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Response of stream macroinvertebrate production to atmospheric nitrogen deposition and channel drying

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Abstract

We assessed the effect of atmospheric nitrogen (N) deposition on secondary production in a first-order intermittent stream at the Bear Brook Watershed in Maine (BBWM). BBWM is a paired-catchment experiment designed to determine the effects of N deposition on a forested ecosystem. Nitrogen as $(NH_4)_2SO_4$ has been applied to the treatment catchment since 1989, with the adjacent catchment serving as a reference (both are drained by a first-order intermittent stream). Secondary production and detritus biomass were quantified for 2 yr. Production did not vary between streams (range = 1.7–2.3 g ash-free dry mass m^{-2} yr^{-1}) but was ~35% higher for both streams in the second year. The distribution of production among functional feeding groups varied little between streams but differed among taxa. Detritus biomass was similar between streams but was ~25% higher in the second year. The $(NH_4)_2SO_4$ treatment had no effect on production in the treatment stream. The statistically identical level of production between streams is presumably because of similar habitat, channel drying, and trophic resources. Difference in production between years was positively related to detritus biomass. Differences in the distribution of production among taxa between streams were likely the result of contrasts in the duration of flowing water, with the treatment stream having the longer duration. Our study indicates that patterns of litter input and channel drying, rather than N deposition, control levels of secondary production in these intermittent streams by altering both resource availability and community structure. These variables apparently override the effects of N deposition in regions where nitrogen is not a limiting nutrient.

First-order streams comprise the majority of total stream length within most drainages (Leopold et al. 1964). This quantitative perspective has been overlooked by major heuristic models of stream ecosystem function, which tend to conceptualize streams as single threads (Fisher 1997). As a consequence, the significance of first-order streams to the ecology of their drainage networks is often all but ignored (Meyer and Wallace 2001). As the primary interface between terrestrial and aquatic ecosystems, first-order streams can be critical sources of water, organic matter, and nutrients to downstream reaches (Takashi et al. 2002). In particular, they play an important role in N cycling (Peterson et al. 2001). Greater than 50% of bioavailable N received by headwater streams can be quickly (minutes to hours) retained or transformed over short transport distances (10–100 m; Peterson et al. 2001). When concentrations of dissolved N rise, however, the capacity for storage can become saturated, resulting in increases in transport distance and potentially leading to eutrophication downstream (Aber et al. 1989).

Nitrogen deposition in northeastern North America has increased exponentially over the past few decades, causing a change in the dynamics of nitrogen cycling in this region (Galloway et al. 2003). The recognition of this has prompted research on the long-term effects of N deposition on terrestrial and aquatic ecosystems (Aber et al. 1989; Galloway et al. 2003). N deposition and subsequent catchment acidification can alter stream ecosystem structure and function in many ways, including changes in detritus quantity and quality (White et al. 1999; Chadwick and Huryn 2003), litter processing rates (Mulholland et al. 1987), and macroinvertebrate community structure and production (Griffith et al. 1995; Smock and Gazzera 1996). In 1987, a whole-catchment experiment was initiated at the Bear Brook Watershed in Maine (BBWM) to investigate the effects of atmospheric deposition on a forest ecosystem. The goal of the BBWM experiment is to evaluate and parameterize acidification models and to evaluate N dynamics at the catchment scale (Norton et al. 1999). Although much attention has been devoted to water chemistry (Norton et al. 1999), the effect of the experiment on other attributes of the stream has not been evaluated. This experiment provided a unique opportunity to examine how N deposition affects the intermittent first-order tributaries of a stream ecosystem.

The primary objective of this study was to use the long-term paired-catchment experiment at BBWM to determine whether a decade-long increase in whole-catchment N deposition altered the structure and function of the macroinvertebrate community of a first-order, intermittent stream. As a secondary objective, we attempted to determine whether differences in intermittent flow patterns between the streams of the treatment and reference catchments had an additional influence on stream productivity by altering community structure and resource availability. We assessed the effects of these factors on the stream macroinvertebrate communities at BBWM by analyzing patterns of their production in

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both the treatment and reference stream over a 2-yr period. Because of the potential for nutrient enrichment, acidification, and flow patterns to have conflicting effects on ecosystem function, we made no a priori predictions about the effects of the N deposition treatment on macroinvertebrate secondary production.

