



5.4 | DIFFERENTIAL EFFECTS OF CONSUMERS ON C, N, AND P DYNAMICS: INSIGHTS FROM LONG-TERM RESEARCH

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From the perspective of ecosystem energetics, animals are often regarded as relatively unimportant. Loss of energy with each trophic transfer results in minor contributions by higher trophic levels to the total energetic budget of a given system (Lindeman, 1942; Teal, 1962; Fisher and Likens, 1973). Increasingly, however, ecologists are recognizing that animals can play very prominent roles in the transformation, translocation, and cycling of essential elements such as carbon (C), nitrogen (N), and phosphorus (P) (Kitchell et al., 1979; Seastedt and Crossley, 1984; Jones et al., 1994; Andersen, 1997; Elser and Urabe, 1999; Strayer et al., 1999; Wallace and Hutchens, 2000; Crowl et al., 2001; Vanni, 2002; Hall et al., 2003). In many cases, the importance of these functional roles far exceeds that of animal biomass in ecosystem energy budgets, and can have major consequences for energy flow, nutrient cycling, and food web dynamics (Power et al., 1996b; Wootton and Downing, 2003). In extreme cases, animals may mediate the availability of essential nutrients (Elser et al., 1998) and ultimately determine the productivity and community composition of entire systems.

When assessing the role of animals in elemental dynamics, it is necessary to recognize that the importance of a given animal or assemblage may vary considerably depending on the particular element or elemental ratio of focus. Moreover, animals may strongly influence a single ecosystem process, but have relatively little influence on others. For example, some lentic fish, such as gizzard shad, are known to be extremely important in the translocation and recycling of P (Shaus and Vanni, 2000), but likely play a comparatively small direct role in lake C dynamics. Thus, in order to elucidate the dominant role of a given species or assemblage, one must consider their effects on multiple elemental currencies and a suite of ecosystem processes and fluxes (Duffy, 2002).

The recent development of ecological stoichiometry (Sturner and Elser, 2002, and references therein) has been a major catalyst for assessing the role of animals in food web and ecosystem dynamics. Although many of the conceptual ideas of ecological stoichiometry date back to Lotka (1925) and Redfield (1958), more recent theoretical and empirical work (Reiners, 1986; Sturner et al., 1998; Elser and Urabe, 1999) has provided a solid framework for hypothesis testing and application. Investigators are now measuring the elemental composition of organisms at all levels within food webs, from basal resources to top predators. This advance has led to considerable progress in estimating the role of animals in nutrient recycling (Elser and Urabe, 1999), understanding elemental constraints in food web and population dynamics (Andersen, 1997; Elser et al., 1998; Sturner et al., 1998; Stelzer and Lamberti, 2002), and comparing consumer-resource elemental imbalances among different ecosystem types (Elser and Hassett, 1994; Elser et al., 2000; Cross et al., 2003; Frost et al., 2003). In addition, by combining estimates of biomass or production of food web components with their elemental composition, assessments can be made about the relative contribution of animals to total particulate pools of C, N, and P (Hessen et al., 1992; Hassett et al., 1997), and the relative efficiency with which these elements are utilized or retained in the system.

Forested headwater streams are important sites of nutrient and organic matter input, storage, transformation, and export (Meyer and Wallace, 2001; Peterson et al., 2001). These first- and second-order streams are also the most abundant aquatic features in many landscapes, and often comprise >75% of the total stream length of larger forested basins (Wallace, 1988). Although animals (primarily invertebrates) inhabiting small streams make up a minor direct contribution to whole-stream carbon or energy budgets (Fisher and Likens, 1973; Webster et al., 1997), they are known to play a major role in the removal, translocation, or downstream export of carbon via leaf-eating (shred-

ding) or particle-gathering activities (Wallace et al., 1982; Webster, 1983; Wallace et al., 1991; Pringle et al., 1999). Little is known, however, about the influence of stream invertebrates on the dynamics of other important elements, such as N and P (but see Grimm, 1988; Crowl et al., 2001), which may limit the productivity of small headwater streams and larger recipient downstream ecosystems.

