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WHOLE-SYSTEM NUTRIENT ENRICHMENT INCREASES SECONDARY PRODUCTION IN A DETRITUS-BASED ECOSYSTEM

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Abstract. Although the effects of nutrient enrichment on consumer–resource dynamics are relatively well studied in ecosystems based on living plants, little is known about the manner in which enrichment influences the dynamics and productivity of consumers and resources in detritus-based ecosystems. Because nutrients can stimulate loss of carbon at the base of detrital food webs, effects on higher consumers may be fundamentally different than what is expected for living-plant-based food webs in which nutrients typically increase basal carbon. We experimentally enriched a detritus-based headwater stream for two years to examine the effects of nutrient-induced changes at the base of the food web on higher metazoan (predominantly invertebrate) consumers. Our paired-catchment design was aimed at quantifying organic matter and invertebrate dynamics in the enriched stream and an adjacent reference stream for two years prior to enrichment and two years during enrichment. Enrichment had a strong negative effect on standing crop of leaf litter, but no apparent effect on that of fine benthic organic matter. Despite large nutrient-induced reductions in the quantity of leaf litter, invertebrate secondary production during the enrichment was the highest ever reported for headwater streams at this Long Term Ecological Research site and was 1.2–3.3 times higher than predicted based on 15 years of data from these streams. Abundance, biomass, and secondary production of invertebrate consumers increased significantly in response to enrichment, and the response was greater among taxa with larval life spans ≤ 1 yr than among those with larval life spans >1 yr. Production of invertebrate predators closely tracked the increased production of their prey. The response of invertebrates was largely habitat-specific with little effect of enrichment on food webs inhabiting bedrock outcrops. Our results demonstrate that positive nutrient-induced changes to food quality likely override negative changes to food quantity for consumers during the initial years of enrichment of detritus-based stream ecosystems. Longer-term enrichment may impact consumers through eventual reductions in the quantity of detritus.

Key words: allochthonous resources; donor control; food web; headwater; heterotrophic; insect; invertebrate; leaf litter; nitrogen; phosphorus; secondary production.

Introduction

Understanding the relative strengths of top-down and bottom-up forces in controlling population and community structure has been a central question among ecologists for decades (Hairston et al. 1960, Hunter and Price 1992, Oksanen and Oksanen 2000, Shurin et al. 2002). Early conceptual (Fretwell 1977) and mathematical (Oksanen et al. 1981) treatments of this subject predicted that (1) system productivity determines the number of possible trophic levels and that (2) consumers or resources are alternately controlled by top-down (i.e., consumers) or bottom-up (i.e., resources) forces depending on the number of trophic levels present. More recently, this predominantly top-down perspective has been modified to include many factors ubiquitous to most food webs (e.g., high species richness, complex reticulate structure, weak interaction strengths, life history omnivory), which tend to dampen the effects of consumers on their resources (e.g., Osenberg and Mittelbach 1996, Polis and Strong 1996, McCann et al. 1998). Such modifications predict that consumers at all trophic positions (i.e., primary and secondary consumers) should respond positively to increased system productivity. These predictions have been corroborated by theoretical and empirical work in aquatic and terrestrial ecosystems, which have shown that both primary and secondary consumers respond positively to increased resource availability (e.g., Hurd and Wolf 1974, Stockner and Macisaac 1996, Moore and de Ruiter 2000). In addition, these results appear to be independent of whether food webs are based on living plants (e.g., Gruner 2004, Slavik et al. 2004) or detritus (e.g., Chen and Wise 1999, Wallace et al. 1999).

Although nutrient gradients (e.g., inorganic nitrogen [N] and phosphorus [P] availability) are rarely consid-

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ered explicitly in trophic dynamic models, it is generally assumed that increased nutrient availability leads to increased primary productivity at the base of the food web. Thus, in the context of trophic dynamic models, nutrients are essentially treated as a positive bottom-up factor enhancing basal productivity, as well as the productivity of intermediate and top consumers. However, many (if not most) food webs are based on nonliving detritus (e.g., those in forested streams, soils, salt marshes; Moore et al. 2004), and in these systems, increased nutrients may affect basal resources and consumers in fundamentally different ways. Mathematical models (e.g., Parnas 1975, 1976) and empirical studies (e.g., Scheu and Schaefer 1998, Gulis and Suberkropp 2003, Stelzer et al. 2003) of detritus-based ecosystems show that nutrient enrichment may enhance the growth of nutrient-limited heterotrophic microbes because of reduced elemental imbalances. Such increased microbial growth has two opposing implications for higher consumers: (1) increased nutrient content of the detritus–microbe complex and (2) increased rates of detritus mineralization. On relatively short time scales, positive changes to detritus quality (i.e., increased nutrient content and microbial biomass; Rosemond et al. 2002, Cross et al. 2003, Gulis and Suberkropp 2003) may lead to higher productivity of consumers because of increased assimilation efficiencies (e.g., Iversen 1974). However, on longer time scales, increased nutrients could cause a decline in detrital biomass at the base of the food web due to stimulated metabolism of heterotrophic consumers and consequent breakdown and respiration of detrital carbon (e.g., Pace and Funke 1991, Gulis and Suberkropp 2003, Mack et al. 2004). Consumers sensitive to such changes in detritus availability may be negatively influenced by nutrient enrichment over long temporal scales.

Detritus represents the dominant carbon source for forested headwater streams in the eastern United States and many other regions of the world (e.g., Wetzel 1995, 2001, Wallace et al. 1997). In these systems, productivity and metabolism are driven by inputs of allochthonous detritus from the terrestrial catchment (e.g., Fisher and Likens 1973, Wallace et al. 1997, 1999), and in-stream autotrophic production is generally very low (e.g., Fisher and Likens 1973, Webster et al. 1997). Previous studies in these ecosystems have shown classic donor-controlled dynamics with biomass and productivity of stream consumers at all trophic positions strongly and positively linked to the availability of detritus (Richardson 1991, Wallace et al. 1999, Eggert and Wallace 2003, Johnson and Wallace 2005). In this study, we examined the effects of nitrogen and phosphorus enrichment of a detritus-based stream ecosystem on detrital resources and consumer secondary production. We predicted that our two-year experimental enrichment would lead to an increased level of secondary production for a given quantity of detritus because of positive changes to detritus quality (see Cross et al. 2003). Although models and empirical studies (predominantly from soil systems) predict a diversity of outcomes with regard to long-term effects of nutrient enrichment on detrital storage (e.g., Ågren et al. 2001, Franklin et al. 2003, Mack et al. 2004, Kuijper et al. 2005), we predicted that during the limited time course of our study, the positive effects of increased detrital quality would outweigh any long-term negative effects of enrichment on detritus quantity.

