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Contrasting response of stream detritivores to long-term nutrient enrichment

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Abstract

We examined growth and production responses of two dominant stream detritivores (chironomids and *Tallaperla* spp. stoneflies) at opposite ends of the "slow-fast" life-history continuum and with distinct feeding characteristics (i.e., consumption of fine particulate organic matter vs. leaf litter) to a 2-yr experimental nutrient enrichment of a headwater stream. Enrichment had large positive effects (~50% increase) on chironomid growth rates but no effects on those of *Tallaperla* spp. On an areal basis, enrichment had a large positive effect on chironomid production (~183% increase) but no detectable effect on the production of *Tallaperla* spp. When production data were examined on a per gram food basis, enrichment had an apparent positive effect on the production of both chironomids and *Tallaperla* spp. Together, these results suggest that nutrient-induced changes to organic matter quality had consistent and substantial positive effects on short-lived chironomids, but effects were limited for longer-lived stoneflies. The lack of a system-wide effect on *Tallaperla* spp. may have been due to nutrient-induced reductions in leaf litter quantity, despite increases in litter quality. Our results indicate that species-specific characteristics such as life span and dominant food type may be important in determining population- and community-level responses of consumers to nutrient enrichment of detritus-based aquatic ecosystems.

Nutrient enrichment of aquatic ecosystems is occurring worldwide as a result of human-induced changes to global nitrogen (N) and phosphorus (P) cycling (e.g., Bennett et al. 2001; Galloway et al. 2003). Fertilizer production and application, fossil fuel combustion, and suburban/urbanization have all contributed to increased mobilization of N and P and elevated concentrations of these elements in streams, lakes, and coastal marine environments (e.g., Caraco 1993; Vitousek et al. 1997; Carpenter et al. 1998). Such changes in nutrient availability can have strong indirect effects on invertebrate primary consumers because many basal food resources (i.e., primary producers and detritus) undergo large changes in quantity and quality as a result of nutrient enrichment (e.g., Carpenter et al. 1998). Our general understanding of enrichment effects on primary consumers is limited, however, because most studies have focused on living plant- or algal-based food webs (e.g., Peterson et al. 1993; Carpenter et al. 1998; Howarth et al. 2002).

In many aquatic ecosystems, detritus (i.e., nonliving organic matter) is a dominant basal resource and provides the energetic basis for diverse and productive detritus-based food webs (e.g., Teal 1962; Wetzel 1995; Hall et al. 2000). Despite the prevalence and importance of detritus in aquatic systems, few studies have investigated the effects of nutrient enrichment on the growth or productivity of invertebrate detritivores.

In the eastern United States and in many other forested regions of the world, detritus-based headwater streams dominate the total length of stream networks (e.g., Meyer and Wallace 2001). In these streams, consumer productivity is driven by pulsed inputs of allochthonous leaf litter, and in-stream autotrophic production can be extremely low (e.g., Webster et al. 1997). Recent studies have shown that nutrient enrichment of detritus-based streams can lead to increased biomass and productivity of microbes (i.e., bacteria and fungi) associated with detritus (e.g., Chadwick and Huryn 2003; Ramírez et al. 2003; Stelzer et al. 2003) and consequent increased rates of organic matter decomposition (e.g., Robinson and Gessner 2000; Grattan and Suberkropp 2001; Gul-

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is and Suberkropp 2003). Thus, nutrient enrichment may positively affect the quality of detritus (i.e., through increased biomass of nutrient-rich microbes) while negatively affecting its quantity (i.e., through increased rates of decomposition). Little is known about how such changes at the base of the food web affect the growth and productivity of invertebrate detritivores (but *see* Ward and Cummins 1979; Rosemond et al. 2001, 2002). Understanding this linkage is critical, because detritivores may limit the flow of energy and materials to higher trophic levels and often play prominent roles in the retention, processing, and export of organic matter and nutrients in forested streams (e.g., Cuffney et al. 1990; Crowl et al. 2001; Cross et al. in press).

We experimentally enriched a headwater stream with N and P for 2 yr and observed profound effects on both the quality and quantity of detritus. Specifically, we observed (1) increased quality of fine particulate organic matter (FPOM) and leaf litter (i.e., increased nutrient : carbon ratios, increased microbial biomass, and activity) (Cross et al. 2003; Gulis and Suberkropp 2003) and (2) reduced quantity of leaf litter (Gulis and Suberkropp 2003; Greenwood 2004) in the treatment stream relative to a control. In this study, we examined the effects of these nutrient-induced changes to detrital resources on the abundance, biomass, growth rates, and secondary production of two prominent stream detritivores. We chose two taxa with distinct life histories (i.e., fast growth and short life span vs. slow growth and long life span) and feeding characteristics (i.e., consumption of FPOM, organic particles <1 mm in diameter] vs. leaf litter) to explore the potential importance of these factors in determining the response of detritivores to enrichment. We predicted that short-lived taxa, which are less dependent on continuous availability of organic matter but which likely can capitalize on increased organic matter quality, would respond more positively to nutrient enrichment than longer-lived taxa. Our detailed analysis is restricted to two taxa, and therefore, any differences in response cannot be directly attributed to a single factor such as life span, feeding mode, or underlying phylogenetic differences. Nonetheless, our study, in combination with information for multiple taxa from a companion study (*see* Cross 2004 and "Discussion"), provides valuable insight into potential taxon-level determinants of detritivore response to nutrient enrichment.