In this chapter, we examine the role of stream invertebrate food webs in the storage, utilization, and translocation of C, N, and P in small Appalachian headwater streams. We combine a number of studies (both published and unpublished) on the production, storage, export, and elemental composition of stream food web components to gain a broader understanding of the role of invertebrates in elemental dynamics of headwater streams. Our basic approach was to combine long-term measurements of food web component biomass and secondary production with their C, N, and P content (Cross et al., 2003). These data were used to assess general patterns in elemental storage and utilization by stream invertebrates. In addition, unpublished data from an experimental invertebrate removal were used to quantify the effects of invertebrates on the downstream translocation of C, N, and P, and the elemental stoichiometry of bulk organic matter export.

METHODS

Study sites

Studies were conducted in three first-order streams draining catchments (C) 53, 54, and 55 at the Coweeta Hydrologic Laboratory, North Carolina. Coweeta is a large (2185 ha), heavily forested basin located in the Blue Ridge physiographic province of the southern Appalachian Mountains. Forest vegetation is dominated by mixed hardwoods (primarily oak, maple, and poplar), and a thick under-story of rhododendron that shades the streams throughout the year. First-order streams at Coweeta are extremely heterotrophic, and receive >90% of their energy base in the form of allochthonous leaf litter from the surrounding catchment (Webster et al., 1997; Hall et al., 2000). In-stream primary production (algae and bryophytes) is very low, and contributes <1% to ecosystem carbon budgets (Webster et al., 1997; Hall et al., 2000). Streams that drain C53, C54, and C55 have very similar physical and chemical characteristics (see Lugthart and Wallace, 1992), but differ in their history of experimental manipulation. This study includes 29 stream-years of data collected from all three catchments between 1984 and 2002 (C53: 11 years, C54: 6 years, C55: 12 years). Years of whole-stream experimental manipulations that were not considered 'reference' conditions included:

1986–1988 in C54 (treated with insecticide, see Cuffney et al., 1990; Wallace et al., 1991), 2000–2002 in C54 (enriched with nitrogen and phosphorus, see Cross et al., 2003; Gulis and Suberkropp, 2003), and 1993–2000 in C55 (exclusion of leaf litter and wood, see Wallace et al., 1999). All other stream-years ($n = 20$) were considered unmanipulated 'reference' conditions.

Background Data

During each year of study, invertebrates and benthic organic matter (primarily detritus) were quantitatively sampled on a monthly basis from the two dominant stream habitats: bedrock outcrops and mixed substrates (i.e., cobble, pebble, gravel, and sand) (see Wallace et al., 1999, for a complete explanation of methods). Annual averages were compiled for the biomass of basal food web components (i.e., total fine particulate organic matter [FPOM, <1mm], total coarse particulate organic matter [CPOM, > 1 mm], leaf litter, moss). Epilithon biomass was quantified every eight weeks during 1999–2002 in C53 and C54 with submerged ceramic tiles (J. Greenwood, University of Georgia, unpublished data). Secondary production of all invertebrate taxa was estimated each year using the size-frequency method (Hamilton, 1969) corrected for the cohort production interval (Benke, 1979) (except non-Tanypod Chironomidae in which the instantaneous growth method was applied, see Huryn, 1990; Benke, 1993).

Carbon, N, and P content of basal food resources and invertebrates were analyzed in C53 and C54 during the period of 1999–2002 (Cross et al., 2003).

Assessing the Role of Invertebrates in Elemental Storage, Utilization, and Export

The percent contribution of invertebrates to total particulate pools of C, N, and P was assessed by calculating the total nutrient content of invertebrates and basal food resources for each year of study. Mean percent C, N, and P of basal food resources and invertebrates in C53 and C54 from 1999–2002 (see Cross et al., 2003) was multiplied by basal resource and invertebrate biomass (dry mass/m²) for each year. Storage of particulate C, N, and P was examined in two distinct habitats (mixed substrates, bedrock outcrops) because these habitats contain functionally distinct invertebrate communities, habitat structure, and fluvial geomorphology (Huryn and Wallace, 1987). For analysis of particulate C, N, and P storage we restricted our data set to the 20 stream-years of 'reference' data from C53, C54, and C55.