Study Sites

This study was conducted in two adjacent headwater streams at the Coweeta Hydrologic Laboratory, a Long-Term Ecological Research site in Macon County, North Carolina, USA. Coweeta is a large (2185 ha), heavily forested basin located in the Blue Ridge physiographic province of the southern Appalachian Mountains (see Swank and Crossley 1988). Forest vegetation is dominated by mixed hardwoods (primarily oak, maple, and poplar) and a dense understory of *Rhododendron maximum* that shades the streams throughout the year. Headwater streams at Coweeta are extremely heterotrophic, and allochthonous inputs of detritus provide >90% of the energy base for microbial and invertebrate production (Wallace et al. 1997, Hall et al. 2000).

The two streams used for this study are first-order and drain catchments (C) 53 and 54 (hereafter C53 and C54) within the Coweeta Hydrologic Laboratory. These streams have similar physical and chemical characteristics (i.e., watershed area, slope, elevation, discharge, temperature, and pH; see Lugthart and Wallace [1992] for more detail), but differ since July 2000 in their concentrations of dissolved N and P as a result of our experimental nutrient enrichment of C54 (see *Methods: Experimental enrichment*, below). Natural concentrations of inorganic N and P in these streams are very low ([NO_3 + NO_2]-N mean, 16.9 μg/L, range, 4–40 μg/L; NH_4-N mean, 10.4 μg/L, range, below detection to 30 μg/L; soluble reactive phosphorus [SRP] mean, 3.7 μg/L, range, below detection to 22 μg/L).

Methods

Experimental enrichment

Our study consisted of an ~2-yr pretreatment period (September 1998–June 2000) and an ~2-yr experimental enrichment (July 2000–August 2002) of C54. Starting in July 2000, nitrogen (NH_4NO_3) and phosphorus (K_2HPO_4 and KH_2PO_4) were dripped continuously into the treatment stream to increase concentrations of dissolved inorganic N and P to ~6–15 times background levels, while keeping stream N:P ratios relatively constant (see Gulis and Suberkropp [2003] for further description of the nutrient drip apparatus). Concentrations of (NO_3 + NO_2)-N, NH_4-N, and SRP were measured once every two weeks at the weir of the reference stream and at several locations in the treatment stream (APHA 1998). Water temperature (in degrees Celsius) was monitored every 30 min in both

streams with Optic StowAway temperature probes (Onset Computer, Pocasset, Massachusetts, USA).

This ecosystem-level experiment was not replicated, employing a paired-catchment design (e.g., Likens et al. 1969) with one treatment stream and one reference stream. This approach has been advocated for its realism and scale (e.g., Carpenter et al. 1995, Schindler 1998, Oksanen 2001), as well as criticized for its lack of treatment replication (Hurlbert 1984, 2004). The limitations of our experimental design are recognized, but we felt that the scale of manipulation (in lieu of strict replication) was essential for observing realistic system-wide effects of enrichment.

Benthic sampling

Quantitative benthic sampling was conducted monthly in each stream for 4 yr between September 1998 and August 2002. Each month samples were taken from two distinct habitats: mixed substrate (i.e., cobble, pebble, gravel, sand) and bedrock outcrops. Mixed substrate samples were collected at four random locations in each stream with a stovepipe core sampler (400 cm^2). The core sampler was firmly placed in the streambed, and all material was removed to a depth of 15 cm by hand or cup and placed in a large plastic jar. Bedrock samples were taken at three randomly determined locations in each stream by brushing and scraping moss and associated particles from a known area (15 × 15 cm) into a plastic bag and Hess net (250-μm mesh size) pressed flush against the bedrock.

Benthic samples were brought to the laboratory, refrigerated, and processed within 24 h according to Lugthart and Wallace (1992). Briefly, samples were rinsed onto nested sieves (pore sizes 1 mm and 250 μm), and material retained on each sieve was elutriated to separate organic from inorganic material. Organic material was then preserved separately for each size fraction (>1 mm and 250 μm–1 mm) in formalin (6–8%). Animals were removed from the >1 mm fraction by hand picking under a dissecting microscope at 15× magnification. Organic material in the smaller size fraction (250 μm–1 mm) was subsampled using a sample splitter (Waters 1969), and animals were removed as above.

The amount of coarse (>1 mm, CBOM) and fine (<250 μm, FBOM) benthic organic matter was quantified in each sample (also see Lugthart and Wallace 1992). After removal of invertebrates, CBOM was dried (50°C), weighed, ashed (at 500°C), and reweighed to quantify ash-free dry mass (AFDM). The FBOM was quantified during sample processing by placing material that was retained or had passed through the 250-μm sieve into a graduated bucket with a known volume of water. This material was stirred, subsampled, filtered onto pre-ashed, preweighed glass fiber filters (Gelman A/E; Pall Corporation, Ann Arbor, Michigan, USA), and AFDM was quantified as above.

Invertebrates and larval salamanders were counted and identified. All insects, except Chironomidae, were identified to the genus or species level. Larval chironomids were identified as either Tanypodinae (predators) or non-Tanypodinae (non-predators). Most noninsect taxa were identified to the order level or higher. Taxa were assigned to functional feeding groups according to Merritt and Cummins (1996) and our knowledge of the local fauna. In this study, all functional feeding group designations (i.e., shredders, collector-gatherers [=gatherers], scrapers, collector-filterers [=filterers], and predators) follow Wallace et al. (1999). The body length of each individual was measured to the nearest millimeter with a dissecting microscope at 12× magnification and a graduated stage. Total snout–vent length and carapace length were measured on salamanders and crayfish, respectively. Biomass (AFDM) was obtained using previously established length–mass regressions for invertebrates at Coweeta, or, for a few taxa, nearby North Carolina streams (Benke et al. 1999; J. B. Wallace, *unpublished data*).