Study organisms

Non-Tanypodinae chironomids (Diptera: Chironomidae) were chosen as representative *r*-selected taxa (i.e., rapid growth and high reproductive rates). Chironomids are among the most abundant macroinvertebrates in most freshwater ecosystems (Armitage et al. 1995) and generally exhibit rapid growth rates (e.g., Huryn 1990; Hauer and Benke 1991; Benke 1998), short larval life spans (e.g., Huryn 1990), and multivoltine life histories (i.e., complete multiple generations per year) (Huryn 1990). Most non-Tanypodinae chironomids are functionally classified as collector-gatherers (Merritt and Cummins 1996), and their diet in many southern Appalachian streams is dominated by amorphous detritus associated with FPOM (e.g., Hall et al. 2000; Rosi-Marshall and Wallace 2002). More than 25 genera of non-Tanypodinae have been collected from the study streams (Wallace et al. 1991), but 7 dominant genera represent >80% of their abundance (*see* Huryn 1990).

Tallaperla spp. (Plecoptera: Peltoperlidae) larvae were chosen as representative *K*-selected taxa (i.e., slow growth and low reproductive rates). These stoneflies exhibit slow growth rates (e.g., O'Hop et al. 1984; Johnson et al. 2003), have relatively long larval life spans (~540 d), and account for a significant proportion of the abundance and biomass of the study stream communities (Lugthart and Wallace 1992; Wallace et al. 1999; this study). *Tallaperla* spp. are functionally classified as leaf-eating shredders (Merritt and Cummins 1996), although early instars may feed on amorphous detritus (Cross pers. obs.). Up to four species of *Tallaperla* spp. potentially co-occur in Coweeta headwater streams: *T. maria, T. anna, T. cornelia,* and *T. elisa* (Huryn and Wallace 1987; Stewart and Stark 2002), although *T. maria* tends to predominate. These species are indistinguishable as larvae but share the same semivoltine life cycle.

Methods

Study site and experimental enrichment—This study was conducted in two adjacent headwater streams (draining catchments [C] 53 and 54) at the Coweeta Hydrologic Laboratory, Macon County, North Carolina (*see* Swank and Crossley 1988). Forest vegetation is dominated by mixed hardwoods (primarily oak, maple, and poplar) and a dense understory of *Rhododendron maximum,* which shades the streams throughout the year. Headwater streams at Coweeta are extremely heterotrophic, and allochthonous inputs of detritus provide >90% of the energy base for microbial and invertebrate production (Wallace et al. 1997; Hall et al. 2000). The streams used in this study have very similar physical and chemical characteristics (i.e., watershed area, slope, elevation, discharge, and temperature) (*see* Lugthart and Wallace [1992] for more detail) but differ (since July 2000) in their concentrations of dissolved N and P as a result of our experimental nutrient enrichment of C54. Natural concentrations of inorganic N and P in these streams are very low ($(NO_3\text{-}N + NO_2)$-N: 16.9 ± 5.2 [mean ± SE] $\mu g\ L^{-1}$ [n = 33; range = 4–40]; NH_4-N: 10.4 ± 2.9 $\mu g\ L^{-1}$ [n = 33; range = below detection, −30]; soluble reactive phosphorus [SRP]: 3.7 ± 0.8 $\mu g\ L^{-1}$ [n = 33; range = below detection, −22]).

Starting in July 2000, nitrogen (NH_4NO_3) and phosphorus (K_2HPO_4 and KH_2PO_4) were dripped continuously along the entire length of the treatment stream (C54) with a solar-powered metering pump to increase the concentrations of dissolved inorganic N and P to ~5–10× background levels while keeping streamwater N : P ratios relatively constant (*see* Gulis and Suberkropp [2003] for a description of the nutrient drip apparatus). Concentrations of $(NO_3 + NO_2)$-N, NH_4-N, and SRP were measured biweekly at the weir of the reference stream and at several locations in the treatment stream (American Public Health Association 1998). Water temperature was monitored every 30 min throughout the study in both streams (Suberkropp unpubl. data) with Optic StowAway temperature probes (Onset Computer Corp.).

Growth rates—In situ daily growth rates (mg mg^{-1} d^{-1}) of chironomids and *Tallaperla* spp. were quantified on a seasonal basis in both streams following methods developed by Huryn and Wallace (1986) and Huryn (1990). Chironomid growth rates were measured between November 1999 and July 2002 (n = 10 seasons; 3 before treatment and 7 during treatment), and *Tallaperla* spp. growth rates were measured between November 1999 and November 2001 (n = 8 seasons; 3 before treatment and 5 during treatment).

During each season, larvae were handpicked from leaf litter and FPOM that were collected in nearby undisturbed Coweeta headwater streams. Body length was measured to the nearest 0.01 mm under a dissecting microscope fitted with an ocular micrometer, and larvae were separated into 1-mm size classes irrespective of species identity. In general, seasonal incubations consisted of three distinct size classes of chironomids and two to four size classes of *Tallaperla* spp. in each stream.

Groups of larvae within a given size class were placed into partially submerged triangular growth chambers constructed of Plexiglas and Nitex mesh (base: 20 × 20 × 14 cm; sides: 16-cm height, described by Huryn and Wallace [1986]). The mesh size of chambers (63 μm) was small enough to prevent immigration or emigration of stream invertebrates but sufficiently large to allow entry of FPOM in the size range used by most chironomid larvae in Coweeta streams. Larval densities in chambers (chironomids: 990–7,180 m^{-2}, *Tallaperla* spp.: 380–3,055 m^{-2}) fell within the range of naturally occurring densities of chironomids and were slightly higher than natural densities of *Tallaperla* spp. in the study streams (Lugthart et al. 1990; Wallace et al. 1999; this study). On occasion, two widely disparate size classes of *Tallaperla* spp. were placed in the same growth chamber to increase the number of size-specific growth estimates during a given season. Because these size classes were easily distinguishable, growth rates could be estimated separately.

