

Nutrient enrichment differentially affects body sizes of primary consumers and predators in a detritus-based stream

John M. Davis,^{a,1,*} Amy D. Rosemond,^a Susan L. Eggert,^b Wyatt F. Cross,^{a,2} and J. Bruce Wallace^c

^aOdum School of Ecology, University of Georgia, Athens, Georgia

^bNorthern Research Station, U.S. Department of Agriculture Forest Service, Grand Rapids, Minnesota

^cDepartment of Entomology, University of Georgia, Athens, Georgia

Abstract

We assessed how a 5-yr nutrient enrichment affected the responses of different size classes of primary consumers and predators in a detritus-based headwater stream. We hypothesized that alterations in detritus availability because of enrichment would decrease the abundance and biomass of large-bodied consumers. In contrast, we found that 2 yr of enrichment increased the biomass and abundance of all consumers regardless of body size. Furthermore, during the fourth and fifth year of enrichment, the abundance and biomass of large-bodied primary consumers continued to increase, while small-bodied primary consumers returned to pretreatment levels. The size structure of a dominant primary consumer (*Pycnopsyche* spp.) also shifted during the 5-yr enrichment: its average and maximum individual body size increased in the treatment stream compared with the reference stream. Positive enrichment effects also occurred on small-bodied predators, but not on large-bodied predators. Thus, enrichment increased prey body size, but these positive effects on large prey did not propagate up to higher trophic levels to affect large predators. Because consumer body size can be an important species-specific trait determining population dynamics and ecosystem processes, these observed shifts in consumer size distributions suggest a potentially important pathway for global increases in nutrient enrichment to alter stream structure and function.

In aquatic ecosystems, nutrient enrichment can alter total consumer biomass and production (Sarda et al. 1996; Slavik et al. 2004; Cross et al. 2006) as well as shift community composition and body size distributions (Sprules and Munawar 1986; Bourassa and Morin 1995; Cyr et al. 1997). In autotrophic ecosystems, reported shifts in body size distributions have largely been attributed to top-down and bottom-up effects via size-selective predation and exploitative competition for resources (Brooks and Dodson 1965; Finlay et al. 2007). Specifically, when predators preferentially consume large-bodied prey, enrichment can increase the relative dominance of smaller bodied prey (Brooks and Dodson 1965; Finlay et al. 2007). Conversely, when predators do not focus on large-bodied prey, enrichment of autotrophic food webs can increase the relative dominance of large primary consumers because of associated increases in the quality (lower C:N, C:P, or both) and quantity of basal resources (Sprules and Munawar 1986; Bourassa and Morin 1995). In addition to such community-level responses, population-level size structure can be altered by enrichment because of increased individual growth rates and maximum body sizes, particularly among those taxa that exhibit indeterminate growth (Lurling and Van Donk 1997; Boersma and Kreutzer 2002; Slavik et al. 2004). Thus, previous studies in autotrophic

ecosystems have largely shown that the effects of nutrient enrichment on body size distributions result from a combination of top-down and bottom-up effects, which simultaneously increase the quantity and quality of algal resources.

Although detrital pathways can dominate energy flow in many ecosystems (Moore et al. 2004), less is known about the effects of enrichment on consumer size distributions in detritus-based ecosystems, in which enrichment might increase resource quality but decrease resource quantity. These ecosystems might respond to enrichment in a fundamentally different manner than living plant-based ecosystems. For instance, enrichment of detritus-based food webs stimulates the production and biomass of heterotrophic microbes on detritus (Pace and Cole 1996; Stelzer et al. 2003; Sundareshwar et al. 2003). Because microbes have a higher nutrient content than their detrital substrate, this greater microbial biomass can improve overall detritus quality (lower carbon to nutrient ratios; Stelzer et al. 2003; Ferreira et al. 2006). This stimulation of heterotrophic microbes also increases detrital processing rates, which can subsequently alter the quantity or the temporal availability of detrital resources, or both (Mack et al. 2004; Turner et al. 2009; Suberkropp et al. 2010). Faster detrital processing rates that accelerate the depletion of these detrital resources could lead to periods of low resource availability, potentially reducing the temporal stability of resources (Suberkropp et al. 2010). In cases in which detrital resource availability limits consumer production or consumers are dependent on predictable temporal availability of detritus, these periods of low resource availability could reduce individual growth rates, decrease maximum body sizes, and depress populations of

* Corresponding author: jmdavis@isu.edu

Present addresses:

¹Stream Ecology Center, Department of Biological Sciences, Idaho State University, Pocatello, Idaho

²Department of Ecology, Montana State University, Bozeman, Montana

large-bodied primary consumers, despite increased resource quality.

Because body size is related to population dynamics and ecosystem function (Peters 1983; Hall et al. 2007), such changes in consumer size distributions can alter ecosystem processes. Specifically, predator–prey body size ratios can be related to predation pressure, trophic interaction strength, and the overall stability of aquatic food webs (Emmerson and Raffaelli 2004; Brose et al. 2006b). Thus, shifts in size distributions because of enrichment have the potential to alter the overall stability of enriched ecosystems. Because body size scales allometrically with consumer metabolic and excretion rates (Brown et al. 2004; Hall et al. 2007), these shifts could also influence nutrient and energy fluxes within these ecosystems. Understanding how enrichment might alter body size distributions of organisms in detritus-based ecosystems will help enhance our ability to predict its effects on the structure and function of aquatic ecosystems.

Here, we report results from a 5-yr experimental nutrient enrichment in which we tested effects on the body sizes of primary consumers and predators in a detritus-based headwater stream. We examined whether consumer response to enrichment varied with body size by grouping organisms into body size classes and assessing which of these classes responded to enrichment. Because enrichment can increase detrital processing rates and affect temporal availability of detrital resources in headwater streams (Greenwood et al. 2007; Suberkropp et al. 2010), we predicted that this protracted period of low resource quantity would decrease the abundance and biomass of large-bodied primary consumers.

Because reduced resource availability can also decrease individual growth rates of consumers (Boersma and Kreutzer 2002), these extended periods of low resource availability could alter population size structure and reduce the maximum individual body size a consumer can obtain in a given year. Therefore, we assessed the effect of nutrient enrichment on the average and maximum individual body size of *Pycnopsyche* spp. (Trichoptera), a dominant consumer in many temperate forested headwater streams (Creed et al. 2009). A previous experimental manipulation that reduced leaf litter inputs to an adjacent headwater stream decreased the production and individual body size of *Pycnopsyche*, which indicated that they were particularly sensitive to reductions in resource quantity (Wallace et al. 1999; Eggert and Wallace 2003). Thus, we believed the size response of this taxon would be an effective integrator of resource quantity effects and help elucidate taxon-level body size responses.

Body size responses of higher trophic levels are more difficult to predict. Specifically, the effects of nutrient enrichment on predator body size likely depend on whether small- or large-bodied primary consumers increased with enrichment because this would affect prey availability. Predators in many ecosystems primarily consume small prey (e.g., prey much smaller than predators; Brose et al. 2006a; Woodward and Warren 2007). In these cases, predators might benefit from the increased biomass and abundance of small prey but might not benefit from similar

increases in large prey. Thus, if reductions in detritus availability increased small primary consumers, this greater prey availability might stimulate predator growth rates, subsequently increasing the abundance and biomass of large predators. Conversely, if enrichment increases large-bodied primary consumers that are not readily eaten by predators, this could decrease the predator's prey base (i.e., small primary consumers). This reduced prey availability might limit predator growth rates and reduce the abundance and biomass of large predators. Accordingly, our study tested the effects of nutrient enrichment on size classes of predators and prey in a detritus-based ecosystem in which predators primarily consume small prey.

Methods

Study site—We conducted this study at the USDA Forest Service Coweeta Hydrologic Laboratory, a Long-Term Ecological Research site located in the southern Appalachian Mountains (Macon County, North Carolina). Coweeta is a heavily forested experimental watershed (21.85 km²) comprising mixed hardwoods (oak, maple, tulip poplar) with a dense understory dominated by *Rhododendron maximum* that limits light availability. This light limitation reduces autotrophic production and increases the food web's reliance on heterotrophic microbes that colonize terrestrial leaf inputs (Wallace et al. 1997; Hall et al. 2000; Cross et al. 2007). Because of the mixed-species forest composition, leaf litter inputs to these stream ecosystems range from low-quality *Rhododendron* detritus to higher quality maple detritus (Greenwood et al. 2007).