Secondary production

Annual secondary production of most taxa was estimated using the size-frequency method (Hamilton 1969) corrected for the cohort production interval (CPI; Benke 1979). Cohort production intervals were identical to those used by Wallace et al. (1999). Annual production of non-Tanypodinae chironomids and *Tallaperla* spp. (Plecoptera: Peltoperlidae) was estimated using the community-level instantaneous growth method (Huryn and Wallace 1986, Huryn 1990, Cross et al. 2005). For a few taxa, production was calculated as the product of mean standing stock biomass and estimated annual production/biomass (P/B) values (as in Wallace et al. 1999).

Annual production of each taxon was estimated separately in each habitat. Habitat-weighted values were calculated according to the relative proportion of each habitat in each stream (e.g., Huryn and Wallace 1987, Lugthart and Wallace 1992).

Statistical analyses

We used randomized intervention analysis (RIA; Carpenter et al. 1989, also see Murtaugh 2003, Stewart-Oaten 2003) to test for effects of nutrient enrichment on benthic organic matter and abundance and biomass of invertebrate taxa and functional feeding groups. In this study, RIA was used to test the null hypothesis of no change in the variable of interest in the treatment stream relative to the reference stream following initiation of nutrient enrichment. Time series data were also visually examined to determine the direction (positive or negative) of response. Data were $\log(x + 1)$-transformed to meet assumptions of normality and homogeneity of variance.

Linear regression analysis was used to analyze relationships between organic matter standing crop and invertebrate production and total invertebrate production and predator production. For the latter, the y-intercept was set equal to zero (i.e., no prey

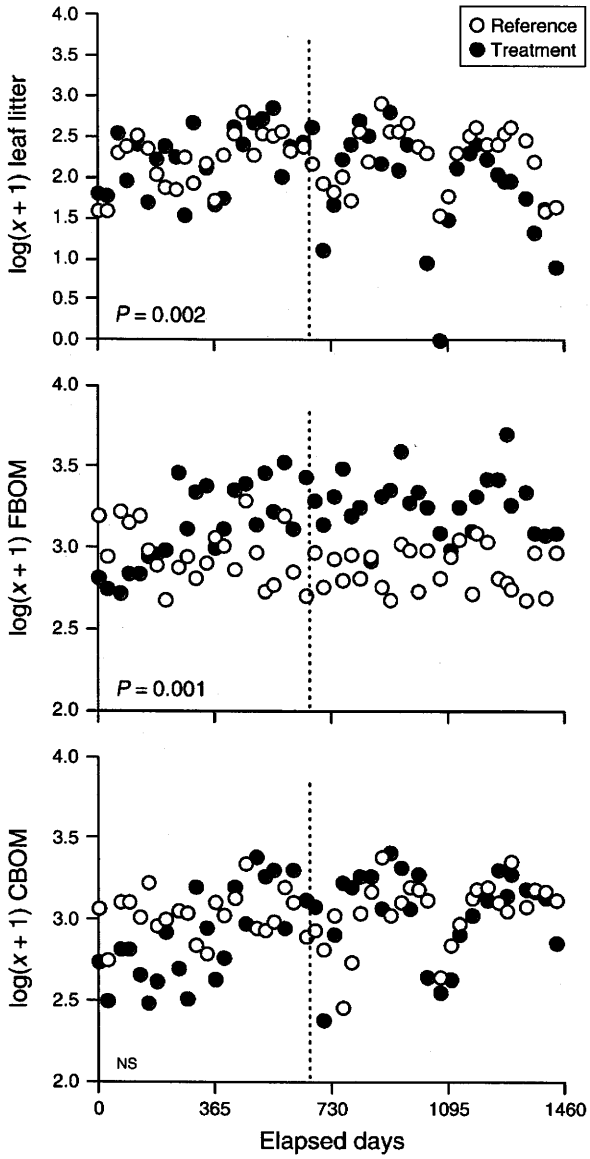

FIG. 1. Time series of monthly log(x + 1)-transformed leaf litter, fine benthic organic matter (FBOM), and coarse benthic organic matter (CBOM) standing crop in the reference stream (open circles) and treatment stream (solid circles) at the Coweeta Hydrologic Laboratory, North Carolina, USA. Measurements were ash-free dry mass (g AFDM/m^2). The vertical dashed line refers to the initiation of nutrient enrichment in the treatment stream. Elapsed days 0 through 1460 are between September 1998 and August 2002. P values are from randomized intervention analysis (RIA) on differences between streams before and after the manipulation; NS, nonsignificant (P > 0.05).

production = no predator production). Although predators are included in both axes of the relationship between total and predator production (predators represent roughly 30% of total production), we felt this analysis was justified based on the prevalence of intraguild predation among predators in these streams (Wallace et al. 1999, Hall et al. 2000).

For each taxon, we calculated proportional differences in production between pre- and post-enrichment periods in the enriched stream (proportional response). To test for significant differences between the proportional response of short-lived (<365 d) and long-lived (>365 d) taxa we used a nonparametric Wilcoxon test.

RESULTS

Concentrations of [$NO_3 + NO_2$]-N (mean, 308.9 μg/L; range, 11–1711 μg/L), NH_4 (mean, 105.5 μg/L; range, 6–566 μg/L), and SRP (mean, 51.2 μg/L, range, below detection to 268 μg/L) were successfully elevated to 10–15 times background levels in the treatment stream. These concentrations were not outside the range of streams in the region that differ in watershed land use (Scott et al. 2002). During enrichment, the molar N:P ratio of streamwater in the treated stream was 19.7:1. This ratio was considerably higher than that of the stock nutrient solution added (11.4:1), suggesting preferential uptake of P in the enriched stream. Throughout the study, water temperature ranged from 1° to 19°C and did not differ between the study streams (K. Suberkropp, University of Alabama, *unpublished data*).