Study site

BBWM is in Hancock County, southeastern Maine, and consists of two forested catchments, each drained by an intermittent first-order stream. East Bear Brook (EBB) is the reference catchment and West Bear Brook (WBB+N) is the treated catchment. WBB+N has received bimonthly additions of ammonium sulfate (∼1,800 equivalents ha^{-1} yr^{-1}; a 300% increase in N deposition) since November 1989. This deposition rate reflects conditions found in areas of New York State, where dry N and S deposition is among the highest in the United States. Both catchments are ∼10 ha in area and have similar soils, topography, aspect, gradient, and hydrology (*see* Norton et al. 1999 for a detailed description). American beech (*Fagus grandifolia*), sugar maple (*Acer sacchrum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and red spruce (*Picea rubens*) are common. The ongoing N experiment in the treated catchment (WBB+N) has decreased stream water pH, acid neutralizing capacity (ANC), and concentrations of dissolved organic carbon (Norton et al. 1999; Chadwick and Huryn 2003). At the same time, specific conductance and concentrations of nitrate, calcium, magnesium, and aluminum have increased (Norton et. al. 1999; Chadwick and Huryn 2003). The streams draining WBB+N and EBB have comparable physical structure and similar inputs, standing stocks, and processing rates of organic matter (Chadwick 2003). Surface flow usually occurs from November to May. Streams are ice covered in winter. During this study (November 1998–July 2000), the streams showed similar patterns in discharge when flowing, and both lost surface flow for extended time periods (Fig. 1). In 1999, both streams lost surface flow by mid-May. In 2000, they continued to flow until July. WBB+N had 95 dry days, with the longest consecutive dry period lasting 22 d. EBB was dry for 174 d, with the longest consecutive dry period lasting 60 d. The threshold discharge to maintain surface flow appears to be ∼2 L s^{-1} (Fig. 1).

Methods

Benthic macroinvertebrates were sampled from each stream approximately monthly from November 1998 to May 1999 (year 1) and October 1999 to July 2000 (year 2) with a Surber sampler (0.09 m^2 with 250-μm mesh). Three samples were taken when streams were flowing from each of the primary habitats (bedrock, debris dams, riffle/runs, and pools). Bedrock was sampled only in year 1. 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) and separation of the remaining organic material into four size fractions (>2, 1–2, 0.5–1, and 0.25–0.5 mm). For large samples, these size fractions were subsampled (1⁄32–1⁄2) with a Folsom plankton wheel. Macroinvertebrates were removed by hand under magnification, identified to the lowest possible taxonomic level, and measured to the nearest 1 mm. Ash-free dry mass (AFDM) was calculated from length–weight relationships (Benke et al. 1999).

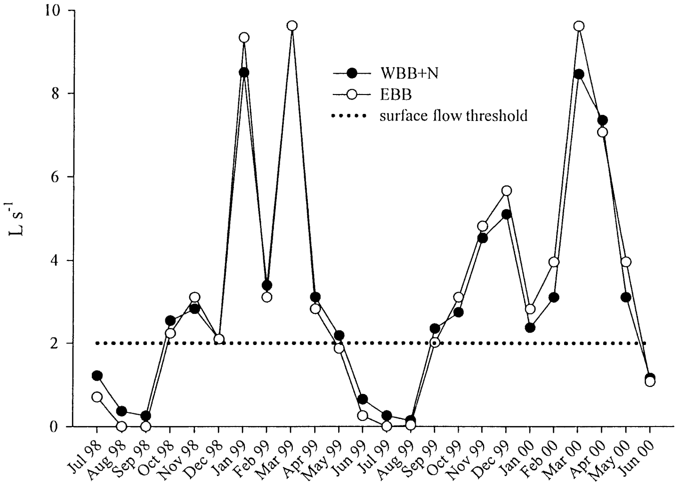

Fig. 1. Mean monthly discharge for West and East Bear Brook. The surface flow threshold is based on observations of each stream channel above the v-notch weir used to measure discharge. WBB+N, treatment stream; EBB, reference stream.

Production was estimated by 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 1993). The size-frequency method was used when a sufficient population size was present, but cohorts could not be followed (Benke 1993). For this method, cohort production intervals equivalent to the period that 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 five (annual production/biomass, P/B; Waters 1977). Production was estimated from all habitats and combined to produce a habitat-weighted value.

Differences in production between taxa, functional feeding groups (FFG), and communities were tested for significance by comparing confidence intervals calculated by bootstrapping for all but rare taxa (Huryn 1996). Control of type II error was achieved by designating an α level of 0.10 prior to sampling. Statistical comparisons between streams were made by comparing 90% confidence intervals, with non-overlapping confidence intervals indicating differences. Because of the absence of pretreatment data on the macroinvertebrate communities of the study stream, we assumed that differences in community attributes between streams would be explained by the N addition to WBB+N.

During the course of the study, we observed differences in the pattern of flow duration between streams and years. We used canonical correspondence analysis (CCA; ter Braak 1986) to determine whether these differences were associated with differences in macroinvertebrate community structure and production. CCA is a multivariate technique used to relate community composition to gradients in environ-