We selected two forested first-order catchments (C53 and C54) that did not differ in their physiochemical properties (see Lughart and Wallace [1992] for further description of study streams). Both study streams were fishless. The primary consumer community comprised ~ 40 taxa, whereas the predator community was dominated by > 20 taxa of invertebrate (e.g., *Beloneuria* [Plecoptera], Ceratopogonidae [Diptera], *Cordulegaster* [Odonata], *Hexatoma* [Diptera], and *Lanthus* [Odonata]) and vertebrate predators (e.g., *Eurycea wilderae* [Plethodontidae] and *Desmognathus quadramaculatus* [Plethodontidae]). Both predator groups, which are representative of predator taxa frequently found in southern Appalachian headwater streams, occupy a similar trophic position because they predominantly eat small-bodied primary consumers (Davis 1991; Hall et al. 2000; Johnson and Wallace 2005).

Dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations did not differ between the reference (C53) and treatment (C54) streams before the experimental enrichment (mean ± SE; C53: DIN, 23.2 ± 8.5 µg L⁻¹; SRP, 6.8 ± 3.0 µg L⁻¹; C54: DIN, 29.3 ± 4.9 µg L⁻¹; SRP, 9.5 ± 2.3 µg L⁻¹). From July 2000 to August 2005 (~ 1877 d), we experimentally enriched a 150-m reach of the treatment stream with nitrogen (NH₄NO₃) and phosphorus (K₂HPO₄ and KH₂PO₄). We added nutrients continuously along the entire 150-m length of the treatment stream with the use of an irrigation line running down the center of the channel. This delivery system increased nutrient concentrations in the treatment

stream to a realistic, moderate-level enrichment (DIN, $506.2 \pm 36.3 \mu\text{g L}^{-1}$; SRP, $80.0 \pm 5.6 \mu\text{g L}^{-1}$), whereas the reference stream concentrations during this same time period were comparable to the pretreatment period (DIN, $31.0 \pm 3.4 \mu\text{g L}^{-1}$; SRP, $8.0 \pm 1.3 \mu\text{g L}^{-1}$). We monitored nutrient concentrations every 2 weeks at three points along the 150-m reach of the treatment stream and at the weir of the reference stream (APHA 1998). Water temperature was measured every 30 min in both streams with Optic StowAway temperature probes (Onset Computer). We measured stream discharge at 5-min intervals with an Isco data logger (Teledyne Isco).

Macroinvertebrate sampling—The macroinvertebrate communities in both streams were sampled every month (approximately midmonth) during an initial 2-yr pretreatment period (September 1998 to June 2000) followed by a 5-yr experimental period (July 2000 to August 2005). On each monthly sampling date, we sampled mixed-cobble substrates according to Cross et al. (2006). With the use of a stovepipe corer (400 cm², Merritt and Cummins 1996), four mixed-cobble substrate samples were randomly collected in each stream on each sampling date. The corer was firmly placed on the stream substrate and all material was removed by hand to a depth of 15 cm. We transported the samples back to the laboratory and processed them within 48 h of collection. Each sample was rinsed onto nested sieves (1-mm and 250- μm mesh size) and elutriated to remove inorganic material. We divided the remaining organic matter into large (> 1 mm) and small (250 μm to 1 mm) size fractions and preserved them with 6–8% formalin. Because of the large number of macroinvertebrates in the small size fraction, we subsampled this fraction with a sample splitter (Waters 1969). All macroinvertebrates were removed from both the large and small size fractions with a dissecting scope at 15 \times magnification. Each organism was identified to genus; however, Chironomidae were identified to either Tanypodinae (predators) or non-Tanypodinae (nonpredators), and most noninsects were identified to the order level or higher (e.g., oligochaetes, nematodes, copepods, etc.). All individuals were enumerated and measured to the nearest millimeter under 12 \times magnification. We calculated consumer biomass using length–mass regressions established for Coweeta streams (Benke et al. 1999; J. B. Wallace unpubl.). We classified all taxa as either primary consumer or predator according to Merritt and Cummins (1996) and on the basis of our previous knowledge from working in this ecosystem (Wallace et al. 1999).

Body size analysis—To first determine potential effects of nutrient enrichment on coarse-scale changes in the body size distribution of the stream macroinvertebrate community, we first compared the total abundance and biomass response of the entire macroinvertebrate community (primary consumers plus predators). Divergent results in these responses (total biomass vs. abundance) would suggest potential changes in mean body size. Increased total biomass without a concomitant increase in total abundance would imply that nutrient enrichment increased

Table 1. Breakdown of the 22 log(body size classes) used for categorizing primary consumers and predators by body size (mg). We based the log transformations on the upper limit of the body size class. Individual body masses of macroinvertebrates in our study streams ranged in body size from < 0.001 to 169.360 mg. Because of insufficient sample sizes that precluded individual statistical analysis of the largest size classes, these larger size classes were further grouped into a single body size class, which allowed for statistical analysis (see Results).

Log(body size class)	Lower limit (>mg)	Upper limit (\leq mg)
–3.00	0.000	0.001
–2.75	0.001	0.002
–2.50	0.002	0.003
–2.25	0.003	0.006
–2.00	0.006	0.010
–1.75	0.010	0.018
–1.50	0.018	0.032
–1.25	0.032	0.056
–1.00	0.056	0.100
–0.75	0.100	0.178
–0.50	0.178	0.316
–0.25	0.316	0.562
0.00	0.562	1.000
0.25	1.000	1.778
0.50	1.778	3.162
0.75	3.162	5.623
1.00	5.623	10.000
1.25	10.000	17.783
1.50	17.783	31.623
1.75	31.623	56.234
2.00	56.234	100.000
2.25	100.000	177.828

the average individual body size of at least some groups of consumers.

We then assessed whether the effects of nutrient enrichment varied with consumer body size by conducting a body size–specific analysis of consumer response. Macroinvertebrate body size is relatively indeterminate and can change under varying environmental conditions (Peckarsky et al. 2001); thus, we did not assign a single body size to a taxon (i.e., an average or maximum body size). Instead, we assigned each individual within a particular taxon to an appropriate size class on the basis of its log-transformed individual body size (mg). Early instars of large-bodied taxa were assigned to the same size class as similar-sized individuals of small-bodied taxa. Accordingly, we first log-transformed the body size (mg) of each individual within each taxon for a given month. On the basis of this transformed body size, we then grouped individuals into one of the 22 separate log size classes (see Table 1 for further descriptions of the specific upper and lower limits for body size used for each class). Then, for all individuals in a specific log size class, we summed either their biomass or abundance, regardless of taxonomic classification. Because we repeated this grouping and summation for each month, we created a taxon-independent monthly time series that followed changes in biomass or abundance within each of the 22 size classes that spanned a 7-yr time period. We conducted this body size analysis separately for primary consumers and predators.

Statistical analysis—We first evaluated whether nutrient enrichment differentially affected total macroinvertebrate biomass and abundance (predators and primary consumers combined) because this would indirectly suggest a shift in body size distributions for the entire macroinvertebrate community. Although our study consisted only of one treatment and one control stream, we felt that the realism gained in a whole-stream manipulation outweighed the statistical benefits of smaller scale, replicated treatments. Randomized intervention analysis (RIA, Carpenter et al. 1989) is a statistical test appropriate for such a design and was applied to the monthly time series of total macroinvertebrate biomass and abundance. To assess the size-specific effects of nutrient enrichment on primary consumers and predators, we also applied RIA to the monthly time series of biomass and abundance data that were grouped by body size into the 22 separate classes. Analyzing each of the body size classes separately allowed us to evaluate how the effects of nutrient enrichment varied between body sizes. Because the effects of nutrient enrichment have been previously shown to vary during the first 2 yr of enrichment (ENR 1 and 2) compared with the fourth and fifth years of enrichment (ENR 4 and 5; Davis et al. 2010), we analyzed the short- and longer term responses separately for each of the RIA comparisons listed above (i.e., total abundance, total biomass, size-specific biomass, size-specific abundance). Specifically, we divided the study into three time periods: pretreatment (PRE 1 and PRE 2; July 1998 to August 2000), short-term response (ENR 1 and ENR 2; September 2000 to August 2002), and longer term response (ENR 4 and ENR 5; September 2003 to August 2005). For each of the above comparisons, RIA then compared the short-term response (26 months) to the pretreatment period (22 months), and the longer term response (24 months) to the pretreatment period. On the basis of these contrasts, RIA calculated probabilities of change for each pairwise comparison with the use of 1000 random permutations of interstream differences (Carpenter et al. 1989). These separate analyses allowed us to isolate the short- and longer term effects of nutrient enrichment on the parameter of interest. The third year of enrichment (ENR 3; September 2002 to August 2003) was not included in our analyses because samples were lost through inadequate preservation. Bias in our analysis because of the exclusion of ENR 3 is unlikely because any trends associated with ENR 3 would likely be captured by the final 2 yr of enrichment (ENR 4 and ENR 5).

