J. N. Am. Benthol. Soc., 2003, 22(4):565–574
© 2003 by The North American Benthological Society

Long-term resource limitation reduces insect detritivore growth in a headwater stream

BRENT R. JOHNSON[1]

Department of Entomology, University of Georgia, Athens, Georgia 30602 USA

WYATT F. CROSS

Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

J. BRUCE WALLACE

Department of Entomology and Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

Abstract. We measured larval growth rates of 2 dominant stream detritivore groups to assess the mechanism underlying declines in invertebrate production following exclusion of terrestrial litter inputs to a forested headwater stream. Larval *Tallaperla* spp. (Plecoptera:Peltoperlidae) were chosen as representative shredders and non-Tanypodinae Chironomidae (Diptera) were selected as representative collector-gatherers. Larval growth rates were measured in the treatment stream and in 2 undisturbed reference streams using in situ growth chambers. Estimates of daily growth rates were derived from change in mean length of larvae over incubation periods. Initial larval length was a significant predictor of growth in each stream for both taxonomic groups (r^2 = 0.43–0.72, $p < 0.05$). Comparison of significant regression lines showed that size-specific growth of both *Tallaperla* spp. and chironomids was significantly reduced in the litter exclusion stream (ANCOVA, $p < 0.05$). Lower chironomid growth rates in the treatment stream than in the control streams indicate that production estimates based on the instantaneous growth method are actually lower than previously reported for the site. Mortality of *Tallaperla* spp. was also significantly higher in the treatment stream than in control streams (ANOVA, $p < 0.05$). Reduced growth of these representative taxa apparently results from reduced quantity of organic matter food resources. These results show that reduced growth is partially responsible for observed declines in detritivore production in the litter-exclusion stream.

Key words: benthos, Chironomidae, detritus, functional groups, litter exclusion, macroinvertebrate, midge, mortality, organic matter, Peltoperlidae, stonefly.

Terrestrial detritus is the principal energy source in shaded headwater streams of the southern Appalachians (Webster et al. 1983, 1995, Webster and Meyer 1997). Many stream invertebrates feed directly on this detritus and play an important role in organic matter processing (Cummins et al. 1973, Vannote et al. 1980, Wallace et al. 1982, Wallace and Webster 1996). In addition, insect detritivores may have life histories that are keyed to autumn leaf fall (Sweeney 1984, Huryn and Wallace 2000). Thus, tight linkages exist between terrestrial detritus inputs, stream detritivores, and ecosystem structure and function (Fisher and Likens 1973, Hynes 1975, Vannote et al. 1980, Cushing et al. 1995, Wallace et al. 1997, 1999). Disturbances (e.g., logging, mining, urbanization, agriculture) that change the quantity or quality of organic matter entering streams can disrupt terrestrial–aquatic linkages and alter ecosystem dynamics (Webster et al. 1983).

In a long-term ecosystem-level manipulation, Wallace et al. (1997, 1999) excluded terrestrial detritus inputs to a headwater stream at the Coweeta Hydrologic Laboratory in western North Carolina. After 4 y of treatment, organic matter standing crop had declined significantly and invertebrate production in mixed substrate habitats was among the lowest reported for streams (Wallace et al. 1999). More specifically, production of shredder and collector-gatherer functional feeding groups (FFGs) declined to 13 and 24% of pretreatment values, respectively. The mechanism responsible for reduced invertebrate production, however, remains uncertain because reduced larval production can result

[1] Present Address: National Exposure Research Laboratory, US Environmental Protection Agency, 26 W. Martin Luther King Dr., Cincinnati, Ohio 45268 USA. E-mail: johnson.brent@epa.gov

from reduced abundance, biomass, or individual growth rate (Benke 1984).

We hypothesized that reduced detritivore growth was contributing to the production decline in the litter-exclusion stream. Daily growth rates were therefore measured for 2 dominant insect detritivores representing shredder and collector-gatherer FFGs. Larval *Tallaperla* spp. (Plecoptera:Peltoperlidae) were chosen as representative shredders. Up to 4 species of *Tallaperla* potentially co-occur in Coweeta headwaters: *T. maria*, *T. anna*, *T. cornelia*, and *T. elisa* (Huryn and Wallace 1987, Stewart and Stark 1993). It is not currently possible to distinguish these species in the larval stage, but all feed on leaf detritus and have similar semivoltine life cycles in these streams (O'Hop et al. 1984 [as *Peltoperla maria*], Huryn and Wallace 1987). Non-Tanypodinae chironomid (Diptera) larvae were chosen as representative collector-gatherers. Midges primarily feed on fine benthic organic matter (FBOM) and undergo rapid growth that results in several generations per year in Coweeta streams (Huryn and Wallace 1986, Huryn 1990). These 2 taxonomic groups were specifically chosen because they compose a large proportion of the abundance, biomass, and production in their respective FFG in the study streams (Wallace et al. 1999).