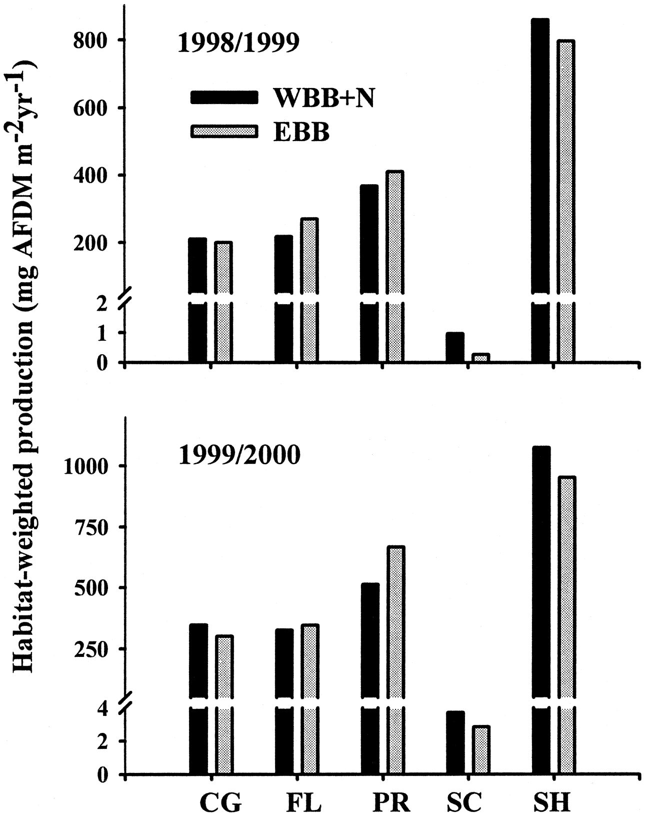

Fig. 2. The distribution of production among functional feeding groups for West and East Bear Brooks in year 1 and year 2. WBB+N, treatment stream; EBB, reference stream; AFDM, ash-free dry mass; CG, collectors; FL, filterers; PR, predators; SC, scrapers; SH, shredders.

mental variables. We 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 then analyzed to assess the relationship between differences in flow patterns between streams and years and macroinvertebrate community attributes.

Results

Total habitat-weighted production of macroinvertebrates varied between years but was not different between streams (year 1: WBB+N = 1,654 ± 111 mg AFDM $m^{-2}yr^{-1}$, EBB = 1,682 ± 179 mg AFDM m^{-2} yr^{-1}; year 2: WBB+N = 2,283 ± 138 mg AFDM m^{-2} yr^{-1}, EBB = 2,271 ± 250 mg AFDM m^{-2} yr^{-1}). The distribution of production among FFG was also similar between streams. Shredders accounted for 50% of production, followed by predators (~25%), filterers (~15%), collectors (~13%), and scrapers (<1%; Fig. 2). Average biomass did not differ between streams and ranged from 383 to 495 mg AFDM m^{-2}, with the lowest occurring in WBB+N in year 1 (Fig. 3A). Annual P/Bs were 3.9 (EBB year 1), 3 (WBB+N year 1), and 6 (both streams year 2). Total richness ranged from 39 to 41 taxa and was similar between streams and years (Fig. 3B). Macroinvertebrate density was similar between streams. The greatest densities occurred in year 2 (Fig. 3C).

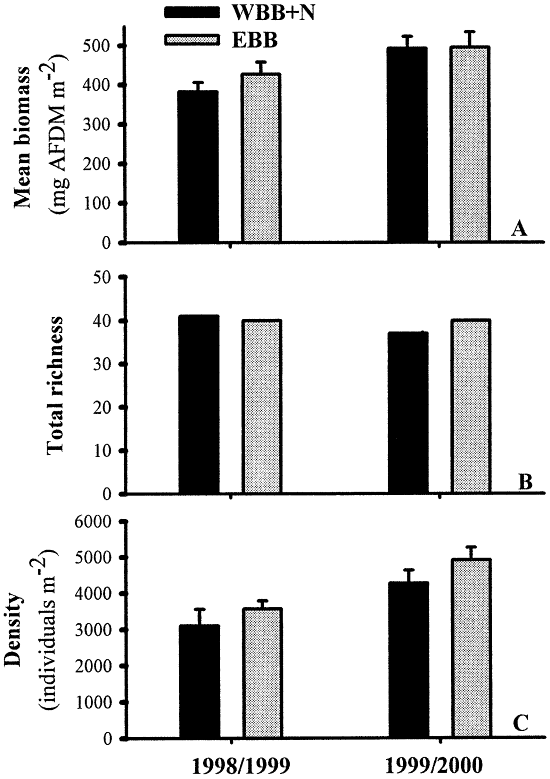

Fig. 3. (A) Average total biomass (+90% CI), (B) total richness, and (C) density (+90% CI) for West and East Bear Brooks in year 1 and year 2. WBB+N, treatment stream; EBB, reference stream; AFDM, ash-free dry mass.

Taxonomic structure—In WBB+N, the shredding stonefly *Leuctra* had the highest production in both years (year 1: 236 mg AFDM m^{-2} yr^{-1} [16% of annual P]; year 2: 338 mg AFDM m^{-2} yr^{-1} [15% of annual P]; Table 1). Seventeen taxa in year 1 and 13 taxa in year 2 had production >1% of total production (i.e., >25 mg AFDM m^{-2} yr^{-1} per taxon; Table 1). In year 1, these included two collectors, three filterers, four predators, and eight shredders (Table 2). In year 2, these included three collectors, two filterers, three predators, and five shredders (Table 2).