Nutrient enrichment had a significant negative effect on standing crop of leaf litter detritus (RIA, $P = 0.002$; Fig. 1) in the mixed substrate habitat. Although both streams attained similar maxima during annual leaf fall (~600 g AFDM/m^2), benthic leaf litter disappeared more rapidly in the treatment stream during the two years of enrichment (Fig. 1). Between-stream differences in leaf litter standing crop were most pronounced during the final year of the study in which the treatment stream contained on average only 43% of leaf litter in the reference stream (101 g AFDM/m^2 vs. 234 g AFDM/m^2). Although RIA showed a significant positive effect of enrichment on total FBOM standing crop (RIA, $P = 0.001$; Fig. 1), visual examination of the data revealed that changes in the treatment stream occurred over a year prior to the enrichment (Fig. 1) and were not attributable to nutrient enrichment. An additional RIA conducted on FBOM data for the final three years of study (i.e., one year prior to enrichment and two years during enrichment) was nonsignificant ($P = 0.486$). Total CBOM standing crop, which included a significant amount of wood, was not affected by nutrient enrichment (RIA, $P > 0.05$; Fig. 1). In bedrock outcrop habitat, standing crop of benthic organic matter (i.e., FBOM and CBOM) was not influenced by nutrient enrichment (RIA, $P > 0.05$).

Nutrient enrichment had a significant positive effect on total invertebrate abundance and biomass in the mixed substrate habitat (RIA, $P < 0.0001$; Fig. 2). During enrichment, abundance and biomass in the treatment stream were 134% and 117% higher than mean pretreatment values (i.e., Pre 1 and Pre 2), respectively. In contrast, invertebrate abundance and biomass in the reference stream decreased or showed no significant change during the two years of enrichment in

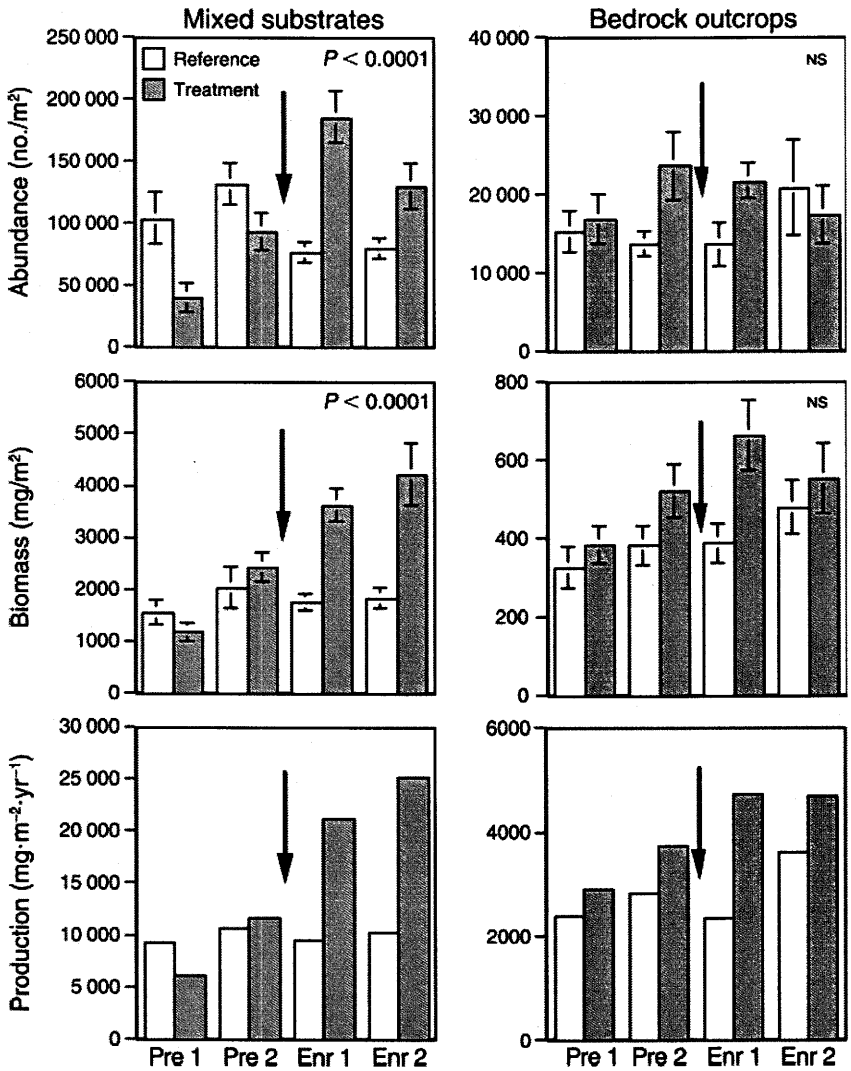

FIG. 2. Abundance (means ± SE), biomass (means ± SE), and annual secondary production during the four years of study in the reference stream (open bars) and treatment stream (solid bars) in mixed substrate and bedrock outcrop habitats. The arrow refers to the initiation of nutrient enrichment in the treatment stream. P values are from randomized intervention analysis (RIA) on differences between streams before and after the manipulation ($n = 48$). Randomized intervention analysis was not possible on annual production data because of limited data points before ($n = 3$) and during ($n = 2$) enrichment. Pre 1, September 1998–August 1999; Pre 2, September 1999–August 2000; Enr 1, September 2000–August 2001; Enr 2, September 2001–August 2002.

comparison to pretreatment values (abundance, −33%; biomass, no change; Fig. 2). Total invertebrate secondary production in the mixed substrate habitat was similar in both streams during the two years of pretreatment (Fig. 2). During enrichment, production in the treatment stream was ~161% higher than pretreatment values and ~135% higher than production in the reference stream (Fig. 2). Total secondary production in the reference stream was similar pre- and post-enrichment.

In sharp contrast to the mixed substrate habitat, nutrient enrichment had no effect on total invertebrate abundance and biomass on bedrock outcrops (RIA, $P > 0.05$; Fig. 2). Secondary production on bedrock outcrops was roughly an order of magnitude lower than production on mixed substrates and was consistently higher in the treatment stream than in the reference stream before and during nutrient enrichment (Fig. 2). The difference in bedrock production between streams was greater during the two years of nutrient enrichment.