Study sites

Our study was conducted in 3 first-order streams draining catchments (C) 53 (reference 1), 54 (reference 2), and 55 (litter exclusion) at the Coweeta Hydrologic Laboratory in Macon County, North Carolina. These 3 streams have similar physical characteristics including catchment size, discharge, and thermal regime (Table 1). Vegetation consists of mixed hardwoods with a dense understory of rhododendron (*Rhododendron maximum* L.) that shades the streams throughout the year. The heavy shading results in extremely low instream primary production. Additional details of the Coweeta catchment are provided in Swank and Crossley (1988). The litter-exclusion treatment in C55 began in August 1993 when an overhead net canopy (2.5-cm mesh) was installed over the uppermost 170 m of the stream. Plastic drift fences (20-cm high with 1-cm mesh) were installed along each side of the treatment stream to prevent lateral inputs. A large (>1 m) space between the fence and canopy allowed recolonization by aerial insects. Riparian vegetation was left in place during canopy installation to prevent changing the natural light regime. Leaves were removed from the canopy once a week in autumn and when needed in other seasons. As a result of these manipulations, organic matter standing crop in the treatment stream was reduced by ~95% compared to pretreatment and reference stream values (Wallace et al. 1999).

TABLE 1. Physical variables of streams draining catchments (C) 53 (reference 1), 54 (reference 2), and 55 (litter-exclusion treatment) at the Coweeta Hydrologic Laboratory. Elevations were measured at the gauging flumes. Data are from Wallace et al. (1999) and WFC (unpublished data). – = missing data.

Variable	C53	C54	C55
Catchment			
Area (ha)	5.2	5.5	7.5
Elevation (m asl)	829	841	810
Channel			
Length (m)	145	282	170
Bankfull area (m^2)	327	443	373
Discharge (L/s)			
Average[a]	1.19	1.45	2.39
Maximum[a]	47.2	35.5	40.2
Temperature (°C)			
Annual average[b]	12.2	–	12.2
Maximum[b]	20.3	19.5	20.1
Minimum[b]	0.7	1.1	0.7
Annual degree-days[b]	4485	4440	4512

[a] C53 average of 12 y (1984–1996), C54 average of 8 y (1985–1992), C55 average of 5 y (1992–1997)
[b] C53 and C55 average of 12 y (1985–1997), C54 average of 8 y (1985–1992)

Methods

Growth rates for *Tallaperla* spp. and non-Tanypodinae chironomids were measured seasonally in each stream beginning in November 1999. *Tallaperla* spp. growth was measured in C55 (litter exclusion) and C53 (reference 1) through April 2001 (n = 6 seasons) and in C54 (reference 2) through June 2000 (n = 3 seasons). Chironomid growth was measured in C55 and C53 through September 2000 (n = 4 seasons) and in C54 through June 2000 (n = 3 seasons). Fewer growth estimates were made in C54 because our study only includes pretreatment data

for an ongoing experiment in that catchment. Mean daily temperatures (recorded hourly in each stream using Ryan® recording thermistors) over each incubation period were averaged to obtain a mean temperature during growth incubations.

Tallaperla spp. and chironomid larvae were collected each season from leaf litter packs in undisturbed Coweeta headwaters. Litter was rinsed through a series of nested sieves using stream water, and the sieve contents were placed under a dissecting microscope for collection of larvae. Length of each larva was then measured to the nearest 0.01 mm with an ocular micrometer and lengths were grouped into 1-mm classes. Size classes were chosen based on the general size distribution in the stream at the time of collection. Three chironomid size classes and from 2 to 4 *Tallaperla* spp. size classes were used in each stream each season.

Larvae of the same size class were incubated separately in the 3 streams using the triangular growth chambers (20 cm × 20 cm × 14 cm sides × 16 cm height) described by Huryn and Wallace (1986). Side panels of the growth chambers consisted of 63-μm Nitex® mesh. Chambers were placed in the stream with their top extending above the water surface and with the triangular wedge oriented directly into the current to reduce drag and prevent mesh clogging. Chambers were anchored to the stream bottom by placing rocks along their external flanges. Two widely disparate *Tallaperla* spp. size classes were sometimes placed in the same chamber to increase the number of growth estimates. Larval densities in the chambers were well within the range of natural densities found in undisturbed Coweeta headwaters (Wallace et al. 1999).

Eight to 10 conditioned leaves were collected each season from the reference streams, rinsed, and placed in each of the reference stream chambers for food and substrate. Leaf species depended on time of year and availability, but consisted primarily of rhododendron, maple (*Acer* spp.), beech (*Fagus grandifolia* Ehrh.), yellow poplar (*Liriodendron tulipifera* L.), oak (*Quercus* spp.), and dogwood (*Cornus florida* L.). In C55 (litter exclusion) where leaves are absent, only stream substrate, consisting of sand, gravel, and FBOM, was placed in each chamber to accurately reflect stream conditions. *Tallaperla* spp. were incubated for ~2 mo, and leaves in reference stream chambers were replaced midway through incubation. There was no replacement of FBOM in C55 chambers because they naturally accumulated FBOM during incubation periods. Midges were incubated for 7 to 14 d, depending on stream temperature. Chironomids >3 mm long were not used in the chambers to prevent emergence during incubation.