Habitat-weighted biomass for different taxa ranged from 9 to 51.2 mg AFDM m^{-2} in year 1 and 8.5 to 73.9 mg AFDM m^{-2} in year 2 (Table 1). *Leuctra* had the highest biomass in both years. Mean densities of all taxa ranged from <1 to 1,103 individuals m^{-2} in year 1 and <1 to 1,362 individual m^{-2} in year 2 (Table 1). For taxa that contributed >1% of total secondary production, Othocladiinae midges had the highest and the shredding caddisfly *Pycnopsyche* had the lowest densities in both years.

In EBB, the shredding stonefly *Paranemoura perfecta* had the highest production in year 1 (217 mg AFDM m^{-2} [13% of annual P]) and the predacious caddisfly *Rhyacophila* had the highest production in year 2 (397 mg AFDM m^{-2} [17% of annual P]; Table 1). In both years, 17 taxa had production >1% of overall production (i.e., >26 and 35 mg AFDM

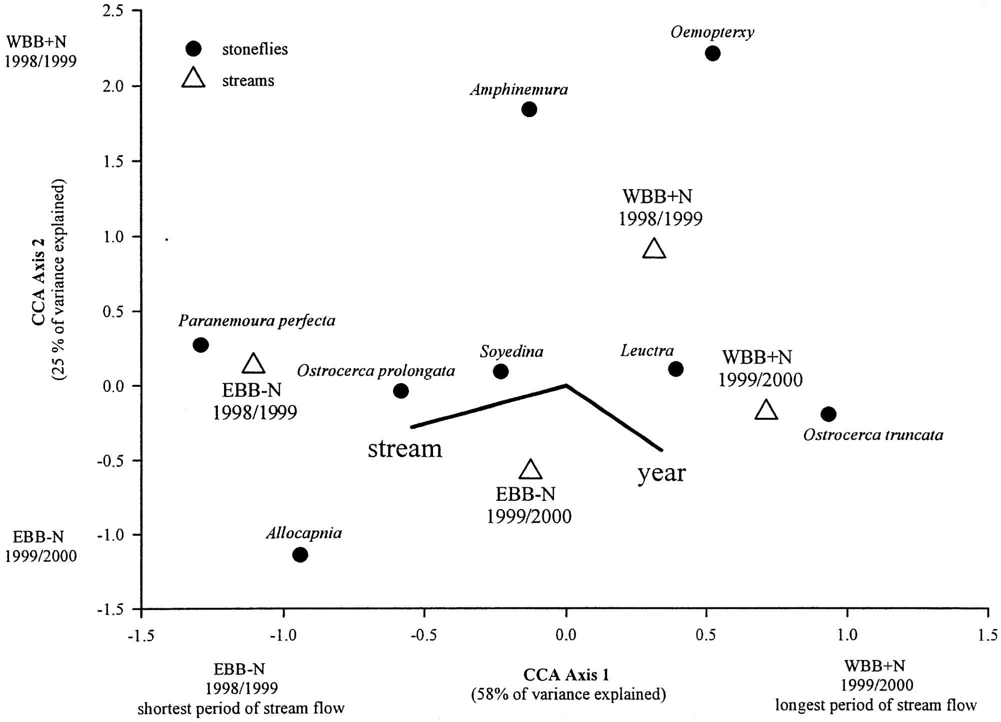

Fig. 4. The taxa–environment ordination from the canonical correspondence analysis. Canonical axes 1 and 2 accounted for 83% of the variance. Most of the variance in taxa production is represented in axis 1 (58%), which shows a gradient of flow duration. For simplicity, only stoneflies are shown (filled circles). Streams are represented as triangles. WBB+N, treatment stream; EBB, reference stream.

m^{-2} yr^{-1} per taxa in years 1 and 2, respectively; Table 1). In year 1, these included three collectors, two filterers, five predators, and seven shredders (Table 2). In year 2, these included three collectors, three filterers, four predators, and seven shredders (Table 2).

Habitat-weighted biomass for different taxa ranged from 1.0 to 73.0 mg AFDM m^{-2} in year 1 and 7.1 to 69.3 mg AFDM m^{-2} in year 2 (Table 1). *P. perfecta* had the highest biomass in year 1. Orthocladiinae had the highest biomass in year 2. Mean densities ranged from <1 to 945 individuals m^{-2} in year 1 and <1 to 2,306 individuals m^{-2} in year 2 (Table 1). In both years, Orthocladiinae had the highest densities. For taxa contributing $>1\%$ to overall production, the filter-feeding caddisfly *Homoplectra* had the lowest densities in year 1 and the shredding caddisfly *Pseudostenophylax* had the lowest densities in year 2.

Canonical correspondence analysis—The total variance associated with macroinvertebrate ordination was small (Inertia; ter Braak 1986). This was expected because of great similarities between WBB+N and EBB. Canonical axes 1 and 2 collectively accounted for 83% of the variance in the taxon–environment ordination (Fig. 4; for simplicity, only stonefly taxa are depicted in the figure). Axis 1 (eigenvalue = 0.172) explained 58% of the variance and separated taxa along a gradient from EBB year 1 to WBB+N year 2. This gradient represents the shortest (EBB year 1) to the longest duration of flow (WBB+N year 2). Axis 2 (eigenvalue = 0.073) explained 25% of the variance and separated taxa along a gradient from EBB year 2 to WBB+N year 1. Axis 2 was strongly influenced by taxa that either occurred in only a single stream (e.g., the stonefly *Oemopteryx*) or had markedly different levels of production between streams (e.g., the stonefly *Allocapnia*).