Relative utilization of C, N, and P by invertebrates was examined indirectly by regressing average annual leaf litter C, N, and P (resource availability) with annual production of invertebrate C, N and P (resource utilization) among years. A comparison of the linear slopes of regressions was used to make general conclusions regarding relative differences in elemental utilization.

Data from an experimental removal of invertebrate consumers (Cuffney et al., 1990) allowed us to estimate the effects of invertebrates on export of fine particulate C, N, and P, as well as elemental stoichiometry of bulk organic matter export. An insecticide (Methoxychlor) was applied seasonally to C54 for a period of three years (1985–1988, Cuffney et al., 1990; Wallace et al., 1991). Insecticide treatment resulted in massive mortality and downstream drift of invertebrates (Wallace et al., 1989), but had no effect on stream microbial activity (Cuffney et al., 1990; Suberkropp and Wallace, 1992). During the treatment, total invertebrate production and shredder production were reduced to 38% and 13% of pretreatment values, respectively (Lugthart and Wallace, 1992). Functional recovery of the invertebrate community was rapid and returned to pre-treatment levels during the second year of recovery (Whiles and Wallace, 1992; Whiles and Wallace, 1995). Cumulative export of fine particulate organic and inorganic material was quantified in the treatment stream (C54) and a reference stream (C55) biweekly during 1987–1990 with a Coshocton proportional sampler (4 mm pore size) connected to three large settling barrels (Cuffney et al., 1990; Wallace et al., 1991). Material at the base of settling barrels was analyzed biweekly for total N and P (APHA 1998); C was assumed to be a constant 50% of organic matter (ash-free dry mass) (Cross, unpublished data). Export data included one year during the insecticide treatment (December 1987–October 1988), and two years after treatment (November 1988–December 1990) during recovery of the invertebrate community. Time series of C, N, and P export in C54 and C55 were analyzed with randomized intervention analysis (RIA, Carpenter et al., 1989). RIA uses paired before-and-after time series data from a manipulated system and a reference system to detect changes caused by the manipulation. In this study, differences between streams during insecticide treatment were compared to differences after treatment.

Previous work demonstrated that invertebrate removal (and consequent declines in detritus consumption) had a large effect (240% increase) on the ratio of CPOM:FPOM exported from the treated stream relative to the reference stream (Wallace et al., 1995). We applied mean molar C:P, C:N, and N:P ratios of CPOM and FPOM (Cross et al., 2003) to export ratios of CPOM:FPOM to obtain weighted estimates of C:P, C:N,

and N:P of bulk (CPOM + FPOM) organic matter export before and during insecticide treatment in both streams.

RESULTS

Elemental Storage

In the mixed substrate habitat, invertebrates contributed relatively small amounts (0.1%, 1.3%, and 2.2%) to total pools of C, N, and P (Figure 1). Most C, N, and P was present in large pools of FPOM and CPOM (primarily leaves and wood). Epilithon was a minor component of particulate C, N, and P in this habitat.

On bedrock outcrops, invertebrates were a very minor proportion of total C (Figure 1). Storage of C was dominated by FPOM, CPOM, and aquatic moss (primarily *Platylomella* sp.). Storage of N and P by invertebrates on bedrock habitat was considerably higher than that in mixed substrates, at 8.2% (N) and 11.2% (P) of total particulate nutrient pools (see Figure 1). However, the majority of N and P was stored in FPOM, CPOM, and moss. Bedrock epilithon was a minor contributor to total pools of particulate C, N, and P (see Figure 1).

Elemental Utilization

A significant positive relationship ($p < 0.001$) was found between mean annual standing crop of leaf litter C and annual invertebrate secondary production of C (Figure 2A). The slope of this relationship was much less than 1 (0.036), indicating that a relatively small proportion of available leaf litter C is converted to invertebrate C in these headwater streams. Leaf litter N and P were also positively related to invertebrate production of N and P ($p < 0.001$, Figure 2B, C), and the slopes of these relationships (N: 0.52, P: 0.90) were at least an order of magnitude higher than that of C, demonstrating relatively high sequestration of N and P by stream invertebrates.