By comparing the differences in the reference and treatment stream during the pretreatment and posttreatment periods, RIA tested the null hypothesis that biomass or abundance in the treatment stream did not change relative to the reference stream during the nutrient enrichment. However, because RIA only established whether there was a significant change in the treatment stream during the posttreatment period compared to the pretreatment period, we examined the monthly time series data to determine the direction of the change (positive or negative) for the biomass and abundance responses within each size class. Briefly, for the biomass or abundance within each individual size class j , we first calculated the difference between the reference and treatment streams (e.g., $\text{reference}_{ij} - \text{treatment}_{ij}$) for each

Table 2. Primary consumer biomass effect sizes that indicate the direction and magnitude of the enrichment response (mean \pm SE) in a given size class. For each size class, negative values indicate a decrease in grouped biomass for the treatment stream relative to the pretreatment period, whereas positive values signify an increase in grouped biomass (see Eq. 1). RIA was applied to the monthly time series in each size class. Asterisks represent a significant difference between the posttreatment period (either short-term [ENR 1 and 2] or longer term response [ENR 4 and 5]) and the pretreatment years (RIA, $p < 0.05$). Because of insufficient sample sizes that precluded individual analysis of the two largest size classes, these classes were further grouped into a single size category (56.234–177.828 mg), which provided a sufficient sample size for analysis. AF, ash-free dry weight.

Body size range (mg) (>min≤max)	Primary consumer biomass effect sizes (mg AF dry wt m ⁻²)	
	Short vs. PRE	Long vs. PRE
0.000–0.001	71.0(13.1)*	–9.0(10.7)
0.001–0.002	7.6(1.7)*	4.5(1.1)*
0.002–0.003	8.0(2.9)*	–1.3(1.9)
0.003–0.006	26.4(8.8)*	–5.8(5.5)
0.006–0.010	5.9(2.3)*	–1.3(1.7)
0.010–0.018	34.1(10.0)*	1.7(9.0)
0.018–0.032	61.9(14.9)*	24.5(15.4)
0.032–0.056	45.5(13.3)*	22.2(12.6)
0.056–0.100	85.5(25.2)*	34.1(12.1)*
0.100–0.178	63.3(31.4)*	–15.2(15.7)
0.178–0.316	58.2(17.1)*	11.5(19.8)
0.316–0.562	68.6(26.2)*	–10.2(25.9)
0.562–1.000	76.7(20.1)*	7.1(22.8)
1.000–1.778	113.8(35.7)*	171.2(105.8)
1.778–3.162	74.1(40.1)	191.4(98.3)*
3.162–5.623	137.3(56.0)*	222.1(115.2)*
5.623–10.000	119.2(48.7)*	514.9(188.3)*
10.000–17.783	259.1(91.8)*	871.7(318.0)*
17.783–31.623	114.4(68.4)	540.0(275.4)*
31.623–56.234	81.1(37.3)*	223.8(79.9)*
56.234–177.828	28.5(84.1)	182.5(100.8)*

month i . We then averaged these monthly differences for each of the three sampling periods—pretreatment (22 months), short-term (26 months), and longer term (24 months)—to obtain an average period difference for each size class j (Δ_j). Using these average period differences, we applied the following equation (Osenberg et al. 1994) to calculate the short-term and longer term effect sizes for each size class j .

$$\text{Effect Size}_j = \Delta_{\text{PRE}j} - \Delta_{\text{POST}j} \quad (1)$$

To calculate the short-term enrichment effect size for each size class j , we compared the short-term difference to the pretreatment difference, whereas the longer term effect size compared the longer term difference to the pretreatment difference. We repeated this calculation for both the abundance and biomass estimates within each of the 22 size classes. These calculated effect sizes helped assess the direction and magnitude of the enrichment response within each class.

On the basis of the RIA results, we observed that the effects of enrichment varied with primary consumer body size (see Results). Because we detected a divergence in the longer term primary consumer response at a size class of 1.778 mg (Tables 2, 3), we categorized macroinvertebrates

Table 3. Primary consumer abundance effect sizes that indicate the direction and magnitude of the nutrient enrichment response (mean \pm SE) within a given size class. RIA was applied to the monthly time series of abundance data within each size class. Asterisks represent a significant difference between the posttreatment period (either short-term [ENR 1 and 2] or the longer term response [ENR 4 and 5]) and the 2-yr pretreatment period (RIA, $p < 0.05$). Because of insufficient sample sizes that precluded individual statistical analysis of the two largest size classes, these two classes were further grouped into a single size class (56.234–177.828 mg), which provided a sufficient sample size for statistical analysis. Other designations as in Table 2.

Body size range (mg) (>min \leq max)	Primary consumer abundance effect sizes (No. m ⁻²)	
	Short vs. PRE	Long vs. PRE
0.000–0.001	89366.90(15912.2)*	–9692.00(13445.5)
0.001–0.002	5058.00(1101.3)*	2984.00(761.9)*
0.002–0.003	2681.10(1128.5)*	–333.50(673.9)
0.003–0.006	6476.40(2099.4)*	–1305.30(1327.8)
0.006–0.010	758.30(297.0)*	–192.80(220.6)
0.010–0.018	2551.40(766.8)*	198.40(694.3)
0.018–0.032	2656.20(625.4)*	944.50(644.0)
0.032–0.056	947.70(283.2)*	413.40(277.6)
0.056–0.100	1220.30(427.3)*	392.50(159.2)*
0.100–0.178	490.30(234.1)*	–124.80(119.1)
0.178–0.316	267.20(77.1)*	79.20(95.4)
0.316–0.562	156.50(62.7)*	–15.00(62.0)
0.562–1.000	107.20(28.0)*	8.60(32.1)
1.000–1.778	86.40(28.0)*	124.90(73.1)
1.778–3.162	28.50(15.8)	78.40(39.4)*
3.162–5.623	30.20(13.2)*	48.30(26.0)*
5.623–10.000	14.90(6.4)*	68.00(25.8)*
10.000–17.783	18.50(6.8)*	56.50(25.3)*
17.783–31.623	5.10(3.0)	23.90(12.3)*
31.623–56.234	2.30(1.0)*	5.80(2.2)*
56.234–177.828	0.10(0.6)	1.40(1.1)*

into two representative groups: small-bodied individuals (individual body size ≤ 1.778 mg) and large-bodied individuals (body size > 1.778 mg). We graphed these overall trends to better illustrate the generalized responses of small and large consumers to enrichment.

Finally, we evaluated the effects of nutrient enrichment on the individual body size of a dominant primary consumer (*Pycnopsyche* spp.) that has previously shown sensitivity to reductions in leaf litter inputs to a similar stream food web (Wallace et al. 1999; Eggert and Wallace 2003). We assumed changes in its individual body size would be a good indicator of the net effect of shifts in resource quality and quantity. We first calculated the maximum body size that *Pycnopsyche* obtained in a given year, which would indicate larval body size at pupation. We also calculated the average individual body size of *Pycnopsyche* in each stream during a particular year. We plotted these changes as maximum and average individual body size.