Chamber contents were preserved in plastic bags containing Kahle's solution at the end of incubation periods. All recovered larvae were then remeasured using the method described above. Initial and final length measurements were converted to ash-free dry mass (AFDM) using known length–mass regressions from undisturbed streams:

Tallaperla $M = 0.0194\ L^{2.853}$ (Benke et al. 1999)
Midges $M = 0.452\ L^{3.099}$ (Huryn and Wallace 1986)

where M is AFDM in μg (midges) or mg (*Tallaperla* spp.) and L is length in mm. Larval growth rate (g/d) for each size class was then calculated for both taxa as:

$$g = (\ln M_f - \ln M_i)/t$$

where M_f is final AFDM, M_i is initial AFDM, and t is the number of days of incubation. This method produces growth estimates that are representative of the 2 taxonomic assemblages. The underlying assumption is that changes in mean mass of similar-sized larvae of different taxonomic composition can be used to estimate mean growth rates that are representative of taxa found in the streams (Huryn and Wallace 1986, Huryn 1990).

Multiple regression models were initially used to measure the influences of initial length and temperature on larval growth rates. Differences in growth rates among streams were then assessed by comparing slopes of significant regression lines by analysis of covariance (ANCOVA) with initial length as the covariate. Initial length was used as the covariate because small larvae generally grow proportionately faster than larger larvae (Huryn and Wallace 1986, Perry et al. 1987, Huryn 1990). Incubation temperatures and larval mortality (%/d) were compared among streams by 1-way analysis of variance (ANOVA) followed by Tukey's multiple comparison tests. Regression models were also used to assess the influence of temperature and initial length on larval survivorship.

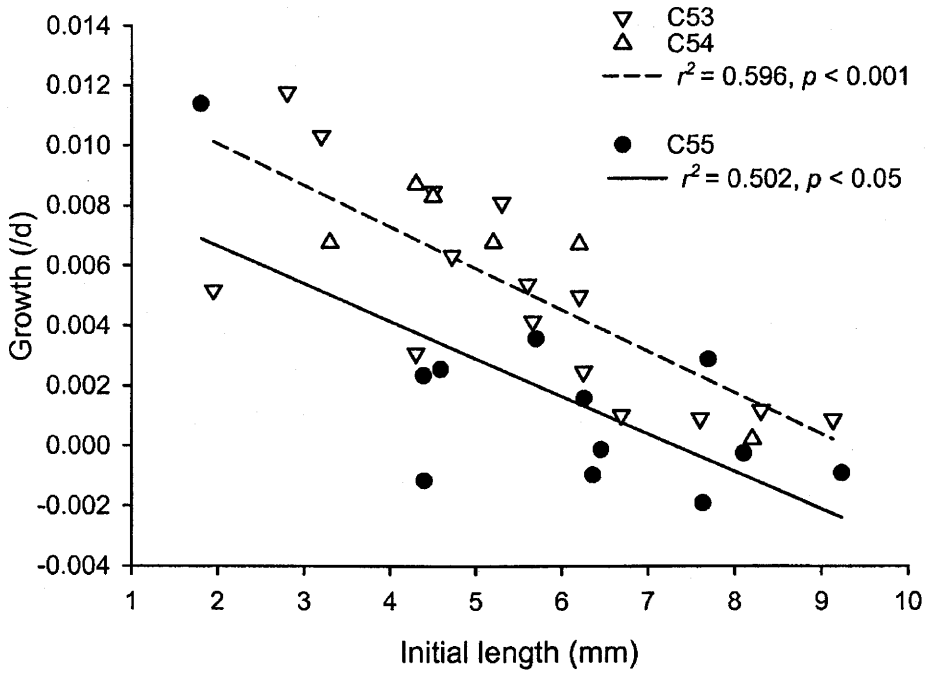

FIG. 1. Relationships between instantaneous growth rate and initial length for *Tallaperla* spp. in 2 reference streams (C53 and C54) and the litter-exclusion stream (C55).

Results

Tallaperla *spp.*

A total of 33 *Tallaperla* spp. growth measurements were taken in the 3 streams (C53, $n = 15$; C54, $n = 6$; C55, $n = 12$) (Appendix). Mean incubation temperatures ranged from 5.0°C to 16.8°C over the 6 incubation periods, and there were no temperature differences among streams (ANOVA, $p > 0.05$). Temperature had little influence on growth in the study streams ($r^2 < 0.15$, $p > 0.05$) and was, therefore, dropped from the growth model. Initial length, however, was a strong predictor of larval growth rate and resulted in significant regression equations for each stream ($r^2 = 0.50$–70, $p < 0.05$). Growth was negatively correlated with initial length indicating that smaller size classes exhibited higher growth rates during incubations.