Effects of Invertebrates on Particulate C, N, and P Export

Invertebrate removal via seasonal application of insecticide resulted in significantly lower export concentrations (g/L) of particulate C, N, and P from the treated stream relative to the reference stream (RIA, p values < 0.01 for all 3 elements, Figure 3). During the insecticide treatment, concentrations of particulate C, N, and P were reduced to 33%, 42%, and

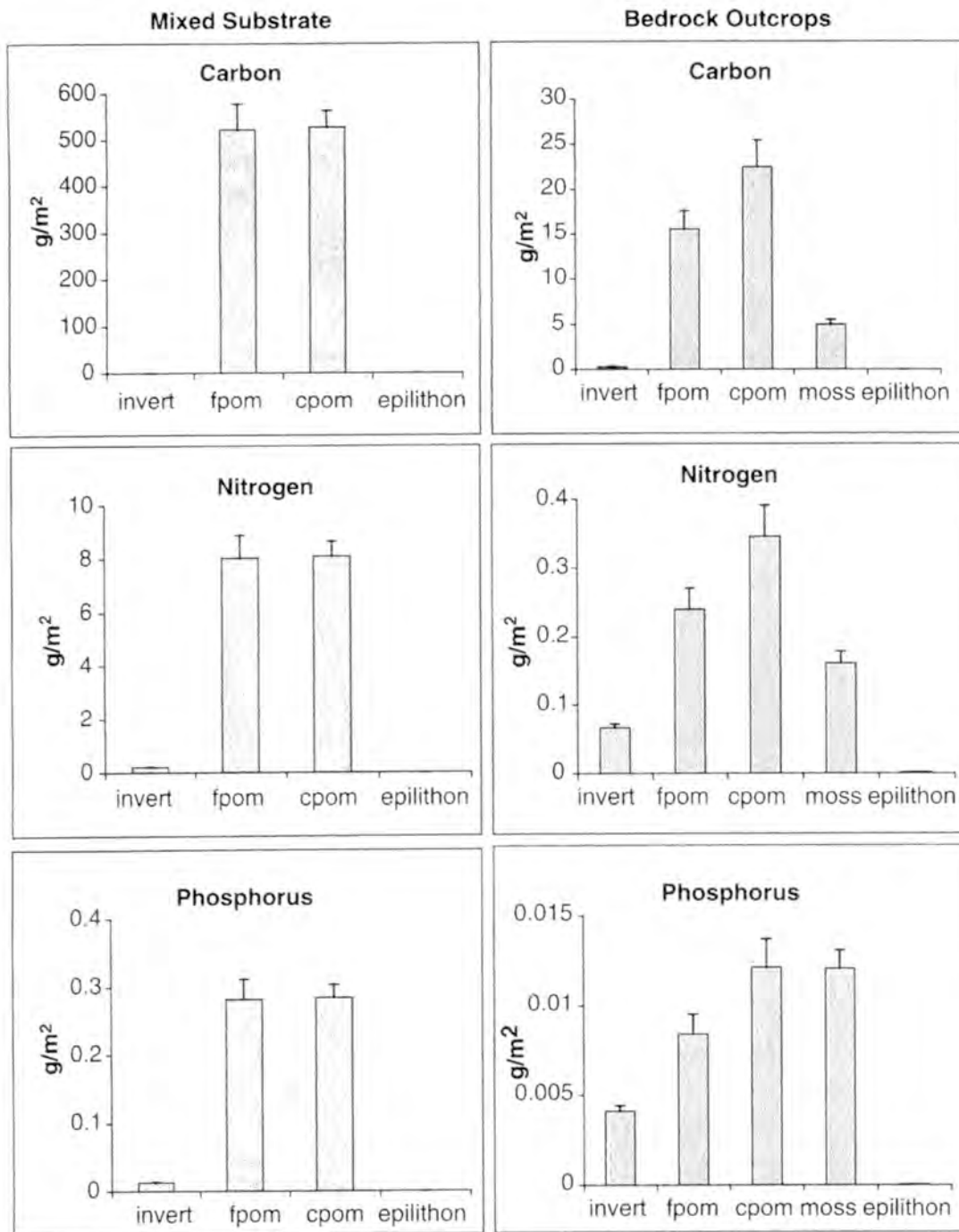


FIGURE 1 | Mean (+ISE) storage of carbon, nitrogen, and phosphorus among food web components in C53, C54, and C55 from the mixed substrate habitat and bedrock outcrops, invert-invertebrates, fpom-fine particulate organic material (<1 mm), cpom-coarse particulate organic material (>1 mm). N=20 years, except epilithon which is based on 3 years of data from C53 (J. Greenwood, University of Georgia, unpublished data). Note large differences in scale among graphs.

