NUTRIENT ENRICHMENT REDUCES CONSTRAINTS ON MATERIAL FLOWS IN A DETRITUS-BASED FOOD WEB

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Abstract. Most aquatic and terrestrial ecosystems are experiencing increased nutrient availability, which is affecting their structure and function. By altering community composition and productivity of consumers, enrichment can indirectly cause changes in the pathways and magnitude of material flows in food webs. These changes, in turn, have major consequences for material storage and cycling in the ecosystem. Understanding mechanisms and predicting consequences of nutrient-induced changes in material flows requires a quantitative food web approach that combines information on consumer energetics and consumer–resource stoichiometry. We examined effects of a whole-system experimental nutrient enrichment on the trophic basis of production and the magnitude and pathways of carbon (C), nitrogen (N), and phosphorus (P) flows in a detritus-based stream food web. We compared the response of the treated stream to an adjacent reference stream throughout the study. Dietary composition and elemental flows varied considerably among invertebrate functional feeding groups. During nutrient enrichment, increased flows of leaf litter and amorphous detritus to shredders and gatherers accounted for most of the altered flows of C from basal resources to consumers. Nutrient enrichment had little effect on patterns of material flows but had large positive effects on the magnitude of C, N, and P flows to consumers (mean increase of 97% for all elements). Nutrient-specific food webs revealed similar flows of N and P to multiple functional groups despite an order of magnitude difference among groups in consumption of C. Secondary production was more strongly related to consumption of nutrients than C, and increased material flows were positively related to the degree of consumer–resource C:P and C:N imbalances. Nutrient enrichment resulted in an increased proportion of detrital C inputs consumed by primary consumers (from ~15% to 35%) and a decreased proportion of invertebrate prey consumed by predators (from ~80% to 55%). Our results demonstrate that nutrient enrichment of detritus-based systems may reduce stoichiometric constraints on material flows, increase the contribution of consumers to C, N, and P cycling, alter the proportion of C inputs metabolized by consumers, and potentially lead to reduced ecosystem-level storage of C.

Key words: detritus-based food webs; ecological stoichiometry; ecosystem enrichment; elemental imbalance; invertebrate; material flow food web; secondary production; stream; trophic basis of production.

INTRODUCTION

Nutrient enrichment of ecosystems is occurring globally, and is strongly affecting the structure, production, and stability of recipient food webs (DeAngelis et al. 1989, Vitousek et al. 1997, Carpenter et al. 1998, Kuijper et al. 2005). If consumers are nutrient limited, enrichment can reduce consumer–resource nutritional imbalances leading to changes in individual growth, production, and the magnitude or direction of material flows in the food web (DeAngelis et al. 1989, Shieh et al. 2002, Cross et al. 2006, Singer and Battin 2007). Although considerable effort has been focused on

predicting the effects of enrichment in living plant-based food webs, less is known about how increased nutrient availability alters detritus-based food webs. This information is critical because the majority of global primary production directly enters detrital pathways (Odum and Biever 1984, Moore et al. 2004) and enrichment of these food webs may cause large-scale changes in carbon (C) accumulation and loss (Mack et al. 2004). In addition, empirical studies of how enrichment alters material flows in detrital food webs will aid in developing predictive models of how these systems respond to natural or anthropogenic perturbations (de Ruiter et al. 1994, Kuijper et al. 2005).

Although there are a diversity of factors that influence productivity and the flows and accumulation of materials in ecosystems, multiple broad-scale analyses have shown that autotroph nutrient content plays a key role in determining consumption rates by heterotrophs (Enriquez et al. 1993, Cebrian et al. 1998, Cebrian and

Lartigue 2004). As a consequence, ecosystems dominated by plants or detritus with high nutrient content tend to accumulate less C (Cebrian et al. 1998, Cebrian and Lartigue 2004). Because plant and detrital (i.e., detritus and microbes) nutrient content are nonhomeostatic with regard to external nutrient supply (Sterner and Elser 2002), enrichment or eutrophication of ecosystems is likely to increase rates of consumption and flows of materials through consumers by altering the nutrient content of basal resources. Such effects have broad implications for system-wide material storage and fluxes. Although these correlative patterns are evident from comprehensive meta-analyses (Cebrian and Lartigue 2004), experimental tests of these patterns in detritus-based ecosystems are lacking.

One way to test these patterns experimentally is to add nutrients to an ecosystem and directly quantify flows of C and nutrients through the food web. To date, most quantitative food web analyses have used energy or C as a common currency to follow flows among resources and consumers (Lindeman 1942, Benke and Wallace 1997, Hall et al. 2000; but see Ulanowicz and Baird 1999). Although this approach is a significant improvement over nonquantitative topological food webs, it does not account for the large degree of variation in nutritional quality (e.g., nutrient content) among basal resources. If flows (and transfer efficiencies) of energy or C through food webs are constrained by mineral elements (e.g., nitrogen or phosphorus; Mattson 1980, Ulanowicz and Baird 1999, Sterner and Elser 2002, Hessen et al. 2004), explicit consideration of these elements in quantitative food webs (i.e., nutrient-specific webs) is necessary for gaining a mechanistic understanding of controls on C storage and flows in ecosystems (sensu Reiners 1986).

In this paper, our primary goal was to examine how long-term nutrient enrichment of a detritus-based stream ecosystem altered the magnitude and pathways of material flows in the food web. In previous work, we found significant positive effects of enrichment on basal resource nutrient content (Cross et al. 2003) and individual growth rates and secondary production of consumers (Cross et al. 2005b, 2006). In this study, we combined novel dietary analysis of consumers with previous estimates of basal resource stoichiometry and consumer production to explicitly examine enrichment effects on the trophic basis of production and flows of C, nitrogen (N), and phosphorus (P) in the food web. Specifically, we combined energetic and stoichiometric approaches to address the following questions: (1) Which food resources provided the basis for the observed positive response of secondary production to nutrient enrichment? (2) Did nutrient enrichment cause changes in the dietary composition of consumers? (3) How did nutrient enrichment alter the magnitude and pathways of material flows to consumers? (4) Were altered material flows due to reduced stoichiometric constraints on consumer production? We predicted that

nutrient enrichment would increase material flows from basal resources to consumers as a result of reduced consumer–resource elemental imbalances (Cross et al. 2003), as opposed to changes in dietary composition. As a consequence, we expected detritivores to consume an increased proportion of allochthonous material inputs in our experimentally enriched system. In addition, due to the abundance of C-rich and nutrient-poor resources in this detritus-based ecosystem, we predicted that consumer production would be more closely linked to consumption of nutrients than C, and that nutrient-induced changes in material flows would be largest among taxa that are typically most constrained by low-nutrient food resources (e.g., those that specialize on nutrient-poor leaf litter).