Comparison of growth equations showed no significant differences between the 2 reference streams (ANCOVA, $p < 0.05$), so these data were combined to yield a single reference growth equation. The relationship between growth and initial length in the reference streams was best described by the linear equation: $y = -0.001x + 0.0128$ ($r^2 = 0.596$, $p < 0.001$) (Fig. 1). The corresponding growth regression equation derived for the litter-exclusion stream was: $y = -0.001x + 0.009$ ($r^2 = 0.502$, $p < 0.05$). Intercepts of reference and litter-exclusion regression equations were significantly different (ANCOVA, $F_{3,32} = 11.29$, $p < 0.01$), showing reduced *Tallaperla* spp. growth in the litter-exclusion stream (Fig. 1). Fifty percent of growth measurements resulted in negative values in the litter-exclusion stream, whereas all 21 measurements showed positive growth in the reference streams.

Larval mortality differed significantly among streams (ANOVA, $p = 0.006$), with mortality in the litter-exclusion stream significantly higher than both reference streams (Tukey test, $p < 0.05$) (Fig. 2). Mortality was expressed as %/d to account for differences in time of incubation over the year. Mean daily mortality in reference streams chambers were both ~0.5%/d, whereas mortality in the litter-exclusion stream was nearly 1%/d (Fig. 2). Larval mortality was negatively correlated with mean incubation temperature in the litter-exclusion stream ($r^2 = 0.417$, $p < 0.05$). No larvae were recovered from either chamber incubated in the litter-exclusion stream in spring 2000 (23 April 2000 to 20 June 2000)

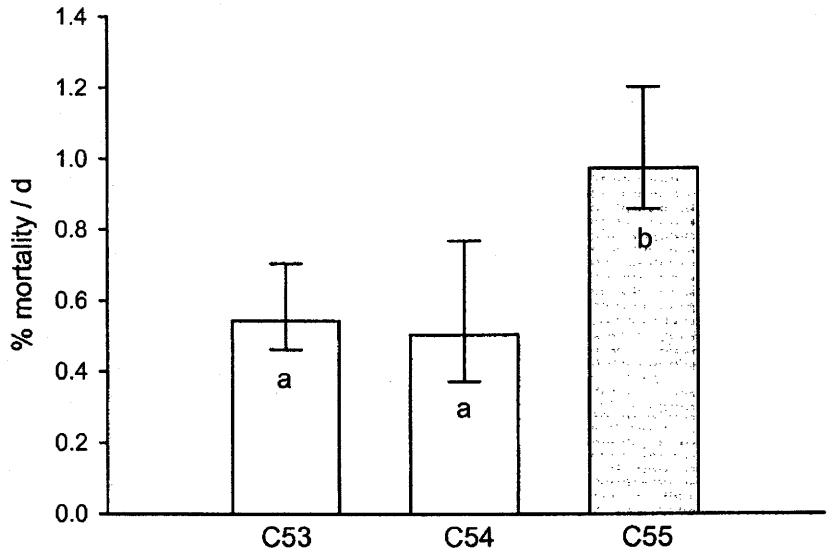

FIG. 2. Mean (±2 SE) daily mortality of larval *Tallaperla* spp. from chambers incubated in 2 reference streams (C53, n = 15 and C54, n = 6) and the litter-exclusion stream (C55, n = 12). Different letters indicate significant differences (Tukey test, $p < 0.05$).

when the mean stream temperature was 13.6°C, and only 17% of the individuals survived for the one chamber recovered in summer 2000 (26 July 2000 to 29 September 2000) when the mean temperature was 16.6°C (the 2nd growth chamber was destroyed by an animal during the summer 2000 incubation period). There was no relationship between temperature and mortality in the reference streams (combined data: $r^2 = 0.003$, $p > 0.05$). Initial length was not related to larval mortality in any stream ($r^2 < 0.070$, $p > 0.05$).

Non-Tanypodinae chironomids

Twenty-nine chironomid growth measurements were taken over the study period (C53, n =10; C54, n = 8; C55, n = 11) (Appendix). Mean incubation temperatures ranged from 8.5 to 16.3°C and there were no temperature differences among streams (ANOVA, $p > 0.05$). As with *Tallaperla* spp., the relationship between chironomid growth and temperature was not significant in the study streams ($r^2 < 0.33$, $p > 0.05$), so temperature was dropped from growth regression equations. Chironomid growth rates were also negatively correlated with initial length in each stream (r^2 = 0.43–0.72, $p < 0.05$).