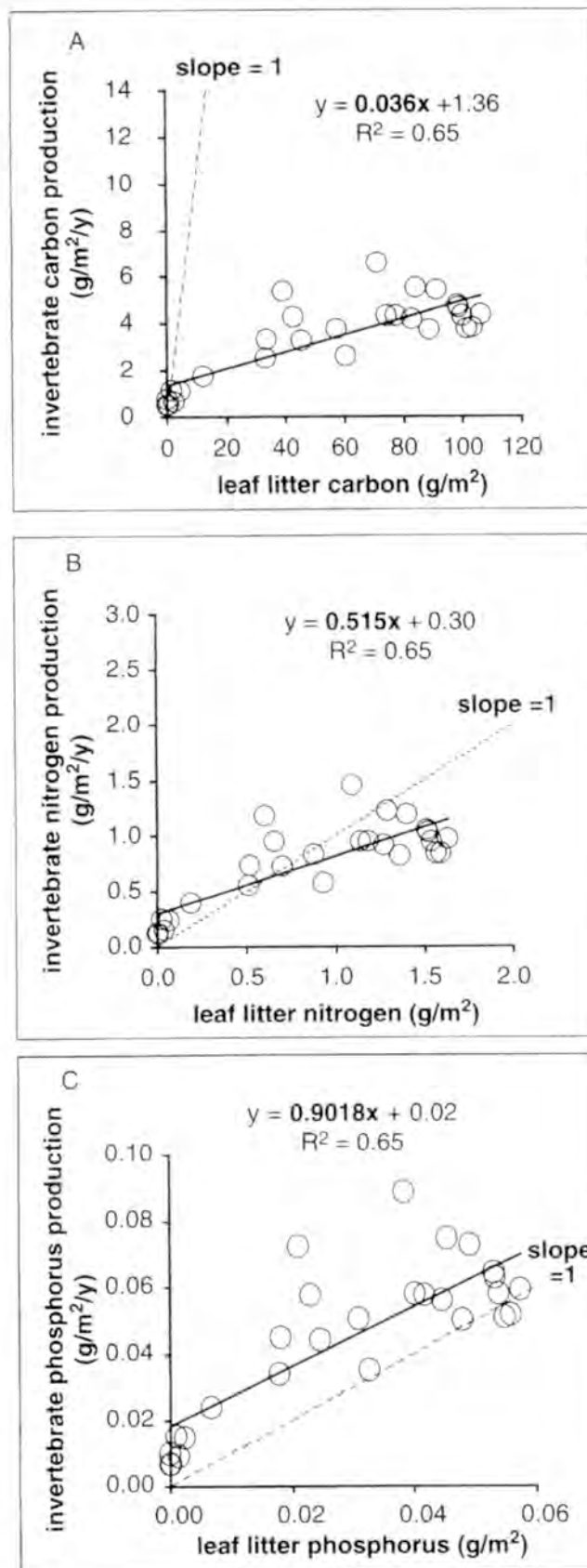


FIGURE 2 | Relationship between mean annual standing crop of leaf litter carbon (A), nitrogen (B), and phosphorus (C) and annual invertebrate secondary production of carbon, nitrogen, and phosphorus in C53, C54, and C55. N-29 years. All linear regressions are significant at $P < 0.001$. For comparative purposes, the dashed line has a slope of 1. Note large differences in scale among graphs.

39% of reference stream concentrations. Throughout the post-treatment period, export concentrations did not differ between the treated and reference streams, although concentrations tended to be higher in the treated stream during this period of rapid invertebrate community recovery (see Figure 3; Whiles and Wallace, 1992; Whiles and Wallace, 1995; Hutchens et al., 1998).