METHODS

Study site and experimental enrichment

We studied two adjacent headwater streams (draining catchments 53 and 54) at the Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA (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 secondary production (Wallace et al. 1997, Hall et al. 2000; see Plate 1). The streams used in this study have similar physical and chemical characteristics (i.e., watershed area, slope, elevation, discharge, temperature; see Lugthart and Wallace [1992] for more detail), but differ since July 2000 in their concentrations of dissolved nitrogen (N) and phosphorus (P) as a result of our experimental nutrient enrichment of catchment 54. 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, from below detection to 30 μg/L; soluble reactive phosphorus mean, 3.7 μg/L; range, from below detection to 22 μg/L).

Starting in July 2000, we continuously added dissolved N (NH_4NO_3) and P (K_2HPO_4 and KH_2PO_4) along the entire length of the treatment stream (catchment 54) with a solar-powered metering pump to increase concentrations of dissolved inorganic N and P, while keeping stream water N:P ratios relatively constant (see Gulis and Suberkropp [2003] for a description of the nutrient pumping apparatus). Nutrient concentrations in the treatment stream during enrichment were as follows: [$NO_3 + NO_2$]-N mean, 308.9 μg/L; range, 11–1711 μg/L; NH_4-N mean, 105.5 μg/L; range, 6–566 μg/L; soluble reactive phosphorus mean, 51.2 μg/L; range, from below detection to 268 μg/L.

Trophic basis of production and material flow food webs

We quantified the trophic basis of production for 22 primary consumer taxa and eight predatory taxa in both

study streams during three distinct time periods: before nutrient enrichment (September 1998–August 2000), during year 1 of enrichment (September 2000–August 2001), and during year 2 of enrichment (September 2001–August 2002). This method requires knowledge of the proportions of food resources consumed, assimilation efficiencies for each food resource, and consumer secondary production.

To quantify the proportions of dominant food resources consumed we used gut content analysis (Cummins 1973, Benke and Wallace 1980). Invertebrate consumers were collected roughly seasonally from both streams between July 1999 and July 2002 ($n = 10$ collection dates). Five to 10 individuals of each of the dominant taxa were collected from each stream on each date and preserved in Kahle's solution (Stehr 1987). Gut contents were teased from invertebrate guts into distilled water, sonicated, and filtered onto 0.45-μm metrical membrane filters (Gelman Sciences, Ann Arbor, Michigan, USA). Filters were air dried, placed on glass slides, cleared with immersion oil, covered, and sealed with clear nail polish. For most taxa, gut contents of one or two individuals were used for each slide; for smaller taxa (e.g., chironomids), a greater number of individuals (2–10) were used. During each season, between one and four slides were made for each taxon. Approximately 50 food particles from each slide were identified and their area measured using a phase-contrast compound microscope (400×) equipped with a digital video camera and image analysis software (Image Pro 3.0, Media Cybernetics, Bethesda, Maryland, USA).

The proportional area of all food types consumed (i.e., leaf, wood, and amorphous detritus, diatoms, fungi, and animal prey) was calculated for each individual. To account for between-stream differences in leaf- and wood-associated fungal biomass, we further partitioned leaf and wood detrital particles into nonliving detritus and fungi by multiplying leaf and wood percentages by the average contribution of fungi to leaf or wood biomass (K. Suberkropp, *unpublished data*). Under non-enriched reference conditions, leaf litter and wood biomass contained 3.9% and 2.3% fungi, respectively. During enrichment of the treatment stream, fungal content increased to 5.3% on leaf litter and 10.2% on wood (Gulis et al. 2004; K. Suberkropp, *unpublished data*). Bacteria and their exopolymers support a large proportion of invertebrate secondary production in these streams (Hall and Meyer 1998). Bacterial contributions to secondary production were shown to be directly proportional to the amount of amorphous detritus in the guts of primary consumers (Hall and Meyer 1998). In this study, we quantified flows of amorphous detritus, but production supported by these flows should be viewed as coming predominantly from bacteria and exopolymers. Gut contents of the dominant predators were examined annually in both streams (R. O. Hall and W. F. Cross, *unpublished data*)

and contained 100% animal material (also see Hall et al. 2000).

Literature-based assimilation efficiencies were used for most food categories (Barlocher and Kendrick 1975, Benke and Wallace 1980, 1997, Slansky and Scriber 1982, Hall et al. 2000). An assimilation efficiency of 80% was used for animal material, 10% for amorphous detritus, 30% for diatoms, and 50% and 70% for bacteria and fungi, respectively. Leaf and wood detritus were assigned an assimilation efficiency of 5%; this value is lower than that generally used for these categories (10%) because we separately assessed flows of nonliving leaf or wood detritus and detritus-bound fungi. Assimilation efficiencies of most food items, including nonliving detritus, were likely higher in the treatment stream than in the reference stream during the enrichment because of increased microbial conditioning and digestibility of detritus. The extent of this difference, however, is unknown and likely to vary significantly among taxa and food types. For this reason, we examined the sensitivity of food web flows to realistic differences in assimilation efficiency (see the *Discussion* and Appendix), and we discuss the implications for quantitative food web analyses in which perturbations alter food quality as well as food quantity.

Annual secondary production of invertebrates was estimated from benthic samples collected monthly in both study streams between September 1998 and August 2002 (see Cross et al. 2006). Secondary production attributed to each food type, and the total amount of each food type consumed each year (i.e., organic matter flows) were quantified following the calculations of Benke and Wallace (1980, 1997). Briefly, the relative fraction of a consumer's annual production attributed to each food type (F_i) was calculated as: $F_i = (G_i \times AE_i \times NPE)$, where G_i is the mean annual percentage of food type i in a consumer's gut, AE_i is the assimilation efficiency of food type i, and NPE is the net production efficiency (held constant at 0.4; Benke and Wallace 1997). To convert each relative fraction (F_i) to a proportion of all food types (PF_i), F_i was divided by $F_i + F_j + F_k \ldots F_n$. To calculate the actual amount of consumer production attributed to each food type, proportions (PF_i) were multiplied by annual consumer secondary production. For the year of September 1998–August 1999, we combined secondary production values from 1998 to 1999 with gut content data from 1999 to 2000 to estimate the trophic basis of production and food web flows.

To construct organic matter flow food webs, we calculated the amount of each food type consumed by a given consumer as: $FC_i = (PF_i \times P)/(AE_i \times NPE)$, where FC_i is the amount of food type i consumed (g ash-free dry mass [AFDM]·m^{-2}·yr^{-1}) and P is the secondary production of the consumer (g AFDM·m^{-2}·yr^{-1}). Next, to quantify flows of individual elements, we multiplied organic matter flows by the percentage of C, N, or P in each food type (Sterner and Elser 2002, Cross et al.