Growth rates did not differ between reference streams (ANCOVA, $p > 0.05$), so these data were combined to produce the linear equation: $y = -0.035x + 0.132$ ($r^2 = 0.642$, $p < 0.001$) (Fig. 3). In the litter-exclusion stream, the corresponding growth equation was: $y = -0.023x + 0.073$ ($r^2 = 0.430$, $p < 0.05$). Growth rates for all larval size classes were generally lower in the litter-exclusion stream than in either reference stream. Comparison of reference and litter-exclusion growth equations showed a difference in line intercepts (ANCOVA, $F_{3,28} = 26.64$, $p < 0.001$), indicating significantly reduced chironomid growth in the litter-exclusion stream (Fig. 3).

There were no differences in midge mortality among streams (ANOVA, $p > 0.05$). Mortality in each of the streams was ~0.5%/d and mortality was not influenced by either temperature ($r^2 < 0.132$, $p > 0.05$) or initial length ($r^2 < 0.068$, $p > 0.05$) in any of the study streams.

Discussion

Detritus limitation resulted in significantly lower growth rates for representatives of both shredder and collector-gatherer FFGs. Reduced individual growth is therefore one mechanism, along with lower biomass and density, responsible for the exceptionally low detritivore production in mixed-substrate habitats of a stream with reduced detrital resources.

After 4 y of litter exclusion, peltoperlid production had declined by ~77% compared to C53 and pretreatment values (Wallace et al. 1999). Coarse benthic organic matter (CBOM) had de-

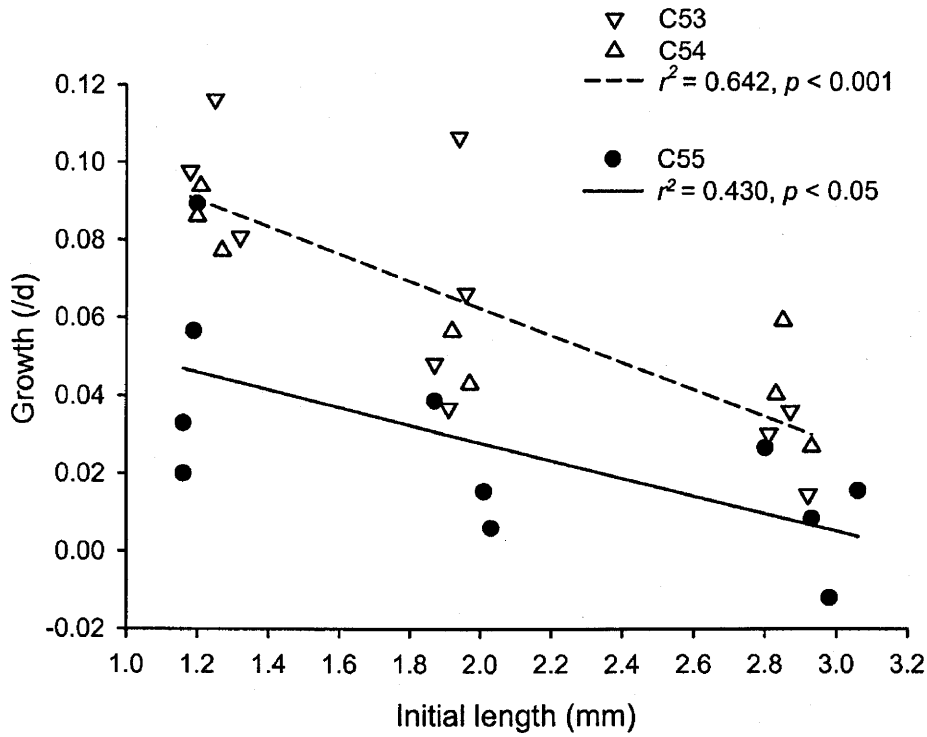

FIG. 3. Relationship between instantaneous growth rate and initial length for non-Tanypodinae Chironomidae in 2 reference streams (C53 and C54) and the litter-exclusion stream (C55).

clined significantly, and leaf detritus had been nearly eliminated from the stream (Wallace et al. 1999). This lack of leaf detritus likely resulted in less growth and higher mortality of *Tallaperla* spp. larvae in the litter-exclusion stream. *Tallaperla* spp. growth rates were characteristically low in all 3 streams, as would be expected for long-lived semivoltine taxa (Sweeney 1984). Yet, growth rates were >3× higher in the reference streams than the litter-exclusion stream. Furthermore, larvae lost mass during incubation in half of the growth chambers in the treatment stream. The higher growth rates observed for early instar peltoperlids may indicate they can rely to some degree on FBOM as a food resource rather than shredding leaf detritus (Fig. 1). Richardson (1991) provided similar evidence of food-limitation effects when he found that growth of another shredding stonefly, *Zapada cinctipes*, increased after the detrital supply was experimentally augmented in streamside channels.

