertebrates were sampled approximately monthly from November 1998 - May 1999 and October 1999 - July 2000 using a Surber sampler (0.9 m<sup>2</sup> with 250 $\mu$ m mesh). Three samples were taken from each of the dominant habitat types present in each stream (bedrock, debris dams, riffle/runs, and pools). Bedrock habitats were sampled only in the first year. Samples were taken from randomly assigned locations and preserved in ~5% formaldehyde. Sample processing included removal of all large organic matter (e.g., leaves, wood, moss), elutriation of inorganics, and separation of the remaining material into 4 size fractions (>2mm, 1–2mm, 0.5–1mm, and 0.25–0.5 mm). For large samples, fractions were split (1/32–1/2) using a Folsom plankton splitter. All organisms were removed by hand under magnification, identified to the lowest possible taxonomic level, and measured to the nearest 1mm. Ash free dry mass (AFDM) was calculated from length-weight regression equations (Benke et al. 1999).

Production was estimated using one of three methods. The instantaneous growth method was used when a cohort could be followed through time and

growth rates could be estimated (Benke 1984, 1993). The size-frequency method was used when a sufficient population size was present, but cohorts could not be followed (Benke 1984, 1993). For this method, cohort production intervals equivalent to the period when flowing water was present were assumed. For rare taxa, production was estimated by multiplying mean annual biomass by an assumed annual biomass turnover rate of 5 (annual production/biomass; P/B; Waters 1977). Production was estimated from all habitats and combined to produce a habitat-weighted value. Confidence intervals were calculated by bootstrapping for all but rare taxa (Huryn 1996). Control of type II error was achieved by designating an  $\alpha$  level of 0.10 prior to the start of this study. Statistical comparisons between streams were made by comparing 90% confidence intervals, with non-overlapping confidence intervals indicating differences.

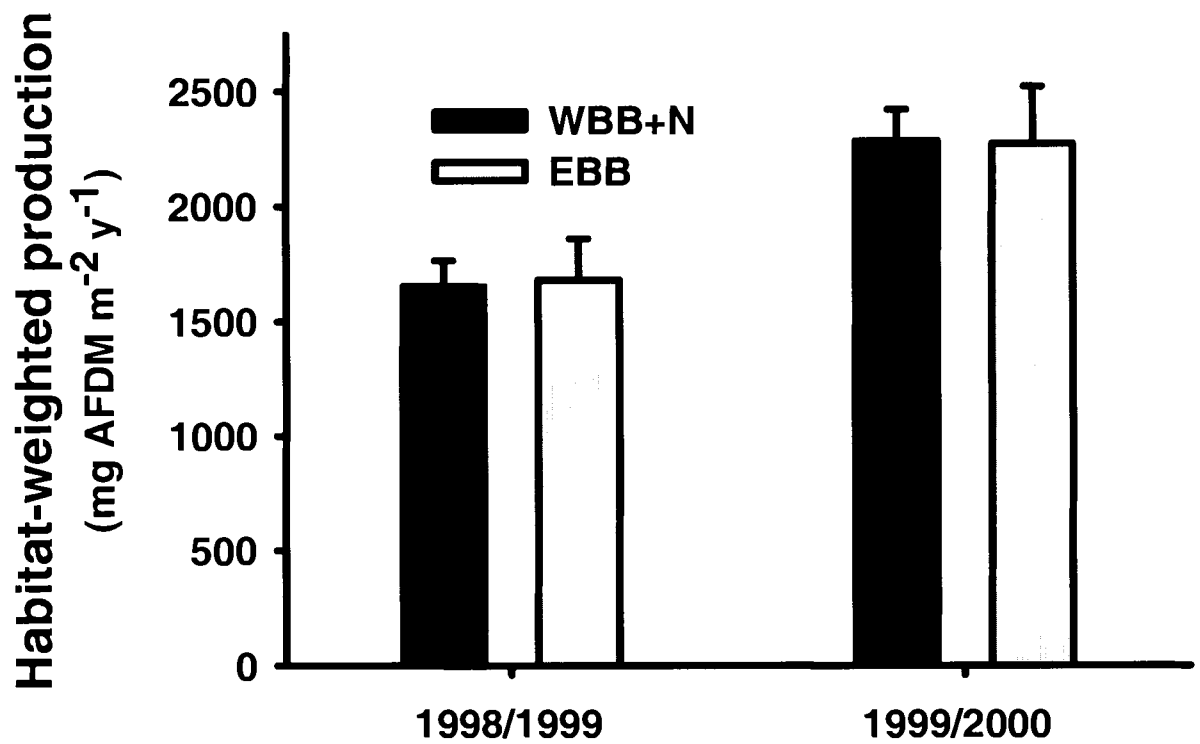
Macroinvertebrate community structure was evaluated using canonical correspondence analysis (CCA; ter Braak 1986). CCA is a multivariate technique used to relate community composition to gradients in environmental variables. I conducted a CCA with taxon-specific production estimates as the community matrix and stream and year, coded as dummy variables, in the environmental matrix. These dummy variables were used to assess if observed gradients in stream permanence (EBB in 1998/1999 - low stream permanence, WBB+N 1998/1999 and EBB 1999/2000 - moderate stream permanence, and WBB+N 1999/2000 high stream permanence) were associated with changes in community structure and production.

## Results

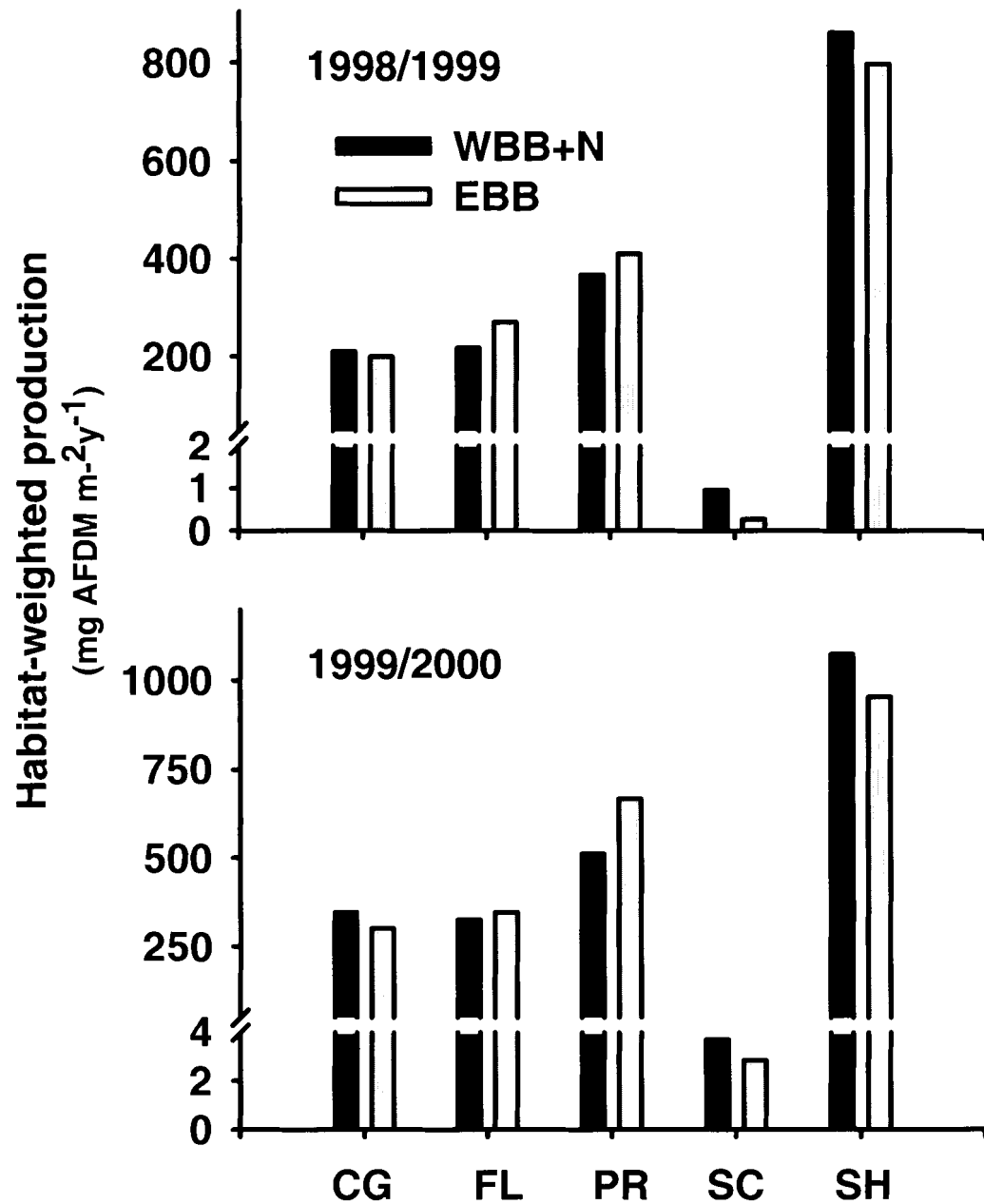
Total habitat-weighted production was remarkably similar between streams, but varied between years (Fig. 4.3). The distribution of production among functional groups was also similar in each stream. Shredders accounted for 50% of production, followed by predators (~25%), filterers (~15%), collectors (~13%), and scrapers (<1%; Fig. 4.4). Average biomass ranged from 383 - 495 mg AFDM/m<sup>2</sup>, with the lowest value occurring in WBB+N in 1998/1999 (Fig. 4.5A). Annual P/Bs were 3.9 (EBB 1998/1999), 4.3 (WBB+N 1998/1999), and 4.6 (both streams 1999/2000). Total richness ranged from 39 to 41 taxa and was similar between streams and years (Fig. 4.5B). Density was also similar between streams, and variable between years. The greatest densities occurred in 1999/2000 (Fig. 4.5C)

### Taxonomic composition

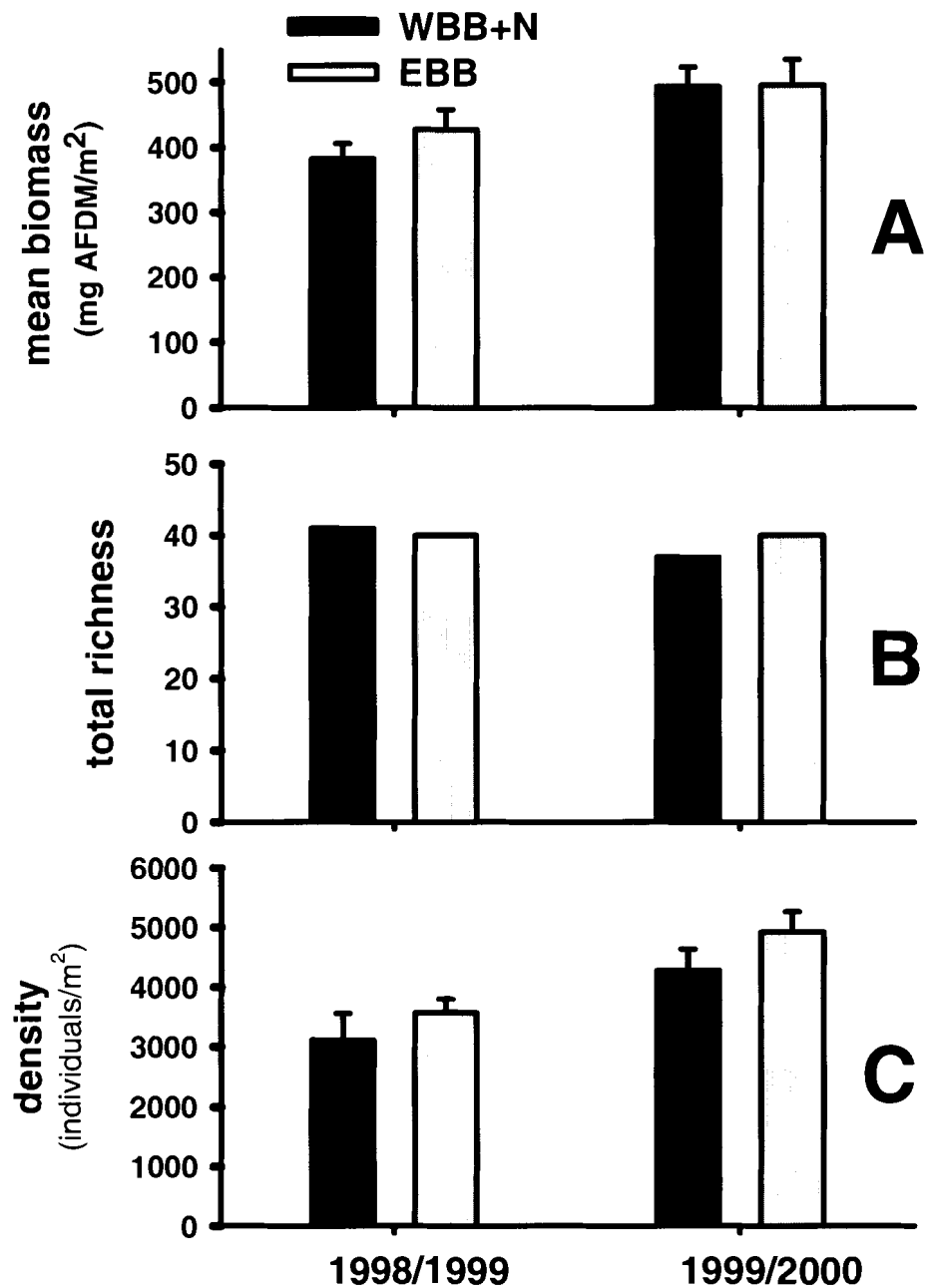
*WBB+N* – In WBB+N, the shredder *Leuctra* had the highest production in both years (1998/1999: 236 mg AFDM m<sup>-2</sup>y<sup>-1</sup> [16% of annual P]; 1999/2000: 338 mg AFDM m<sup>-2</sup>y<sup>-1</sup> [15% of annual P], Table 4.1). Seventeen taxa in 1998/999 and 13 taxa in 1999/2000 had production > 1% of total production which corresponded to > 25 mg AFDM m<sup>-2</sup>y<sup>-1</sup> per taxon (Table 4.1). In 1998/1999, these taxa consisted of 2 collectors, 3 filterers, 4 predators, and 8 shredders (Table 4.2). In 1999/2000, these taxa included 3 collectors, 2 filterers, 3 predators, and 5 shredders (Table 4.2).