Results

Total abundance vs. total biomass trends—Total macroinvertebrate (primary consumer plus predators) biomass

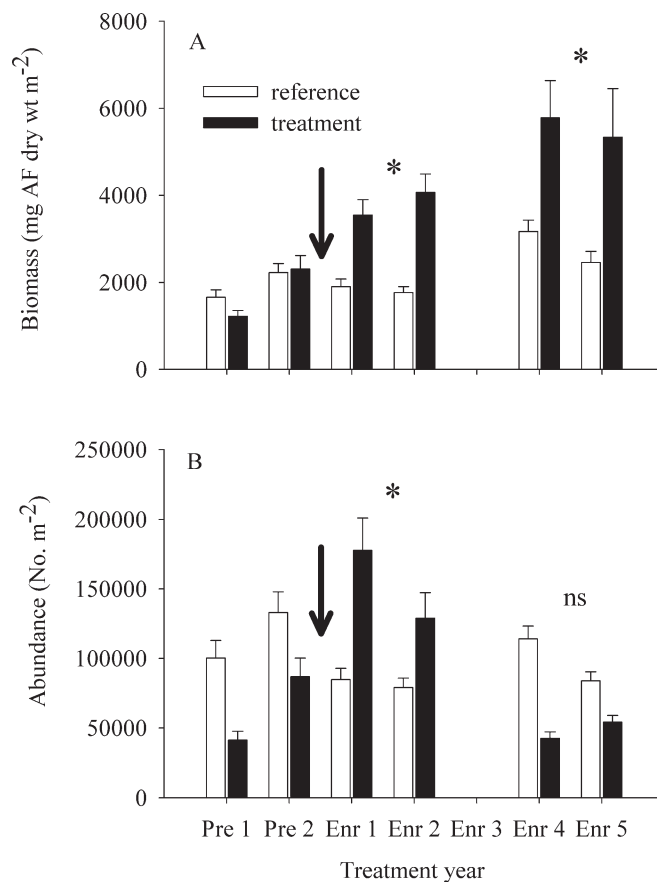


Fig. 1. Average annual (A) biomass and (B) abundance of all macroinvertebrates (primary consumers plus predators; mean \pm 1 SE). The arrow indicates the beginning of nutrient enrichment. The short-term sampling period encompasses ENR 1 and 2, whereas the longer term sampling period encompasses ENR 4 and 5. Asterisks above each sampling period represent a significant difference between the posttreatment period (either short-term or longer term response) and the pretreatment period (Pre 1 and 2; RIA, $p < 0.05$). ns, nonsignificant difference between the sampling periods.

was significantly higher in the treatment compared with the reference stream during both the short-term (ENR 1 and 2; Cross et al. 2006) and longer term enrichments (ENR 4 and 5; RIA, $p < 0.05$; Fig. 1A). However, total abundance increased during the short-term enrichment (RIA, $p < 0.05$; Cross et al. 2006) but was not significantly different from the pretreatment years during the longer term enrichment (Fig. 1B). These sustained increases in total biomass, but lack of a total abundance response to the longer term nutrient enrichment, indicated that nutrient enrichment increased the average individual body size of stream consumers.

Size-specific analysis—The body size analyses showed that the effect of nutrient enrichment on consumers was related to body size. This analysis categorized biomass and abundance estimates into 22 separate size classes that ranged in size from < 0.001 mg to 169.360 mg. Because of insufficient sample sizes that precluded individual analysis

Table 4. Predator biomass effect sizes that indicate the direction and magnitude of the nutrient enrichment response (mean \pm SE) within a given size class. RIA was applied to the monthly time series of biomass data within each size class. Asterisks represent a significant difference between the posttreatment period (either short-term or longer term response) and the pretreatment period (RIA, $p < 0.05$). Because of insufficient sample sizes that precluded individual statistical analysis of the three largest size classes, these three classes were further grouped into a single size class (31.623–177.828 mg), which provided a sufficient sample size for statistical analysis. We excluded one body size class (0.001–0.002 mg) from the RIA analysis (represented by nd) because of insufficient sample sizes (*see* Results). Other designations as in Table 2.

Body size range (mg) (>min≤max)	Predator biomass effect sizes (mg AF dry wt m ⁻²)	
	Short vs. PRE	Long vs. PRE
0.000–0.001	2.4(0.6)*	1.9(0.6)*
0.001–0.002	0.2(0.1)nd	0.1(0.1)nd
0.002–0.003	10.3(3.0)*	7.8(2.5)*
0.003–0.006	6.0(1.6)*	4.0(1.3)*
0.006–0.010	3.6(1.1)*	2.6(1.2)*
0.010–0.018	36.0(9.0)*	22.8(7.5)*
0.018–0.032	9.1(4.1)*	1.2(3.0)
0.032–0.056	43.0(14.5)*	27.8(15.0)
0.056–0.100	43.9(20.9)*	19.5(14.6)
0.100–0.178	21.5(17.3)	–20.6(15.1)
0.178–0.316	75.1(25.3)*	12.0(21.2)
0.316–0.562	68.7(20.5)*	–31.8(12.5)*
0.562–1.000	78.6(22.0)*	2.8(11.3)
1.000–1.778	63.6(16.9)*	29.7(17.4)
1.778–3.162	57.4(15.2)*	31.1(22.1)
3.162–5.623	–19.6(24.2)	–90.0(21.6)*
5.623–10.000	27.5(23.5)	–42.8(22.4)
10.000–17.783	94.6(40.5)*	–14.9(38.0)
17.783–31.623	27.0(64.5)	–3.3(49.5)
31.623–177.828	47.3(95.2)	69.9(110.2)

of the largest primary consumers and predators, these size classes were further grouped into a single size class (primary consumers, 56.234–177.828 mg; predators, 31.623–177.828 mg). This regrouping provided a sufficient sample size for statistical analysis. We still excluded one small size class of predators (0.001–0.002 mg) from the analysis because combining these data with an adjoining class would have masked the low occurrence of predators in this size category (represented by not determined [nd] in Tables 4 and 5). Because the biomass and abundance in this size class was low compared with the adjacent classes, their exclusion did not alter the analysis.

Primary consumer size-specific response—During the short-term enrichment (ENR 1 and 2), the response of primary consumer biomass and abundance did not vary with body size (Tables 2, 3). Specifically, short-term enrichment increased the biomass and abundance of primary consumers in most of the body sizes tested (with the exception of two size classes [1.778–3.162 and 17.783–31.623 mg] that did not respond to nutrient enrichment). However, during the longer term enrichment (ENR 4 and 5), primary consumer response varied with body size. In

Table 5. Predator abundance effect sizes that indicate the direction and magnitude of the nutrient enrichment response (mean \pm SE) within a given size class. RIA was applied to the monthly time series of abundance data within each size class. Asterisks represent a significant difference between the posttreatment period (either short-term [ENR 1 and 2] or a longer term response [ENR 4 and 5]) and the 2-yr pretreatment period (RIA, $p < 0.05$). Because of insufficient sample sizes that precluded individual statistical analysis of the three largest size classes, these three classes were further grouped into a single size class (31.623–177.828 mg), which provided a sufficient sample size for statistical analysis. We excluded one body size class (0.001–0.002 mg) from the RIA analysis (represented by nd) because of insufficient sample sizes (*see* Results). Other designations as in Table 2.

Body size range (mg) (>min≤max)	Predator abundance effect sizes (No. m ⁻²)	
	Short vs. PRE	Long vs. PRE
0.000–0.001	3986.20(1073.4)*	3122.60(1052.6)*
0.001–0.002	123.70(58.8)nd	46.00(57.8)nd
0.002–0.003	3839.20(1092.7)*	2891.10(927.9)*
0.003–0.006	1372.80(359.9)*	906.40(287.3)*
0.006–0.010	412.60(125.7)*	339.90(142.4)*
0.010–0.018	2480.90(620.9)*	1571.60(512.3)*
0.018–0.032	338.30(143.5)*	44.20(109.0)
0.032–0.056	1073.90(371.7)*	715.20(384.7)
0.056–0.100	598.60(273.4)*	221.40(192.3)
0.100–0.178	171.00(133.2)	–152.80(116.5)
0.178–0.316	331.60(116.9)*	47.80(98.8)
0.316–0.562	165.10(47.7)*	–70.40(33.7)*
0.562–1.000	101.50(28.1)*	4.60(14.8)
1.000–1.778	48.90(12.8)*	23.00(13.2)
1.778–3.162	23.10(6.4)*	14.10(9.7)
3.162–5.623	–3.30(5.3)	–18.40(5.0)*
5.623–10.000	3.80(3.0)	–5.20(2.9)
10.000–17.783	6.70(3.1)*	–1.40(2.8)
17.783–31.623	0.20(2.6)	–0.80(2.0)
31.623–177.828	1.30(2.0)	0.40(1.9)

this case, the biomass and abundance of large-bodied primary consumers (defined here as body size > 1.778 mg) continued to increase with the longer term enrichment, but most small-bodied primary consumers did not (defined here as body size ≤ 1.778 mg). There were two exceptions to this general lack of response of small primary consumers, in that the abundance and biomass of two size classes (0.001–0.002 and 0.056–1.000 mg) continued to respond positively to longer term nutrient enrichment (Tables 2, 3).

Because the abundance and biomass of large primary consumers (body size > 1.778 mg) disproportionately increased during the fourth and fifth years of enrichment (Tables 2, 3), the relative dominance of large compared with small primary consumers increased in the treatment stream (Fig. 2A,B). Before enrichment, large primary consumers contributed 56% of primary consumer community biomass in the treatment stream, but this percentage increased to 82% during the final 2 yr of enrichment in the treatment stream. This substantially greater response of large primary consumers skewed the community biomass composition toward these larger sized consumers during the longer term enrichment (Fig. 2A,B).