Tallaperla spp. larvae are adapted to cold streams and are capable of growth through winter months (O'Hop et al. 1984, Huryn and Wallace 1987). The fact that we found no relationship between larval growth and incubation temperature may result from the relatively stable thermal regime in these groundwater-dominated streams. The lack of temperature effect may indicate that growth in these headwater streams may be influenced more by timing and availability of leaf litter inputs than by temperature alone.

Tallaperla spp. mortality was also significantly higher in the litter-exclusion than in reference streams (Fig. 2). Mortality increased with increasing stream temperature only in the litter-exclusion stream. Greater mortality in the summer likely resulted from lack of available food, an inability to catabolize alternative resources, and increased metabolic demands associated with increased stream temperatures. The observed mortality was likely a function of the growth chambers. Free from chamber effects, *Tallaperla* spp. larvae drifted from the litter-exclusion stream in search of food resources (Siler et al. 2001).

Non-Tanypodinae chironomid growth rates in the reference streams were characteristically high and indicative of fast turnover rates. Chironomid growth rates in reference streams were within the range of growth estimates previously

reported at Coweeta (Huryn and Wallace 1986, Huryn 1990) and in other temperate streams (Berg and Hellenthal 1992). As with *Tallaperla* spp., there was no relationship between growth and temperature in any of the study streams. This result is not surprising because chironomid larvae in the chambers were representative of the community and thus contained many taxa that may have different thermal optima (Rempel and Harrison 1987, Berg and Hellenthal 1992, but see Huryn 1990).

Non-tanypodine chironomid production in mixed-substrate habitats of the litter-exclusion stream had declined by ~82% compared to reference and pretreatment values (Wallace et al. 1999). Growth rates in the litter-exclusion stream averaged <1/2 of those in reference streams. FBOM, like CBOM, declined significantly as a result of treatment (Wallace et al. 1999). FBOM in the litter-exclusion stream was only 32% of that in the reference stream following 3 y of treatment (Meyer et al. 1998). Chironomid larvae may ingest greater quantities of inorganic sediments with a reduction in the FBOM food resource. This lower-quality diet may explain the reduced individual growth rates. Meyer et al. (2000) found no difference in FBOM quality after 3 y of litter exclusion based on laboratory growth assays using *Chironomus tentans*. The growth assays, however, provided an excess of FBOM in the absence of inorganic particles and probably did not accurately reflect stream conditions. Our in situ measurements may have suffered from lack of treatment replication, but they provided greater ecological realism than laboratory assays (Carpenter 1996, Schindler 1998). Overall, there were no differences in midge mortality among streams, suggesting that larvae may survive equally well on a lower-quality diet, but at the expense of reduced growth.

Litter exclusion resulted in some of the lowest secondary production estimates reported for stream ecosystems. By the 4th year of treatment, Wallace et al. (1999) estimated that total production of the benthic community in mixed-substrate habitats had declined to 1.1 g AFDM m^{-2} y^{-1} (a decline of 78% from pretreatment values). Chironomids alone accounted for >16% of that production. Chironomid production in Wallace et al. (1999) was calculated by the instantaneous growth method (Benke 1984) using growth rates established for undisturbed Coweeta streams by Huryn and Wallace (1986) and modified by Huryn (1990). The fact that our results showed reduced chironomid growth rates in the litter-exclusion stream means that Wallace et al. (1999) actually overestimated chironomid production, and that total benthic production in the litter-exclusion stream is even lower than previously reported. Application of our newly derived chironomid growth rates for C55 to the 1998 to 1999 benthic data lowered chironomid production estimates nearly 3× in mixed-substrate habitats, from 194 to 68 mg AFDM m^{-2} y^{-1}.

Riparian vegetation is often removed by urban development, logging, and agricultural activities. Failure to maintain appropriate riparian vegetation alters the connectivity between streams and the surrounding landscape and results in loss of the detrital subsidy. Several studies have now demonstrated the importance of detritus for stream ecosystem productivity (Hynes 1963, Fisher and Likens 1973, Wallace et al. 1997, 1999). Our results support those findings, and show that reduced growth of insect detritivores is yet another consequence of severing the terrestrial–aquatic linkage.

Acknowledgements

We thank Darold Batzer, Wayne Berisford, Judy Meyer, Cathy Pringle, and John Hutchens for their helpful comments. We also thank David Rosenberg, John Richardson, Arthur Brown, and an anonymous reviewer for their valuable comments on earlier versions of this paper. The litter exclusion aspect of this work was funded by National Science Foundation grant DEB-9629268.

Literature Cited

BENKE, A. C. 1984. Secondary production of aquatic insects. Pages 289–322 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger, New York.

BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

BERG, M. E., AND R. A. HELLENTHAL. 1992. Life histories and growth of lotic chironomids (Diptera: Chironomidae). Annals of the Entomological Society of America 85:578–589.

CARPENTER, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680.

CUMMINS, K. W., R. C. PETERSON, F. O. HOWARD, J. C. WUYCHECK, AND V. I. HOLT. 1973. The utilization of leaf litter by stream detritivores. Ecology 54: 336–345.