At the beginning of growth incubations, 8–10 leaves collected from each stream were rinsed to remove invertebrates and placed in each of the chambers. Leaves placed in the chambers represented a mixture of species readily available during the time of incubation. The most commonly used leaf types were maple (*Acer* spp.), beech (*Fagus granifolia* Ehrh.), oak (*Quercus* spp.), *R. maximum,* yellow poplar (*Liriodendron tulipifera* L.), and dogwood (*Cornus florida* L.). Efforts were made to keep leaf species relatively constant among chambers and between streams.

Growth incubations lasted ~1–2 weeks for chironomids and ~2 months for *Tallaperla* spp. Leaves were replaced halfway through *Tallaperla* spp. incubations to prevent food limitation of larvae. At the end of growth incubations, larvae were preserved in Kahle's solution (Stehr 1987). Final body lengths of preserved individuals were measured as described above. Initial and final lengths were converted to biomass estimates (ash-free dry mass [AFDM]) using previously established length–mass regressions for these taxa (Benke et al. 1999). Size-specific daily growth rates (g) were calculated as $g = (\ln M_f - \ln M_i)/t$, where M_f is the mean final AFDM of surviving larvae, M_i is the mean initial AFDM of larvae introduced into chambers, and t is the duration of the incubation in days. Linear equations were derived from relationships between ln(initial length[mm]) and daily growth rate. This assemblage-based method of estimating growth rates assumes that changes in the average weight of similarly sized mixtures of species accurately reflect size-specific growth rates of the entire taxonomic group (Huryn and Wallace 1986). Larval mortality was calculated as the percentage of initial numbers in each chamber missing or obviously dead at the end of each incubation. Food was always provided in excess during growth incubations to control for food quantity; thus, between-stream differences in growth were viewed as a test for effects of food quality.

Benthic sampling and secondary production—Quantitative benthic sampling was conducted monthly in each stream for 4 yr between September 1998 and August 2002. Each month, samples were taken in two distinct stream habitats (i.e., mixed substrate [cobble, pebble, gravel, sand, silt] and bedrock outcrops, following Lugthart and Wallace [1992]).

Benthic samples were brought to the laboratory, refrigerated, and processed within 24 h. Samples were rinsed onto nested metal sieves (pore sizes = 1 mm and 250 μm), and material retained on each sieve was elutriated to separate organic from inorganic material. Organic material was then preserved separately for each size fraction (i.e., from 250 μm to 1 mm and >1 mm) with formalin solution (6–8%). All invertebrates were removed from the >1-mm fraction by handpicking under a dissecting microscope at ×15 magnification. Organic material in the smaller size fraction (from 250 μm to 1 mm) was subsampled (1/8 to 1/64 of whole samples) (Waters 1969), and animals were removed from subsamples with a dissecting microscope at ×15 magnification. The amounts of leaf litter and FPOM (i.e., food resources) in each sample were also quantified according to Lugthart and Wallace (1992). Although these food resource data are used in calculations presented below, the detailed methodology and time-series results are presented elsewhere (Cross 2004).

All non-Tanypodinae chironomids and *Tallaperla* spp. were counted, and their body lengths were measured to the nearest millimeter using a graduated microscope stage. Biomass (mg of AFDM) of individual larvae was determined with length–mass relationships as described above, and total biomass per square meter was calculated for each sample. Secondary production was estimated for each sampling interval (i.e., interval production, P_{int}) using the community-level instantaneous growth method (Huryn and Wallace 1986; Benke 1993). All sampling intervals were roughly 1 month. Interval production (mg AFDM m^{-2} $interval^{-1}$) was calculated as follows: $P_{int} = \Sigma_{i=1 \text{ to } n} ([B_{i(t+1)} + B_{i(t)}]/2) \times g_i \times d$, where n = 1-mm size classes, $B_{i(t+1)}$ = mean larval biomass of size class i at sampling interval $t + 1$, $B_{i(t)}$ = mean larval biomass of size class i at sampling interval t, g_i = size-specific instantaneous growth rate, and d = number of days in the interval. Annual production was calculated as the sum of all P_{int} values for a given year. Size-specific growth rates were obtained from empirically derived linear growth equations described above. Habitat-weighted values of larval abundance (no. m^{-2}), biomass (mg AFDM m^{-2}), and interval or annual secondary production (mg AFDM m^{-2}

interval^{-1} [d] or mg AFDM m^{-2} yr^{-1}) were calculated according to the relative proportion of each habitat in each stream (e.g., Huryn and Wallace 1987). Production : biomass ($P:B$) ratios were calculated for each year of study.

Annual consumer production per gram of available food resource (Cross 2004) was also calculated as a relative proxy for differences in assimilation of carbon between streams. Higher production per gram of food resource during the enrichment, in comparison to preenrichment values, is suggestive of higher food conversion efficiencies, and hence, food quality. Production of chironomids and *Tallaperla* spp. was expressed per gram of FPOM and leaf litter, respectively, because gut content analyses (Cross 2004) indicated that these food items accounted for ~80–90% of consumer diets.

Statistical analyses—We used stepwise multiple regression analysis to build parsimonious models for predicting growth rates or mortality from mean daily stream temperature, number of degree days, density of larvae in chambers, and initial length of larvae (mm) ($\alpha \leq 0.1$ to enter model). A two-way analysis of covariance (ANCOVA) was used to test for differences in growth rates between streams before and during enrichment; initial length was used as the covariate because early instars tend to grow faster than late instars for both taxonomic groups examined (e.g., Huryn 1990; Johnson et al. 2003). Two-way analyses of variance (ANOVAs) were used to test for the effects of stream (i.e., reference or treatment) and enrichment on larval mortality.