2003, Gulis and Suberkropp 2003; also see Table 1). This analysis yielded separate flows of C, N, and P for individual taxa during each time period. Mean annual flow food webs were constructed for two time periods in each stream: before (September 1998–August 2000) and during (September 2000–August 2002) nutrient enrichment. Due to the timing of our secondary production estimates (September–August each year), we included July and August 2000 in the "before-treatment" period. This has little effect on our results because gut contents were quantified seasonally and averaged throughout the year. Furthermore, nutrient-induced changes in primary consumer biomass (and production) were lagged by a few months (Cross et al. 2006), indicating that inclusion of these months in the before-treatment period does not affect our conclusions. Note that throughout this paper we use the terms "flow" and "consumption" synonymously.

We present dietary proportions, trophic basis of production, and flow food webs for composite functional feeding groups (sensu Merritt and Cummins 1996). Functional feeding groups in these streams consist of leaf-shredding taxa (shredders), collector gatherers (gatherers), collector filterers (filterers), scrapers, and predators, each of which rely on relatively different combinations of food resources. For this study, functional feeding groups were determined a priori based on previous gut content analyses under reference conditions (see Wallace et al. 1997, Hall et al. 2000). Trophic basis of production values represent means across all taxa in a given functional feeding group, weighted by the annual production of each taxon. Annual flows were summed across all taxa within a given functional feeding group.

We examined the degree to which nutrient-induced changes in the magnitude of organic matter flows were related to consumer–resource elemental imbalances. For each taxon, we calculated elemental imbalance as the difference between the consumer's body C:P (or C:N) ratio (Cross et al. 2003) and the flow-weighted C:P (or C:N) ratio of their food resources based on gut content analyses. We then calculated the mean proportional increase in total flows to a given consumer as the mean of flows during treatment minus flows before treatment divided by the mean of flows before treatment, across all food types. Correlations between elemental imbalance and proportional increase in flows were determined.

To assess whether invertebrate production was more closely linked to consumption of C or nutrients, we examined relationships between functional feeding group secondary production and C, N, and P consumption for all years of the study. In this analysis, we were most interested in the relative differences in strength among relationships for different elements, as opposed to the actual slope, significance, or explained variation in any one relationship. To determine whether residual variation in the relationship between secondary production and C consumption could be explained by

consumption of nutrients, we examined relationships between N or P consumption and residuals from the C relationship.

To examine whether detritivores consumed an increased proportion of detrital C inputs during enrichment (sensu Cebrian et al. 1998), we divided annual leaf litter C consumption before and during nutrient enrichment in both streams by previously quantified mean annual leaf litter C inputs to catchment 53 and catchment 54 (mean = 206 g C·m^{-2}·yr^{-1}; Cuffney et al. 1990).

Statistical analyses

We used proportional similarity analysis (Whittaker 1975) to compare diet overlap between streams during three separate time periods (i.e., before enrichment, during year 1 of enrichment, and during year 2 of enrichment). For this analysis we used the average proportions (weighted by secondary production) of food items across all taxa within a given functional feeding group. A proportional similarity of 1.0 is indicative of complete diet overlap. Dietary proportions were compared seasonally for each functional feeding group using nonparametric Wilcoxon signed-ranks test. Linear regression was used to examine relationships between C, N, and P consumption and secondary production, as well as relationships between nutrient consumption and C residuals. In these regressions we violated the assumption that there is no error in our independent variable; data points represent annual means across taxa and seasons. However, violation of this assumption principally limits our interpretation of the slope values from these relationships (Pascual and Kareiva 1996), and error in the independent variable would tend to bias the slope toward lower values. Because we are not interested in the absolute values of slopes, we abstain from their interpretation. We also violated the assumption of non-independence among our points (before- and during-enrichment years plotted together), which may alter the strength of relationships. However, our primary interest was in differences among the relationships in both relative significance and size of residuals, rather than the strength of the relationship in any given plot.

RESULTS

We examined the diet and estimated trophic basis of production for 22 primary consumer taxa and eight predatory taxa. Together, these taxa constituted 86% of community-wide annual secondary production (Cross et al. 2006).

Dietary composition

Primary consumer functional feeding groups exhibited strong differences in dietary composition throughout the study (Fig. 1). On average, shredder guts were dominated by leaf litter, with smaller contributions from amorphous detritus, wood, and fungi. In contrast, gut
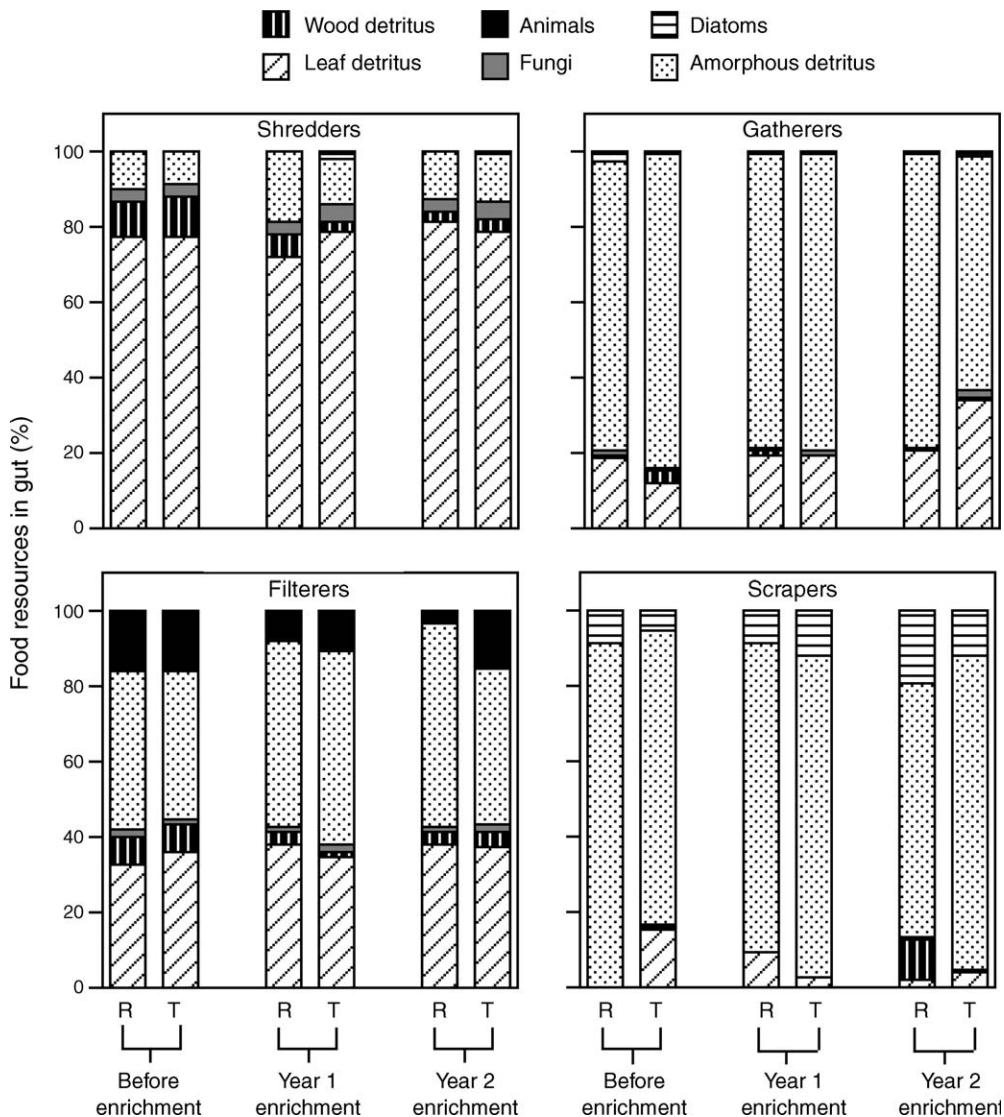
FIG. 1. Percentages of different food resources consumed by four invertebrate functional feeding groups in the reference stream (R) and the treatment stream (T) before enrichment (September 1999–August 2000), during year 1 of the nutrient enrichment (September 2000–August 2001), and during year 2 of the nutrient enrichment (September 2001–August 2002). Percentages were averaged across four seasonal sampling dates in each year.