Discussion

Estimates of community production and its distribution among FFG were virtually identical between EBB and WBB+N. The decade-long addition of ammonium sulfate to the WBB+N catchment had no measurable effect on gross bioenergetics and functional attributes of the macroinvertebrate community of this stream. This was unexpected given the marked differences in water chemistry caused by this long-term experiment (e.g., pH, nitrate, calcium, magnesium, aluminum). In addition to being statistically identical between streams, macroinvertebrate production in EBB and WBB+N was also among the lowest reported for natural streams (range = 1.7–2.3 g AFDM m^{-2} yr^{-1}). Estimates of production for headwater streams range from 1 to 10 g dry mass m^{-2} yr^{-1}, with few ranging below 3 g dry mass m^{-2} yr^{-1} (Benke 1993; Huryn and Wallace 2000). Although community production and its distribution among FFG were similar between streams, how production was apportioned among taxa was significantly different. Two general questions are raised by our results: (1) Why was there no treat-

Table 1. Average abundance (N, individuals m^{-2}), biomass (B, mg AFDM m^{-2}), and production (P, mg AFDM m^{-2} yr^{-1}) for taxa sampled from the treatment (WBB+N) and reference (EBB) streams at the Bear Brook Watershed in Maine. Values in parentheses are 90% confidence intervals. FFG, functional feeding group; CG, collector gatherer; FL, filterer; PR, predator; SC, scraper; and SH, shredder.

			WBB+N/EBB					
			1998–1999			1999–2000		
FFG	Order	Taxon	N	B	P	N	B	P
CG	Ephemeroptera	*Eurylophella*	—/1.0	—/0.04	—/0.22	0.3/1.5	0.02/0.28	0.11/1.42
	Trichoptera	*Oligostomis*	—/0.01	—/0.04	—/0.18	—/—	—/—	—/—
	Diptera	*Antocha*	0.4/—	0.16/—	0.79/—	—/—	—/—	—/—
		Tipula	0.5/0.1	1.16/0.34	5.81/0.84	2.3/0.2	1.40/0.04	7.00/0.21
		Orthocladiinae	1103/945	39.8/35.4	132.5/119.8	1362/2306	39.1/69.3	138.7/187.3
			(426/157)	(15/6.7)	(61.2/22.0)	(205/309)	(6.7/11.3)	(20.3/28.8)
		Tanytarsini	150/368	3.3/6.6	13.1/38.6	519/261	12.3/11.3	65.1/48.3
			(90/91)	(2.2/2.3)	(8.9/23.2)	(258/54)	(5.3/3.3)	(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	55/35.4	233/132	27.2/12.6	135.9/62.9
FL	Trichoptera	*Wormaldia*	2.8/19.7	2.01/3.87	8.18/15.63	10/25.1	6.16/10.12	30.9/50.8
			(—/12.7)	(—/2.06)	(—/7.72)	(—/—)	(—/—)	(—/—)
		Homoplectra	6.2/1.3	22.2/5.33	111.0/26.6	8.2/10.3	31.4/22.4	157.1/112.1
		Parapsyche	3.4/<0.1	12.01/0.01	505/0.05	0.7/0.4	2.12/1.70	10.3/8.5
		Prosimulium	48/130	9.2/31.8	46/130	148/281	29.6/40.2	128.2/175.1
			(20/34)	(2.9/9.6)	(15.0/50.5)	(42.4/68.8)	(11.0/12.7)	(42.4/49.3)
PR	Plecoptera	*Sweltsa*	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	*Polycentropus*	—/13.4	—/19.1	—/97.9	0.8/3.4	0.7/7.1	3.6/35.4
			(—/12.5)	(—/18.5)	(—/90.8)	(—/—)	(—/—)	(—/—)
		Rhyacophila	19.2/45	11.0/37.6	68.9/190.1	48.9/3.7	36.6/49.2	260/396.9
			(7.6/12.4)	(3.3/12.8)	(20/102.3)	(9.5/11.6)	(9.4/20.4)	(74/201.4)
	Coleoptera	*Hydaticus*	2.5/0.4	1.8/1.7	9.0/8.2	1.5/—	0.9/—	7/—
	Diptera	*Dicranota*	8.0/38.3	2.0/6.7	12.4/42.0	35.6/25.7	8.5/3.9	37.9/23.3
			(2.6/8.5)	(0.8/1.9)	(6.1/18)	(15.9/7.0)	(3/1.63)	(17.0/11.5)
		Hexatoma	1.4/0.9	1.0/1.0	5.01/2.59	2.8/8.5	0.7/1.3	3.6/6.5
		Limnophila	0.5/—	0.2/—	0.8/—	—/—	—/—	—/—
		Oreogeton	9/1	2.6/1.4	15.6/7.7	10.3/17.1	2.8/3.0	12/18
		Pedicia	5.7/6.6	16.4/7.7	89.2/41.4	3/5.0	19.9/10	99.5/70.1
			(2.3/3.8)	(8.9/1.2)	(49.0/6.2)	(—/—)	(—/—)	(—/—)
		Probezzia	2.3/1.8	1.0/0.4	8/2.2	11.2/8	1.0/1.1	5.2/5.7
		Tanypodinae	135/141	19.1/16.3	95.7/97.7	91/113	6.4/7.1	18.2/27.8
			(29.6/36.0)	(3.0/9.0)	(22.3/29.8)	(25.5/28.4)	(2.1/2.0)	(5.4/11.5)
	Chilopoda		0.3/—	6/1.6	23.0/7.7	1.0/1.3	6/7.5	23.2/37.7
			(12.7/7.6)	(2.62/1.10)	(12.0/10.0)	(—/—)	(—/—)	(—/—)
	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
SC	Trichoptera	*Neophylax*	—/0.1	—/0.01	—/0.2	—/5.6	—/0.5	—/2.6
		Palaeagapetus	0.8/<0.1	0.16/<1	1.0/0.02	2.7/1.2	0.7/0.3	3.7/0.3
	Coleoptera	*Oulimnius*	—/0.1	—/0.02	—/0.08	—/—	—/—	—/—
SH	Plecoptera	*Amphinemura*	102/52	10.4/2.4	45.5/11.4	5.2/15.2	0.6/1.5	2.8/7.5
			(41/19)	(5.1/0.9)	(23.9/7)	(—/—)	(—/—)	(—/—)
		Ostrocerca prolongata	166/365	25.8/49.4	60/101	118/222	8.2/25	45.2/112.9
			(36/77)	(5.6/10.9)	(14/49.7)	(36/26)	(2.4/3.6)	(17.1/20.4)
		Ostrocerca truncata	207/6	33.1/2.5	105.7/5.6	470/303	78.9/40.3	256.2/129.6
			(44/3)	(6.0/1.3)	(29.5/2)	(70/38)	(10/5.4)	(68.2/23.3)
		Paranemoura perfecta	123/568	17.7/73.0	48.5/217.3	68/148	6.9/28.2	21.2/90.8
			(27/95)	(5.1/11.1)	(18.0/65)	(11/27)	(1.1/6.9)	(5.7/25.7)
		Soyedina	25/35	3.4/5.9	13.4/36.1	28/31	5.6/4	32.4/20.2
			(16/12)	(1.5/1.8)	(7.0/13.0)	(4/13)	(2.1/1.3)	(12/6.5)
		Oemopteryx	0.7/—	2.9/—	14/—	0.2/1.3	0.5/0.2	2.3/0.9
		Allocapnia	2.0/10	0.6/3.3	3.0/16.3	1.1/47	0.4/8.4	1.9/36.3
			(—/—)	(—/—)	(—/—)	(—/11)	(—/2.0)	(—/10.4)
		Leuctra	485/231	51.2/23.8	262.2/106.9	350/329	73.9/56.7	337.9/258.7
			(93/53)	(9.3/5.70)	(53/31.5)	(94/106)	(19.5/28.7)	(72.1/139.3)
	Trichoptera	*Lepidostoma*	42/35)	9/1	26.2/28.2	15/14	1.3/2	10.7/26.1