The average ratio of CPOM:FPOM exported from the treated stream increased from 0.053 before treatment to 0.18 during treatment, while little change occurred in reference stream ratios (0.028 before treatment, 0.048 during treatment) (Wallace et al., 1995). Altered export CPOM:FPOM ratios in the treated stream caused relatively large increases in C:P (40%, from 1219 to 1706), C:N (14%, from 36 to 41), and N:P (16%, from 30 to 35) ratios of total (CPOM + FPOM) exported particulate organic matter.

In order to gain a basin-wide perspective on the importance of invertebrates to elemental export, we calculated mean export of C, N, and P per square meter, and extrapolated these data to all headwater streams within the Coweeta basin. Mean annual export of fine particulate C, N, and P ($\text{g}/\text{m}^2/\text{y}$) was quantified from headwater streams during 13 unmanipulated stream-years in C53, C54, and C55 (Table 1). On a per-square meter basis, these first-order streams deliver a large subsidy of fine particulate C, N, and P to downstream river ecosystems (see Table 1). When all first-order streams within the Coweeta basin (length: 33.2 km; average wetted-channel width: 1.5 m) are considered, massive amounts of particulate C, N, and P are exported each year (see Table 1). Based on results from the insecticide treatment, it is possible to estimate the role of invertebrates in the total particulate C, N, and P export from the Coweeta basin. Applying percent differences in the treated versus the reference stream from above, it is evident that a major proportion of particulate C, N, and P export is due to invertebrate feeding and/or bioturbation activities (see Table 1).

DISCUSSION AND CONCLUSIONS

The implication that animal-derived effects on nutrient fluxes can dominate in ecosystems is receiving a considerable amount of support. In diverse ecosystems including lakes (Kitchell et al., 1979; Strayer et al., 1999; Vanni, 2002), streams (Grimm, 1988; Cuffney et al., 1990; Gende et al., 2002; Hall et al., 2003; this study), forests (Swank et al., 1981; Lovett et al., 2002), coral reefs (Meyer and Schultz, 1985), and estuaries (Dame