**Figure 4.3.** Total habitat-weighted production (+ 90% CI) for the Bear Brook Watershed in Maine in 1998/1999 and 1999/2000. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass.



**Figure 4.4.** The distribution of production among functional groups for West and East Bear Brooks in 1998/1999 and 1999/2000. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass, CG = collectors, FL = filterers, PR = predators, SC = scrapers, SH = shredders..



**Figure 4.5.** A) Average total biomass (+ 90% CI), B) total richness, and C) density (+ 90% CI) for West and East Bear Brooks in 1998/1999 and 1999/2000. WBB+N = treatment stream, EBB = reference stream, AFDM = ash-free dry mass.

Habitat-weighted average biomass for different taxa ranged from 4.9 to 51.2 mg AFDM/m<sup>2</sup> in 1998/1999 and 8.5 to 73.9 mg AFDM/m<sup>2</sup> in 1999/2000 (Table 4.1). *Leuctra* had the highest biomass in both years. Mean densities ranged from <1 to 1,103 individuals/m<sup>2</sup> in 1998/1999 and <1 to 1,362 individual/m<sup>2</sup> in 1999/2000 (Table 4.1). For taxa that contributed > 1% of total secondary production, Orthoclaadiinae had the highest and *Pycnopsyche* had the lowest densities in both years.

*EBB* – In EBB, the shredder *Paranemoura perfecta* had the highest production in 1998/1999 (217 g AFDM m<sup>-2</sup>y<sup>-1</sup> [13% of annual P]) and the predator *Rhyacophila* had the highest production in 1999/2000 (397 g AFDM m<sup>-2</sup>y<sup>-1</sup> [17% of annual P]; Table 4.1). In both years, 17 taxa had production > 1% of overall production which corresponded to > 26 mg AFDM m<sup>-2</sup>y<sup>-1</sup> per taxa in 1998/1999 and 35 mg AFDM m<sup>-2</sup>y<sup>-1</sup> per taxa in 1999/2000 (Table 4.1). In 1998/1999, these taxa consisted of 3 collectors, 2 filterers, 5 predators, and 7 shredders 7 (Table 4.2). In 1999/2000, these taxa included 3 collectors, 3 filterers, 4 predators, and 7 shredders (Table 4.2).

Habitat-weighted average biomass for different taxa ranged from 4.1 to 73.0 mg AFDM/m<sup>2</sup> in 1998/1999 and 7.1 to 69.3 mg AFD/m<sup>2</sup> in 1999/2000 (Table 4.1). *Paranemoura perfecta* had the highest biomass in 1998/1999. Orthoclaadiinae had the highest biomass in 1999/2000. Mean densities ranged from <1 to 945 individuals/m<sup>2</sup> in 1998/1999 and <1 to 2,306 individual/m<sup>2</sup> in 1999/2000 (Table 4.1). In both years Orthoclaadiinae had the highest densities.

**Table 4.1.** Average abundance (N=ind/m<sup>2</sup>), biomass (B=mg AFDM/m<sup>2</sup>), and production (P=mg AFDM m<sup>-2</sup> y<sup>-1</sup>) for taxa sampled from the treatment (WBB+N) and reference (EBB) streams at the Bear Brook Watershed in Maine. Values underneath and in italics are 90% confidence intervals. FFG is functional feeding group with CG = collector gather, FL = filterers, PR =predators, SC=scrapper, and SH=shredders. \* indicates taxonomy higher than the Order level. AFDM = ash-free dry mass.

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WBB+N / EBB								
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FFG	Order	Taxon	1998 – 1999 N	B	P	1999 – 2000 N	B	P
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CG	Ephemeroptera	<i>Eurylophella</i>	-- / 1.0	-- / 0.04	-- / 0.22	0.3 / 1.5	0.02 / 0.28	0.11 / 1.42
	Trichoptera	<i>Oligostomas</i>	-- / 0.01	-- / 0.04	-- / 0.18	-- / --	-- / --	-- / --
	Diptera	<i>Antocha</i>	0.4 / --	0.16 / --	0.79 / --	-- / --	-- / --	-- / --
		<i>Tipula</i>	0.5 / 0.1	1.16 / 0.34	5.81 / 0.84	2.3 / 0.2	1.40 / 0.04	7.00 / 0.21
		Orthoclaadiinae	1103 / 945 426 / 157	39.8 / 35.4 14.5 / 6.7	132.5 / 119.8 61.2 / 22.0	1362 / 2306 205 / 309	39.1 / 69.3 6.7 / 11.3	138.7 / 187.3 20.3 / 28.8
		Tanytarsini	150 / 368 90 / 91	3.3 / 6.6 2.2 / 2.3	13.1 / 38.6 8.9 / 23.2	519 / 261 258 / 54	12.3 / 11.3 5.3 / 3.3	65.1 / 48.3 28.2 / 12.8
		Chironomidae	3.2 / 7.8	0.01 / 1.00	0.07 / 5.01	3.2 / 8.7	0.03 / 0.19	0.16 / 0.93
	Oligochaeta*		105 / 77	10.9 / 7.1	54.5 / 35.4	233 / 132	27.2 / 12.6	135.9 / 62.9

Table 4.1. continued

=====								
WBB+N / EBB								
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FFG	Order	Taxon	1998 – 1999 N	B	P	1999 – 2000 N	B	P
-----								
FL	Trichoptera	<i>Wormaldia</i>	2.8 / 19.7 -- / 12.7	2.01 / 3.87 -- / 2.06	8.18 / 15.63 -- / 7.72	14.0 / 25.1 -- / --	6.16 / 10.12 -- / --	30.9 / 50.8 -- / --
		<i>Homoplectra</i>	6.2 / 1.3	22.2 / 5.33	111.0 / 26.6	8.2 / 10.3	31.4 / 22.4	157.1 / 112.1
		<i>Parapsyche</i>	3.4 / < 0.1	12.01 / 0.01	54.05 / 0.05	0.7 / 0.4	2.12 / 1.70	10.3 / 8.5
		<i>Prosimulium</i>	48 / 130 20 / 34	9.2 / 31.8 2.9 / 9.6	44.6 / 130 15.0 / 50.5	148 / 281 42.4 / 68.8	29.6 / 40.2 11.0 / 12.7	128.2 / 175.1 42.4 / 49.3
PR	Plecoptera	<i>Sweltsa</i>	7.2 / 7.3	2.4 / 6.5	12.0 / 20.8	3.2 / 7.6	1.0 / 3.1	5.1 / 15.7
	Trichoptera	<i>Polycentropus</i>	-- / 13.4 -- / 12.5	-- / 19.1 -- / 18.5	-- / 97.9 -- / 90.8	0.8 / 3.4 -- / --	0.7 / 7.1 -- / --	3.6 / 35.4 -- / --
		<i>Rhyacophila</i>	19.2 / 45 7.6 / 12.4	11.0 / 37.6 3.3 / 12.8	68.9 / 190.1 24.0 / 102.3	48.9 / 3.7 9.5 / 11.6	36.6 / 49.2 9.4 / 20.4	264.0 / 396.9 74.4 / 201.4
	Coleoptera	<i>Hydaticus</i>	2.5 / 0.4	1.8 / 1.7	9.0 / 8.2	1.5 / --	0.9 / --	4.7 / --
	Diptera	<i>Dicranota</i>	8.0 / 38.3 2.6 / 8.5	2.0 / 6.7 0.8 / 1.9	12.4 / 42.0 6.1 / 14.8	35.6 / 25.7 15.9 / 7.0	8.5 / 3.9 4.3 / 1.63	37.9 / 23.3 17.0 / 11.5
		<i>Hexatoma</i>	1.4 / 0.9	1.0 / 1.0	5.01 / 2.59	2.8 / 8.5	0.7 / 1.3	3.6 / 6.5
		<i>Limnophila</i>	0.5 / --	0.2 / --	0.8 / --	-- / --	-- / --	-- / --
		<i>Oreogeton</i>	4.9 / 4.1	2.6 / 1.4	15.6 / 7.7	10.3 / 17.1	2.8 / 3.0	14.2 / 14.8
		<i>Pedicia</i>	5.7 / 6.6 2.3 / 3.8	16.4 / 7.7 8.9 / 1.2	89.2 / 41.4 49.0 / 6.2	4.3 / 5.0 -- / --	19.9 / 14.0 -- / --	99.5 / 70.1 -- / --

Table4.1. continued

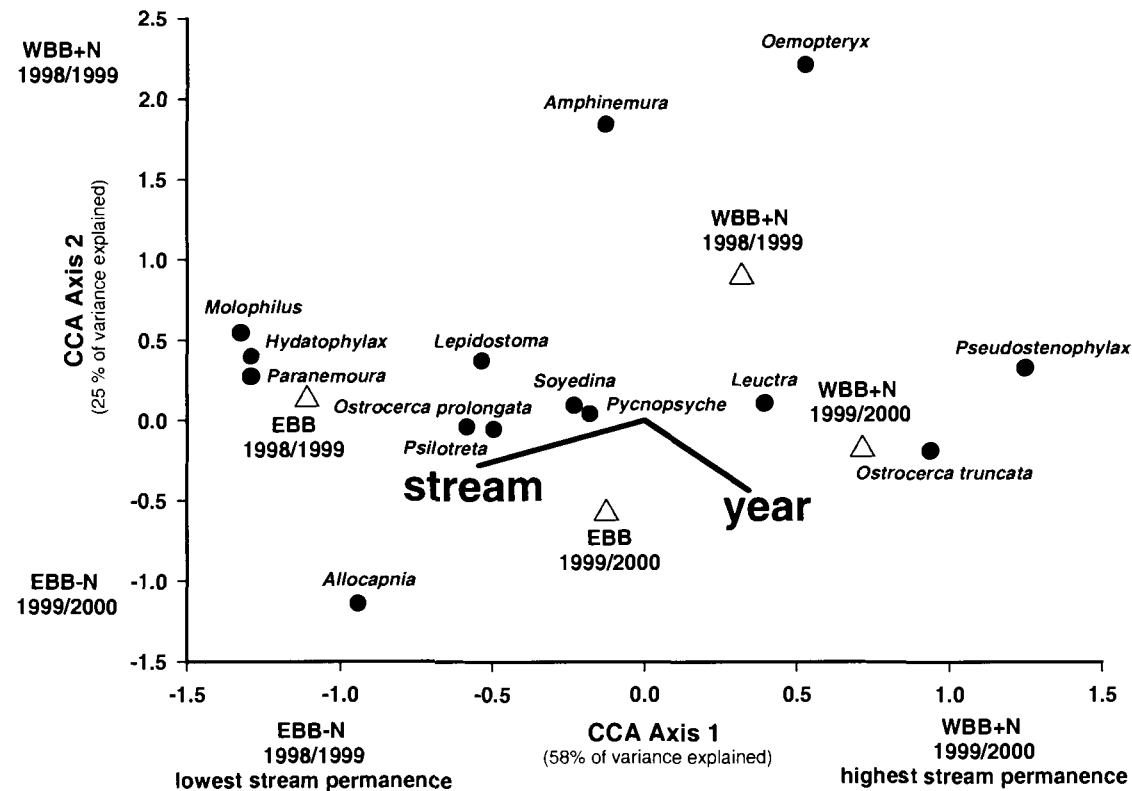
WBB+N / EBB								
FFG	Order	Taxon	1998 – 1999 N	B	P	1999 – 2000 N	B	P
SC		<i>Probezzia</i>	2.3 / 1.8	1.0 / 0.4	4.8 / 2.2	11.2 / 4.8	1.0 / 1.1	5.2 / 5.7
		Tanypodinae	135 / 141 29.6 / 36.0	19.1 / 16.3 4.3 / 4.9	95.7 / 97.7 22.3 / 29.8	91 / 113 25.5 / 28.4	6.4 / 7.1 2.1 / 2.0	18.2 / 27.8 5.4 / 11.5
		Chilopoda	0.3 / -- 12.7 / 7.6	4.6 / 1.6 2.62 / 1.10	23.0 / 7.7 12.0 / 10.0	1.0 / 1.3 -- / --	4.6 / 7.5 -- / --	23.2 / 37.7 -- / --
		Hydracarina*	287 / 406	0.4 / 0.5	1.9 / 2.7	508 / 501	0.6 / 0.6	3.2 / 3.2
		Turbellaria*	0.5 / 12.7	0.04 / 1.6	0.2 / 7.8	-- / 18.1	-- / 2.2	-- / 10.8
	Trichoptera	<i>Neophylax</i>	-- / 0.1	-- / 0.01	-- / 0.2	-- / 5.6	-- / 0.5	-- / 2.6
		<i>Palaeagapetus</i>	0.8 / < 0.1	0.16 / < 1	1.0 / 0.02	2.7 / 1.2	0.7 / 0.3	3.7 / 0.3
	Coleoptera	<i>Ouliminous</i>	-- / 0.1	-- / 0.02	-- / 0.08	-- / --	-- / --	-- / --
	Plecoptera	<i>Amphinemura</i>	102 / 52 41 / 19	10.4 / 2.4 5.1 / 0.9	45.5 / 11.4 23.9 / 4.7	5.2 / 15.2 -- / --	0.6 / 1.5 -- / --	2.8 / 7.5 -- / --
		<i>Ostrocerca prolongata</i>	166 / 365 36 / 77	25.8 / 49.4 5.6 / 10.9	64.0 / 104.1 14.4 / 49.7	118 / 222 36 / 26	8.2 / 24.5 2.4 / 3.6	45.2 / 112.9 17.1 / 20.4
SH		<i>Ostrocerca truncata</i>	207 / 6 44 / 3	33.1 / 2.5 6.0 / 1.3	105.7 / 5.6 29.5 / 4.2	470 / 303 70 / 38	78.9 / 40.3 14.0 / 5.4	256.2 / 129.6 68.2 / 23.3
		<i>Paranemoura</i>	123 / 568 27 / 95	17.7 / 73.0 5.1 / 11.1	48.5 / 217.3 18.0 / 64.5	68 / 148 11 / 27	6.9 / 28.2 1.1 / 6.9	21.2 / 90.8 5.7 / 25.7