contents of gatherers and scrapers were dominated by amorphous detritus (Fig. 1). Filterer taxa had a more diverse diet with significant contributions from leaf litter, amorphous detritus, and animal prey. Wood, fungi, and diatoms represented a small dietary component of all functional feeding groups.

Nutrient enrichment had no effect on the proportions of food resources in the guts of consumers (Fig. 1). Proportional similarities of gut contents for each functional feeding group were consistently high between treatment periods within each stream (reference stream: 0.74–0.92; nutrient-enriched stream: 0.63–0.92) and between the reference and treatment streams during each time period (0.77–0.95; all Wilcoxon signed-ranks tests had $P > 0.2$).

Trophic basis of production

On average, production of shredders in both streams was primarily attributed to leaf litter (46%), fungi (31%), and amorphous detritus (17%; Fig. 2). Gatherer and scraper production was predominantly supported by amorphous detritus (81% and 73%), and ~23% of scraper production was attributed to diatoms (Fig. 2). Production of filterer taxa was largely supported by amorphous detritus (38%) and animal prey (41%).

Although nutrient enrichment had little effect on the proportions of food resources supporting invertebrate production, the absolute amount of production supported by food resources increased in the treatment stream relative to the reference stream during the
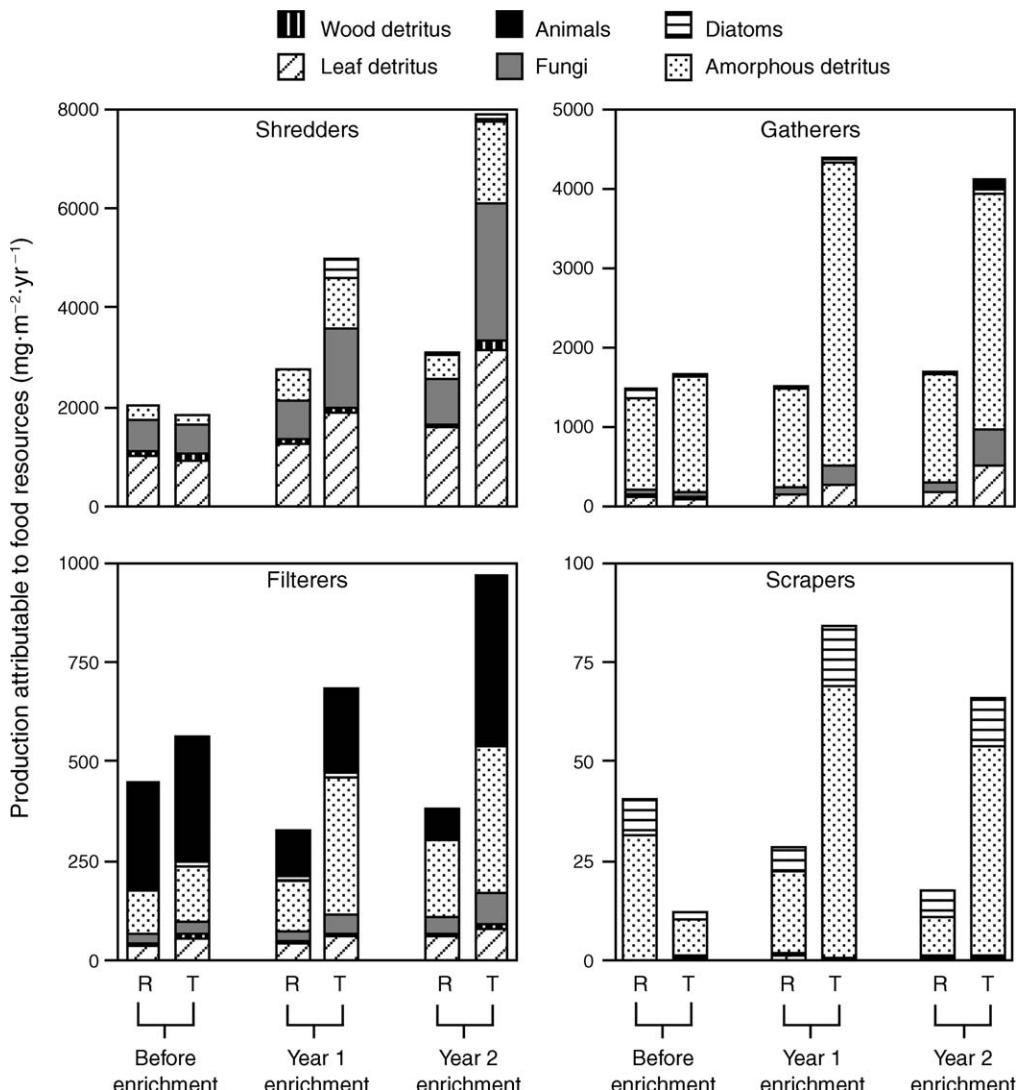
FIG. 2. Invertebrate secondary production (ash-free dry mass) attributed to food resources among four functional feeding groups in the reference stream (R) and treatment stream (T) before enrichment (average of September 1998–August 1999 and September 1999–August 2000), during year 1 of enrichment (September 2000–August 2001), and during year 2 of enrichment (September 2001–August 2002). Average gut content proportions from September 1999–August 2000 were applied to production data from September 1998–August 1999 to estimate production attributed to food resources during the earlier reference year. Note the difference in scale among functional groups.

enrichment (Fig. 2). For example, the amount of shredder production attributed to fungi increased from a mean of 603 mg ash-free dry mass (AFDM)·m^{-2}·yr^{-1} before enrichment to 2194 mg AFDM·m^{-2}·yr^{-1} in the treatment stream during enrichment. Among gatherers, production attributable to amorphous detritus increased from ~1293 mg AFDM·m^{-2}·yr^{-1} before enrichment to ~3404 mg AFDM·m^{-2}·yr^{-1} during enrichment. The magnitude of trophic support increased similarly for most food types among all functional feeding groups during nutrient enrichment of the treatment stream (Fig. 2).