On a habitat-weighted basis, both primary consumers and their predators exhibited highly significant increases in abundance and biomass in response to enrichment (RIA, $P < 0.05$; Fig. 3). The response of primary consumers was driven by increases in abundance and biomass of shredders and gatherers (as opposed to filterers and scrapers) in the treatment stream relative to

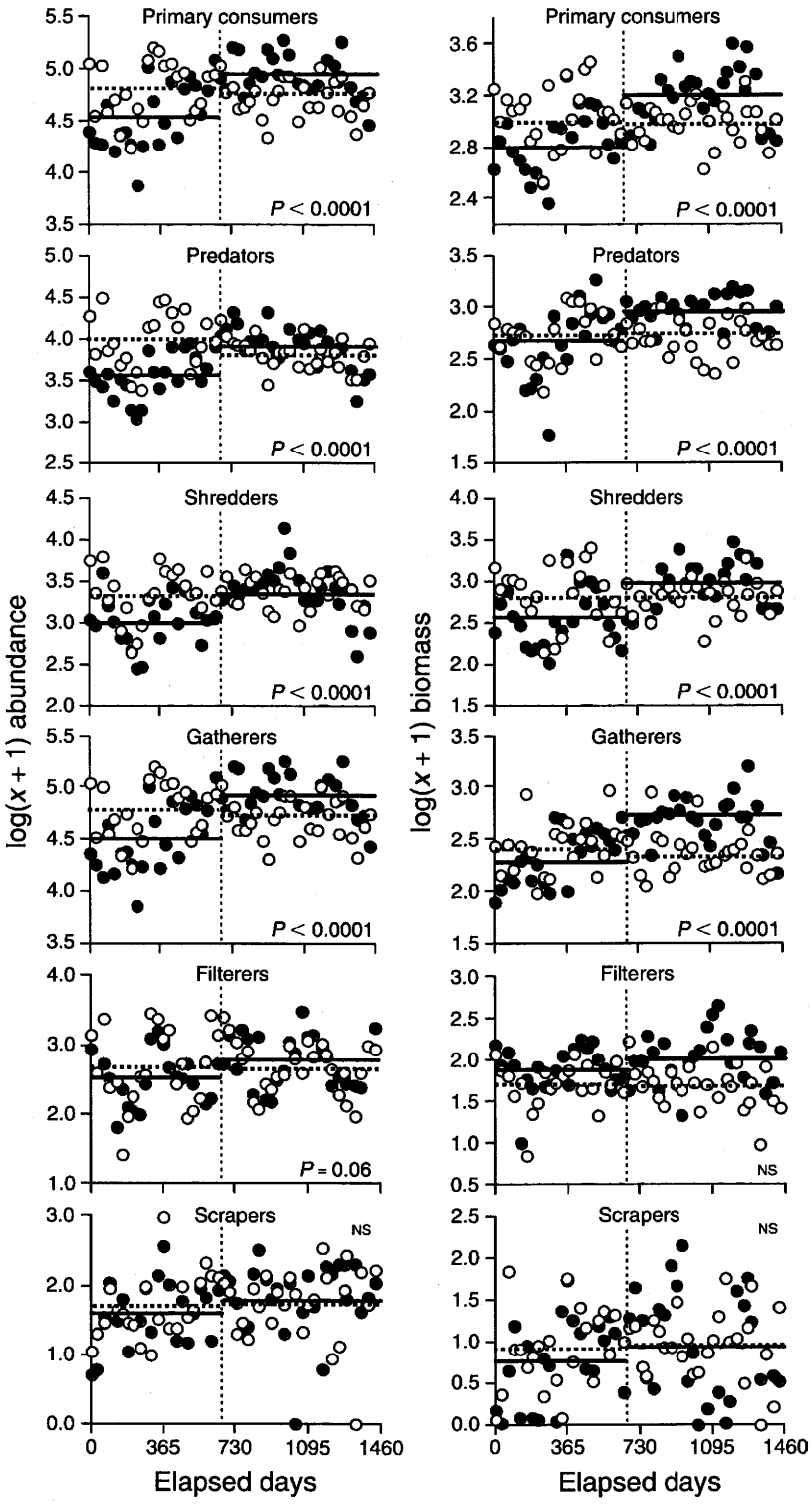

FIG. 3. Time series of habitat-weighted $\log(x+1)$-transformed abundance (no./m^2) and biomass (mg/m^2) of primary consumers and individual functional feeding groups in the reference stream (open circles) and treatment stream (solid circles). The vertical dotted lines refer to the initiation of nutrient enrichment in the treatment stream. The horizontal dashed lines represent mean values in the reference stream before and during enrichment. The horizontal solid lines represent mean values in the treatment stream before and during treatment. P values are from randomized intervention analysis (RIA) on differences between streams before and after the manipulation.

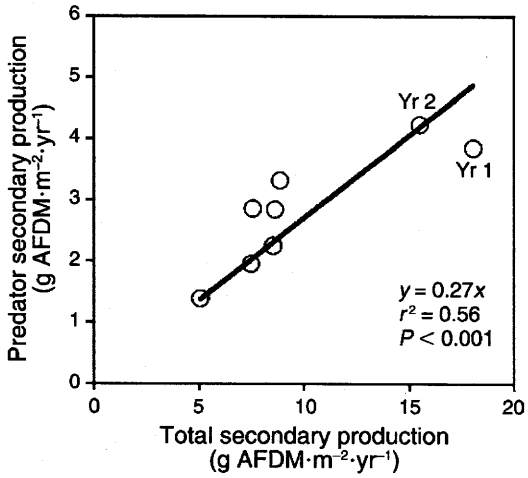

FIG. 4. Relationship between predator production and habitat-weighted total secondary production in the reference and enriched streams throughout the study. Yr 1 is the first year of enrichment in the treatment stream; Yr 2 is the second year of enrichment in the treatment stream; AFDM is ash-free dry mass.

the reference stream (Fig. 3; see Appendix for detailed data on functional feeding groups and specific taxa).