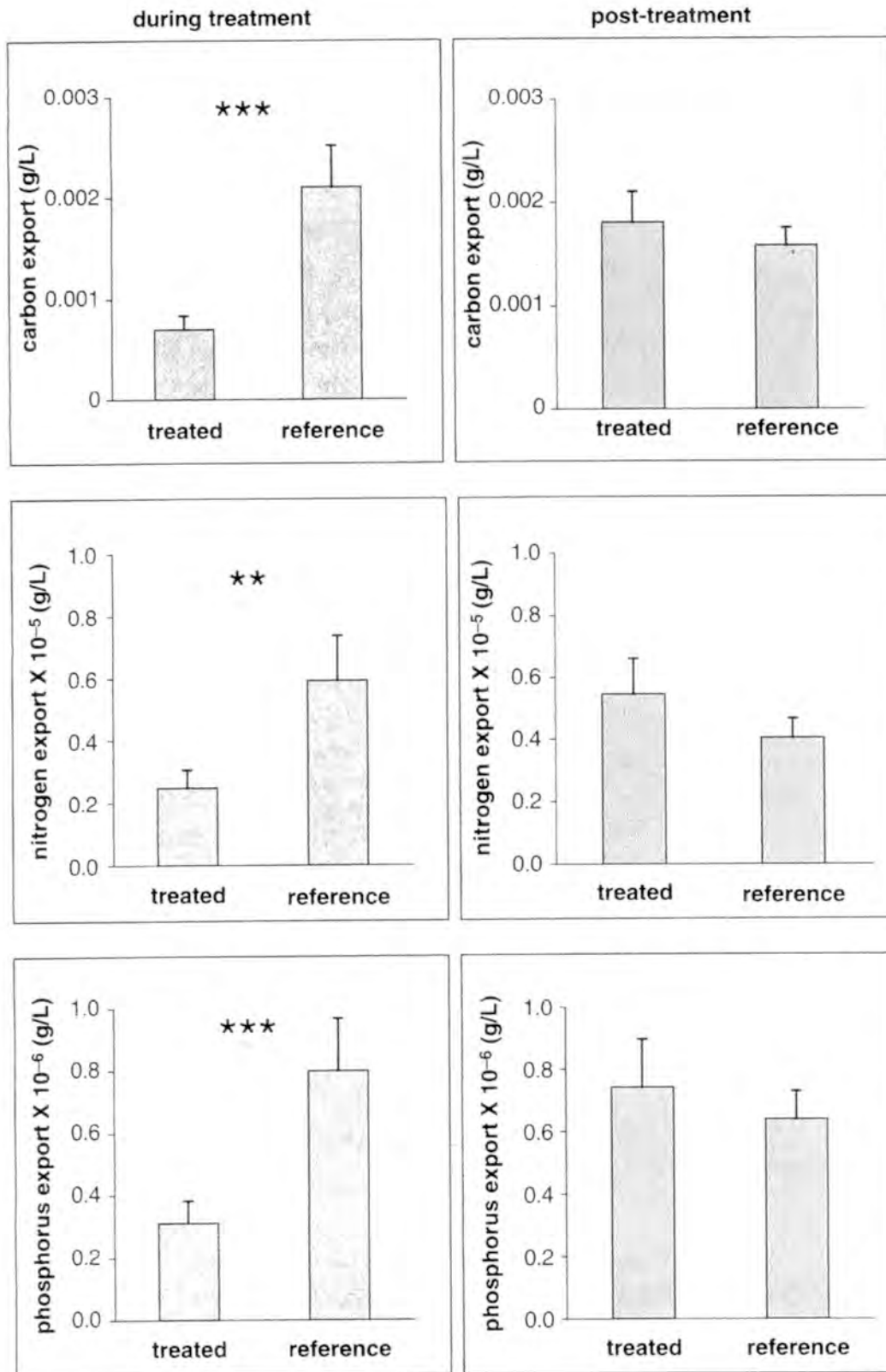


FIGURE 3 | Mean (+ISE) export concentration (g/L) of carbon, nitrogen, and phosphorus in the treated stream (C54) and a reference stream (C55) during invertebrate removal treatment (1987-1988) and after treatment (1988-1990). ** $P < 0.01$, *** $P < 0.001$, randomized intervention analysis. Note large differences in scale among graphs.

Table 1. Export of particulate carbon, nitrogen, and phosphorus (<4mm) from headwater streams at Coweeta Hydrologic Laboratory.*

	Mean export (g/m ² /y) ±SE	Total area of 1 st order streams at Coweeta† (m ²)	Total basin wide export from 1 st order streams (Kg/y) ±SE	Predicted basin-wide export from 1 st order streams without inverte- brates (Kg/y)
Carbon	173.8 ± 20.6	49800	8655.2 ± 1024.2	2856.2
Nitrogen	3.6 ± 0.7	49800	179.3 ± 32.4	75.3
Phosphorus	0.5 ± 0.09	49800	24.9 ± 4.7	9.7

*Based on 13 reference condition stream-years in C53, C54, and C55.

†Wallace 1988, assuming average wetted-width of 1st order streams is 1.5 m.

and Libes, 1993), animals contribute significantly to the dynamics of ecosystem-wide biogeochemical cycles, as well as many other ecosystem processes (Duffy, 2002). The magnitude of these contributions, however, can vary tremendously in space and time, and may be underappreciated if focus is limited to one elemental currency or ecosystem process.

One way animals can affect nutrient dynamics is by preferential utilization and storage of elements that are limited in supply. Essential elements, such as N or P, are often more efficiently or tightly cycled in ecosystems than other more abundant elements, such as C. In this study, detrital N and P were sequestered in invertebrate biomass much more readily than C. This is to be expected if N and P are in high demand relative to their availability in the system. Although stream microbes (i.e., bacteria, fungi, algae) can dominate the short-term uptake and cycling of N and P (Mulholland et al., 2000; Peterson et al., 2001; Gulis and Suberkropp, 2003), their turnover rates may be sufficiently high such that elements are quickly recycled and not retained for any significant period of time. In contrast, many invertebrates in headwater streams live for a longer period of time (approximately one to three years), and elemental storage by these invertebrates may be an important mode of nutrient retention in the system (Peterson et al., 1997) as well as a stable source of nutrients for in-stream predators.