Material flow food webs

Overall, leaf litter (52%) and amorphous detritus (35%) dominated organic matter flows to primary consumers, followed by animal prey (5%), wood detritus (4%), fungi (3%), and diatoms (~1%; Fig. 3). The pattern and magnitude of flows from the dominant food resources to consumers were very similar in the reference stream and the treatment stream before enrichment (Fig. 3). In contrast, during nutrient enrichment organic matter flows to consumers were twice as high in the treatment stream, while flows in the reference stream only increased ~25% (Fig. 3).
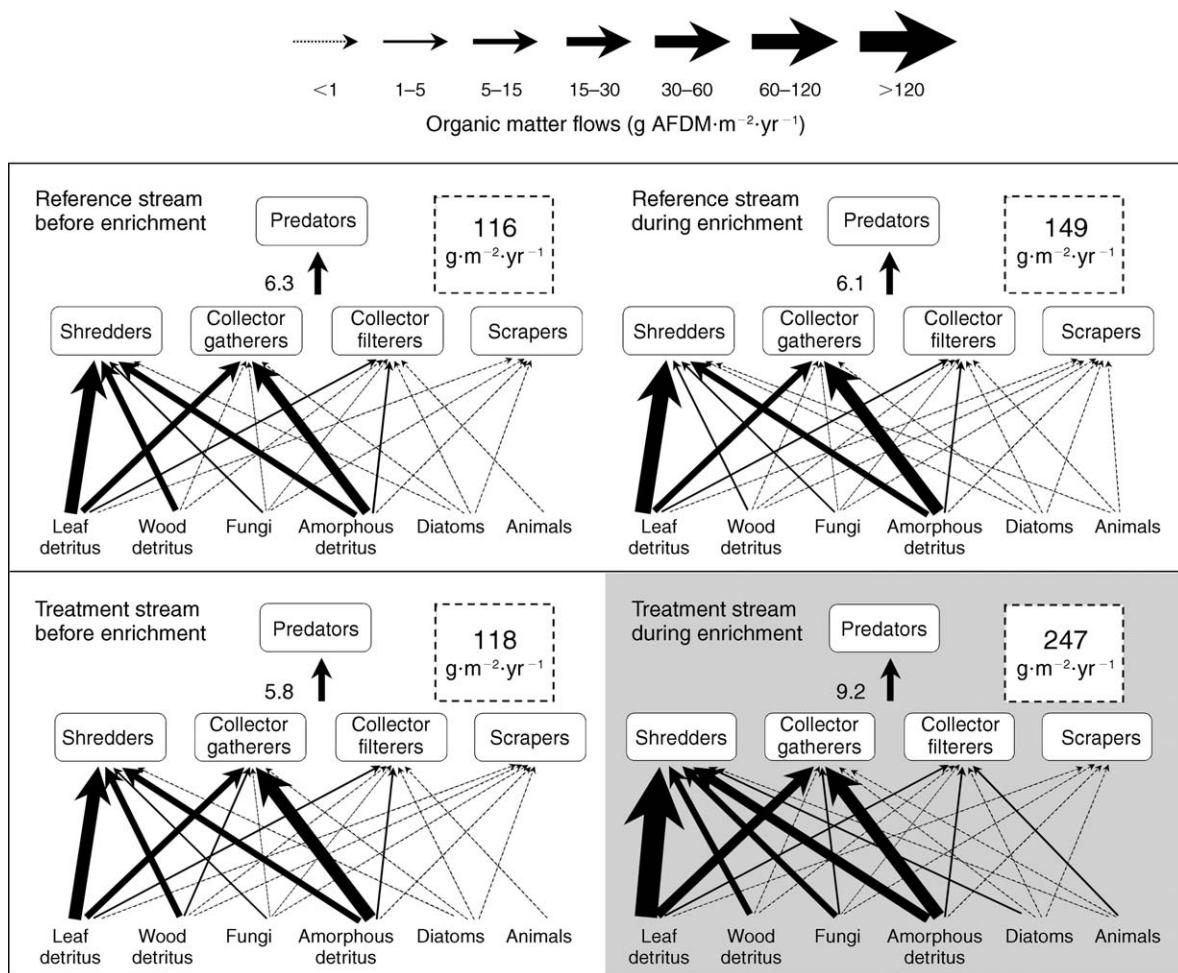
Fig. 3. Organic matter flow food webs (g AFDM·m^{-2}·yr^{-1}) for invertebrate functional feeding groups in the reference stream and treatment stream before (September 1998–August 2000) and during (September 2000–August 2002) nutrient enrichment of the treatment stream. Flow webs were averaged across years during each time period. Numbers within the dashed boxes represent the mean annual organic matter flows to all functional feeding groups. The smaller numbers by the small upper arrows represent the total amount of organic matter flowing from invertebrate prey to predators. Widths of arrows from food sources to invertebrate groups indicate the magnitude of organic matter flows.

Flows of invertebrate prey to predators represented a small proportion of the total food web flows (Fig. 3). Nonetheless, these values indicated that before enrichment predators consumed 79% and 85% of total prey production in the reference stream and treatment stream, respectively. During nutrient enrichment, flows to predators increased substantially in the treatment stream (from 5.8 to 9.2 g·m^{-2}·yr^{-1}; Fig. 3), but they consumed only (55%) of total prey production.

Before nutrient enrichment, primary consumers in the reference and treatment streams consumed 14% and 19%, respectively, of total leaf litter carbon (C) inputs. During enrichment, primary consumers in the treatment stream consumed 35% of leaf C inputs, while only 13% of inputs were consumed in the reference stream.

Nutrient-specific flow food webs revealed patterns that were not readily apparent with flow webs based on organic matter (Table 1). The dominant C flows were consistently from leaf litter to shredders. Nitrogen (N) flows were generally largest from invertebrate prey to predators (Table 1), reflecting the high nutrient content of invertebrate prey relative to other food resources (Cross et al. 2003). Total flows of phosphorus (P) were similar for shredders, gatherers, and predators, which resulted from large flows of P-poor detritus to shredders and gatherers and small flows of P-rich invertebrate prey to predators. Total flows of C, N, and P to consumer functional feeding groups consistently increased in the treatment stream in response to enrichment (13–350%; Table 1), with a mean production-weighted increase of 97% for all elements. Flow differences in the reference stream between time periods were relatively small (mean production-weighted increase of 21%; Table 1).