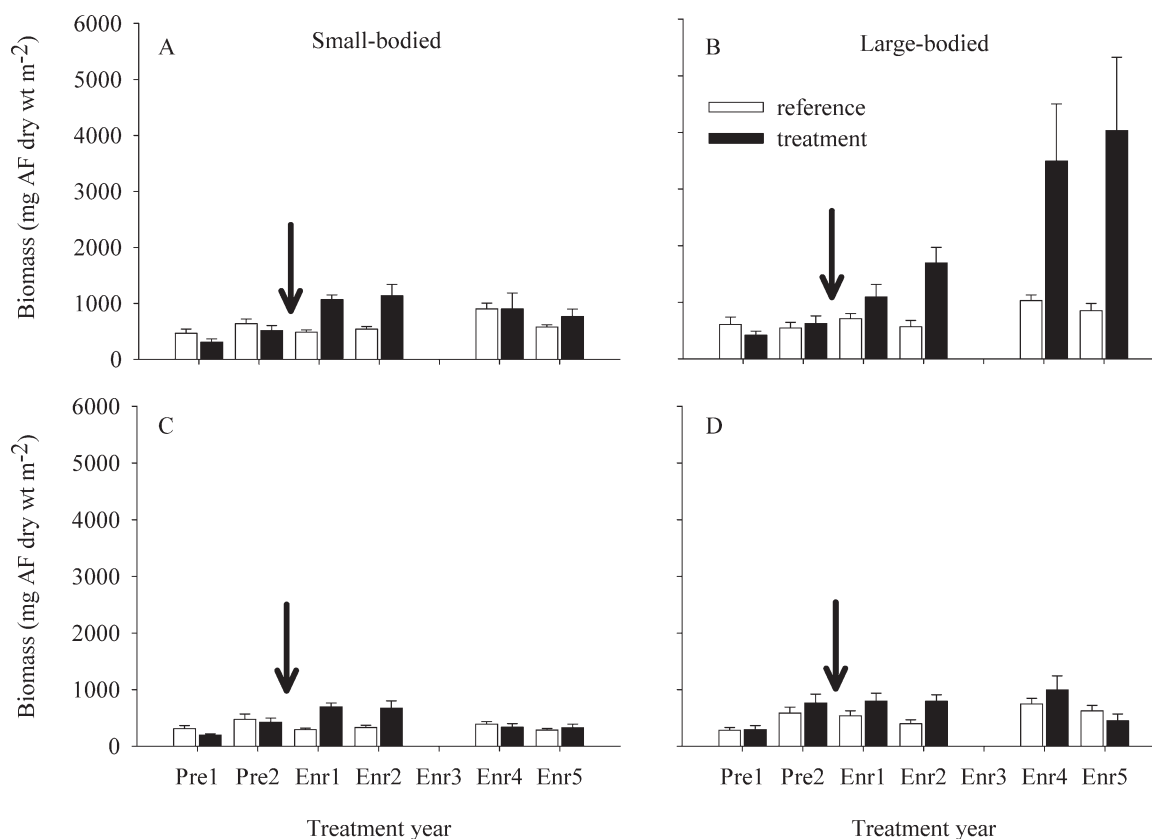


Fig. 2. Average annual biomass (mean \pm 1 SE) of small- and large-bodied (A, B) primary consumers and (C, D) predators. Small- and large-bodied individuals were classified on the basis of the results of the RIA. Our RIA results indicated that primary consumer response to longer term nutrient enrichment diverged at a body size class of 1.778 mg (see Tables 2, 3). Thus, we defined small-bodied consumers as those individuals with body size \leq 1.778 mg, and large-bodied individuals as those individuals with body size $>$ 1.778 mg. The arrow represents the beginning of nutrient enrichment. AF dry wt, ash-free dry weight.

Predator size-specific response—In accordance with the short-term primary consumer response, the biomass and abundance of predators in most body size groups increased with short-term nutrient enrichment, which suggested that the effects of nutrient enrichment did not vary with predator size (Tables 4, 5). In contrast, during the longer term enrichment, predator response varied with body size. The biomass and abundance of small predators (body size \leq 0.018 mg) increased during the longer term enrichment, but large predators did not (body size $>$ 0.018 mg; Tables 4, 5). The abundance and biomass of predators in two of the larger size classes (0.316–0.562 and 3.162–5.623 mg, respectively) were the only classes (primary consumer or predator) that declined significantly below pretreatment levels.

Compared with primary consumers, in which the enrichment responses diverged at a body size of 1.778 mg (Table 2), predator response diverged at a smaller size (0.018 mg; Table 4). Because we were primarily interested in comparing the responses of predators and primary consumers with similar body size, we elected to use the same 1.778-mg division for both trophic levels. However, even when the smaller division (0.018 mg) was used, we observed a similar graphical trend as that observed with the separation at 1.778 mg because of the relatively low

contribution of small predators to overall community biomass.

Using the above body size partition, we found that, similar to primary consumers, the biomass of small-bodied (size \leq 1.778 mg) and large-bodied predators (size $>$ 1.778 mg) increased during the short-term enrichment (Fig. 2C,D). Conversely, the biomass of large predators did not increase during the longer term enrichment (Fig. 2C,D). Thus, although primary consumers and predators of both body sizes exhibited similar positive responses during the short-term enrichment, longer term enrichment did not increase the biomass of large predators, despite continued increases in large primary consumers (Tables 2–5; Fig. 2A–D).

Effects on Pycnosyche individual body size—Nutrient enrichment also altered the size structure of *Pycnosyche* spp. (Fig. 3A,B). Because of the relative greater abundance of large individuals, enrichment increased the annual average individual body size of *Pycnosyche* during the 5-yr enrichment relative to the reference stream and pretreatment period (Fig. 3A). The maximum size of *Pycnosyche* also increased with nutrient enrichment, but this increase was most evident during the final 2 yr of enrichment. Specifically, the maximum size of *Pycnosyche*

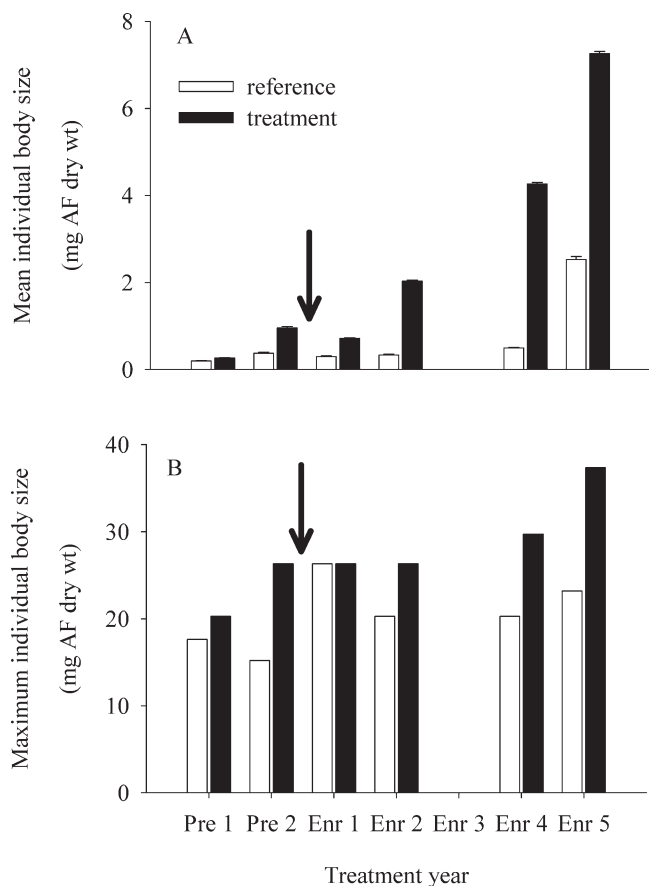


Fig. 3. (A) Mean (\pm SE) and (B) maximum individual body size of *Pycnopsyche* spp. calculated on a yearly basis. The arrow represents the beginning of nutrient enrichment. AF dry wt, ash-free dry weight.

in the fifth year of enrichment was 61% greater in the treatment stream relative to the reference stream (37.4 compared with 23.2 mg, respectively) and was 42% larger than the maximum size observed during the pretreatment period (26.3 mg; Fig. 3B). In the reference stream, *Pycnopsyche* size never exceeded 26.3 mg during the 7-yr experiment.