Table 1. Continued.

			WBB+N/EBB					
			1998–1999			1999–2000		
FFG	Order	Taxon	N	B	P	N	B	P
			(15/13)	(2.7/1.9)	(11.4/13.9)	(7/3)	(0.5/1.2)	(6/9.3)
		Psilotreta	2.1/3.1	2/1.6	15.9/6.3	—/1.9	—/5	—/22.4
		Hydatophylax	5.0/7.9	6.3/30.2	15.8/75.6	0.7/3.4	1.4/3.6	9.5/17.8
		Pseudostenophlyax	5.3/—	21.1/—	105.3/—	9.6/0.8	43/8.6	221.7/43.0
		Pycnopsyche	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	*Limonia*	0.1/—	0.3/—	1.6/—	—/—	—/—	—/—
		Molophilus	2.0/4	0.5/2.6	2.3/13.1	0.6/1.2	0.5/0.7	2.5/3.6

* Taxonomy higher than the Order level.

ment effect, and why is macroinvertebrate production so low at BBWM? and (2) What factors are responsible for differences in community structure between WBB+N and EBB?

Factors contributing to the lack of a treatment effect and low secondary production are probably interrelated and will be considered together. Low production results from low biomass, low growth rates, or both (Huryn and Wallace 2000). Factors likely responsible for the low production estimated for the streams at BBWM include poor food quality (lowers growth rates), low pH (typically <5.7) and nutrient concentrations (lowers growth rates), channel drying (lowers biomass), and winter temperatures near 0°C for ~4 months of a 9-month period of flow (lowers growth rates).