Time series of monthly habitat-weighted chironomid and *Tallaperla* spp. abundance, biomass, and secondary production were analyzed with randomized intervention analysis (RIA) (Carpenter et al. 1989; *see also* Murtaugh 2003; Stewart-Oaten 2003). In this study, RIA was used to test the null hypothesis that no change in abundance, biomass, or secondary production (per m^2 and per gram of food resource) of chironomids or *Tallaperla* spp. occurred in the treatment stream relative to the reference stream following the initiation of nutrient enrichment. All data were appropriately transformed (log[x + 1] or arcsin-square root) when necessary to meet assumptions of normality and homoscedasticity.

Results

Physical/chemical conditions—Throughout the study, water temperature was similar in both study streams and averaged 12.0°C (range = 2.6–18.6°C) (Suberkropp unpubl. data). Average streamwater N and P concentrations were successfully elevated to ~5–10× background levels in the treatment stream during the enrichment ($(NO_3 + NO_2)$-N: 308.9 ± 57.0 μg L^{-1} [n = 44; range = 11–1,711]; NH_4-N: 105.5 ± 18.0 μg L^{-1} [n = 44; range = 6–566]; SRP: 51.2 ± 8.4 μg L^{-1} [n = 44; range = below detection, −268]) and were well within the range of natural concentrations in streams in the region (Scott et al. 2002). N : P ratios of streamwater (~17.9) were consistently higher than N : P ratios of the nutrient solution added (~11.4), suggesting the preferential uptake of P relative to N.

Growth rates—Numbers of chironomid larvae introduced into individual growth chambers ranged from 13 to 94 (mean = 47) per season tested. Average mortality of chironomids was relatively high at 69% (range = 37–100%), and daily mortality rates averaged 6.1% d^{-1} (range = 2.5–11.8% d^{-1}). Rates of mortality were not influenced by larval density, larval initial length, or number of degree days of growth incubations (regression analysis: all $r^2 < 0.1$, $p > 0.05$). Additionally, chironomid mortality did not differ between streams or with nutrient enrichment (two-way ANOVA: $F_{3,49} = 1.038$, $p > 0.05$). Mean daily stream temperature (°C) during incubations had an overall significant positive effect on mortality rates ($r^2 = 0.18$, $p = 0.002$), but this effect did not differ between pre- and postenrichment periods ($p > 0.05$).

Growth rates of chironomid larvae in the reference and treatment streams were relatively high (0.07 ± 0.005 mg mg^{-1} d^{-1}; n = 50; range = 0.015–0.153; Fig. 1A). Mean daily temperature (°C), number of degree days, and larval density did not affect chironomid growth rates (all $r^2 < 0.1$, $p > 0.1$) and were therefore dropped from the growth model. ANCOVA showed a significant interaction between control and treatment streams and pre- versus postenrichment periods (ANCOVA: $F_{1,49} = 6.82$, $p = 0.01$), indicating similar growth rates between streams before enrichment but divergent growth rates during the enrichment (Fig. 1A). Because no differences were found between streams prior to enrichment, these data were combined to yield a single "nonenriched" growth equation: $g = (-0.054 \pm 0.009$ [coefficients ± SE] × ln(initial length [mm]) + (0.095 ± 0.007) ($r^2 = 0.50$, $p < 0.0001$, Fig. 1A: dotted line).

Nutrient enrichment had a significant positive effect on chironomid growth rates in the treatment stream (ANCOVA: $F_{1,49} = 7.12$, $p = 0.01$). On average, chironomids grew 53% faster in the treatment stream during enrichment than in the reference and treatment streams before enrichment (Fig. 1A). This relationship was best described by the following equation: $g = (-0.083 \pm 0.011) \times$ ln(initial length [mm]) + (0.143 ± 0.008) ($r^2 = 0.78$, $p < 0.0001$, Fig. 1A: solid line). Differences between enriched and nonenriched conditions were most pronounced among small larvae.

Numbers of *Tallaperla* spp. introduced into growth chambers ranged from 5 to 40 (mean = 25). Average mortality of *Tallaperla* spp. was lower than that of chironomids at 42% (range = 6–100%), and daily mortality rates averaged 0.7% d^{-1} (range = 0.1–1.4% d^{-1}). Rates of mortality were not significantly affected by initial length or density of larvae, mean daily temperature (°C), or degree days during incubation (all $r^2 < 0.1$, $p > 0.05$). There was no difference in mortality between streams; however, mortality was significantly higher (~40%) in both streams during the period of nutrient enrichment (two-way ANOVA: $F_{3,32} = 3.79$, stream $p > 0.05$, enrichment $p = 0.008$, interaction $p > 0.05$).

Growth rates of *Tallaperla* spp. were an order of magnitude lower than those of chironomids (0.006 ± 0.0007 mg mg^{-1} d^{-1}; n = 33; range = 0–0.015) (Fig. 1B). There were no significant effects of larval density, mean daily temperature (°C), or number of degree days on *Tallaperla* spp. growth rates (all $r^2 < 0.1$, $p > 0.1$). Growth rates of *Tallaperla* spp. did not differ significantly among the reference stream, the treatment stream before enrichment, or the treat-