Throughout the study, predator production tracked the availability of potential prey production ($r^2 = 0.56$, $P < 0.001$; Fig. 4). The slope of this relationship (0.27) is close to known bioenergetic efficiencies (production/ingestion $\approx$ 0.35) of invertebrate predators (Slansky and Scriber 1982, Wallace et al. 1999).

On average, the proportional response of taxa with life spans >1 yr was significantly lower (mean = 13% increase) than that of taxa with life spans $\leq$1 yr (mean = 209% increase, $P < 0.001$, Wilcoxon test).

When years of non-enriched conditions from this study (both streams) were combined with long-term data from Coweeta headwater streams (Wallace et al. 1999; includes years of experimental leaf litter removal), leaf litter standing crop explained a large and significant amount of the variation in annual secondary production ($r^2 = 0.88$, $P < 0.001$; Fig. 5A) and shredder production ($r^2 = 0.79$, $P < 0.001$; Fig. 5B). In sharp contrast, total secondary production during the two years of enrichment was 118% (year 1) and 334% (year 2) higher than predicted production based on the long-term relationship (Fig. 5A). Shredder production during the two years of enrichment was even further from predicted values at 136% and 539% of predicted production (Fig. 5B). Production values during nutrient enrichment fell far outside the long-term 99% prediction intervals (Fig. 5).

DISCUSSION

Our study examined the effects of nutrient enrichment on dynamics of consumers and resources in a detritus-based ecosystem. Previous work in this system has shown that the productivity of consumers at all trophic positions (i.e., primary consumers, omnivores, top predators) is strongly and positively related to the quantity of detritus at the base of the food web (Wallace et al. 1997, 1999). Such data, which span decades (J. B. Wallace, *unpublished data*), is rarely available for testing the influence of perturbations (e.g., nutrient enrichment) on trophic dynamics. We have shown that two years of nutrient enrichment of this system, likely through its effects on the quality of detrital resources, led to extremely high levels of secondary production. These results deviated strongly from well-established long-term

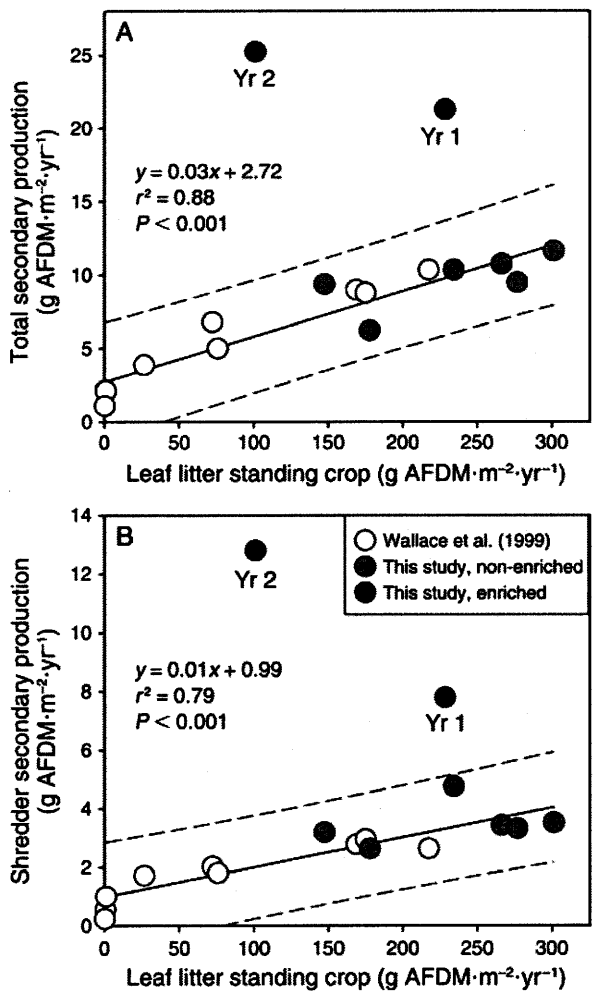

FIG. 5. Long-term relationships between mean leaf litter standing crop and (A) total secondary production and (B) shredder secondary production in the mixed substrate habitat. Data include nine years of production estimates from another similar headwater stream at Coweeta (stream C55); some years are from an experimental leaf litter removal (Wallace et al. 1999). Open circles represent previously published data, gray circles represent non-enriched years of this study in both streams (n = 6), and black circles represent two years of experimental nutrient enrichment ($n = 2$). The black circles are, from right to left, year 1 of enrichment (Yr 1) and year 2 of enrichment (Yr 2). Regressions do not include the two years of enrichment that were statistical outliers. AFDM is ash-free dry mass.

relationships between detritus quantity and consumer secondary production.

Nutrient-induced changes in organic matter quality were likely responsible for increased community secondary production. Our experimental enrichment led to significant increases in microbial biomass and production (Gulis and Suberkropp 2003, Greenwood 2004; K. Suberkropp, *unpublished data*), nutrient content of fine and coarse particulate organic matter (Cross et al. 2003, Gulis and Suberkropp 2003, Greenwood 2004), and leaf decomposition rates (Gulis and Suberkropp 2003, Greenwood 2004). For the macroconsumer community, the positive effects of enrichment on detrital quality (i.e., increased microbial activity and nutrient content) appeared to outweigh the negative effects of enrichment on carbon loss (i.e., increased decomposition and respiration). Despite an ~45% reduction in leaf litter at the base of the food web due to both increased microbial and invertebrate consumption, invertebrate production in the mixed substrate habitat was, on average, 226% higher in the treatment stream than in the reference stream. Moreover, production data during the two years of enrichment were extreme outliers when compared to long-term data from streams at Coweeta (Fig. 5). For invertebrates that consume leaf litter (i.e., many shredders), these results suggest that either (1) assimilation efficiencies and/or survivorship were much higher on nutrient-rich leaf litter or (2) shredders switched diets to include other high-quality food items such as wood biofilm (e.g., Tank and Webster 1998, Eggert 2003). The former explanation is the most plausible based on gut content analyses (Cross 2004) in which no dietary shifts were observed among shredders.