Table 4.1 continued

		WBB+N / EBB							
FFG	Order	Taxon	1998 – 1999		1999 – 2000				P
			N	B	N	P	N	B	
		<i>Soyedina</i>	25 / 35 16 / 12	3.4 / 5.9 1.5 / 1.8	13.4 / 36.1 7.0 / 13.0	28 / 31 4 / 13	5.6 / 4.4 2.1 / 1.3	32.4 / 20.2 14.2 / 6.5	
		<i>Oemopteryx</i>	0.7 / --	2.9 / --	14.4 / --	0.2 / 1.3	0.5 / 0.2	2.3 / 0.9	
		<i>Allocapnia</i>	2.0 / 10 -- / --	0.6 / 3.3 -- / --	3.0 / 16.3 -- / --	1.1 / 47 -- / 11	0.4 / 8.4 -- / 2.0	1.9 / 36.3 -- / 10.4	
		<i>Leuctra</i>	485 / 231 93 / 53	51.2 / 23.8 9.3 / 5.70	262.2 / 106.9 54.3 / 31.5	350 / 329 94 / 106	73.9 / 56.7 19.5 / 28.7	337.9 / 258.7 72.1 / 139.3	
	Trichoptera	<i>Lepidostoma</i>	42 / 35 15 / 13	4.9 / 4.1 2.7 / 1.9	26.2 / 28.2 11.4 / 13.9	15 / 14 7 / 3	1.3 / 4.2 0.5 / 1.2	10.7 / 26.1 4.6 / 9.3	
		<i>Psilotreta</i>	2.1 / 3.1	4.2 / 1.6	15.9 / 6.3	-- / 1.9	-- / 4.5	-- / 22.4	
		<i>Hydatophylax</i>	5.0 / 7.9	6.3 / 30.2	15.8 / 75.6	0.7 / 3.4	1.5 / 3.6	9.5 / 17.8	
		<i>Pseudostenophylax</i>	5.3 / --	21.1 / --	105.3 / --	9.6 / 0.8	44.3 / 8.6	221.7 / 43.0	
		<i>Pycnopsycha</i>	1.8 / 2.0	31.1 / 30.7	136.7 / 135.1	0.9 / 1.8	26.1 / 36.7	130.4 / 183.7	
	Diptera	<i>Limonia</i>	0.1 / --	0.3 / --	1.6 / --	-- / --	-- / --	-- / --	
		<i>Molophilus</i>	2.0 / 4.4	0.5 / 2.6	2.3 / 13.1	0.6 / 1.2	0.5 / 0.7	2.5 / 3.6	

**Table 4.2.** Percent of total production P for taxa sampled from the treatment WBB+N and reference EBB streams at the Bear Brook Watershed in Maine. FFG is functional feeding group with CG = collector gather FL = filterers PR =predators SC=scraper and SH=shredders. \* indicates taxonomy higher than the Order level.

		WBB+N		EBB	
		1998/1999	1999/2000	1998/1999	1999/2000
FFG	Taxa	% of P	Taxa	% of P	Taxa
CG	Orthocladinae	8	Orthocladinae	6	Orthocladinae
	Oligochaeta*	3	Oligochaeta*	6	Oligochaeta*
			Tanytarsini*	3	Tanytarsini
FL	Homoplectra	7	Homoplectra	7	Prosimulium
	Parapsyche	3	Prosimulium	6	Homoplectra
	Prosimulium	3			Wormaldia
PR	Tanypodinae*	6	Rhyacophila	12	Rhyacophila
	Pedicia	5	Pedicia	4	Pedicia
	Rhyacophila	4	Dicranota	2	Chilopoda*
	Clinocera	2			Polycentropus
					Pedicia
SH	Leuctra	16	Leuctra	15	Leuctra
	Pycnopsyche	8	Ostrocerca truncata	11	Pycnopsyche
	Ostrocerca truncata	6	Pseudostenophylax	10	Ostrocerca truncata
	Pseudostenophylax	6	Pycnopsyche	6	Ostrocerca prolongata
	Ostrocerca prolongata	4	Ostrocerca prolongata	2	Paranemoura perfecta
	Paranemoura perfecta	3			Pseudostenophylax
	Amphinemura	3			Allocapnia
	Lepidostoma	2			



**Figure 4.6.** The taxa-environment ordination from the canonical correspondence analysis. Canonical axis 1 and 2 accounted for 83% of the variance. Most of the variance in taxa production is represented in axis 1 (58%), which shows a gradient from low stream permanence to high stream permanence. For clarity, only shredders are shown (filled circles). Streams are represented as triangles. WBB+N = treatment stream, EBB = reference stream.

For taxa contributing > 1% to overall production, *Homoplectra* had the lowest densities in 1998/1999 and *Pseudostenophylax* had the lowest densities in 1999/2000.

### Canonical correspondence analysis

The total variance associated with taxon-specific macroinvertebrate production ordination was small (inertia; ter Braak 1986). This was expected, however, due to the similarities among habitats in both streams. Canonical axes 1 and 2 accounted for 83% of the variance in the taxa-environment ordination (Fig. 4.6). Axis 1 (eigenvalue=0.172) explained 58% of the variance and separated taxa along a gradient from EBB 1998/1999 to WBB+N 1999/2000. This gradient represents the lowest stream permanence (EBB 1998/1999) to the highest stream permanence (WBB+N 1999/2000). Axis 2 (eigenvalue =0.073) explained 25% of the variance and separated taxa along a gradient from EBB 1999/2000 to WBB+N 1998/1999. Axis 2 was strongly influenced by taxa that either did not occur in both streams (e.g., *Oemopteryx*) or had higher production in one of the streams (e.g., *Allocapnia*).

### **Discussion**

My production estimates are among the lowest values reported (1.9 and 2.6 g dry mass (dry mass)  $\text{m}^{-2} \text{y}^{-1}$  1998/1999 and 1999/2000, respectively; dry mass values are standardized based on Waters 1977). Production for headwater streams tends to vary from 1-10 g DM  $\text{m}^{-2} \text{y}^{-1}$  and few are < 3 g DM  $\text{m}^{-2} \text{y}^{-1}$

(Benke 1993, Huryn and Wallace 2000 and references within, Buffagni and Comin 2000, Hall et al. 2001, Woodcock 2002). Factors that reduce biomass, growth rates or both contribute to low secondary productivity (Huryn and Wallace 2000). These factors include low stream temperatures (Harvey et al. 1998), food limitation (Smock et al. 1985, Wallace et al. 1999, Buffagni and Comin 2000, Hall et al. 2001), poor water quality (Smock et al. 1985, Woodcock 2002), and hydraulic disturbance (Buffagni and Comin 2000, Hall et al. 2001). Factors that may be responsible for the similarities I found in invertebrate secondary production between WBB+N and EBB, as well as the lack of any apparent treatment effect, include acidic and oligotrophic stream conditions, similar levels of food availability (e.g., detritus biomass), similar hydraulic disturbance regimes, and summer channel drying.

#### Acidic and oligotrophic stream conditions

Secondary production was not affected by the whole-catchment manipulation, even though there are marked differences in water quality (e.g., pH, nitrate, calcium, magnesium, aluminum). During this study, both streams were acidic, with pH generally < 5.8. These conditions likely limit acid-sensitive taxa and lessen acidification impacts due to the treatment. Similarly, concentrations of dissolved P are typically < 5  $\mu\text{g/L}$  (unpublished data). Consequently, P rather than N is likely the limiting nutrient for ecosystem productivity in both streams. The similar and low invertebrate productivity measured in each stream are likely driven by low pH and nutrient availability which work together to limit community productivity (Huryn and Wallace 2000).

Low pH has been shown to change macroinvertebrate community structure (Smith et al. 1990, Guérol et al. 1995, Griffith et al. 1995, Smock and Gazzera 1996). For example, both streams at BBWM have a conspicuous lack of acid-sensitive mayfly taxa. Several mayfly taxa (e.g., Baetidae, Leptophlebiidae, Siphonuridae) have been reported from intermittent streams elsewhere (Clifford 1966, Delucchi and Peckarsky 1989, Dieterich and Anderson 1995, Feminella 1996) which suggests that acidic conditions may prohibit these taxa from occurring in either stream at BBWM. Similarly, scrapers are absent from these systems. The lack of scrapers is presumably due to low levels of autotrophic productivity in each stream (Chapter 3).

Decreased growth rates, due to increased metabolic demands associated with acidic conditions, food limitations, and/or poor food quality may also result in low levels of secondary production. Reduced microbial activity on stream detritus has been observed in acidic and nutrient poor conditions (Mulholland et al. 1987, Palumbo et al. 1987, Groom and Hildrew 1989, Maltby and Booth 1991, Chamier and Tipping 1997, Suberkropp 1998). A decrease in microbial activity could result in decreased food quality, and subsequently reduce invertebrate growth rates, especially for shredders (i.e., Griffith et al. 1993, Thomsen and Friberg 2002). However, no evidence of lower microbial activity in either stream for both maple and American beech detritus was found (Chapter 1). Further, differences in taxon-specific production between streams appear to be driven mainly by differences in biomass and not growth (Table 4.1). For example,