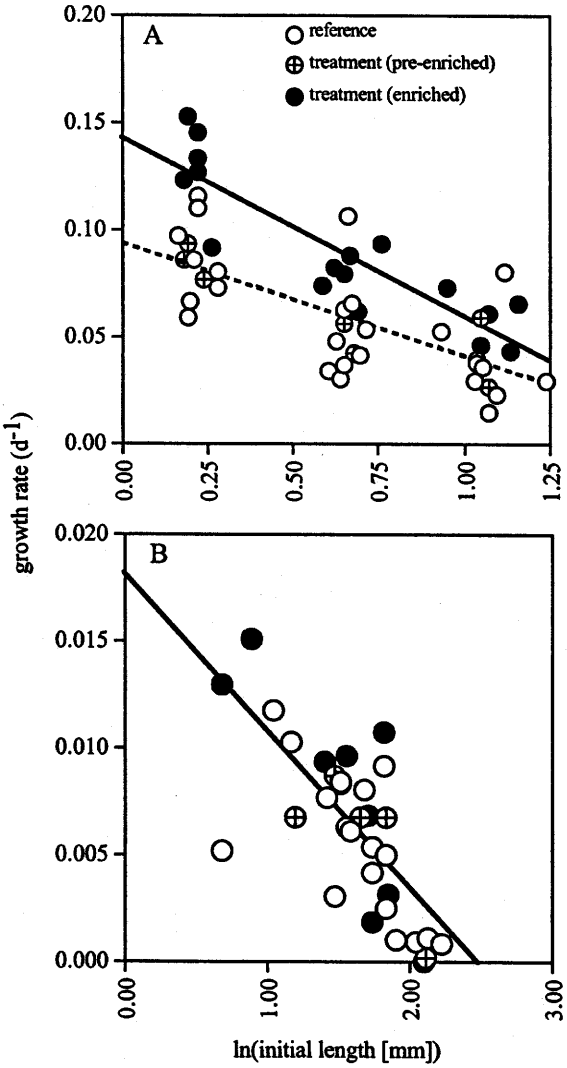

Fig. 1. Size-specific daily growth rates (d^{-1}) of (A) non-Tanypodinae chironomids and (B) *Tallaperla* spp. in the reference stream (C53), the treatment stream before enrichment (C54), and the treatment stream during the experimental enrichment (C54). Lines represent significant linear regressions (*see text for equations*). For chironomids (A), the dashed line represents data from the reference stream and the treatment stream before enrichment (open and cross-hatched circles), and the solid line represents data from the treatment stream during enrichment (filled circles). For *Tallaperla* spp. (B), the solid line represents data from all time periods.

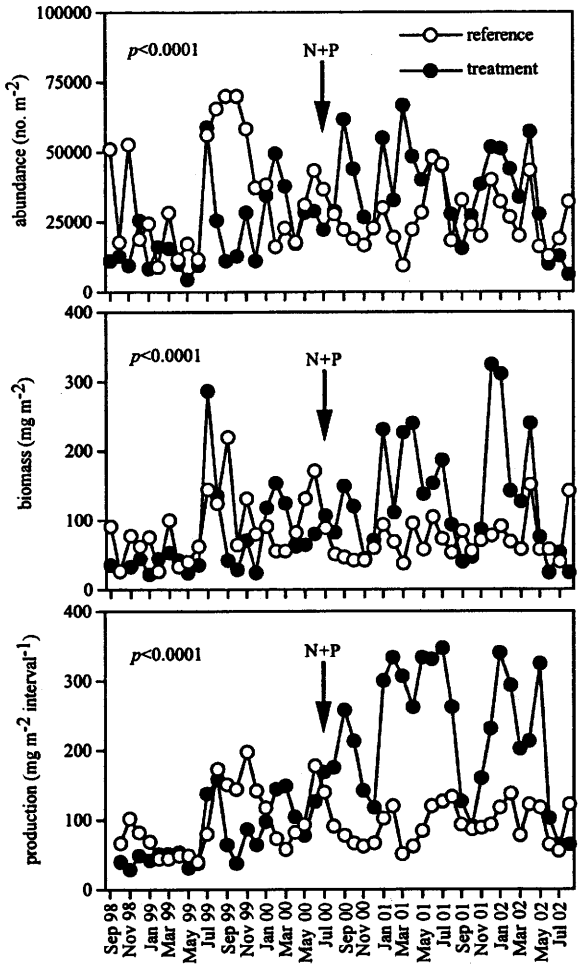

Fig. 2. Mean monthly habitat-weighted abundance and biomass and interval secondary production of non-Tanypodinae chironomids in the reference stream (C53) and the treatment stream (C54) from September 1998 to August 2002. The arrow indicates the initiation of nutrient enrichment of C54. Differences between streams were tested with randomized intervention analysis (RIA) (Carpenter et al. 1989).

ment stream during enrichment (ANCOVA: $F_{1,32} = 0.98$, $p > 0.05$, Fig. 1B). A large proportion of the variation in growth rates was explained by the initial length of larvae ($r^2 = 0.52$, $p < 0.0001$, Fig. 1B), and this negative relationship was best described by the following equation: $g = (-0.007 \pm 0.001) \times \ln(\text{initial length [mm]}) + (0.018 \pm 0.002)$.

Chironomids—abundance, biomass, and secondary production—Nutrient enrichment had a large positive effect on habitat-weighted chironomid abundance, biomass, and interval secondary production per m² (RIA, all $p < 0.0001$, Fig. 2). The greatest response was observed in chironomid production (183% increase; on the basis of the mean values from July 2000 through August 2002 in comparison to September 1998 through June 2000), followed by biomass (86% increase) and abundance (70% increase). Annual habitat-weighted chironomid production in the reference stream was similar before (mean of years 1 and 2: 1,098 mg of AFDM m^{-2} yr^{-1}) and during (mean of years 3 and 4: 1,050 mg of AFDM m^{-2} yr^{-1}) the experimental enrichment (Table 1). Annual habitat-weighted production in the treatment stream increased considerably from an average of 968 mg m^{-2} yr^{-1} before enrichment to 2,531 mg of AFDM m^{-2} yr^{-1} during enrichment (Table 1).