Discussion

Differences between primary consumer and predator response—Results from our 5-yr ecosystem-level manipulation provided strong evidence that consumer response to chronic nutrient enrichment was related to body size. This response differed for primary consumers and predators and was only evident after 2 yr of continuous enrichment. One possible mechanism to explain the contrasting size responses of primary consumers and predators was the potential existence of predator size-refugia that reduced the predation risk of large prey. The streams used for this study were dominated by > 20 taxa of invertebrate and vertebrate predators (see Methods for taxon list) that primarily eat small prey (Davic 1991; Hall et al. 2000; Johnson and Wallace 2005). Thus, rather than top-down effects of predation diminishing the positive nutrient response of

large prey (if predators preferentially ate them) and increasing the abundance of small prey (Brooks and Dodson 1965), predation likely facilitated the increased dominance of large prey in our streams. Energy flow from prey to predators in these stream food webs can also be highly efficient (Wallace et al. 1997). This suggests that if predators primarily eat small prey, these prey might be more limited by top-down predator control. Conversely, the production of large primary consumers might be coupled more to changes in resource quality because they could obtain predator size-refugia that reduce their predation risk. Because these trends agree with an enrichment of an autotrophic-based stream (Bourassa and Morin 1995), it suggests that body size could determine consumer response to enrichment in a variety of food web types.

Size-selective predation can also help explain why large predators did not respond to enrichment, because predators frequently eat prey smaller than themselves (Emmerson and Raffaelli 2004; Brose et al. 2006a; Woodward and Warren 2007). The increased dominance of large primary consumers might reduce the vulnerability of the prey community, subsequently reducing prey availability and minimizing the positive effects of enrichment on large predators. It is less clear why the abundance and biomass of small predators increased with enrichment in both the short- and longer term experimental periods, because the lack of a significant response of small prey during the longer term period should have minimized any positive effects on small predators. However, because these small predators were dominated by predatory mites (Acari), Ceratopogonidae (Diptera), and Tanypodinae chironomids (Diptera), they might have been eating substantially smaller meiofauna that were not adequately sampled by our 250- μ m sieves. Because early instars of certain small-bodied predators (i.e., Tanypodinae chironomids) can also shift to eating fine particulate organic matter when meiofauna availability declines (Schmid-Araya et al. 2002; Woodward and Hildrew 2002), this dietary switch might have helped to maintain their positive nutrient response.

Omnivory (i.e., cannibalism) has been related to bimodal body size distributions and the emergence of "giants" in other ecosystems (Claessen et al. 2000); thus, such dietary plasticity could potentially explain size-specific primary consumer responses. For instance, some large-bodied detritivores, which primarily consume detritus at early instars, switch to cannibalism and intraguild predation during later instars (Wissinger et al. 1996). Therefore, one could interpret the positive responses of large primary consumers (i.e., later instars) in the treatment stream to ontogenetic omnivory and consumption of small-bodied primary consumers. However, several factors suggest that such a mechanism is highly unlikely in our study streams. In a previous experiment that reduced leaf litter availability in an adjacent stream ecosystem, primary consumers did not switch to animal material, even when leaf availability declined to levels below those measured in the current study (Hall et al. 2000). Although later instars of one primary consumer taxon, *Parapsyche cardis* (Trichoptera), can cannibalize early instars (Hall et al. 2000), this taxon was

not readily found in mixed cobble habitat as sampled here (< 1% of primary consumer biomass; Davis 2009). Consumer diets also did not shift during the first 2 yr of enrichment, despite significant temporal changes in leaf litter availability (Cross et al. 2007; Suberkropp et al. 2010). This lack of diet switching, even when detrital resources declined, suggests that omnivory is an unlikely driver of the size-specific responses of primary consumers that we observed. However, increased intraguild predation could be a proximate driver of predator responses. If reductions in small primary consumers decreased the prey base of large predators, this could increase the prevalence of intraguild predation, subsequently increasing predation pressure on predator taxa and reducing their response to enrichment. Despite this potential role of intraguild predation in the response of large predators, this mechanism still assumes that large primary consumers are predator resistant and reduce the predator's prey base. We therefore think that intraguild predation cannot explain the overall patterns we observed.

Short-term vs. longer term responses—The abundance and biomass of primary consumers and predators within most size classes initially increased because of enrichment (ENR 1 and 2), but longer term enrichment (ENR 4 and 5) positively affected only the abundance and biomass of large primary consumers and small predators. In fact, previous results from the first 2 yr of enrichment, which showed significant increases in the production and growth rates of small prey (e.g., non-Tanypodinae chironomids [Diptera]), led us to predict initially their increased dominance with a longer term enrichment (Cross et al. 2005). These contrasting results suggest that the importance of consumer body size in affecting primary consumer and predator responses might have been delayed and driven in part by shifts in stream habitat dynamics. Specifically, temporal declines in leaf litter standing crop during the experimental enrichment (Suberkropp et al. 2010) might have reduced stream consumer habitat and increased predation risk. Within stream ecosystems, leaf litter can provide a combination of food resources and habitat complexity to consumers (Richardson 1992), such that reductions in debris dams can reduce macroinvertebrate production (Smock et al. 1989; Wallace et al. 1999). Because greater habitat complexity can also provide spatial refugia (Beaty et al. 2006), increased leaf litter standing crop might reduce predation risk. Because predators in these streams primarily eat small prey, these prey could benefit more from leaf litter refugia than larger prey, which might be capable of reducing their predation risk independent of leaf litter availability (i.e., via body size refugia). Although the short-term enrichment reduced leaf litter standing crop (Suberkropp et al. 2010), there could still have been adequate spatial refugia that reduced predation risk and allowed small prey to respond positively to increases in detrital quality. However, leaf litter standing crop reached even lower levels in the treatment stream as our experimental enrichment progressed through time (Suberkropp et al. 2010), which might have decreased habitat complexity beyond a threshold that could no longer provide adequate

spatial refugia for small prey. This decline in spatial refugia might have disproportionately increased the predation risk of small prey and counteracted their positive nutrient response over the longer term enrichment.

Observed increases in the biomass and abundance of large primary consumers, despite substantial shifts in the quantity and timing of detrital resource availability, suggests that consumer body size responses could be primarily related to increased resource quality. For instance, declines in leaf litter standing crop occurred during the winter and spring months (Suberkropp et al. 2010) when many stream consumers increase their body size in preparation for emergence (Huryn and Wallace 1988); therefore, we initially predicted that these seasonal declines in resource quantity would reduce consumer size. However, certain consumers still obtained a larger size during the short time that resources were abundant (fall and early winter), which might have allowed them to survive through later periods of low resource availability. For instance, invertebrate body size can be positively related to their lipid and energy content (Otto 1974). Lipid content is also positively related to body size, starvation resistance, and survival of *Daphnia* (Tessier et al. 1983). This suggests that the larger size of consumers in our treatment stream might have subsequently increased their lipid storage capacity and allowed them to maintain their positive nutrient response despite the later seasonal reductions in resource quantity. Indeed, we observed more robust individuals from several taxa that appeared to have greater fat stores in the treatment stream during the fourth and fifth years of enrichment (J. Davis and S. Eggert pers. obs.). These results contribute to the growing empirical evidence indicating the relatively greater importance of resource quality vs. quantity in stimulating consumer production in aquatic ecosystems (Boersma and Kreutzer 2002). Moreover, the ability of consumers to maintain greater productivity (Davis et al. 2010) and obtain larger body sizes despite substantial reductions in the quantity and temporal availability of resources are particularly salient for detritus-based ecosystems, in which nutrient enrichment has facilitated carbon loss in a variety of biomes (Mack et al. 2004; Benstead et al. 2009; Turner et al. 2009).