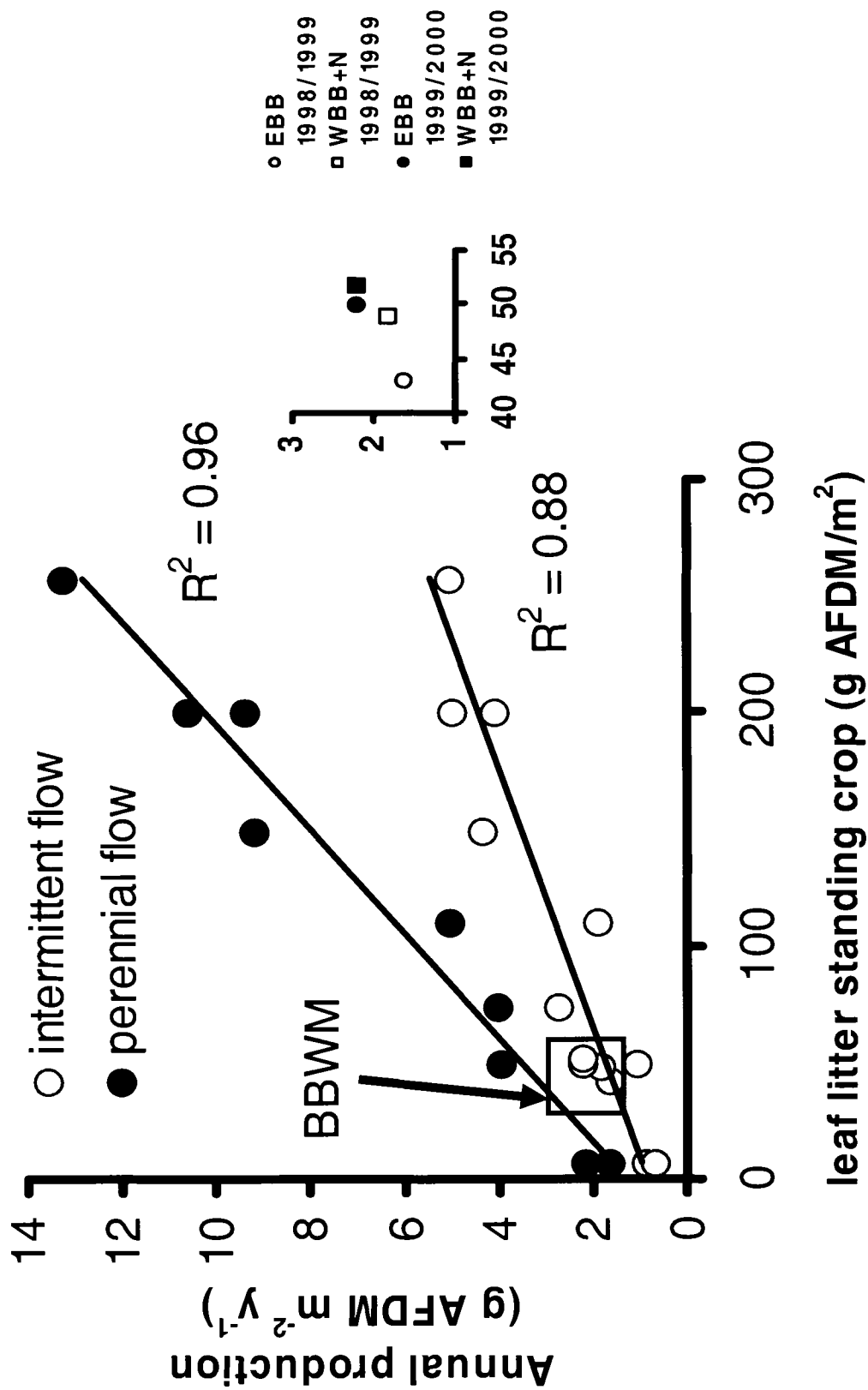
*Leuctra* production ranged from 107–338 g AFDM m<sup>-2</sup> y<sup>-1</sup> while biomass ranged from 24–74 g AFDM/m<sup>2</sup>, but P/B varied little between streams (~ 5).

#### Detritus availability and quality

The productivity of forested, headwater streams is “donor-controlled” (sensu Wallace et al. 1997) due to reliance of consumer production on allochthonous organic matter. For example, Wallace et al. (1999) showed that levels of invertebrate productivity are positively correlated with the availability of stream detritus. Similarly, Hall et al. (2001) found that invertebrate productivity was limited by the availability of detrital resources. The availability of stream detritus is similar between the 2 streams at BBWM (Chapter 3), so similar levels of secondary production between these streams are not surprising. In fact, the increase in production between years is associated with an increase in the detrital biomass found in each stream (Fig. 4.7 inset graph) as would be predicted from previous studies (Wallace et al. 1999, Hall et al. 2001) .

Even though detrital biomass is similar to other headwater streams (Chapter 3), secondary production may still be limited because of low food quality. The dominant leaf source for both streams is American beech (*Fagus grandifolia*; Chapter 3) which is a refractory food source based on its slow decomposition rates. For example, Dangles and Guérold (1998) found that beech leaves in acidic stream conditions experience only a ~5% mass loss over a 225 day period. At BBWM I found similarly slow processing rates (~0.002/day; Chapter 2). The refractory quality of this detritus could certainly limit shredder productivity, and may limit system productivity.





A reduction in shredder productivity could lead to a reduction in collector productivity. In headwater streams, shredders and collectors are predicted to dominate headwater reaches due to direct links to CPOM resources ((e.g., feeding on detritus; Vannote et al. 1980). For example, Huryn and Wallace (1989) found that trichopteran shredders accounted for ~30% of total secondary production, while trichopterans feeding on FPOM accounted for ~40% of total annual secondary production in a forested headwater stream. Similarly, Dieterich et al. (1997) showed that in a forested intermittent stream, ~70% of the emerging insects (by biomass) were shredders and collectors and that in this system shredders emerged before collectors. To further elucidate this pattern, laboratory experiments showed that shredder presence could increase collector growth (Dieterich et al. 1997). This linking of shredder activities to collector feeding has major implications for the total metabolic importance of CPOM processing. In a whole stream litter exclusion experiment, Wallace et al. (1997) showed a direct link between CPOM availability and shredders and FPOM feeding organisms. WBB+N and EBB are dominated by shredders (Fig. 4.4), so the similarities in detritus quantity and quality (see Chapter 3) in each stream may regulate secondary productivity (i.e., bottom-up control).

#### Stream channel drying

Drying influences invertebrate community structure by filtering out taxa that lack appropriate strategies (i.e., desiccation resistance, diapause, access to refugia) to persist through dry periods (Delucci 1988, Richardson 1990, Feminella 1996, Rincón and Cressa 2000, Dieterich and Anderson 2000, Meyer

and Meyer 2001). Shifts in taxon-specific production in WBB+N and EBB appear to be based on differences in stream permanence (Fig. 4.6). For example, nemourid stoneflies had higher production in the most intermittent conditions, while *Leuctra* showed highest production with high permanence. To further investigate how changes in community structure due to stream drying affect invertebrate secondary production, I re-estimated invertebrate production for 4 perennial, headwater streams (C55 and C53 Coweeta Hydrologic Laboratory, NC – Wallace et al. 1999; Bear Brook and Hubbard Brook, NH – Hall et al. 2001) by excluding all taxa with life-histories that would prohibit their success in intermittent streams. Additionally, I assumed that production for remaining taxa would not be altered by removal of perennial stream taxa from the community (e.g., no competition, etc.). Using the re-estimated invertebrate production values, I then assessed the relationship of production to levels of detrital resources. I found that the linear relationship was similar to one found for perennial streams (Fig. 4.7,  $R^2=0.89$ ). Further, the trend line passed directly through the production estimates for WBB+N and EBB. This evidence suggests that channel drying could be a primary factor responsible for low levels of invertebrate production measured at BBWM. Further, the strong pressure of drying may act to override any effects because of atmospheric N deposition.

The goal of this study was to assess the effect of atmospheric N deposition on stream invertebrate production in a first-order, intermittent stream. Previous studies have shown that rates of annual macroinvertebrate production can differ markedly between systems with contrasting water chemistry (e.g.,

hard-water versus soft-water streams; Kreuger and Waters 1983, Eggerts and Burton 1994, Griffiths et al. 1993, 1994). However, stream inorganic N concentration seemed to play a minimal role, if any, in influencing invertebrate production in WBB+N. Presumably, the similar levels of invertebrate productivity between streams are due to similar habitat templates, stream channel drying, and limiting trophic resources. Although I did not detect a difference in productivity because of the N-deposition manipulation, a gradient in stream permanence did result in changes in invertebrate production and community structure. Between years, differences in drying resulted in secondary production (1998/1999 < 1999/2000). Between streams, I found that differences in drying altered the distribution of production among taxa (e.g., *Paranemoura* in the driest conditions to *Leuctra* in more moderate conditions). My results support previous findings that invertebrate community structure can be regulated by stream channel drying. Further, this study shows that stream channel drying plays an important role in controlling levels of invertebrate productivity.

**Chapter 5:**

**ROLE OF HABITAT IN DETERMINING  
MACROINVERTEBRATE PRODUCTION ALONG  
AN INTERMITTENT STREAM CONTINUUM**



Whiskey Spring by C.L. Chadwick

## Introduction

Intermittent streams can have widely varying degrees of flow permanence. Variation in permanence produces physico-chemical environments that can be similar to or vastly different from nearby perennial streams, and result in tax-specific responses that alter invertebrate community structure (Delucchi and Peckarsky 1989, Dieterich and Anderson 1995, Erman and Erman 1995, Jacobi and Cary 1996). Some studies have found similar assemblages between intermittent and nearby perennial streams (Deluchi 1988, Feminella 1996, Shivoga 2001). However, both increases and decreases in invertebrate richness have been attributed to stream drying (Dieterich and Anderson 2000, Meyer and Meyer 2000, Rincón and Cressa 2000). Factors responsible for the observed changes in community structure for temporary streams have been suggested to be physical, chemical, and biological (reviewed in Williams 1996), and these factors should also evoke functional responses.

A few studies have examined functional responses to stream drying. For example, storage of benthic organic matter in 2 streams in southeastern, Australian has been shown to increase during periods of decreased flow resulting in increases in benthic detritivores (Bolton and Lake 1992). Contrary to this, reduced detritus processing rates due to a reduction in shredder richness and biomass have been observed in another intermittent stream in Michigan (Richardson 1990). I am unaware, however, of any studies that have quantified the functional response of macroinvertebrate secondary production to stream channel drying.

Secondary production is a comprehensive measure of ecosystem function because it integrates density, biomass, growth, reproduction, development, and mortality into one measurement (Waters 1977, Benke 1984, 1993). A variety of ecological questions have been addressed in studies of macroinvertebrate secondary production, including responses of populations to environmental stress and assessment of natural differences in productive capacity.

Macroinvertebrate productivity can vary with habitat structure, substrate type, and leaf detritus (Smock et al. 1985, Huryn and Wallace 1987). Stream drying could be predicted to increase invertebrate productivity, because small-bodied taxa with short generation times and fast growth rates should predominate (Williams 1996) which would result in high system productivity (dynamic systems sensu Huryn and Wallace 1999). Alternatively, stream drying could result in conditions that are inhospitable for large taxa with long generation times and high biomass. The loss of these taxa could lower system-wide biomass and result in low secondary production (inertial systems sensu Huryn and Wallace 1999). The effects of drying on secondary production will thus depend on which taxa can persist in intermittent streams and overall community structure.

Along with the direct effects of drying on invertebrate productivity, effects of drying on organic matter standing crop may also play an important role in regulating secondary production. Levels of invertebrate productivity for intermittent streams that drain forested catchments should depend on allochthonous organic material (i.e., donor controlled systems; Wallace et al. 1997). Increases in organic matter have been observed because of stream

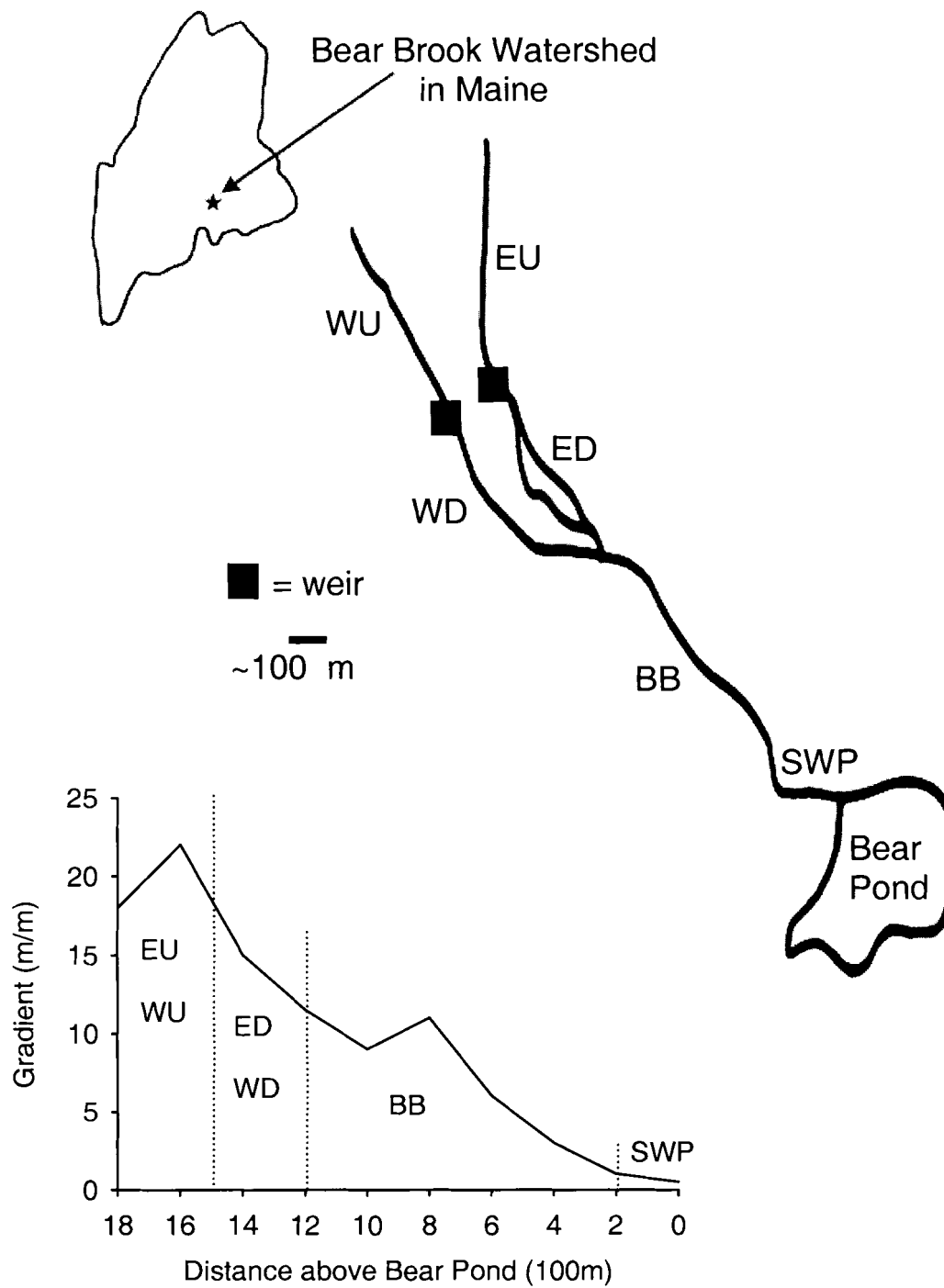
drying (see above) and this could lead to increased productivity for resident populations that tolerate drying.