Annual secondary production of chironomids was also expressed per gram of FPOM (Fig. 3A). Although there was a higher standing crop of FPOM in the treatment stream (1,675

Table 1. Annual habitat-weighted secondary production, P (mg m^{-2} yr^{-1}) and production : biomass ($P:B$) ratios for chironomids and *Tallaperla* spp. during each year of the study in the reference (C53) and treatment (C54) streams. Year 1 = Sep 98–Aug 99, year 2 = Sep 99–Aug 00, year 3 = Sep 00–Aug 01, year 4 = Sep 01–Aug 02. Years 1 and 2 are before the experimental nutrient enrichment.

		Year 1		Year 2		Year 3		Year 4	
		P	$P:B$	P	$P:B$	P	$P:B$	P	$P:B$
Chironomidae	Reference	838.2	9.9	1,356.8	13.2	1,007.9	15.3	1,090.7	13.5
	Treatment	692.8	11.1	1,243.0	8.8	2,963.2	20.0	2,098.8	16.6
Tallaperla spp.	Reference	197.3	2.5	286.9	2.7	397.0	2.8	352.4	2.2
	Treatment	84.3	1.8	191.6	2.2	249.3	2.0	175.7	2.1

g of AFDM m^{-2}) versus the reference stream (844 g of AFDM m^{-2}) throughout the study (before and after enrichment), nutrient enrichment had no effect on the quantity of FPOM (Cross 2004). During the two pretreatment years, chironomid production per gram of FPOM was considerably lower (48% on average) in the treatment stream than in the reference stream (years 1 and 2, Fig. 3A). During the enrichment, chironomid production per gram of FPOM increased in the treatment stream to levels comparable to those of the reference stream (years 3 and 4, Fig. 3A). The relative change between streams in chironomid production per gram of FPOM was significant by RIA (p = 0.001).

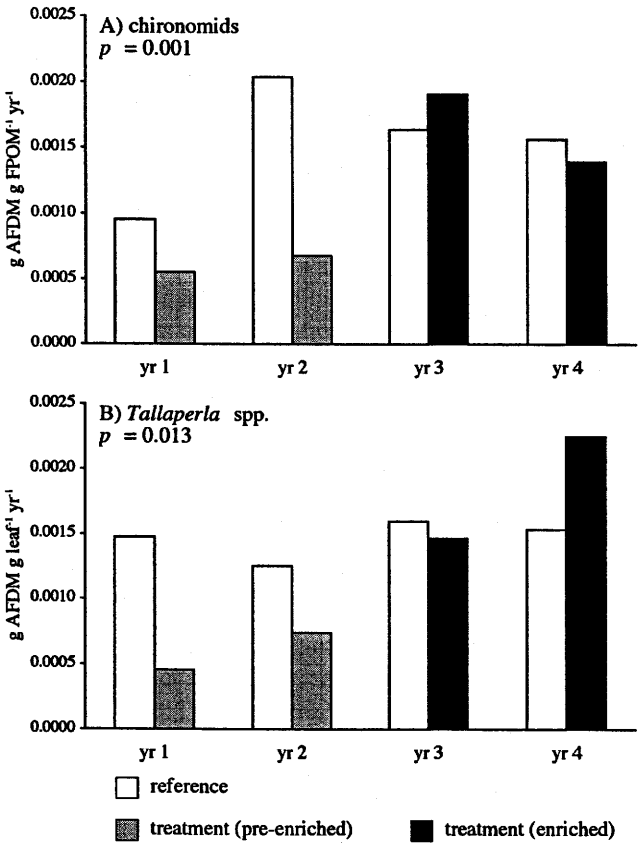

Fig. 3. Annual secondary production of (A) non-Tanypodinae chironomids and (B) *Tallaperla* spp. expressed per gram of food (i.e., FPOM or leaf litter) during 4 yr of study in the reference stream, treatment stream before enrichment, and treatment stream during enrichment. Year 1 = September 1998–August 1999; year 2 = September 1999–August 2000; year 3 = September 2000–August 2001; year 4 = September 2001–August 2002. p values correspond to RIA on monthly time-series data (n = 60 months) contrasting production per gram of food resource in the reference and treatment streams.

Tallaperla *spp.—abundance, biomass, and secondary production*—Nutrient enrichment did not have a significant effect on habitat-weighted *Tallaperla* spp. biomass or secondary production per square meter (RIA, all $p > 0.05$, Fig. 4). Habitat-weighted abundance increased 60% in the treatment stream (RIA, p = 0.01, Fig. 4), while abundance in the reference stream decreased by 37% during enrichment. Throughout the study, annual habitat-weighted production of *Tallaperla* spp. was consistently higher (~75%) in the reference stream (mean: 308 mg of AFDM m^{-2} yr^{-1}) than in the enriched stream (175 mg of AFDM m^{-2} yr^{-1}), and nutrient enrichment had no significant effect on this difference (Table 1).

Annual production of *Tallaperla* spp. was also expressed per gram of leaf litter (Fig. 3B). The standing crop of leaf litter in the treatment stream was significantly reduced from ~244 g of AFDM m^{-2} before enrichment to ~100 g of AFDM m^{-2} during the second year of enrichment (Cross 2004). Production of *Tallaperla* spp. per gram of leaf litter in the mixed substrate habitat was lower (55% on average) in the treatment stream than in the reference stream during the 2 yr of nonenriched conditions (years 1 and 2, Fig. 3B). In contrast, production of *Tallaperla* spp. per gram of leaf litter increased in the treatment stream during nutrient enrichment relative to the reference stream and was 47% greater than that of the reference stream during the second year of enrichment (year 4, Fig. 3B). The relative change between streams in *Tallaperla* spp. production per gram of leaf litter was significant by RIA (p = 0.013).