Nutrient enrichment also had a positive effect on production of invertebrate predators, whose trophic position is generally multiple links removed from the ultimate source of enrichment; however, the magnitude of this effect was not as great as that observed for most primary consumers. This pattern essentially reflects a loss of energy with each trophic transfer, consistent with basic thermodynamic principles. Predator production also appeared to track prey production closely over the course of the study in both streams. Others have observed increased abundance and biomass of terrestrial invertebrate predators in response to an enhanced resource base (Polis and Hurd 1995, Scheu and Schaefer 1998, Chen and Wise 1999). In addition, experimental reduction of leaf litter drastically reduced production of both invertebrate and vertebrate predators in a nearby detritus-based stream at Coweeta (Wallace et al. 1999, Johnson and Wallace 2005). Our study also showed that increased nutrients had effects that transcended two consumer trophic levels, presumably due to the positive effects of nutrient enrichment on microbial assemblages, despite reduced carbon availability.

Consumers with relatively long life spans (>1 yr) responded less to enrichment than those with shorter life spans. Such a result may be simply driven by differences in the time necessary for long-lived consumers to exhibit population-level responses to enrichment. However, for some long-lived taxa, particularly those that specialize on leaf litter, nutrient enrichment may lead to temporary resource shortages between annual pulses of allochthonous leaf litter, limiting their potential to respond. This may occur because the single pulsed input of litter is more rapidly metabolized or exported from the system under enriched conditions. Thus, the timing and frequency of pulsed detrital inputs relative to consumer life histories may be important in detrital food web dynamics, as well as in determining the responses of consumers to nutrient enrichment (Cross et al. 2005). In other detritus-based ecosystems where allochthonous inputs are not pulsed, but are relatively continuous (e.g., some tropical streams, estuarine benthic communities), consumers may not have such contrasting responses to nutrient enrichment.

During the two years of nutrient enrichment in this study we saw greatly increased invertebrate production. However, questions remain concerning the long-term sustainability of this boost in secondary production. How far must the system be perturbed for the positive effects of nutrients on detritus quality to no longer outweigh the negative effects on detritus quantity? Nutrient enrichment of detritus-based systems can result in increases, decreases, or no change in long-term or transient storage of carbon as evidenced by models and empirical studies in detritus-based soil ecosystems (e.g., Parnas 1975, Ågren et al. 2001, Franklin et al. 2003, Mack et al. 2004, Kuijper et al. 2005). However, most of these studies actually predict an increase in carbon storage with enrichment because of reduced microbial activity. In contrast, available evidence for detritus-based stream ecosystems suggests that long-term enrichment may lead to a reduction in total secondary production via loss of carbon, with potential shifts in community structure. In our study system, benthic samples, leaf litter surveys (K. Suberkropp, *unpublished data*), and litter bag decomposition studies (Gulis and Suberkropp 2003, Greenwood 2004) all demonstrated elevated breakdown and metabolism of carbon during the enrichment. In addition, whole systems carbon budgets (A. D. Rosemond, *unpublished data*) indicated a net loss of carbon from the treatment stream during the enrichment period, and faster breakdown rates of organic matter occurred with each successive year of enrichment (Greenwood 2004). Interestingly, despite higher overall secondary production during the second year of enrichment in comparison to the first year of enrichment, ~50% of invertebrate species had lower production during the second year of enrichment (including species at all trophic positions; see Appendix). This result coincides with lower organic matter standing crop in the treatment stream during the second year of enrichment in comparison to the first year and suggests that reductions in detritus quantity likely modulate the positive effects of nutrient-induced changes to detritus quality. With similar inputs of allochthonous leaf litter

each year and increasingly rapid rates of detrital loss (Greenwood 2004), we speculate that continued nutrient enrichment should lead to an alternate equilibrium quantity of total benthic organic matter that is lower than reference stream conditions. We also expect that mean annual secondary production will be lower than that seen during the first few years of enrichment (e.g., in this study), but still higher than reference stream conditions. In addition, we expect changes in invertebrate community structure that favor relatively short-lived consumers (also see Cross et al. 2005). Detailed analysis of carbon budgets (A. D. Rosemond, *unpublished data*) combined with realistic simulation models (e.g., Karlsson et al. 2005) will be critical for understanding the ultimate fates of nutrient-induced carbon losses in these detritus-based ecosystems.

Our study provides evidence that bottom-up effects of nutrient enrichment in a detritus-based ecosystem can stimulate whole-community production through detrital–microbial pathways. Although nutrient enrichment of detritus-based ecosystems is common, and its effects may be less visually obvious than in living-plant-based ecosystems, enrichment has the potential to cause large changes in carbon balance and consumer productivity.

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Literature Cited

Ågren, G. A., E. Bosatta, and A. H. Magill. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia **128**:94–98.

APHA [American Public Health Association]. 1998. Standard methods for the examination of water and wastewater. 20th edition. American Public Health Association, Washington, D.C., USA.

Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography **24**:168–171.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society **18**:308–343.

Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science **269**: 324–327.

Carpenter, S. R., T. M. Frost, D. Heisey, and T. K. Kratz. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecology **70**:1142–1152.

Chen, B., and D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus- based terrestrial food web. Ecology **80**:761–772.

Cross, W. F. 2004. Nutrient enrichment of a detritus-based stream ecosystem: effects on invertebrate community structure and function. Dissertation. University of Georgia, Athens, Georgia, USA.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer–resource stoichiometry in detritus-based streams. Ecology Letters **6**:721–732.

Cross, W. F., B. R. Johnson, J. B. Wallace, and A. D. Rosemond. 2005. Contrasting response of stream detritivores to long-term nutrient enrichment. Limnology and Oceanography **50**:1730–1739.

Eggert, S. L. 2003. Resource use by detritivorous macroinvertebrates in southern Appalachian headwater streams. Dissertation. University of Georgia, Athens, Georgia, USA.

Eggert, S. L., and J. B. Wallace. 2003. Reduced detrital resources limit *Pycnopsyche gentilis* (Trichoptera: Limnephilidae) production and growth. Journal of the North American Benthological Society **22**:388–400.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: integrative approach to stream ecosystem metabolism. Ecological Monographs **43**:421–439.