Drying regimes and organic matter standing crop are factors that can be controlled by geomorphology and climate, and are responsible for regulating habitat heterogeneity among stream reaches (Ward 1989, Poff and Ward 1989, Hildrew and Giller 1994, Frisell et al. 1996). In perennial streams, numerous studies have investigated how habitat heterogeneity affects macroinvertebrate community structure (e.g., Carter et al. 1996, Richards et al. 1997, Pardo and Armitage 1997, Beisel et al. 2000) and secondary production (Smock et al. 1985, Huryn and Wallace 1987, Wohl et al. 1995, Buffagni and Comin 2000). However, few studies have investigated how habitat heterogeneity can affect invertebrate community structure or productivity for streams that dry. Habitat heterogeneity should moderate drying effects because more heterogeneity should lead to increased refugia.

In this study, macroinvertebrate community structure, secondary productivity, and benthic organic matter standing crop were quantified in an intermittent stream system. Specifically, I determined if community structure and productivity vary along a continuum of stream drying at different levels of habitat heterogeneity. Further, the importance of organic matter standing crop in regulating the response of invertebrate community structure and productivity to stream drying was evaluated.

## Study Site

This study was conducted in an intermittent stream system located in the Narraguagus River basin in southeastern Maine. The stream system drains Lead Mountain and is composed of 2 headwater streams and their confluence (Fig. 5.1). The upper portions of each headwater stream are part of a long-term ecosystem manipulation that is investigating the effects of atmospheric deposition on forest ecosystems (Bear Brook Watershed in Maine; see Norton and Fernandez 1999 for more information). Both streams have V-notch weirs located ~ 300 meters above their confluence. The second-order reach flows ~1,000 m and empties into Bear Pond. Slope decreases in the last ~200 meters of this second-order stream and there is an abrupt switch in riparian vegetation from hardwoods (American beech [*Fagus grandifolia*] and maple [*Acer* spp.]) to softwoods (Red spruce [*Picea rubens*] and Atlantic white cedar [*Chamaecyparis thyroides*.]; Fig. 5.1 inset graph). I divided the system into six reaches based on stream order and habitat heterogeneity (i.e., the distribution of bedrock, debris dams, riffle/runs, and pools; Table 5.1). The reaches are: 1) East Bear Brook above the weir (EU), 2) West Bear Brook above the weir (WU), 3) East Bear Brook below the weir (ED), 4) West Bear Brook below the weir (WD), 5) Bear Brook (upper 800 m of the second order confluence; BB), and 6) the swamp reach ( lower 200 m of the second-order confluence that flows directly into Bear Pond; SWP).



**Figure 5.1.** Map of the location reaches at the Bear Brook Watershed in Maine.

The inset graph shows how gradient varies across all reaches.

**Table 5.1.** Stream order, habitat heterogeneity, and reach-specific and habitat-weighted channel drying ranks. Reach-specific drying ranks are based on my observation of the timing of drying and rewetting in each reach. Habitat-weighted drying ranks are the sums of % habitat occurrence X habitat drying rank. Habitat drying ranks are based on my observation of drying for habitats in each reach and appear in parentheses after each habitat.

		EU	WU	ED	WD	BB	SWP
Stream order		1	1	1	1	2	2
Habitat heterogeneity as percent occurrence							
112	Bedrock (1)	6	10	0	0	0	0
	Riffle/run (2)	48	44	60	75	72	41
	Pool (3)	28	25	28	17	19	59
	Debris dams (4)	18	21	12	8	9	0
Reach drying rank		1	2	3	4	5	6
Habitat-weighted drying rank		2.78	2.76	2.84	2.91	2.90	2.41

## **Methods**

### Stream channel drying

Evaluation of stream channel drying was made from monthly visual observations of stream flow in all habitats along each reach. Discharge recorded by weirs located at the start of EU and WU was also used to evaluate flow permanence (Chapter 4).

### Benthic organic matter

Benthic organic matter (BOM) was sampled in each reach approximately monthly from November 1998 to May 1999 using a Surber sampler (0.9 m<sup>2</sup> with 250 $\mu$ m mesh). Three samples were taken from each habitat (e.g., bedrock, debris dams, riffle/runs, and pools). Sample locations were determined randomly prior to sampling. Samples were preserved in ~5% formaldehyde in the field. In the lab, material was sorted into BOM types (American beech leaves, maple leaves, small woody debris, >2 mm miscellaneous, or < 2 mm miscellaneous), dried at 60° C to constant mass, and then weighed. A portion from each sample was ashed (550° C) and weighed to calculate ash free dry mass (AFDM).

Average biomass for each BOM type was calculated from 1,000 monthly, habitat-weighted estimates generated by resampling with replacement. Total BOM was then calculated by summing across BOM types to create 1,000 estimates for each stream. Statistical comparisons between reaches and habitats for BOM types and total BOM were made by comparing 90% confidence intervals. Nonoverlapping confidence intervals were taken to indicate a

significant difference. I used  $\chi^2$  test to assess differences in the distribution of BOM among litter types. Control of type II error was achieved by establishing an  $\alpha$  level of 0.10 prior to this study.

#### Macroinvertebrate productivity

Benthic macroinvertebrates were sampled in the same manner as BOM (see above). Samples were elutriated to remove inorganic particles. The remaining material was sieved into 4 fractions (>2mm, 1–2mm, 0.5–1mm, and 0.25–0.5 mm). For large samples, fractions were split (1/32–1/2) using a Folsom plankton splitter. All organisms were removed by hand under magnification, identified to the lowest possible taxonomic level, assigned to functional feeding groups (Merritt and Cummins 1999), and measured to the nearest 1mm. Ash free dry mass (AFDM) was calculated from length-weight regression equations (Benke et al. 1999).

Production was estimated using one of three methods. The instantaneous growth method was used when a cohort could be followed through time and growth rates could be estimated (Benke 1984, 1993). The size-frequency method was used when a sufficient population size was present, but cohorts could not be followed (Benke 1984, 1993). For this method, cohort production intervals equivalent to the period when flowing water was present were assumed. For rare taxa, production was estimated by multiplying mean annual biomass by an assumed annual biomass turnover rate of 5 (annual production/biomass; P/B; Waters 1977). Production was estimated for all habitats and also combined to

produce a habitat-weighted value. Confidence intervals were calculated by bootstrapping for all but rare taxa (Huryh 1996). Statistical comparisons between reaches were made using the same techniques used for BOM (see above). Differences in the distribution of production among functional feeding groups were assessed using  $\chi^2$  tests. An  $\alpha$  level of 0.10 for all production comparisons were set prior to the start of the study.

### Invertebrate community structure

Invertebrate community structure was evaluated using canonical correspondence analysis (CCA; ter Braak 1986). CCA is a multivariate technique used to relate community composition to gradients in environmental variables. I conducted a CCA using both habitat-specific and habitat-weighted taxon production estimates in the community matrix and benthic organic matter, stream order, and ranks of habitat and reach permanence in the environmental matrix. This analysis allowed an assessment of the importance of habitats and reaches in structuring community assemblages.

## **Results**

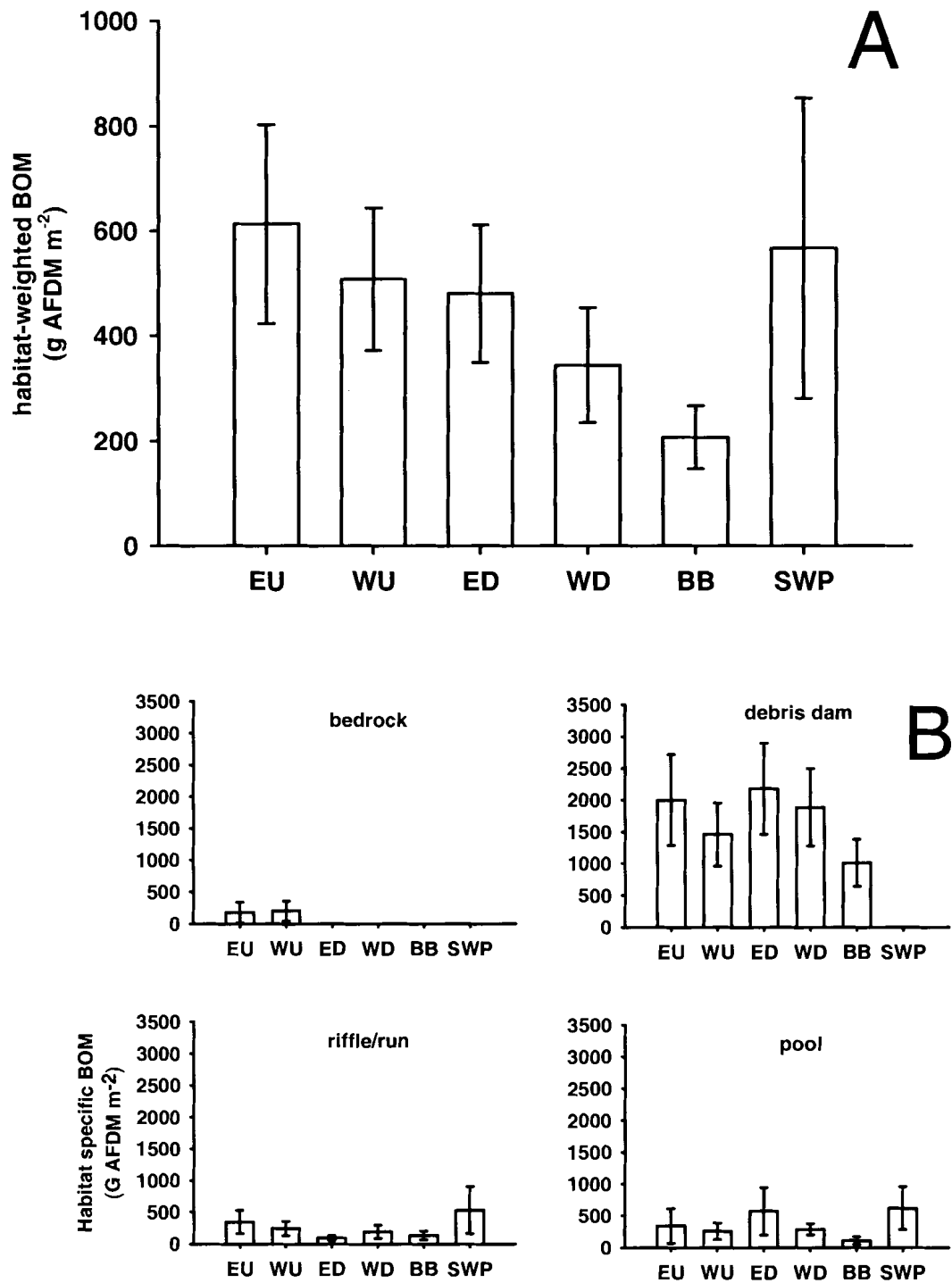
### Stream channel drying

Based on visual observations, each reach experienced periods when the entire stream channel was dry. The upper reaches (EU, ED, WU and WD) began to dry in April and each stream channel was completely dry by May. Surface water did not return until the following fall. BB and SWP had reduced