The major factor explaining low consumer productivity in EBB and WBB+N is probably food quality and quantity. The productivity of forested, headwater streams is ''donor controlled'' because of a reliance of consumer production on allochthonous organic matter (Wallace et al. 1999). As an 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 detritus. Productivity in WBB+N and EBB is dominated by shredders (Fig. 2), so the similarities in detritus quantity and quality between streams (Chadwick 2003) indicate that similar levels of production should be expected. And in fact, the highest production between years was associated with the highest detrital biomass in each stream. When compared with data from other perennial streams, however, the data for BBWM were outliers—levels of the ratio of production to detritus biomass were lower than would be predicted by the regression (Fig. 5). This can be attributed to low detritus quality, intermittent flow, or both.

Detritus quality is dependent on two primary factors: litter type and water chemistry. The dominant litter species entering the study streams is American beech (Chadwick 2003). Detritus derived from beech litter is a low-quality food source (as indicated by processing rates) compared with litter from other deciduous tree taxa (Chadwick and Huryn 2003). The refractory quality of this detritus could certainly limit shredder productivity, as well as that of other consumers that feed on the detritus that they process (i.e., collector–gatherers and filter feeders; Wallace et al. 1999).

The mean pH of EBB and WBB+N was acidic (mean pH < 5.8). Reduced microbial activity on detritus has been reported from acidic streams (Mulholland et al. 1987). A decrease in microbial activity reduces food quality of detritus, which might have an important effect on shredders and collectors (e.g., Griffith et al. 1993). Any effect on detritus quality as a result of low pH will be compounded by low nutrient supply. The streams of BBWM are oligotrophic, with concentrations of dissolved inorganic P in both EBB and WBB+N typically <5 μg L^{-1} (Chadwick unpubl. data). Consequently, P, rather than N, is likely the limiting nutrient for ecosystem productivity in these streams, which probably explains the lack of any treatment effect observed in this study. Finally, acidic water chemistry might also lower secondary production by a reduction in consumer growth rates because of increased metabolic demands associated with low pH stress (Griffith et al. 1993).

Intermittent flow influences stream community structure by generating conditions that are too harsh for taxa that lack strategies (i.e., desiccation resistance, diapause, access to refugia; Williams 1996), allowing them to persist through dry periods (Delucci 1988; Feminella 1996; Dieterich and Anderson 2000). This constraint on community structure, combined with the additional constraint of a production interval limited to periods of surface water and favorable temperatures, might decouple any relationship between detritivore production and detritus biomass, as shown elsewhere (Wallace et al. 1999; Hall et al. 2001). This scenario has some support from a prior study. Richardson (1990) showed that intermittent streams can have reduced detritus processing rates compared with perennial streams because of a reduction in shredder richness and biomass, which suggests that detritus biomass and shredder production might have been decoupled in this system. In contrast to Richardson (1990), however, Bolton and Lake (1992) showed that storage of benthic organic matter increased during decreased flow periods and was associated with an increase in detritivore biomass.

To conceptualize how changes in community structure because of the cessation of surface flow might affect macroinvertebrate production, we recalculated community production for four perennial headwater streams (C55 and C53 Coweeta Hydrologic Laboratory, North Carolina—Wallace et al. 1999; Bear Brook and Hubbard Brook, New Hampshire—Hall et al. 2001) by excluding all taxa with life his-

Table 2. Percentage of total production (% P) for taxa sampled from the treatment (WBB+N) and reference (EBB) streams at the Bear Brook Watershed in Maine. FFG, functional feeding group; CG, collector-gatherer; FI, filterer; PR, predator; SH, shredder.

	WBB+N				EBB			
	1998/1999		1999–2000		1998/1999		1999–2000	
FFG	Taxa	%P	Taxa	%P	Taxa	%P	Taxa	%P
CG	Orthocladiinae*	8	Orthocladiinae*	6	Orthocladiinae*	7	Orthocladiinae*	8
	Oligochaeta*	3	Oligochaeta*	6	Tanytarsini*	2	Oligochaeta*	3
			Tanytarsini*	3	Oligochaeta*	3	Tanytarsini*	2
FL	*Homoplectra*	7	*Homoplectra*	7	*Prosimulium*	8	*Prosimulium*	8
	Parapsyche	3	*Prosimulium*	6	*Homoplectra*	2	*Homoplectra*	5
	Prosimulium	3					*Wormaldia*	2
PR	Tanypodinae*	6	*Rhyacophila*	12	*Rhyacophila*	11	*Rhyacophila*	17
	Pedicia	5	*Pedicia*	4	Tanypodinae*	6	*Pedicia*	3
	Rhyacophila	4	*Dicranota*	2	*Polycentropus*	6	Chilopoda*	2
	Clinocera	2			*Dicranota*	2	*Polycentropus*	2
					Pedicia	2		
SH	*Leuctra*	16	*Leuctra*	15	*P. perfect*	13	*Leuctra*	11
	Pycnopsyche	8	*O. truncata*	11	*Pycnopsyche*	8	*Pycnopsyche*	8
	O. truncata	6	*Pseudostenophylax*	10	*Leuctra*	6	*O. truncata*	6
	Pseudostenophylax	6	*Pycnopsyche*	6	*O. prolongata*	6	*O. prolongata*	5
	O. prolongata	4	*O. prolongata*	2	*Hydatophylax*	4	*P. perfecta*	4
	P. perfecta	3			*Soyedina*	2	*Pseudostenophylax*	2
	Amphinemura	3			*Lepidostoma*	2	*Allocapnia*	2
	Lepidostoma	2						

* Taxonomy higher than the Genus level.