Annual $P:B$ ratios of chironomids ranged from 8.8 to 20.0, and the two highest values corresponded to the treatment stream during enrichment (Table 1). Annual $P:B$ ratios of *Tallaperla* spp. were considerably lower than those of chironomids (range = 1.8–2.8, Table 1), and there was no consistent pattern associated with the experimental enrichment.

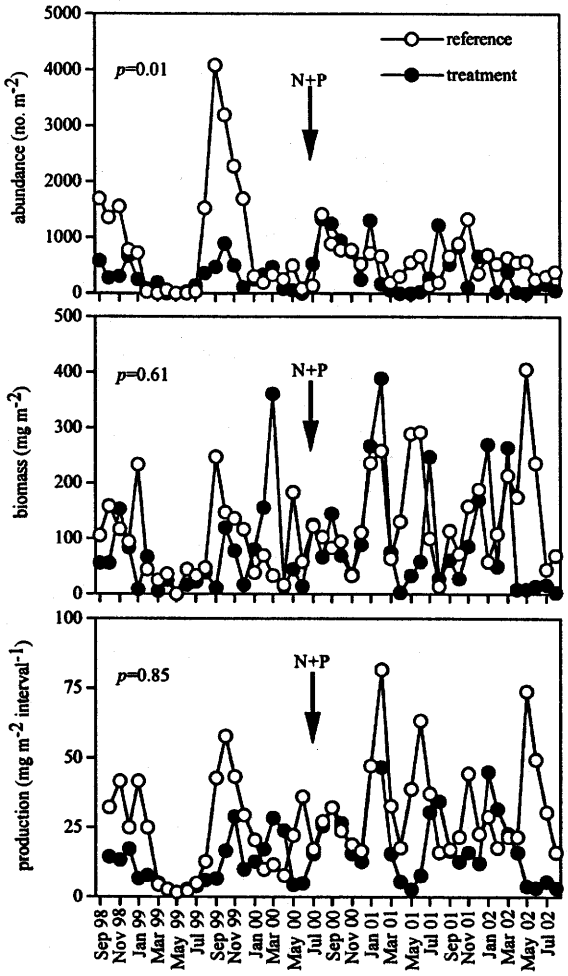

Fig. 4. Mean monthly habitat-weighted abundance and biomass and interval secondary production of *Tallaperla* spp. in the reference stream (C53) and the treatment stream (C54). The arrow indicates the initiation of nutrient enrichment of C54. Differences between streams were tested with RIA (Carpenter et al. 1989).

Discussion

Although a number of studies have demonstrated a causal link between nutrient enrichment and increased microbial activity, detrital quality, and decomposition rates, few studies have examined the consequences of these basal changes on the growth and production of detritivorous macroconsumers (but *see* Rosemond et al. 2002). In this study, we observed marked differences between the response of chironomids and *Tallaperla* spp. to enrichment. Nutrient enrichment had a positive effect on short-lived chironomids, as evidenced by increased growth rates as well as the increased production per square meter and per gram of food resource. In contrast, there was limited evidence for an effect of enrichment on *Tallaperla* spp.; no response was observed in *Tallaperla* spp. growth rates or secondary production per square meter. Our results, in combination with a companion study (*see below;* Cross 2004), suggest that species-specific characteristics are important in determining the response of primary consumers to nutrient enrichment.

We found strong differences in the response of two taxa that have distinct larval life spans and feeding characteristics (i.e., FPOM vs. leaf litter). However, without consideration of additional taxa (i.e., short-lived shredders or long-lived collectors), it is impossible to ascertain whether these differences in response were due to larval life span, food type, phylogeny, or some interaction among these factors. Results from a concurrent study (Cross 2004; Cross unpubl. data) of enrichment effects on whole-community production help shed light on this question. These additional data represent the annual production response (averaged over the same 2 yr of enrichment) for >50 taxa for which larval life span and diet are known. These results include a broad range of taxa with similar diets and distinct life spans, or vice versa (Cross 2004; Cross unpubl. data). When the response of multiple shredder (i.e., leaf eating) taxa was examined across a range of larval life spans, there was no significant effect of enrichment on the production of long-lived shredders (>1-yr larval life span), which include *Tallaperla* spp. In contrast, enrichment had consistently positive effects on the production of all short-lived shredders (<1-yr larval life span). Interestingly, one of the main contributors to increased production in the treatment stream was *Pycnopsyche* spp., a shredder with a relatively short life span (275 d) (Cross 2004). The dominant species of this taxon completes larval growth prior to the summer months when leaf litter becomes scarce. Thus, it appears that larval life span may be critical for determining the response of shredders to enrichment; taxa that can take advantage of nutrient-rich leaf litter and complete larval growth before it is depleted have a distinct advantage over those that are present during periods of low leaf litter standing crop and are potentially food-limited.

When we examined the response of multiple collector–gatherer taxa across a range of life spans, no consistent pattern was apparent (Cross 2004). Long-lived collectors showed little response to enrichment, and there was considerable variability among short-lived taxa. Thus, for collectors (e.g., chironomids) that are not likely to become food-limited with enrichment, other factors in addition to larval life span may be more important in determining variation in response to enrichment.