Correlations between consumer–resource elemental imbalances (as molar C:P and C:N ratios) and proportional changes in material flows with nutrient

TABLE 1. Mean annual flows of carbon, nitrogen, and phosphorus to consumer functional feeding groups in the reference and treatment streams before (September 1998–August 2000) and during (September 2000–August 2002) nutrient enrichment of the treatment stream.

Elements and functional feeding groups	Mean annual flows (g·m^{-2}·yr^{-1})				Percentage change†	
	Reference stream		Treatment stream			
	Before	During	Before	During	Reference	Treatment
Carbon					*16*	*95*
Shredders	29.523	39.974	27.552	70.632	35	156
C gatherers	8.725	10.021	9.474	18.176	15	92
C filterers	1.980	2.310	2.695	3.257	17	21
Scrapers	0.151	0.100	0.064	0.174	−34	172
Predators	3.005	2.924	2.791	4.424	−3	59
Nitrogen					*23*	*99*
Shredders	0.384	0.575	0.353	1.067	50	202
C gatherers	0.300	0.331	0.341	0.536	10	57
C filterers	0.119	0.081	0.147	0.166	−32	13
Scrapers	0.008	0.004	0.002	0.009	−50	350
Predators	0.626	0.609	0.581	0.922	−3	59
Phosphorus					*25*	*97*
Shredders	0.025	0.041	0.023	0.073	64	217
C gatherers	0.037	0.042	0.046	0.063	14	37
C filterers	0.009	0.008	0.011	0.013	−11	18
Scrapers	0.001	0.001	0.000	0.001	−50	233
Predators	0.038	0.037	0.035	0.055	−3	57

Notes: Annual material flows were calculated by multiplying annual organic matter flows of each food resource to each functional feeding group (based on Benke and Wallace [1980]) by the percentage C, N, or P of each food resource (based on Sterner and Elser [2002], Cross et al. [2003], Gulis and Suberkropp [2003], and Gulis et al. [2004]). Values used for C: leaf detritus, 48.0%; wood detritus, 46.0%; fungi, 46.0%; amorphous detritus, 17.0%; diatoms, 20.0%; animals, 50.0%. Values used for N: leaf detritus, 0.5%; wood detritus, 0.15%; fungi, 3.0%; amorphous detritus, 0.8%; diatoms, 2.0%; animals, 10.0%. Values used for P: leaf detritus, 0.02%; wood detritus, 0.01%; fungi, 0.3%; amorphous detritus, 0.12%; diatoms, 0.1%; animals, 0.6%). Annual flows of C, N, and P were then summed across all food resources for each functional group. Also shown is the percentage change in flows before vs. during the enrichment period in both streams; the community-wide production-weighted percentage change is shown in italics for each element.

† Flow during treatment minus flow before treatment, divided by flow before treatment, × 100.

enrichment were positive and significant (Fig. 4), suggesting that increased flows were most prominent for taxa that consume nutrient-poor resources (i.e., largest elemental imbalances). These relationships, however, were largely driven by differences between a few leaf-eating taxa (i.e., shredders) and predators (Fig. 4). When the two points of highest proportional change were removed, relationships were not significant.

Regressions between element-specific consumption and functional feeding group production revealed strong significant relationships between N and P consumption and secondary production (all P values < 0.01); this relationship was weaker for C (Fig. 5A–C). Removal of the data point with highest consumption reduced the amount of variation explained in relationships for C (Fig. 5A; r^2 from 0.56 to 0.29) and N (Fig. 5B; r^2 from 0.83 to 0.76), but not for P (Fig. 5C). The absolute value of residuals from these regressions was significantly higher for C than for N or P (Fig. 5D; ANOVA P < 0.001, Tukey's post hoc test). A significant amount of the variation in the C relationship residuals was explained by consumption of N ($r^2 = 0.47$) and P ($r^2 = 0.57$; Fig. 5E, F), such that large positive residuals were associated with greater consumption of N and P, and

negative residuals were associated with the lowest N and P consumption.

DISCUSSION

Our study revealed strong positive effects of nutrient enrichment on the magnitude of material flows to consumers. Results suggest that these changes in material flows were likely driven by shifts in basal resource quality and not by fundamental shifts in consumer diets (e.g., switching from leaf litter to diatoms). Our approach highlights the usefulness of combining traditional energetic flow food webs with stoichiometric data to explicitly address mechanisms for nutrient-induced changes in material flows in ecosystems. Our analysis demonstrated that experimental changes in nutrient content of detritus (see Cross et al. 2003) resulted in an increased proportion of carbon (C) inputs consumed by invertebrate detritivores, as shown correlatively in a diversity of ecosystem types (Cebrian et al. 1998). Such nutrient-driven changes, over sufficient time periods, have the potential to alter storage, transformation, and export of C in detritus-based ecosystems.

Nutrient enrichment of detrital food webs can alter the nutritional quality of detritus via a number of mechanisms that are not mutually exclusive. First, enrichment can increase the biomass and activity of detritus-associated microbes (i.e., fungi and bacteria; Gulis and Suberkropp 2003, Stelzer et al. 2003), which are often selectively ingested by detritivores (Arsuffi and Suberkropp 1985) or assimilated at a higher efficiency than nonliving detritus. Second, microbes contain high levels of nutrients and other biochemicals (Brett and Mueller-Navarra 1997, Sterner and Elser 2002, Cross et al. 2005a) that may directly limit the growth and production of consumers (Iversen 1974, Urabe et al. 1997). Lastly, nutrients may stimulate the production of microbial exoenzymes, which degrade complex carbohydrates and increase the digestibility of detritus (Barlocher 1985, Sinsabaugh et al. 1985, Suberkropp 1992). In our study, it is likely that all of these factors reduced constraints on material flows to consumers. Concurrent research in the treatment stream showed positive effects of enrichment on microbial biomass associated with leaf and wood detritus (Gulis and Suberkropp 2003, Gulis et al. 2004) and nutrient content of both leaf litter and fine particulate organic matter (Cross et al. 2003, Greenwood et al. 2007). We showed that increased flows in the treatment stream were partially driven by reduced consumer–resource elemental imbalances (Fig. 4). Moreover, our analyses indicated that invertebrate production was more strongly linked to consumption of nutrients (e.g., P and N) than C (Fig. 5), and N and P consumption explained a significant amount of variation in residuals between C consumption and production. Taken together, our results strongly suggest that higher nutrient content and changes in nutritional quality of food resources in the treatment stream were responsible for increased production and material flows. In addition, these results demonstrate that explicit consideration of nutrients in food webs can add significant insight towards understanding limits to energy flow in ecosystems.