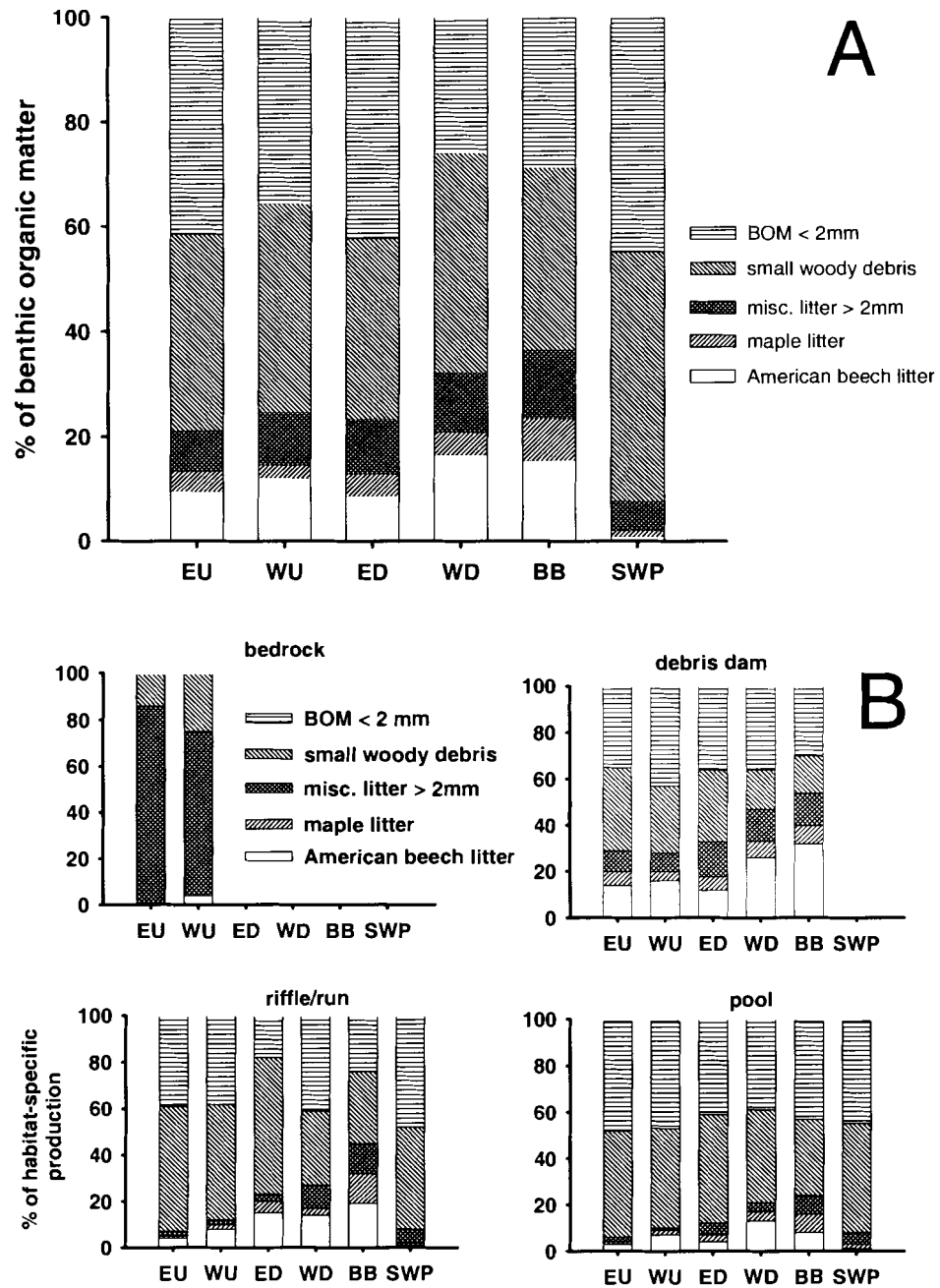
water levels starting in late April, but retained some water until June. From June until the following fall no water was found in these reaches. Observations from all reaches indicated that bedrock and riffle/runs dried before pools, and debris dams retained moisture longer than other habitats (Table 5.1). Discharge from the weirs confirmed my visual observations of stream permanence (Chapter 4). EU also showed a lower degree of permanence than WU (Table 5.1, Chapter 4). Based on these observations, I ranked the reaches in order of highest stream permanence to lowest stream permanence as BB > SWP > WD > ED > WU > EU (Table 5.1).

#### Benthic organic matter

Average habitat-weighted BOM (207–613 g AFMD/m<sup>2</sup>) decreased from the upper reaches to BB, but then increased in SWP (Fig. 5.2A). Average habitat-specific BOM showed similar patterns across reaches with debris dams > pools = riffle/runs > bedrock (Fig. 5.2B). ED, however, had higher BOM in pool than riffle/runs. The distribution of habitat-weighted BOM among litter types was similar between EU, WU, ED, WD, and BB ( $\chi^2 = 15.9$ ,  $p = 0.46$ ), but these reaches were different than SWP ( $\chi^2 = 1.3$ ,  $p = 0.05$ ; Fig 5.3A). Habitat-specific distribution of BOM among litter types differed in debris dams ( $\chi^2 = 30.4$ ,  $p = 0.02$ ), riffle/runs ( $\chi^2 = 99.0$ ,  $p < 0.001$ ) and pool ( $\chi^2 = 36.7$ ,  $p = 0.01$ ), but not in bedrock ( $\chi^2 = 6.3$ ,  $p = 0.18$ ; Fig 5.3B). Riffle/runs and pools in SWP and pools in all other reaches were dominated by BOM < 2mm and small woody debris. Bedrock habitats were dominated by miscellaneous litter (mainly moss).



**Figure 5.2.** Benthic organic matter standing crop for (A) habitat-weighted (reach-specific), and (B) habitat-specific values for each reach. Error bars are 90% confidence intervals.



**Figure 5.3.** The distribution of organic matter among BOM types (American beech leaves, maple leaves, small woody debris, >2mm miscellaneous, or < 2mm miscellaneous) for (A) habitat-weighted (reach-specific), and (B) habitat-specific values.

In debris dams and riffle/runs for all reaches except SWP, small woody debris decreased and leaf litter increased from upstream to downstream.

### Invertebrates

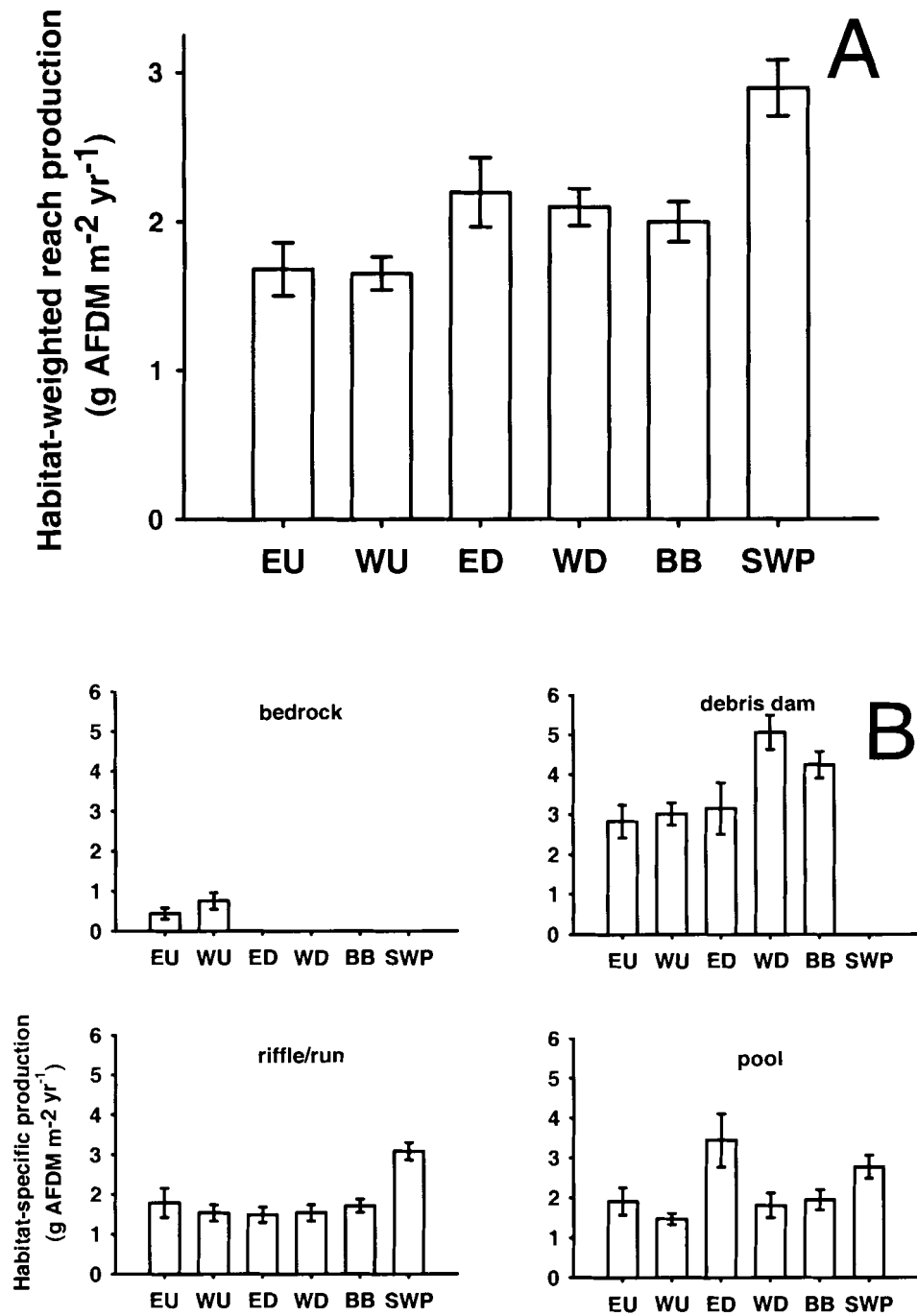
Total invertebrate richness was similar among reaches and ranged from 39 to 49 taxa (Table 5.2). Habitat-weighted biomass ranged from 0.38–0.65 g AFDM/m<sup>2</sup>, with the lowest value occurring in WU and the highest in SWP (Table 5.2). Habitat-weighted density varied from ~3500–6000 individuals/m<sup>2</sup> among reaches (Table 5.2).

Habitat-specific invertebrate richness ranged from 24 to 46 taxa with bedrock having the lowest richness and other habitats having similar values (Table 5.2). Habitat -specific biomass followed a pattern similar to that of benthic organic matter with debris dams > pools = riffle/runs > bedrock (Table 5.2). Habitat-specific densities varied across reaches. Debris dams tended to have the most individuals while other habitats had similar density. However, ED had the highest density in pool rather than debris dams (Table 5.2).

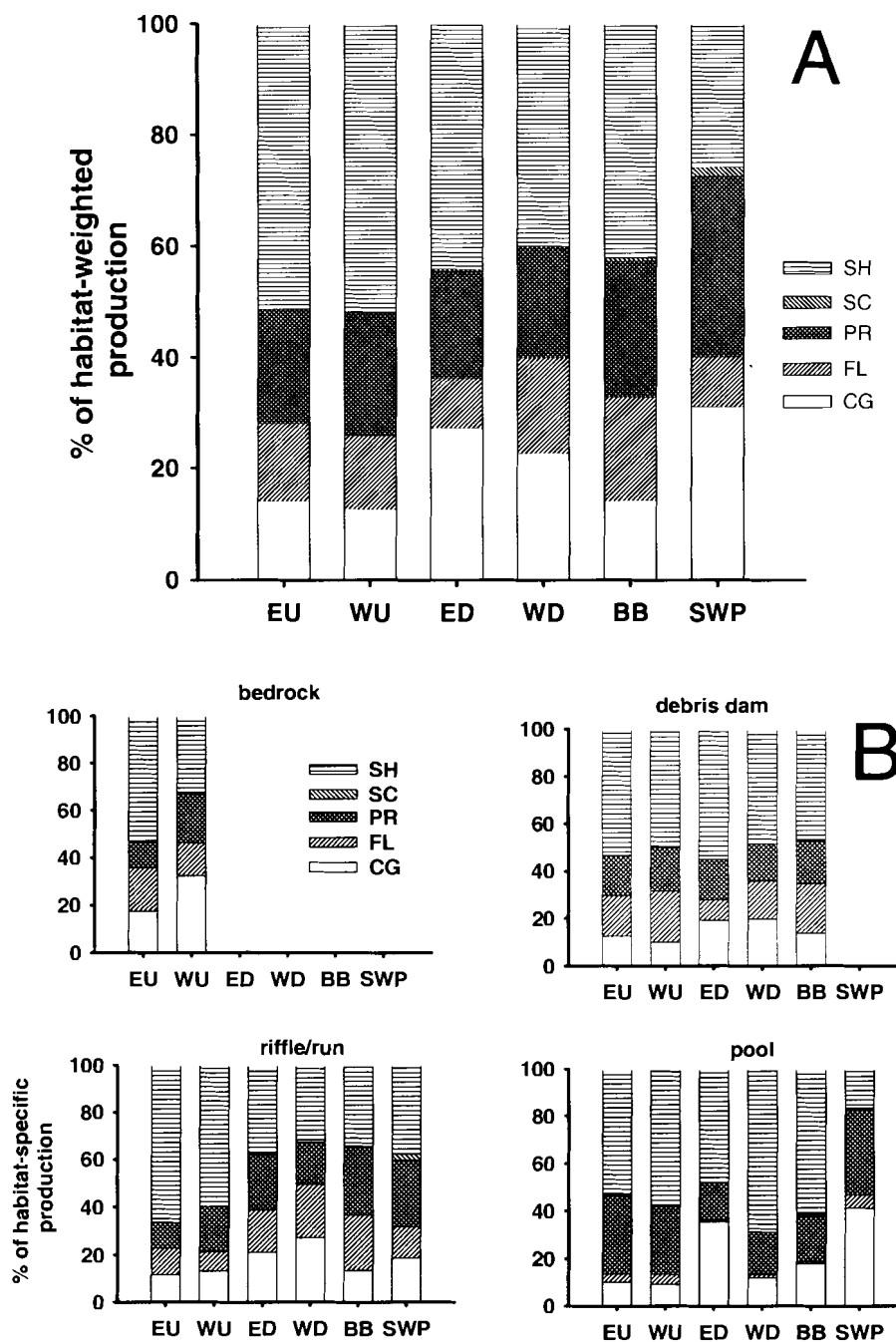
Total habitat-weighted production increased along the stream permanence gradient (Fig. 5.4A). The lowest production was found in EU and WU ( $1.68 \pm 0.18$  and  $1.65 \pm 0.11$  g AFDM m<sup>-2</sup>y<sup>-1</sup>  $\pm$  90% C.I.), followed by ED, WD, and BB ( $2.19 \pm 0.23$ ,  $2.09 \pm 0.12$ , and  $2.0 \pm 0.13$ ) and SWP ( $2.89 \pm 0.19$ ). The distribution of habitat-weighted production among functional groups also differed among reaches ( $\chi^2 = 43.3$ ,  $p < 0.01$ ; Fig 5.5A).