CUSHING, C. E., K. W. CUMMINS, AND G. W. MINSHALL. (EDITORS). 1995. Ecosystems of the world 22: river and stream ecosystems. Elsevier, Amsterdam, The Netherlands.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

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

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

HURYN, A. D., AND J. B. WALLACE. 1987. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. Aquatic Insects 9:229–251.

HURYN, A. D., AND J. B. WALLACE. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83–110.

HYNES, H. B. N. 1963. Imported organic matter and secondary productivity in streams. International Congress of Zoology 16:324–329.

HYNES, H. B. N. 1975. The stream and its valley. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 19:1–15.

MEYER, J. L., C. HAX, J. B. WALLACE, S. L. EGGERT, AND J. R. WEBSTER. 2000. Terrestrial litter inputs as determinants of food quality of organic matter in a forest stream. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 27:1346–1350.

MEYER, J. L., J. B. WALLACE, AND S. L. EGGERT. 1998. Leaf litter as a source of dissolved organic carbon in streams. Ecosystems 1:240–249.

O'HOP, J., J. B. WALLACE, AND J. D. HAEFNER. 1984. Production of a stream shredder, *Peltoperla maria* (Plecoptera:Peltoperlidae) in disturbed and undisturbed hardwood catchments. Freshwater Biology 14:13–21.

PERRY, W. B., E. F. BENFIELD, S. A. PERRY, AND J. R. WEBSTER. 1987. Energetics, growth, and production of a leaf-shredding stonefly in an Appalachian mountain stream. Journal of the North American Benthological Society 6:12–25.

REMPEL, R. S., AND A. D. HARRISON. 1987. Structural and functional composition of the Chironomidae (Diptera) in a Canadian Shield stream. Canadian Journal of Zoology 65:2545–2554.

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

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

SILER, E. R., J. B. WALLACE, AND S. L. EGGERT. 2001. Long-term effects of resource limitation on stream invertebrate drift. Canadian Journal of Fisheries and Aquatic Sciences 58:1624–1637.

STEWART, K. W., AND B. P. STARK. 1993. Nymphs of North American Stonefly Genera (Plecoptera). University of North Texas Press, Denton, Texas.

SWANK, W. T., AND D. A. CROSSLEY. (EDITORS). 1988. Forest hydrology and ecology at Coweeta. Ecological Studies Series Volume 66. Springer-Verlag, New York.

SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56–100 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger, New York.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

WALLACE, J. B., AND J. R. WEBSTER. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115–139.

WALLACE, J. B., J. R. WEBSTER, AND T. F. CUFFNEY. 1982. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia (Berlin) 53:197–200.

WEBSTER, J. R., M. E. GURTZ, J. J. HAINES, J. L. MEYER, W. T. SWANK, J. B. WAIDE, AND J. B. WALLACE. 1983. Stability of stream ecosystems. Pages 355–395 *in* J. R. Barnes and G. W. Minshall (editors). Stream ecology. Plenum, New York.

WEBSTER, J. R. AND J. L. MEYER. (EDITORS). 1997. Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

WEBSTER, J. R., J. B. WALLACE, AND E. F. BENFIELD. 1995. Streams and rivers of eastern United States. Pages 117–187 *in* C. E. Cushing, K. Cummins, and G. W. Minshall (editors). River and stream ecosystems. Elsevier Press, Amsterdam, The Netherlands.

Received: 15 January 2003
Accepted: 20 August 2003

APPENDIX. Size- and temperature-specific growth data used to derive non-Tanypodinae Chironomidae (A) and *Tallaperla* spp. (B) growth regression equations. Li = average initial length (mm); Mi and Mf = average initial and final mass (ash-free dry mass [AFDM] in μg for chironomids and mg for *Tallaperla* spp.) of individuals used in growth chambers; ni and nf = initial and final numbers of individuals observed; t = number of days incubated; g = daily growth rate (/d); T = average stream temperature (°C) during incubation; X = no recovery. C53 and C54 = reference streams, C55 = litter-exclusion stream.