Nutrient-induced change in food quality is the most probable mechanism responsible for the increased growth and production of chironomids. FPOM is extremely abundant in headwater streams at Coweeta (ca. 1,000 g m^{-2}), and its quantity is relatively stable throughout the year (e.g., Wallace et al. 1999; Cross 2004). While nutrient enrichment had little effect on FPOM quantity (Cross 2004), the P content and, to a lesser extent, N content of FPOM increased in the treatment stream during the enrichment (~40% increase in %P, ~10 increase in %N) (Cross et al. 2003). Together, these data suggest that changes in food nutrient content (most likely P) were responsible for the positive effects of enrichment on chironomid growth rates and production. In addition, we found that chironomid production per gram of FPOM increased in the treatment stream during enrichment (Fig. 3), further supporting the postulate that changes in production were driven by increased food quality. Others have also

found that growth rates of chironomids are sensitive to changes in food nutrient content, microbial activity, and lipid content (e.g., Ward and Cummins 1979; Vos et al. 2000).

In contrast to the clear positive response of chironomids, we found that enrichment had little effect on *Tallaperla* spp., as evidenced by no response in growth rates or areal secondary production. However, we did observe an increase in *Tallaperla* spp. production per gram of leaf litter during the treatment period (Fig. 3). These data suggest that a reduced standing crop of leaf litter during enrichment supported the same amount of production as a high standing crop of leaf litter before the experimental enrichment. For such an effect to be attributable to differences in litter quality, as opposed to a numerical concentration of larvae on reduced leaf resources, the population in question must be food-limited. If a population is not food-limited, decreases in leaf litter biomass without changes in secondary production would necessarily result in higher production per gram of leaf litter, regardless of food quality. In our case, long-term data for shredders in streams at Coweeta demonstrate a strong positive relationship between litter quantity and total shredder production (on the basis of log values of mean annual litter standing crop and annual shredder production: production = $0.51 \times$ leaf litter + 2.28; $r^2 = 0.74$, $p < 0.001$) (Wallace unpubl. data), suggesting food limitation. Thus, changes in production per gram of leaf litter may have been attributable to increased food quality of leaf litter. Concurrent research showed that enrichment led to large increases in leaf litter nutrient content (Cross et al. 2003; Gulis and Suberkropp 2003) as well as increased leaf-associated fungal and bacterial biomass (Gulis and Suberkropp 2003; Suberkropp unpubl. data). Both nutrient content and microbial biomass of leaf litter have been shown to affect the condition (Pearson and Connolly 2000), growth (e.g., Iversen 1974), and abundance (Robinson and Gessner 2000) of leaf consumers in streams.

Despite the increased production per gram of leaf litter of *Tallaperla* spp., our results suggest that the overall production per m^2 was limited by food quantity. Because *Tallaperla* spp. are semivoltine and that they complete less than one generation per year (O'Hop et al. 1984), they require consistent availability of leaf litter throughout the year. In our study, nutrient enrichment led to major reductions in benthic leaf litter via increased leaf decomposition rates (Gulis and Suberkropp 2003; Greenwood 2004). In fact, during the summer months of the enrichment (particularly during the second year of enrichment), leaf litter was reduced to unprecedented low quantities in the treatment stream (Cross 2004; Suberkropp unpubl. data). Nonetheless, the total secondary production of *Tallaperla* spp. m^{-2} was unaffected by enrichment. Thus, one possibility to explain the lack of response by *Tallaperla* spp. is that positive effects of nutrient enrichment on *Tallaperla* spp. via increased food quality were offset by negative effects of enrichment on food quantity. In this case, prolonged larval development may be a constraint for *Tallaperla* spp. in terms of their ability to take full advantage of increased food quality. However, additional research is required to explore this hypothesis more extensively.

In terms of growth rate response, between-taxon differences may have been due to fundamental differences in elemental requirements (sensu Elser et al. 1996). Chironomids at Coweeta grow rapidly and, in accordance with stoichiometric theory, have relatively high amounts of body P (1.1%) and low C:P ratios (113) (Elser et al. 1996; Cross et al. 2003). In contrast, *Tallaperla* spp. have slow growth rates and, on average, lower body P (0.5%) and higher C:P ratios (419) (Cross et al. 2003). Theory predicts that invertebrates with high amounts of body P (or N) require P-rich (or N rich) food for optimal growth (Elser et al. 1996; Sterner and Elser 2002). Those that contain low amounts of these elements are thought to be less constrained by low-nutrient resources and may not exhibit a growth response to increased food nutrient content. Thus, the absence of an enrichment effect on the growth rates of *Tallaperla* spp. may have been due to a low physiological requirement for essential nutrients (i.e., N and P) and a lack of pronounced nutrient limitation. Notwithstanding, considerable research is required that compares consumer elemental content with true elemental requirements in order to test this hypothesis. For example, it is quite possible that consumers with low body P (and high C:P) is still limited by P if they have a low P assimilation efficiency or if they have difficulty getting rid of excess C in food resources (Frost et al. 2005).

In detritus-based stream ecosystems, nutrient enrichment is capable of stimulating microbial biomass and activity (e.g., Ramírez et al. 2003; Stelzer et al. 2003), invertebrate biomass and production (e.g., Pearson and Connolly 2000; Rosemond et al. 2002; Cross 2004), and leaf litter decomposition (e.g., Elwood et al. 1981; Gulis and Suberkropp 2003). During a sufficient time period, these factors may lead to a net loss of carbon from the system (Rosemond unpubl. data; Greenwood 2004), as detrital resources are metabolized, assimilated, or exported. This carbon loss has the potential to cause shifts in community structure by favoring species with short life spans that do not require continuous availability of coarse particulate organic matter. With persistent enrichment, we speculate that production will be dominated by short-lived shredders and a mixture of short- and long-lived taxa from other functional groups that can sustain growth during periods of leaf litter scarcity. Such functional changes in the detritivore community, if persistent, will profoundly change the storage, processing, and export of organic matter from headwater streams (e.g., Cuffney et al. 1990; Wallace and Webster 1996).

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