Implications for other ecosystem types—Our findings have general applicability to food web pathways across a wide geographic area and in other aquatic ecosystems. Our specific study ecosystem, a deciduous forested headwater stream, generally dominates overall stream miles in a variety of river networks (Meyer and Wallace 2001). Thus, our specific results likely elucidate size-specific responses across a broad geographic range. However, our study streams are very different from many aquatic ecosystems in other ways, including the fact that they are fishless. Despite this, similar results could potentially be found in ecosystems with fish predators. For example, the underlying driver of size-specific predator responses was likely the increased dominance of predator-resistant prey. Gape-limited predators, predator-resistant prey, and size-selective predation occur in a variety of aquatic ecosystems

(Emmerson and Raffaelli 2004; Brose et al. 2006b), such that the increased dominance of large prey can negatively affect fish predators in many types of aquatic ecosystems (Wootton et al. 1996; Persson et al. 2007). Thus, similar size-specific predator responses might manifest when enrichment disproportionately increases predator-resistant prey in food webs exhibiting such size-selective predation. Conversely, when enrichment does not increase the dominance of predator-resistant prey (Slavik et al. 2004) or when predators have diets that encompass larger prey (Brooks and Dodson 1965), predators could capitalize on this increased prey biomass and be less likely to exhibit these size-specific responses. In fact, enrichment of the Kuparuk River (Alaska) increased Arctic grayling (*Thymallus arcticus*) growth rates and individual body size (Slavik et al. 2004), likely because they could eat a broader range of prey body sizes. Thus, these context-dependent results suggest that the direction of predator body size responses are not absolute but instead depend on a combination of the prey size structure, their relative enrichment responses, and the breadth of the predator's dietary niche.

Effects on ecosystem processes—These shifts toward greater dominance of large primary consumers indicate a little-recognized pathway for nutrient enrichment to alter stream function because consumer size structure can alter ecosystem processes (Poff et al. 1993; Hall et al. 2007). Because body size is negatively related to mass-specific metabolic rates (Brown et al. 2004), food webs dominated by larger organisms might have lower community-level respiration rates and slower biomass turnover rates (Poff et al. 1993; Huryń and Benke 2007). Consumer assemblages that possess similar levels of consumer biomass, but differ in body size distributions, can also have substantially different consumer nutrient excretion rates (Hall et al. 2007). Thus, enrichment might alter energy and nutrient flows within nutrient-enriched food webs through shifts in size distributions. Given the overall importance of body size in many ecosystem-level processes, these changes in size distributions facilitated by enrichment might further alter aquatic ecosystem function.

We found that consumer response to nutrient enrichment depended on body size. Enrichment also increased the individual body size of a dominant stream consumer that had previously exhibited sensitivity to resource limitation. Thus, contrary to our original prediction that longer term enrichment would not stimulate large consumers because of extended periods of reduced resource availability, enrichment increased the biomass and abundance of large primary consumers throughout our 5-yr manipulation. Body size responses were not homogeneous across trophic levels, because large predators did not respond to the longer term enrichment. Despite reduced detrital resource availability, enrichment continued to stimulate large primary consumers, likely because of associated increases in resource quality and reductions in predation pressure. Because predator responses also contrasted with the results from another experimental enrichment (Slavik et al. 2004), enrichment might not always increase the dominance of large predators. Instead, the

direction of predator size shifts are likely related to the size distribution of prey, the relative nutrient response of prey, and the breadth of the predator's diet.

Acknowledgments

S. Dye, N. Taylor, R. Hilten, J. Benstead, and C. Tant helped in the field. We are also grateful to our numerous laboratory assistants, but especially to E. Baker, A. Ely, J. Hoehn, and J. Holland. Contributions from our collaborators, J. Benstead, D. Conners, J. Greenwood, V. Gulis, K. Suberkropp, and C. Tant, made this experiment possible. The Coweeta Hydrologic Laboratory provided logistical support. Water chemistry analyses were conducted at the University of Georgia (UGA) Analytical Chemistry Lab. S. Dye, C. Anderson, R. Creed, J. Allgeier, D. Batzer, M. Bradford, J. Frisch, A. Helton, A. Mehring, S. Norlin, G. Small, C. Tant, A. Trice, and two anonymous reviewers provided insightful comments on an earlier draft of this manuscript.

Funding was provided by the National Science Foundation (NSF; DEB-9806610, DEB-0318063, DEB-9629268, and DEB-0212315). J.M.D. was supported by an NSF graduate research fellowship and a UGA presidential fellowship. During the final preparation of this manuscript, additional support was provided to J.M.D. by the NSF Experimental Program to Stimulate Competitive Research (EPSCoR) in Idaho (EPS-0814387).

References

- APHA. 1998. Standard methods for the examination of water and wastewater, 20th ed. American Public Health Association.
- BEATY, S. R., K. FORTINO, AND A. E. HERSHEY. 2006. Distribution and growth of benthic macroinvertebrates among different patch types of the littoral zones of two arctic lakes. *Freshw. Biol.* **51**: 2347–2361, doi:10.1111/j.1365-2427.2006.01664.x
- BENKE, A., 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. *J. North Am. Benthol. Soc.* **18**: 308–343, doi:10.2307/1468447
- BENSTEAD, J. P., AND OTHERS. 2009. Nutrient enrichment alters storage and fluxes of detritus in a headwater stream ecosystem. *Ecology* **90**: 2556–2566, doi:10.1890/08-0862.1
- BOERSMA, M., AND C. KREUTZER. 2002. Life at the edge: Is food quality really of minor importance at low quantities? *Ecology* **83**: 2552–2561, doi:10.1890/0012-9658(2002)083[2552:LATEIF]2.0.CO;2
- BOURASSA, N., AND A. MORIN. 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *J. North Am. Benthol. Soc.* **14**: 393–403, doi:10.2307/1467205
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28–35, doi:10.1126/science.150.3692.28
- BROSE, U., AND OTHERS. 2006a. Consumer–resource body–size relationships in natural food webs. *Ecology* **87**: 2411–2417, doi:10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2
- , R. J. WILLIAMS, AND N. D. MARTINEZ. 2006b. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9**: 1228–1236, doi:10.1111/j.1461-0248.2006.00978.x
- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology* **85**: 1771–1789, doi:10.1890/03-9000
- 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, doi:10.2307/1941382