**Table 5.2.** Habitat-weighted (reach-specific) and habitat-specific invertebrate richness , biomass (mg AFDM/m<sup>2</sup>), and density (individuals/m<sup>2</sup>). Values in parentheses are 90% confidence intervals.

<b>Reach</b>	<b>Habitat</b>	<b>Richness</b> No. of taxa	<b>Biomass</b> mg AFDM/m <sup>2</sup>	<b>Density</b> ind./m <sup>2</sup>
EU	Habitat-weighted	40	427 (31)	3570 (221)
	Bedrock	24	88 (23)	1324 (654)
	Riffle/run	31	680 (167)	3191 (809)
	Pool	32	467 (154)	2240 (902)
	Debris dams	36	573 (72)	7082 (2182)
WU	Habitat-weighted	41	382 (25)	3189 (449)
	Bedrock	25	183 (53)	3339 (1192)
	Riffle/run	38	330 (102)	3209 (1582)
	Pool	37	341 (29)	2186 (824)
	Debris dams	36	717 (57)	4040 (1912)
ED	Habitat-weighted	41	538 (137)	5870 (1873)
	Riffle/run	39	421 (162)	3338 (851)
	Pool	29	841 (306)	10418 (5684)
	Debris dams	33	868 (363)	7921 (2414)
WD	Habitat-weighted	39	467 (70)	3482 (556)
	Riffle/run	36	732 (242)	3175 (607)
	Pool	30	377 (91)	2671 (773)
	Debris dams	37	1244 (246)	8074 (1987)
BB	Habitat-weighted	46	456 (100)	2834 (675)
	Riffle/run	38	436 (149)	2702 (852)
	Pool	42	454 (135)	2462 (920)
	Debris dams	42	999 (245)	4677 (1598)
SWP	Habitat-weighted	49	651 (122)	6135 (1390)
	Riffle/run	46	688 (131)	6301 (1746)
	Pool	42	626 (156)	6020 (1922)



**Figure 5.4.** Invertebrate secondary production for (A) habitat-weighted (reach-specific), and (B) habitat-specific values for each reach. Error bars are 90% confidence intervals.



**Figure 5.5.** The distribution of invertebrate secondary production among functional feeding groups for (A) habitat-weighted (reach-specific), and (B) habitat-specific values. CG = collectors, FL = filter feeders, PR = predators, SC = scrappers, SH = shredders

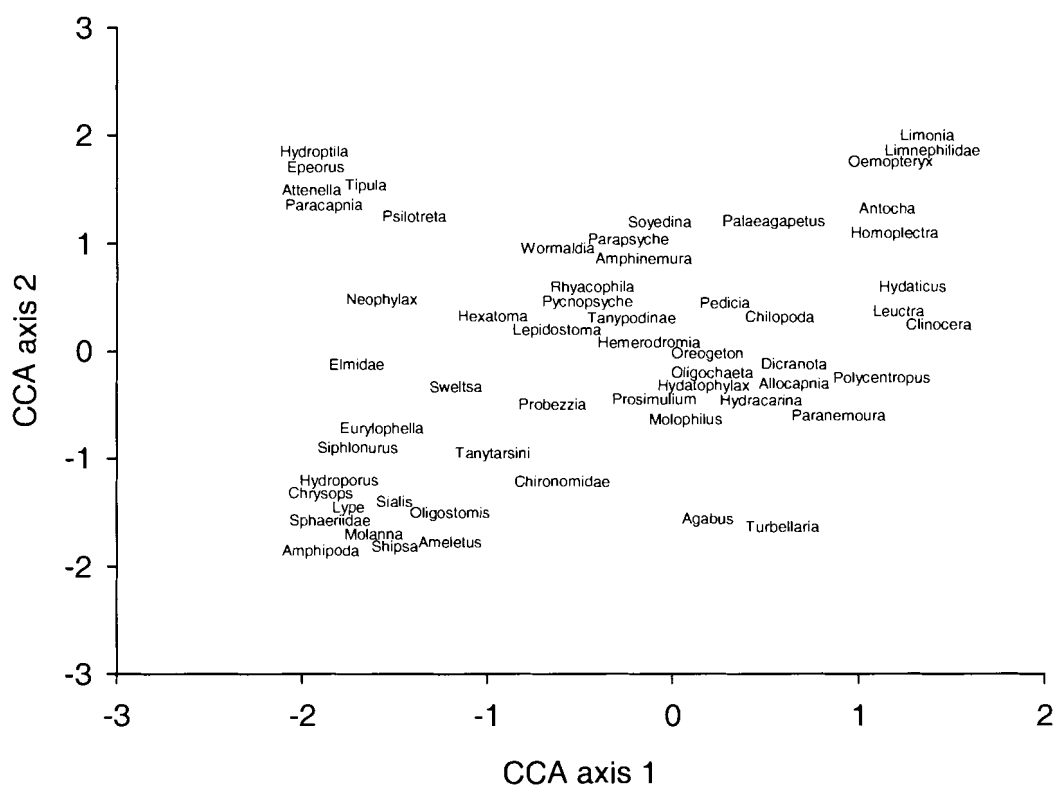
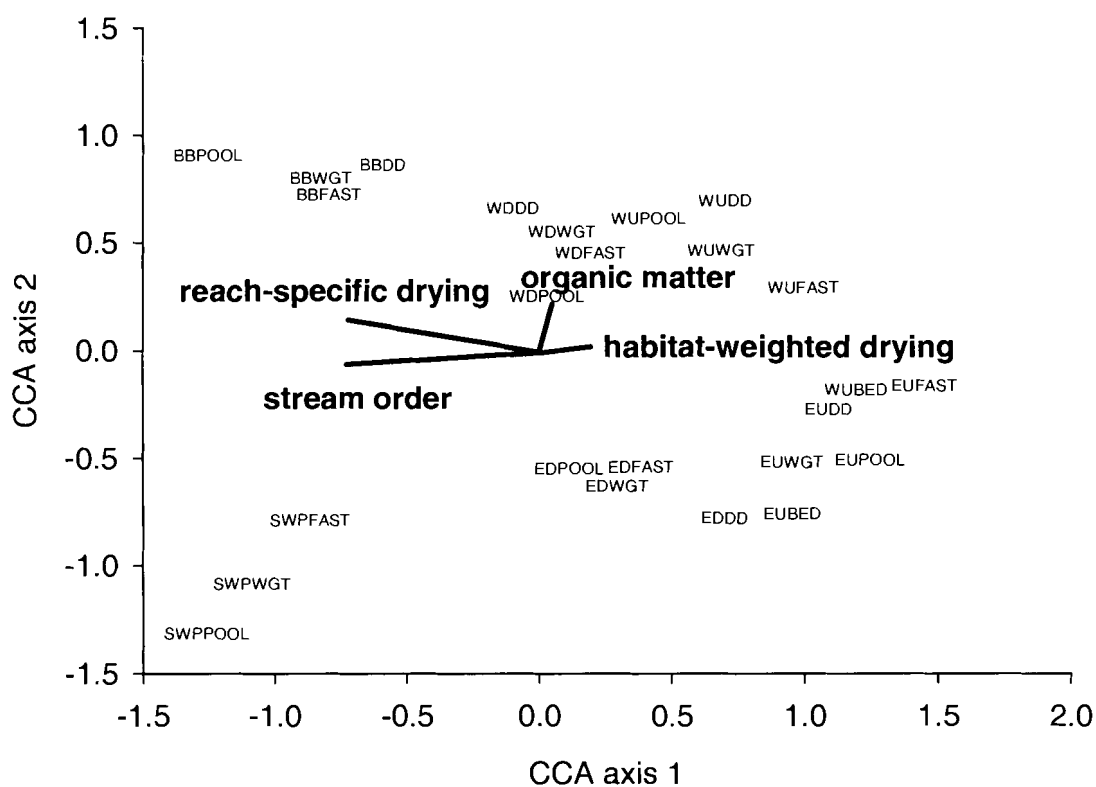
In the reaches with the lowest production (WU and EU), shredders accounted for 50% of production, followed by predators (~25%), filter feeders (~15%), collectors (~13%), and scrapers (<1%; Fig. 5.5A). In ED, WD, and BB, proportions of collectors and shredders decreased, while predators and filter feeders increased (Fig. 5.5A). SWP was dominated by collectors (~31%) and predators (32%; Fig 5.5A).

Habitat-specific annual production ranged from ~0.5 g AFDM/m<sup>2</sup> in EU bedrock to 5.0 g AFDM/m<sup>2</sup> in WD debris dams (Fig 5.4B). Productivity tended to track organic matter standing crop with debris dams > pool > riffle/runs > bedrock. Further, the highest production occurred in reaches with high stream permanence (WD and BB and SWP). Productivity in debris dams was dominated by shredders (~50%), and was similar among reaches (Fig 5.5B). Pools had fewer filter feeders than any other habitat (Fig. 5.65). For riffle/runs and bedrock, shredder production decreases while the other functional feeding groups increased with increased stream permanence (Fig. 5.5B).

### Community structure

Canonical axes 1 and 2 accounted for 29% of the variance in the tax-environment ordination (total inertia=1.7; Fig. 5.6). Axis 1 (eigenvalue=0.30).

**Figure 5.6.** The taxa-environment ordination from the canonical correspondence analysis. The upper figure shows the locations of habitat assemblages. Lines in the graph show the relationship of the environmental variables in the ordination. The lower figure shows the locations of taxa within the ordination.



explained 18% of the variance and separated taxa along a longitudinal gradient (upstream to downstream) that also corresponds to stream drying. Axis 2 (eigenvalue=0.19) explained 11% of the variance and separated taxa based on benthic organic matter standing crop and reach habitat-specific patterns in drying. Based the first 2 axes, drying appears more important than habitat in structuring macroinvertebrate production in this stream system

## **Discussion**

### Invertebrate community structure

A number of studies have shown that stream channel drying can influence invertebrate community structure (e.g., Delucchi 1988, Feminella 1996, Rincón and Cressa 2000, Shivoga 2001). I found similar results using taxon-specific production rather than biomass or abundance. In this intermittent stream system, community structure varied with channel drying, position in the watershed, and organic matter standing crop. Reach-specific drying and position in the watershed explain similar patterns of invertebrate community structure (Fig. 5.6). This is not surprising because these parameters are tightly linked (i.e., reaches lower in the system had higher degrees of permanence). Habitat-weighted drying and organic matter contributed less to explaining community structure, and both are probably related to debris dams (Fig. 5.6). Increases in the amount of debris dam habitat within a reach certainly elevate organic matter and may provide refuges from drying. Both organic matter and refuge from drying are

important factors that regulate invertebrate populations and community structure (Williams 1996, Wallace et al. 1999)

Ordination of taxon-based habitat- and reach-specific production showed that invertebrate communities were more similar within reaches than habitats (Fig. 5.6). This suggests that similarities of habitat-specific production within reaches act to “filter” invertebrate populations and subsequently regulate community structure in this intermittent stream system (sensu Poff 1997). Comparable degrees of drying within a reach are plausibly responsible for similar invertebrate communities that occur among habitats within any given reach. The differences in drying that occur among the 6 reaches could thus be the primary factor that regulates community structure in this intermittent streams system.

#### Invertebrate production

Production estimates from each reach in this intermittent stream system are among the lowest ever recorded (Benke 1993, Huryn and Wallace 2000). For headwater streams, secondary production tends to vary from 1-10 g DM m<sup>-2</sup> y<sup>-1</sup> and few are <3 g DM m<sup>-2</sup> y<sup>-1</sup> (Benke 1993, Huryn and Wallace 2000). Low productivity in streams can be due to reduced macroinvertebrate biomass and/or growth rates (Huryn and Wallace 2000). In this intermittent stream system, low secondary production is likely because of low biomass driven by stream-drying which excludes taxa that require perennial flow (Table 5.2 and Chapter 4).