We also found that invertebrates played a minor role in the storage of C in both dominant stream habitats, but contributed moderately to storage of N and P on bedrock outcrops (N = 8.2%, P = 11.2%). The contribution of invertebrates to particulate pools of N and P on bedrock outcrops is comparable to average values reported for zooplankton N and P in lake pelagic zones (N ~ 6%, P ~ 20%, Hessen et al., 1992; Andersen, 1997). These two habitats are somewhat similar in that nutrients are readily lost through physical erosive (to downstream) or sedimentary (to the lake benthos) processes. In these 'erosional' habitats, the retention of nutrients by consumers makes nutrients available to higher trophic levels and provides a source of recycled nutrients. In contrast, the mixed substrate stream habitat acts as a depositional zone for organic matter, and may be similar in function to lake benthic zones. In these 'depositional' sink habitats, the retention of nutrients by biota is potentially less critical for the maintenance of consumer productivity and nutrient recycling. More studies are needed which quantify the contribution of animals to total pools of particulate nutrients to assess patterns in nutrient storage among systems.

A number of recent studies have demonstrated that small headwater streams are extremely efficient sites for the retention of dissolved carbon and nutrients (Hall and Meyer, 1998; Peterson et al., 2001; Valett et al., 2002; Bernhardt et al., 2003; Webster et al., 2003). These streams are also the most prevalent aquatic features in many regions, and therefore play a strong role in the uptake and retention of these dissolved elements at a landscape scale (Meyer and Wallace, 2001). In this study we have shown that in addition to the importance of headwater streams in the retention of dissolved nutrients, these streams act as critical providers of particulate C, N, and P to downstream food webs (also see Wipfli and Gregovich, 2002). Animals (i.e., invertebrates) are prominent players in this process because they facilitate the transformation of large organic particles to small egested particles which are more readily exported downstream. Indeed, our results indicate that >50% of total fine particulate C, N, and P export from Coweeta headwater streams can be attributed to invertebrate consumptive processes (also see Cuffney et al., 1990). In contrast to the fate of dissolved nutrients, these particles are likely to be physically retained in larger streams and provide a dependable food resource for downstream consumers.

Our ability to quantify the large importance of invertebrates to downstream elemental export was made possible by a large-scale experimental invertebrate removal (Cuffney et al., 1990). Such 'deletion' experiments are critical for assessing interaction strengths among consumers and resources, and may be considerably more

informative than other food web approaches (e.g., energetic flow food webs or topological webs) in determining the regulation of material flows (Paine, 1992; Polis, 1994). In forested headwater streams, the actual flow of energy (or carbon) to invertebrates is insignificant in terms of the whole-system energetic budget. In sharp contrast, their influence on the dynamics of detrital food resources and nutrients is highly significant.

Animals are also capable of affecting ecosystem nutrient dynamics by altering elemental ratios and stoichiometric balance of available nutrients (e.g., Elser et al., 1998, Vanni, 2002). In this study, invertebrates affected bulk elemental ratios of exported particulate nutrients by maintaining low CPOM:FPOM export ratios. In Coweeta streams, average C:P (1015 or 0.09% P) and C:N (34 or 2.9% N) of FPOM are much lower than CPOM (C:P=4858, or 0.02% P; C:N=73, or 1.37% N) as a result of increased surface area:volume ratios and a higher proportion of microbes on these small particles (Sinsabaugh and Linkens, 1990; Cross et al., 2003; 2005). Transformation of CPOM to FPOM by feeding activities of detritivorous invertebrates effectively facilitates the production and export of small nutrient-rich particles. Invertebrate removal caused a major reduction in this transformation, and a consequent increase in C:P, C:N, and N:P ratios of bulk organic matter export because nutrient-poor CPOM constituted a higher proportion of the total particulate organic matter being exported.

In summary, our analyses support the idea that animals play diverse roles in ecosystems and may have surprisingly large effects on processes (i.e., nutrient dynamics) that would not be predicted from their limited energetic contribution to many systems. Understanding linkages between animal species or assemblages and ecosystem processes will benefit greatly from studies that examine a suite of response variables, including multiple elemental currencies and multiple processes.

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