Date	Li	Mi	ni	Mf	nf	t	g	T
A: Non-Tanypodinae Chironomidae								
C53								
7 Nov 99	1.25	1.18	30	5.99	18	14	0.116	10.9
7 Nov 99	1.91	3.77	50	6.32	12	14	0.037	10.9
7 Nov 99	2.92	11.89	19	14.59	4	14	0.015	10.9
21 Feb 00	1.18	1.00	51	4.33	27	14	0.098	9.6
21 Feb 00	1.87	3.60	94	7.43	21	14	0.048	9.6
21 Feb 00	2.87	11.30	29	19.41	8	14	0.036	9.6
25 May 00	1.96	4.14	59	9.17	16	12	0.066	14.8
25 May 00	2.81	10.64	26	15.29	15	12	0.030	14.8
9 Sept 00	1.32	1.32	40	2.52	16	8	0.081	16.3
9 Sept 00	1.94	3.97	82	9.32	10	8	0.107	16.3
C54								
7 Nov 99	1.20	1.05	30	3.52	13	14	0.086	10.7
7 Nov 99	2.83	10.99	20	19.35	3	14	0.040	10.7
20 Feb 00	1.21	1.05	53	4.31	22	15	0.094	9.6
20 Feb 00	1.92	3.85	71	9.01	31	15	0.057	9.6
20 Feb 00	2.93	12.03	29	17.99	13	15	0.027	9.6
25 May 00	1.27	1.20	40	3.04	5	12	0.077	13.9
25 May 00	1.97	4.16	59	6.98	8	12	0.043	13.9
25 May 00	2.85	11.14	30	22.69	4	12	0.059	13.9
C55								
7 Nov 99	1.16	0.96	30	1.52	9	14	0.033	10.2
7 Nov 99	2.01	4.33	51	5.37	8	14	0.015	10.2
7 Nov 99	2.98	12.61	20	10.66	3	14	−0.012	10.2
21 Feb 00	1.16	0.94	36	1.27	13	14	0.020	8.5
21 Feb 00	2.03	4.50	90	4.93	29	14	0.006	8.5
21 Feb 00	3.06	13.58	23	17.16	12	14	0.016	8.5
25 May 00	1.19	1.02	31	2.02	10	12	0.057	14.5
25 May 00	2.80	10.53	34	14.50	14	12	0.027	14.5
9 Sept 00	1.20	1.01	28	2.08	4	8	0.089	16.3
9 Sept 00	1.87	3.66	56	5.00	20	8	0.039	16.3
9 Sept 00	2.93	11.97	28	12.81	9	8	0.008	16.3
B: *Tallaperla* spp.								
C53								
3 Nov 99	4.30	1.31	30	1.62	22	67	0.003	9.2
3 Nov 99	8.30	8.12	15	8.80	9	67	0.001	9.2
7 Feb 00	4.50	1.45	40	2.33	21	55	0.008	9.8
7 Feb 00	6.20	3.58	27	4.74	24	55	0.005	9.8
23 April 00	3.20	0.55	36	1.00	33	58	0.010	14
23 April 00	5.30	2.25	30	3.61	22	58	0.008	14
26 July 00	2.80	0.36	20	0.77	7	65	0.012	16.8
26 July 00	5.66	2.74	18	3.59	7	65	0.004	16.8
26 July 00	6.69	4.39	5	4.70	4	65	0.001	16.8
6 Nov 00	4.72	1.63	9	2.47	5	65	0.006	5.7
6 Nov 00	6.25	3.64	35	4.27	30	65	0.002	5.7
6 Nov 00	9.13	10.69	6	11.31	2	65	0.001	5.7

APPENDIX. Continued.

Date	Li	Mi	ni	Mf	nf	t	g	T
10 Feb 01	1.95	0.14	39	0.19	23	61	0.005	9.2
10 Feb 01	5.60	2.67	25	3.71	23	61	0.005	9.2
10 Feb 01	7.60	6.40	10	6.77	7	61	0.001	9.2
C54								
3 Nov 99	4.30	1.23	30	2.22	10	67	0.009	9.3
3 Nov 99	8.20	7.90	17	8.02	9	67	0.0002	9.3
7 Feb 00	4.50	1.42	40	2.26	27	55	0.008	9.7
7 Feb 00	6.20	3.48	26	5.07	21	55	0.007	9.7
23 April 00	3.30	0.61	35	0.90	33	58	0.007	13.2
23 April 00	5.20	2.19	30	3.25	25	58	0.007	13.2
C55								
3 Nov 99	4.40	1.35	30	1.23	6	67	−0.001	8.2
3 Nov 99	8.10	7.66	15	7.53	7	67	−0.0002	8.2
7 Feb 00	4.39	1.33	42	1.52	27	55	0.002	8.8
7 Feb 00	6.26	3.65	32	4.00	27	55	0.002	8.8
23 April 00	3.97	0.99	35	X	0	58	X	13.6
23 April 00	6.64	4.31	30	X	0	58	X	13.6
26 July 00	6.45	4.04	29	4.01	5	65	−0.0001	16.6
6 Nov 00	4.59	1.52	12	1.79	7	65	0.003	5.0
6 Nov 00	6.36	3.82	37	3.59	19	65	−0.001	5.0
6 Nov 00	7.63	6.42	29	5.68	19	65	−0.002	5.0
6 Nov 00	9.23	11.04	10	10.41	4	65	−0.001	5.0
10 Feb 01	1.81	0.11	51	0.23	22	61	0.011	8.4
10 Feb 01	5.70	2.80	26	3.48	5	61	0.004	8.4
10 Feb 01	7.69	6.56	15	7.82	7	61	0.003	8.4