Reach productivity varied with habitat heterogeneity. Secondary production for reaches has been shown to be a function the distribution of habitat

within reaches (Huryn and Wallace 1987), and these results concur. The most productive habitats for all reaches were debris dams (Fig. 5.4) which had the highest stream permanence and organic matter standing crop (Table 5.1, Fig. 5.2). Production was similar for the other habitats (riffle/runs, pools, and bedrock; Fig. 5.4) which is likely because of similarities in drying and organic matter.

Other studies have not reported such similar levels of secondary production among different habitats. In this study riffle/runs and pools had production estimates of  $\sim 1.5\text{--}3.0 \text{ g AFDM m}^{-2} \text{ y}^{-1}$ . For comparison, 2 headwater reaches in North Carolina had secondary production estimates from  $5.7\text{--}7.5 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  in all habitats (Wohl et al. 1995). In another study of a headwater stream in North Carolina, Huryn and Wallace (1987) found that production was  $5.7 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  in bedrock habitats,  $7.2 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  in riffles, and  $9.3 \text{ g AFDM m}^{-2} \text{ y}^{-1}$  in pools. Also, riffle habitats in a 2nd-order stream in New Hampshire yielded production of  $\sim 4.0 \text{ g AFDM/m}^2 \text{ y}^{-1}$  (Fisher and Likens 1973, Hall et al. 2001). These production estimates from similar streams located in the Appalachian Mountains provide evidence that stream-drying reduces secondary production in this stream system.

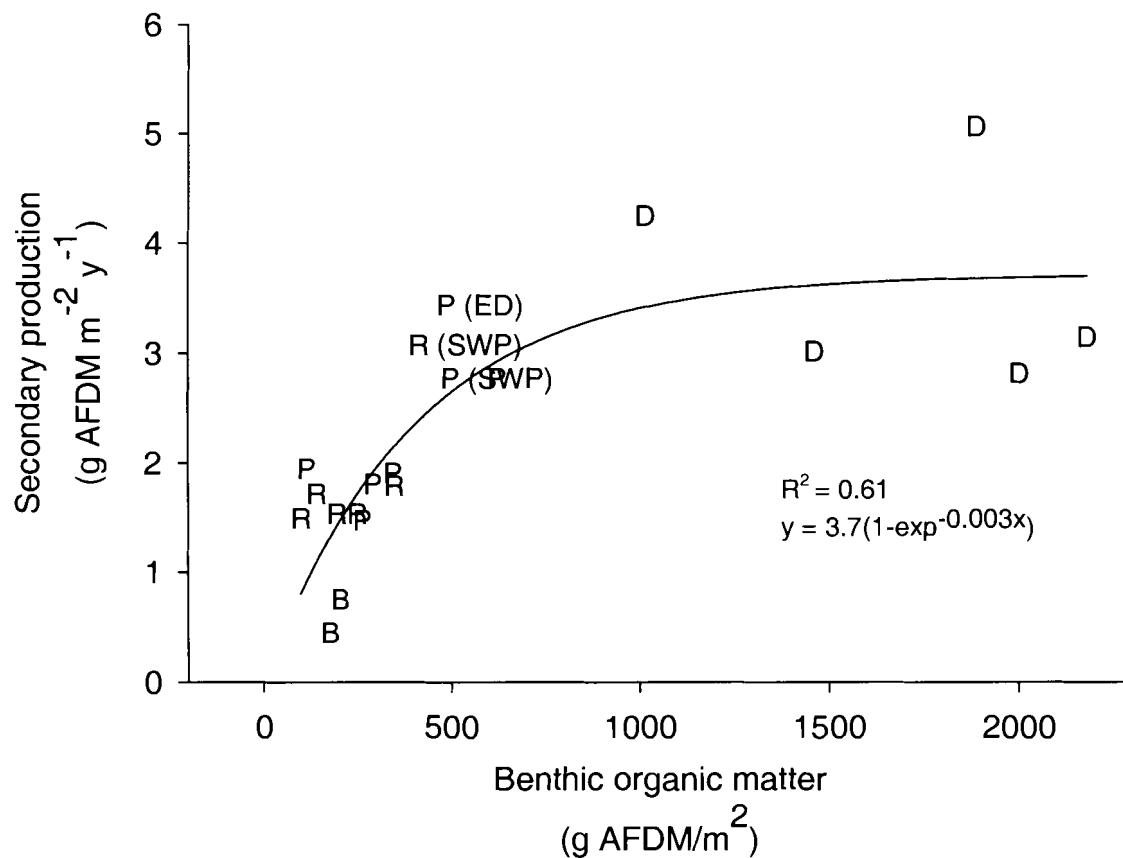
Debris dams may have provided a refuge from drying because moisture was retained for long periods within the organic matter when stream flow ceased. Because of their ability to retain water, debris dam invertebrate assemblages had a pronounced response to the drying gradient. The clearest example from this study is the high productivity for debris dams in WD and BB (i.e., less intermittent

reaches) when compared to other reaches (Fig 5.4B). The potential for stream drying to be the principal factor driving the differences in secondary production is strengthened given that WD and BB have low and intermediate levels of benthic organic matter (Fig. 5.3, 5.4).

While drying reduced differences that were expected for habitat-specific estimates of production, levels of organic matter standing crop still influenced overall patterns of invertebrate productivity (Fig. 5.7). Productivity among bedrock, riffle/run, and pool habitats was positively associated with benthic organic matter (Fig. 5.7). This relationship between organic matter and invertebrate productivity has been shown for perennial stream ecosystems (Wallace et al. 1999, Hall et al. 2001), and these results further support the relationship. Within debris dam habitats, however, secondary production did not increase with organic matter. This lack of relationship may be because debris dams are composed of organic matter which provides both food and space for organisms. Much of the organic matter biomass associated with debris dams is not palatable (e.g., wood), so increasing standing crop in these habitats may not result in the same increases in secondary production observed in other habitats.

The goal of this study was to assess how stream channel drying affects invertebrate productivity and community structure. Drying appears to act as an ecosystem filter for taxa along gradients of stream permanence. Because of this, invertebrate community structure was more sensitive to drying effects than production. Drying also reduced invertebrate production differences among habitats that have been found in other studies (Hurytn and Wallace 1987).

Production was, however, positively associated with organic matter, as seen in other headwater streams (Wallace et al 1999, Hall et al. 2001). Overall, I found that both drying regimes and organic matter standing crop are important for regulating habitat heterogeneity in intermittent streams. Differing degrees of habitat heterogeneity can thus regulate both invertebrate community structure and productivity.



**Figure 5.7.** The exponential rise to max relationship between invertebrate secondary production and organic matter for habitat-specific values. B = bedrock, D = debris dam, R = riffle/run. P = pool.

## **Chapter 6:**

### **GENERAL CONCLUSIONS**

The Bear Brook Watershed in Maine (BBWM) is a paired catchment study investigating ecosystem effects of N and S deposition. Due to the long-term addition of ammonium sulfate, the treatment catchment has higher stream nitrate and enriched foliar N concentrations. The treatment stream also has a higher degree of permanence. Below the established study catchments, an intermittent stream system, that includes four more stream reaches, has differing degrees of flow permanence. The objective of this work was to investigate how N deposition and stream drying affect organic matter dynamics. Specifically, I examined leaf-litter processing, organic matter input, storage and exports, and invertebrate production and community structure.

#### **Litter Processing**

I investigated how both stream N and foliar N affect stream detritus. Differences in litter processing were assessed by measuring mass loss, tissue softness, and shredder biomass. To examine both “stream effects” and “leaf source effects”, N-enriched and reference litter bags were prepared for three leaf species and placed in the treatment and reference streams. Red maple leaves were examined in 1997, 1998, and 1999. Sugar maple and American beech were examined in 1999. In all years, the only stream effects were increased mass loss for sugar maple and higher shredder biomass for red maple in 1998, both occurring only in the treatment stream. Several leaf source effects were

observed. N-enriched leaves of sugar maple, American beech, and red maple in 1998 had significantly higher microbial activity, as indicated by softer tissue, and had higher total mass loss. Further, shredder biomass tended to be highest in N-enriched litter bags. Although significant effects were detected, these results suggest that elevated dissolved N concentrations due to N deposition play a minimal role in regulating stream detritus processing at BBWM. Increased foliar N, however, did influence rates of stream detritus processing by increasing microbial activity, and possibly increasing shredder biomass. This study showed how N deposited on entire watersheds can affect the stream ecosystem function of litter processing.

### **Organic Matter Dynamics**

I predicted that the increased N loading to the treatment catchment would elevate inputs of organic matter, result in higher levels of stream coarse organic matter biomass, and increase litter processing rates relative to the reference catchment. This study found that the streams draining BBWM did not have statistically different inputs or coarse organic matter biomass, and only modest differences in export potential. System-level processing rates for maple (*Acer* spp.) litter were similar to rates previously quantified from litterbags. However, system-level processing rates for American beech (*Fagus grandifolia*) litter were faster than litterbag rates. This difference was likely due to movement of these leaves from riffle/runs and pools into debris dams, rather than changes in leaf tissue processing. Further, organic matter dynamics of the intermittent streams

at BBWM were similar to other headwater, forested streams. These results suggest that the ongoing N manipulation at BBWM is not altering inputs, storage or processing of stream coarse organic matter and consequently physical characteristics of these stream ecosystems regulate organic matter dynamics.

### **Stream Invertebrates and the N Deposition Experiment**

Invertebrate secondary production was the same in both streams, but varied between years (1998/1999:  $1.66 \pm 0.11$  and  $1.68 \pm 0.18$  g AFDM  $\text{m}^{-2}\text{y}^{-1}$ ; 1999/2000:  $2.28 \pm 0.14$  and  $2.27 \pm 0.25$  [mean  $\pm$  90% C.I., treatment and reference streams, respectively]). In both years, *Leuctra* had the highest production in the treatment stream. In the reference stream, *Paranemoura* had the highest production in the first year, but *Rhyacophila* and *Leuctra* had the highest production in the second year. Overall, shredders accounted for roughly half and predators a quarter of total production. The increase in production in the second year was attributed to both increased stream permanence and higher levels of organic matter. These results suggest that N deposition at BBWM has little effect on stream invertebrate production. However, differences in drying regimes for these intermittent streams did affect both the level of production and the distribution of production among taxa. Further, these findings suggest that although invertebrate production is limited in intermittent streams, it is still positively correlated with organic matter biomass.

## **The Role of Habitat along an Intermittent Stream Continuum**

I examined macroinvertebrate secondary production and community structure in an intermittent stream system that drains Lead Mountain. The intermittent stream system includes 2 first-order streams and their second-order confluence. Six reaches were defined within the system: 2 high-and 2 moderate-gradient, first-order reaches, a moderate to low gradient, second-order reach and a pond inlet. Each of the reaches had unique combinations of habitats (bedrock, riffle/runs, debris dams, and pools). In general, the percent riffle/runs increased and debris dams decreased while pools were similar from upstream to downstream. The upper reaches lost surface flow before the second-order reach and the pond inlet. Among all reaches, pools and debris dams retained water longer than fast flow habitats (riffle/runs and bedrock). Further, debris dams retained moisture after surface flow ceased. Reach-specific organic matter ranged from ~200 to 600 g AFDM/m<sup>2</sup> and decreased with increasing stream permanence. Habitat-specific organic matter was highest in debris dams and lowest for bedrock, but did not have as distinct longitudinal patterns as the reach-specific measurements. Reach-specific macroinvertebrate production ranged from ~1.7 to 2.9 g AFDM m<sup>-2</sup> y<sup>-1</sup> among all reaches, while habitat-specific macroinvertebrate production ranged from ~0.5 to 5.0 g AFDM m<sup>-2</sup> y<sup>-1</sup> (bedrock and debris dams, respectively). Flow permanence and detritus biomass appear to control invertebrate production within habitats, whereas differing distributions of habitats have strong control on reach-specific invertebrate production.

## Synthesis

A main result from this work is clear; the ongoing ecosystem manipulation at BBWM has yet to affect organic matter dynamics of these streams. This finding was unexpected due to the amount of prior research that has suggested that elevated N should cause a system-wide response. Continued additions of ammonium sulfate and further development of N-saturation conditions, however, should eventually alter the WBB+N stream ecosystem because of the changes expected in the surrounding forest. Throughout this dissertation I have offered several possible explanations for the lack of a measurable effect including: P limitation, pre-existing acidic conditions, and stream channel drying. Each of these plausible explanations, however, is without refutable proof.

The other main result from this work is also clear; stream channel drying can reduce macroinvertebrate secondary production and alter community structure. The timing of channel drying in this stream system filters taxa that lack appropriate life histories or traits to deal with prolonged dry periods. This filtering structures the macroinvertebrate community and regulates productivity.

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