Material flows to consumers increased in both the reference and treatment streams throughout the study, but the magnitude of increase was much higher in the treatment stream. We attribute the small increases in the reference stream to interannual variability in consumer production, which was well within the range of natural variability seen for Coweeta headwater streams (Wallace et al. 1999). In contrast, flows and production in the treatment stream during enrichment were far outside of the natural range of variability (Cross et al. 2006). Similar increased production and C flows have been shown to result from nutrient pollution in Colorado streams (Shieh et al. 2002). Our data suggest that specifically nutrient consumption, rather than C consumption, can be the most important factor driving increased energy flow to consumers in nutrient-enriched environments.
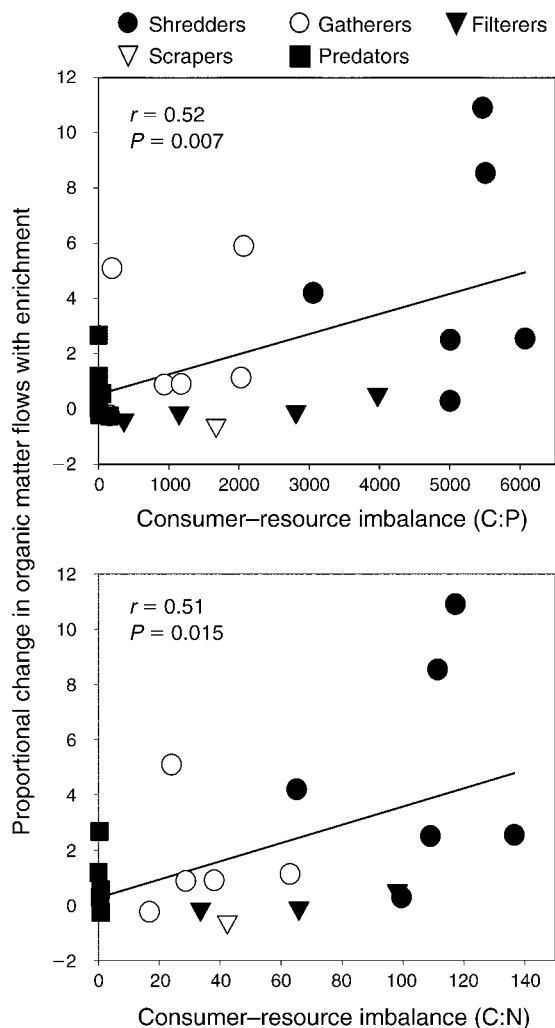

Fig. 4. Relationships between consumer–resource elemental imbalances under ambient nutrient conditions (expressed as molar C:P or C:N ratios; see *Methods: Trophic basis of production and material flow food webs*) and the proportional increase in total flows with nutrient enrichment for 25 consumer taxa in the treatment stream. The *y*-axis scale goes from a twofold decline to a 12-fold increase in flows. For each taxon, we calculated the annual consumption (as organic matter) of all food resources found in the guts. Molar C:P and C:N ratios for each food resource were estimated directly or taken from the literature (see *Notes* for Table 1). Mean dietary C:P (or C:N) ratios were calculated by weighting the resource stoichiometry values by the annual consumption (i.e., flow) of each resource. Elemental imbalances were calculated as the difference between the flow-weighted dietary C:P (or C:N) ratio and the consumers' body C:P (or C:N) ratio. Taxa included in these figures represent 85% of total invertebrate production. Much of this relationship was driven by two leaf-eating taxa with high elemental imbalances (*Fattigia pele* and *Tipula* sp.) and predatory taxa that clustered around zero elemental imbalance.

In addition to quantifying flows of organic matter, we calculated taxon-specific and functional-group-specific flows of C, N, and P. This type of analysis can provide additional information on the fate and pathways of individual elements in the food web, and may reveal
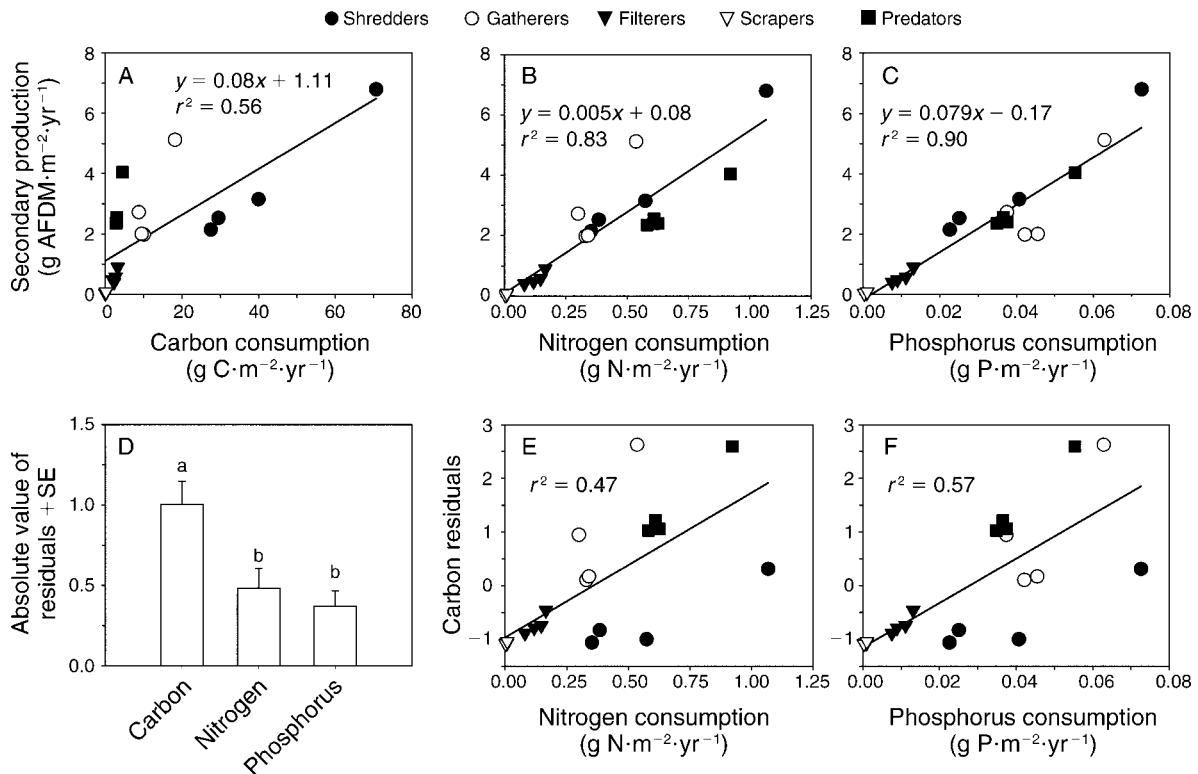
FIG. 5. Upper row: relationships between functional feeding group secondary production and annual consumption of (A) carbon, (B) nitrogen, and (C) phosphorus. Each point represents the mean for a given functional feeding group during a given treatment period ($n = 20$, 5 functional feeding groups × 2 streams × 2 treatment periods [before enrichment, September 1998–August 2000; during enrichment, September 2000–August 2002]). Lower row: (D) absolute value (+SE) of residuals for panels A, B, and C, with different lowercase letters representing significantly different means with ANOVA ($P < 0.01$) and Tukey's post hoc test; (E and F) relationships between the carbon residuals and consumption of nitrogen and phosphorus. For each functional feeding group, the point with highest secondary production represents the treatment stream during the experimental nutrient enrichment. All regressions are statistically significant ($P < 0.01$).