Franklin, O., P. Högberg, A. Ekblad, and G. I. Ågren. 2003. Pine forest floor carbon accumulation in response to N and PK additions: bomb ^{14}C modelling and respiration studies. Ecosystems **6**:644–658.

Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine **20**:169–185.

Greenwood, J. 2004. The response of heterotrophic and autotrophic resources to a long-term nutrient enrichment in an Appalachian headwater stream ecosystem. Dissertation. University of Georgia, Athens, Georgia, USA.

Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology **85**:3010–3022.

Gulis, V., and K. Suberkropp. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshwater Biology **48**:123–134.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **44**:421–425.

Hall, R. O., Jr., J. B. Wallace, and S. L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. Ecology **81**:3445–3463.

Hamilton, A. L. 1969. On estimating annual production. Limnology and Oceanography **14**:771–782.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**: 724–732.

Hurd, L. E., and L. L. Wolf. 1974. Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. Ecological Monographs **44**:465–482.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–211.

Hurlbert, S. H. 2004. On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. Oikos **104**:591–597.

Huryn, A. D. 1990. Growth and voltinism of lotic midge larvae: patterns across an Appalachian mountain basin. Limnology and Oceanography **35**:339–351.

Huryn, A. D., and J. B. Wallace. 1986. A method for obtaining in situ growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. Limnology and Oceanography **31**:216–222.

Huryn, A. D., and J. B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology **68**:1932–1942.

Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. Oikos **25**:278–282.

Johnson, B. R., and J. B. Wallace. 2005. Bottom-up limitation of a stream salamander in a detritus-based food web.

Canadian Journal of Fisheries and Aquatic Sciences **62**:301–311.

Karlsson, O. M., J. S. Richardson, and P. M. Kiffney. 2005. Modelling organic matter dynamics in headwater streams of south-western British Columbia, Canada. Ecological Modelling **183**:463–476.

Kuijper, L. J., M. P. Berg, E. Morriën, B. W. Kooi, and H. A. Verhoef. 2005. Global change effects on a mechanistic decomposer food web model. Global Change Biology **11**: 249–265.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1969. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecological Monographs **40**:23–47.

Lugthart, G. J., and J. B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. Journal of the North American Benthological Society **11**:138–164.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin, III. 2004. Ecosystem carbon storage in artic tundra reduced by long-term nutrient fertilization. Nature **431**:440–443.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature **395**: 794–798.

Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America. Third edition. Kendall/Hunt, Dubuque, Iowa, USA.

Moore, J. C., and P. C. de Ruiter. 2000. Invertebrates in detrital food webs along gradients of productivity. Pages 161–184 *in* D. C. Coleman and P. F. Hendrix, editors. Invertebrates as webmasters in ecosystems. CAB International, New York, New York, USA.

Moore, J. C., et al. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters **7**:584–600.

Murtaugh, P. A. 2003. On rejection rates of paired intervention analysis: reply. Ecology **84**:2799–2802.

Oksanen, L. 2001. Logic of experiments in ecology: Is pseudoreplication a pseudoissue? Oikos **94**:27–38.

Oksanen, L., S. D. Fretwell, J. Arruda, and A. P. Niemel. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist **155**:703–723.

Osenberg, C. W., and G. G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pages 134–148 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

Pace, M. L., and E. Funke. 1991. Regulation of planktonic microbial communities by nutrients and herbivores. Ecology **73**:904–914.

Parnas, H. 1975. Model for decomposition of organic material by microorganisms. Soil Biology and Biochemistry **7**:161–169.

Parnas, H. 1976. A theoretical explanation for the priming effect based on microbial growth with two limiting substrates. Soil Biology and Biochemistry **8**:139–144.

Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences (USA) **92**:4382–4386.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology **72**:873–887.

Rosemond, A. D., C. M. Pringle, A. Ramirez, M. J. Paul, and J. L. Meyer. 2002. Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. Limnology and Oceanography **47**:278–289.

Scheu, S., and M. Schaefer. 1998. Bottom-up control of the soil macrofauna community in a beechwood on limestone: manipulation of food resources. Ecology **79**:1573–1585.

Schindler, D. W. 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems **1**:323–334.

Scott, M. C., G. S. Helfman, M. E. McTammany, E. F. Benfield, and P. V. Bolstad. 2002. Multiscale influences on physical and chemical stream conditions across blue ridge landscapes. Journal of the American Water Resources Association **38**:1379–1392.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785–791.

Slansky, F., and J. M. Scriber. 1982. Selected bibliography and summary of quantitative food utilization by immature insects. Bulletin of the Entomological Society of America **28**:43–55.

Slavik, K., B. J. Peterson, L. A. Deegan, W. B. Bowden, A. E. Hershey, and J. E. Hobbie. 2004. Long-term responses of the Kuparuk river ecosystem to phosphorus enrichment. Ecology **85**:939–954.

Stelzer, R. S., J. Heffernan, and G. E. Likens. 2003. The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. Freshwater Biology **48**:1925–1937.

Stewart-Oaten, A. 2003. On rejection rates of paired intervention analysis: comment. Ecology **84**:2795–2799.

Stockner, J. G., and E. A. Macisaac. 1996. British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. Regulated Rivers Research and Management **12**:547–561.

Swank, W. T., and D. A. Crossley. 1988. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Tank, J. L., and J. R. Webster. 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. Ecology **79**:2168–2179.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science **277**:102–104.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs **69**:409–442.

Waters, T. F. 1969. Subsampler for dividing large samples of stream invertebrate drift. Limnology and Oceanography **14**: 813–815.

Webster, J. R., J. L. Meyer, J. B. Wallace, and E. F. Benfield. 1997. Organic matter dynamics in Hugh White Creek, Coweeta Hydrologic Laboratory, North Carolina, USA. Journal of the North American Benthological Society **16**:74–78.

Wetzel, R. G. 1995. Death, detritus, and energy flow in aquatic ecosystems. Freshwater Biology **33**:83–89.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. Third edition. Academic Press, San Diego, California, USA.

APPENDIX

A table showing abundance, biomass, and secondary production of all taxa in the reference stream and the treatment stream before and during nutrient enrichment (*Ecological Archives* E087-093-A1).