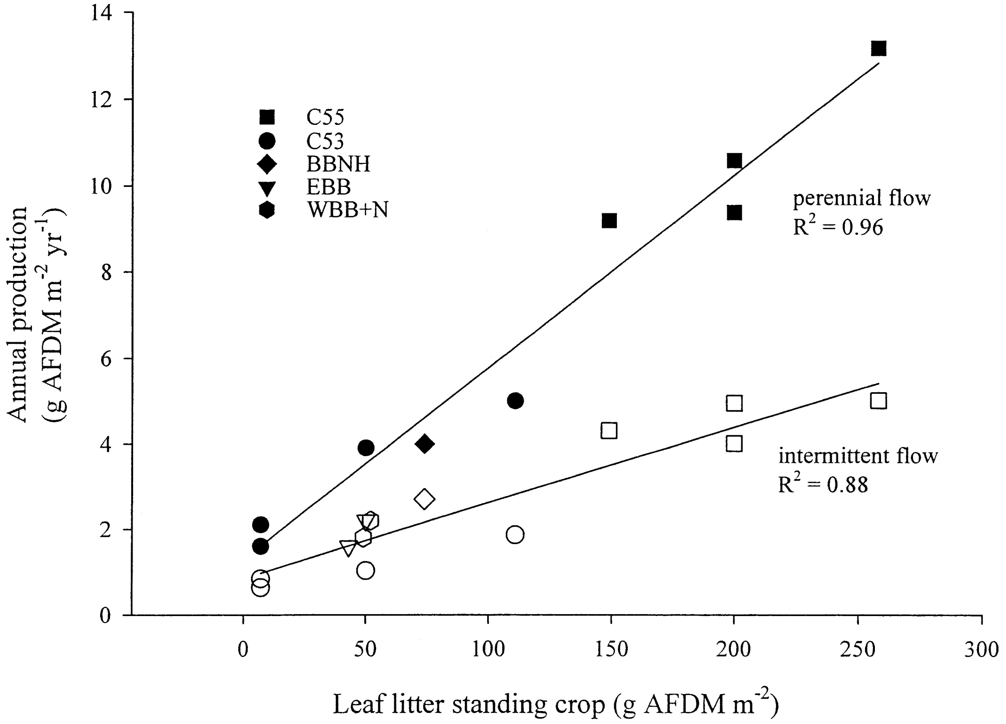

Fig. 5. The relationship between detrital resources and invertebrate secondary production. Filled symbols are for perennial invertebrate communities, and open symbols are for intermittent invertebrate communities. C55 and C53 are at the Coweeta Hydrological Laboratory (Wallace et al. 1999). BBNH is at the Hubbard Brook Experimental Forest (Hall et al. 2001). WBB+N, treatment stream; EBB, reference stream; AFDM, ash-free dry mass.

tories that would exclude them from intermittent streams (e.g., taxa with life cycles longer than the duration of flow or that are not known to possess strategies to avoid desiccation or both). We also assumed that production for remaining taxa would not be altered by removal of perennial stream obligates from the different communities (e.g., no competition). With these values, we assessed the relationship between the recalculated production values and detritus biomass and found that the trend line passed directly through the production estimates for WBB+N and EBB (Fig. 5; $R^2 = 0.89$). This result provides some support for the prediction that channel drying could be a primary factor responsible for the low levels of invertebrate production measured at BBWM.

The difference in community structure between EBB and WBB+N is substantial—even surprising given their habitat structure, the functional similarities of their macroinvertebrate productivity, and their close proximity ($<$100 m). This finding might be attributed to the ammonium sulfate treatment; however, it more likely results from differences in the duration of flowing water between streams, with WBB+N having a longer period of flow than EBB (Fig. 1). Contrasting flow conditions between channels could thus be responsible for the pattern shown by axis 1 of the CCA analysis of the distribution of shredder production between streams and years. Although many of the stoneflies occurring in the streams of BBWM have long been known to persist in intermittent streams elsewhere, our results suggest that subtle differences in the duration of channel drying and the occurrence of refugia might be important in determining relative contributions of these different intermittent-stream specialists to community production (e.g., *Paranemoura* in the driest conditions to *Leuctra* in more moderate conditions). On the strength of the large body of literature showing the importance of flow duration on stream community structure (Williams 1996), we suggest that differences in community structure between EBB and WBB+N are probably a response to different intensities of channel drying rather than the effects of the ammonium sulfate treatment on stream chemistry.

Before beginning our study, we did not expect the subtle difference in the drying regime between streams to have a large effect on their ecology because both streams had true intermittent flow. However, we found that differences in drying regimes likely decoupled the relationship between detritivore production and detritus biomass and substantially altered the distribution of production among taxa. Nevertheless, community function, as indicated by FFG composition, remained constant between streams and years.

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