patterns that would be overlooked with traditional analysis of organic matter flows. Although C is generally ~50% of organic matter, N and P content can vary widely among food resources and taxa (Sterner and Elser 2002, Cross et al. 2005a). Thus, while C-based food webs may directly reflect patterns in organic matter flow, N- or P-specific food webs will take into account the variation in nutrient content across different food types. Interestingly, nutrient flows were often similar for taxa with strongly contrasting consumption rates of organic matter. For example, flows of P from invertebrate prey to predators were nearly identical to flows of P from leaves to shredders (averaged across streams and time periods: 0.04 g·m⁻²·yr⁻¹ for both prey to predators and leaves to shredders), despite an order of magnitude difference in organic matter consumption by these groups. These data further suggest that production may be limited by the nutrient content of food resources, as opposed to total C or energy content.

Consumer–resource elemental imbalances were positively related to proportional changes in organic matter flows with nutrient enrichment (Fig. 4). This pattern

suggests that the consumers most likely to be nutrient limited (as defined by imbalances between consumer and food stoichiometry) showed the largest response to enrichment in terms of secondary production and flows of resources to consumers. Interestingly, we found no relationship when limiting our analysis to just consumer body stoichiometry vs. proportional flow changes (data not shown), suggesting that elemental imbalances using detailed gut analyses may increase our ability to detect patterns of consumer nutrient limitation. It is worth noting, however, that simple elemental imbalances may not accurately reflect actual nutrient requirements among taxa (Frost et al. 2005). Threshold elemental ratio models, which combine species-specific information on body stoichiometry and bioenergetics, show considerable promise for predicting the degree of nutrient limitation among taxa, as well as which taxa are most likely to respond to increased nutrient availability (see Urabe and Watanabe 1992, Sterner 1997, Sterner and Elser 2002, Frost et al. 2006).

One limitation of the trophic basis of production method, at least when using gut content analysis, is the

reliance of flow estimates on a single literature-based assimilation efficiency for each food category (Benke and Wallace 1997, Rosi-Marshall and Wallace 2002; and this study). For example, leaf litter and animal prey are often assigned assimilation efficiency values of 0.1 and 0.8, respectively, based on few actual measurements. While these estimates are valuable for incorporating inherent qualitative differences among major food categories, they are limited in that they do not account for subtle differences in nutritional quality within a given food type. For example, the quality of leaf litter for a consumer may vary depending on the amount of microbial biomass associated with the leaf litter (Arsuffi and Suberkropp 1985), leaf nutrient content (Iversen 1974, Quinn et al. 2000), or leaf condition (Hutchens et al. 1997); generally, assimilation efficiency is assumed to be equivalent for all leaves, and flows are calculated accordingly. Such limitations make comparisons of trophic basis of production or flow food webs among systems or sites difficult, especially when differences are manifested in the quality of food types as opposed to their quantity.

How much do assimilation efficiency values influence estimates of consumption, and do realistic nutrient-induced changes in assimilation alter our results? To approach these questions, we took advantage of existing data that relate nutrient content of basal resources to carbon-based assimilation efficiency (Pandian and Marian 1986, Boersma et al. 2001; see analysis in the Appendix). Based on our observed changes in N content of basal resources (e.g., 12.5% increase in N content of amorphous detritus) and considerable error around these values (up to a 50% increase in percentage N), our analysis indicates that realistic increases in assimilation efficiency (~5%) would only lead to an 8–20% decline in flows of dominant basal resources. Although existing data are more limited for the relationship between basal resource P content and assimilation efficiency, an estimated 3–5% increase in assimilation efficiency with enrichment (see Boersma et al. 2001) would lead to a reduction of flows by 23–33%. In our study, flows to consumers increased, on average, ~100% with nutrient enrichment. If, in fact, assimilation efficiencies increased with enrichment, we would still conclude that flows increased by ~67–92% (instead of ~100%). Thus, large increases in material flows were still needed to account for the observed increase in consumer production, and our overall conclusion that enrichment caused large increases in material flows is robust to realistic changes in assimilation efficiency.

Nutrient enrichment often leads to a shift in community structure, favoring competitive dominants or pollution-tolerant taxa (Miltner and Rankin 1998). In such situations, changes in the identity of dominant consumers may strongly alter the pathways or magnitude of material flows in the food web. For example, increased proportional representation of fast-growing species will lead to increased material flows channeled

PLATE 1. Detritus-based headwater stream draining catchment 54 at Coweeta Hydrologic Laboratory, North Carolina, USA. Photo credit: John Davis.

through these taxa (Singer and Battin 2007). If these fast-growing taxa have high nutrient requirements, as suggested by recent studies (Elser et al. 2003), community shifts could alter the fate of nutrients in the food web (Hall et al. 2003, Singer and Battin 2007). During the first two years of enrichment we saw very little change in the structure of the community (also see Pearson and Connolly 2000), but large increases in secondary production of many taxa (Cross et al. 2005b, 2006). Thus, the pathways of material flows have remained relatively similar with large increases in their magnitude. However, recent work examining food web dynamics into the third, fourth, and fifth years of experimental enrichment has shown increased dominance of certain taxa and reduced evenness of the community (J. M. Davis, A. D. Rosemond, and J. B. Wallace, *unpublished data*). These time-lagged changes may ultimately influence the pathways of material flows in the food web, and underscore the importance of long-term studies in assessing the effects of perturbations such as nutrient enrichment (Slavik et al. 2004).

In summary, we showed that whole-system nutrient enrichment of a detritus-based ecosystem led to increased flows of organic matter and essential elements to invertebrate consumers. Changes in material flows were likely driven by released stoichiometric constraints

(i.e., reduced consumer–resource elemental imbalances) on invertebrate production. During enrichment, invertebrates consumed an increased, and substantial (35%), percentage of detrital C inputs. In ecosystems with large pools of refractory detrital C, increased availability of N and P may speed up the rate at which C is passed on to, and processed by, higher trophic levels, and may ultimately alter patterns of system-wide C accumulation.

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APPENDIX

Sensitivity analysis examining effects of realistic changes in assimilation efficiencies on material flows in the nutrient-enriched stream (*Ecological Archives* E088-154-A1).