- CLAESSENS, D., A. M. DE ROOS, AND L. PERSSON. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. *Am. Nat.* **155**: 219–237, doi:10.1086/303315
- CREED, R. P., R. P. CHERRY, J. R. PFLAUM, AND C. J. WOOD. 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. *Oikos* **118**: 723–732, doi:10.1111/j.1600-0706.2008.17212.x
- CROSS, W. F., B. R. JOHNSON, J. B. WALLACE, AND A. D. ROSEMOND. 2005. Contrasting response of stream detritivores to long-term nutrient enrichment. *Limnol. Oceanogr.* **50**: 1730–1739, doi:10.4319/lo.2005.50.6.1730
- , J. B. WALLACE, AND A. D. ROSEMOND. 2007. Nutrient enrichment reduces constraints on material flows in a detritus-based food web. *Ecology* **88**: 2563–2575, doi:10.1890/06-1348.1
- , ———, ———, AND S. L. EGGERT. 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. *Ecology* **87**: 1556–1565, doi:10.1890/0012-9658(2006)87[1556:WNEISP]2.0.CO;2
- CYR, H., J. A. DOWNING, AND R. H. PETERS. 1997. Density–body size relationships in local aquatic communities. *Oikos* **79**: 333–346, doi:10.2307/3546017
- DAVIC, R. D. 1991. Ontogenetic shift in diet of *Desmognathus quadramaculatus*. *J. Herpetol.* **25**: 108–111, doi:10.2307/1564806
- DAVIS, J. M. 2009. Food web response to long-term experimental enrichment of a detritus-based stream ecosystem. Ph.D. thesis. Univ. of Georgia.
- , A. D. ROSEMOND, S. L. EGGERT, W. F. CROSS, AND J. B. WALLACE. 2010. Long-term nutrient enrichment decouples predator and prey production. *Proc. Natl. Acad. Sci. USA* **107**: 121–126, doi:10.1073/pnas.0908497107
- EGGERT, S. L., AND J. B. WALLACE. 2003. Reduced detrital resources limit *Pycnopsyche gentilis* (Trichoptera: Limnephilidae) production and growth. *J. North Am. Benthol. Soc.* **22**: 388–400, doi:10.2307/1468269
- EMMERSON, M., AND D. RAFFAELLI. 2004. Predator–prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* **73**: 399–409, doi:10.1111/j.0021-8790.2004.00818.x
- FERREIRA, V., V. GULIS, AND M. A. S. GRACA. 2006. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* **149**: 718–729, doi:10.1007/s00442-006-0478-0
- FINLAY, K., B. E. BEISNER, A. PATOINE, AND B. PINEL-ALLOUL. 2007. Regional ecosystem variability drives the relative importance of bottom-up and top-down factors for zooplankton size spectra. *Can. J. Fish. Aquat. Sci.* **64**: 516–529, doi:10.1139/F07-028
- GREENWOOD, J. L., A. D. ROSEMOND, J. B. WALLACE, W. F. CROSS, AND H. S. WEYERS. 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways. *Oecologia* **151**: 637–649, doi:10.1007/s00442-006-0609-7
- HALL, R. O., B. J. KOCH, M. C. MARSHALL, B. W. TAYLOR, AND L. M. TRONSTAD. 2007. How body size mediates the role of animals in nutrient cycling in aquatic ecosystems, p. 286–305. *In* A. Hildrew, D. Raffaelli, and R. Edmonds-Brown [eds.], *Body size: The structure and function of aquatic ecosystems*. Cambridge Univ. Press.
- , J. B. WALLACE, AND S. L. EGGERT. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**: 3445–3463, doi:10.1890/0012-9658(2000)081[3445:OMFISF]2.0.CO;2
- HURYN, A. D., AND A. C. BENKE. 2007. Relationship between biomass turnover and body size for stream communities, p. 55–76. *In* A. Hildrew, D. Raffaelli, and R. Edmonds-Brown [eds.], *Body size: The structure and function of aquatic ecosystems*. Cambridge Univ. Press.
- , AND J. B. WALLACE. 1988. Community structure of Trichoptera in a mountain stream: Spatial patterns of production and functional organization. *Freshw. Biol.* **20**: 141–155, doi:10.1111/j.1365-2427.1988.tb00438.x
- JOHNSON, B. R., AND J. B. WALLACE. 2005. Bottom-up limitation of a stream salamander in a detritus-based food web. *Can. J. Fish. Aquat. Sci.* **62**: 301–311, doi:10.1139/f04-197
- LUGTHART, G. J., AND J. B. WALLACE. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. *J. North Am. Benthol. Soc.* **11**: 138–164, doi:10.2307/1467381
- LURLING, M., AND E. VAN DONK. 1997. Life history consequences for *Daphnia pulex* feeding on nutrient-limited phytoplankton. *Freshw. Biol.* **38**: 693–709, doi:10.1046/j.1365-2427.1997.00242.x
- MACK, M. C., E. A. G. SCHUUR, M. S. BRET-HARTE, G. R. SHAVER, AND S. CHAPIN III. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**: 440–443, doi:10.1038/nature02887
- MERRITT, R. W. AND K. W. CUMMINS [EDS.]. 1996. An introduction to the aquatic insects of North America, 3rd ed. Kendall Hunt.
- MEYER, J. L., AND J. B. WALLACE. 2001. Lost linkages and lotic ecology: Rediscovering small streams, p. 295–317. *In* M. C. Press, N. J. Huntly, and S. Levin [eds.], *Ecology: Achievement and challenge*. Blackwell Science.
- MOORE, J. C., AND OTHERS. 2004. Detritus, trophic dynamics, and biodiversity. *Ecol. Lett.* **7**: 584–600, doi:10.1111/j.1461-0248.2004.00606.x
- OSENBERG, C. W., R. J. SCHMITT, S. J. HOLBROOK, K. E. ABUSABA, AND A. R. FLEGAL. 1994. Detection of environmental impacts: Natural variability, effect size, and power analysis. *Ecol. Appl.* **4**: 16–30, doi:10.2307/1942111
- OTTO, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph) (Trichoptera) in a south Swedish stream. *J. Anim. Ecol.* **43**: 339–361, doi:10.2307/3369
- PACE, M. L., AND J. J. COLE. 1996. Regulation of bacteria by resources and predation tested in whole-lake experiments. *Limnol. Oceanogr.* **41**: 1448–1460, doi:10.4319/lo.1996.41.7.1448
- PECKARSKY, B. L., B. W. TAYLOR, A. R. MCINTOSH, M. A. MCPEEK, AND D. A. LYTLE. 2001. Variation in mayfly size at metamorphosis as a development response to risk of predation. *Ecology* **82**: 740–757, doi:10.1890/0012-9658(2001)082[0740:VIMSAM]2.0.CO;2
- PERSSON, L., P. A. AMUNDSEN, A. M. DE ROOS, A. KLEMETSEN, R. KNUDSEN, AND R. PRIMICERIO. 2007. Culling prey promotes predator recovery: Alternative states in a whole-lake experiment. *Science* **316**: 1743–1746, doi:10.1126/science.1141412
- PETERS, R. H. 1983. *The ecological implications of body size*. Cambridge Univ. Press.
- POFF, N. L., AND OTHERS. 1993. Size structure of the metazoan community in a Piedmont stream. *Oecologia* **95**: 202–209, doi:10.1007/BF00323491
- RICHARDSON, J. S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshw. Biol.* **27**: 169–176, doi:10.1111/j.1365-2427.1992.tb00531.x
- SARDA, R., I. VALIELA, AND K. FOREMAN. 1996. Decadal shifts in a salt marsh macrofaunal community in response to sustained long-term experimental nutrient enrichment. *J. Exp. Mar. Biol. Ecol.* **205**: 63–81, doi:10.1016/S0022-0981(96)02600-7
- SCHMID-ARAYA, J. M., A. G. HILDREW, A. ROBERTSON, P. E. SCHMID, AND J. WINTERBOTTOM. 2002. The importance of meiofauna in food webs: Evidence from an acid stream. *Ecology* **83**: 1271–1285, doi:10.1890/0012-9658(2002)083[1271:TOMIF]2.0.CO;2

- SLAVIK, J., B. J. PETERSON, L. A. DEEGAN, W. B. BOWDEN, A. E. HERSHEY, AND J. E. HOBBI. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* **85**: 939–954, doi:10.1890/02-4039
- SMOCK, L. A., G. M. METZLER, AND J. E. GLADDEN. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* **70**: 764–775, doi:10.2307/1940226
- SPRULES, W. G., AND M. MUNAWAR. 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Can. J. Fish. Aquat. Sci.* **43**: 1789–1794, doi:10.1139/f86-222
- 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. *Freshw. Biol.* **48**: 1925–1937, doi:10.1046/j.1365-2427.2003.01141.x
- SUBERKROPP, K., V. GULIS, A. D. ROSEMOND, AND J. P. BENSTEAD. 2010. Nutrient enrichment shifts microbial and detrital pathways in a headwater stream ecosystem. *Limnol. Oceanogr.* **55**: 149–160.
- SUNDARESHWAR, P. V., J. T. MORRIS, E. K. KOEPFLER, AND B. FORNWALT. 2003. Phosphorus limitation of coastal ecosystem processes. *Science* **299**: 563–565, doi:10.1126/science.1079100
- TESSIER, A. J., L. L. HENRY, C. E. GOULDEN, AND M. W. DURAND. 1983. Starvation in *Daphnia*: Energy reserves and reproductive allocation. *Limnol. Oceanogr.* **28**: 667–676, doi:10.4319/lo.1983.28.4.0667
- TURNER, R. E., B. L. HOWES, J. M. TEAL, C. S. MILAN, E. M. SWENSON, AND D. D. GOEHRINGER-TONER. 2009. Salt marshes and eutrophication: An unsustainable outcome. *Limnol. Oceanogr.* **54**: 1634–1642.
- 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, doi:10.1126/science.277.5322.102
- , ———, ———, AND ———. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecol. Monogr.* **69**: 409–442, doi:10.1890/0012-9615(1999)069[0409:EORLOA]2.0.CO;2
- WATERS, T. F. 1969. Sub-sampler for dividing large samples of stream invertebrate drift. *Limnol. Oceanogr.* **14**: 813–815, doi:10.4319/lo.1969.14.5.0813
- WISSINGER, S. A., G. B. SPARKS, G. L. ROUSE, W. S. BROWN, AND H. STELTZER. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. *Ecology* **77**: 2421–2430, doi:10.2307/2265743
- WOODWARD, G., AND A. G. HILDREW. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* **71**: 1063–1074, doi:10.1046/j.1365-2656.2002.00669.x
- , AND P. WARREN. 2007. Body size and predatory interactions in freshwaters: Scaling from individuals to communities, p. 98–117. *In* A. G. Hildrew, D. G. Raffaelli, and R. Edmonds-Brown [eds.], *Body size: The structure and function of aquatic ecosystems*. Cambridge Univ. Press.
- WOOTTON, J. T., M. S. PARKER, AND M. E. POWER. 1996. Effects of disturbance on river food webs. *Science* **273**: 1558–1561, doi:10.1126/science.273.5281.1558

Associate editor: Alexander D. Huryn

Received: 02 February 2010

Accepted: 16 June 2010

Amended: 19 July 2010