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Reduced detrital resources limit *Pycnopsyche gentilis* (Trichoptera: Limnephilidae) production and growth

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Abstract. Leaf inputs in temperate forest streams may limit caddisfly production because leaf detritus serves both as a food and case-material resource. We estimated *Pycnopsyche gentilis* production in a stream experimentally decoupled from its riparian habitat and a reference stream for 8 y in the southern Appalachians. We also examined laboratory survivorship, growth, and case-building activities of *P. gentilis* in substrate containing various quantities of leaf material. *Pycnopsyche gentilis* production declined to 0 within 3 y of the start of litter exclusion. Abundance, biomass, and production of *P. gentilis* were positively related to leaf litter standing crops. Maximum individual length of *P. gentilis* was reduced when annual leaf standing crops fell below 25 to 50 g AFDM/m^2. Observations of case construction for instars removed from their original leaf cases and kept in substrate with low leaf standing crop, showed that *P. gentilis* was capable of rebuilding a case of available substrate and surviving for 3 to 4 wk before dying of starvation. Survivorship and growth were significantly greater for larvae reared at high and intermediate leaf standing crops, than at low leaf standing crop. Older instars had higher survivorship rates but lower growth rates than younger instars in the low litter substrates. Survivorship and growth rates were lower for some individuals forced to rebuild new cases, indicating an energetic cost associated with case-building activities. Our results demonstrate that the linkage between terrestrially derived organic matter and production of a caddisfly shredder was a consequence of food availability.

Key words: case-building behavior, caddisfly, organic matter, macroinvertebrates, stream, resource limitation.

Detrital resources and benthic invertebrates in streams are closely linked (e.g., Egglishaw 1964, Anderson and Sedell 1979, Cummins et al. 1989, Richardson 1991, Dobson and Hildrew 1992, Wallace et al. 1999). Organic matter inputs from riparian habitats provide ~90% of the energy source of southern Appalachian headwater streams (Webster et al. 1983). Rapid development in this region has hastened the decoupling of riparian habitats from streams and rivers. Privately owned land in the region has <60% forest cover in the 30-m riparian zone (SAMAB 1996). The extent of riparian loss worldwide is not well known (Nilsson and Berggren 2000, NRC 2002), although it has been suggested that >80% of riparian areas in North America and Europe have been lost in the last 200 y (Naiman et al. 1993). The loss of riparian forest cover and associated litter inputs to streams puts the survival of sensitive stream invertebrates such as caddisflies at risk (Morse et al. 1993).

Many caddisfly genera are restricted to particular terrestrial biomes (Ross 1963). Larvae of *Pycnopsyche gentilis* (MacLachlan) inhabit leaf packs in temperate forest streams throughout the eastern United States (Flint 1960, Ross 1963, Mackay 1972, Mackay and Kalff 1973). Leaf litter is a dominant part of their diet (Mackay and Kalff 1973). In headwater streams at Coweeta, 86 to 100% of their diet consists of leaf detritus (Hutchens et al. 1997). The type of available organic material influences habitat selection by *Pycnopsyche* spp. (Cummins 1964, Mackay and Kalff 1973). Second- through 4th-instar *P. gentilis* construct 3-sided leaf disk cases (Mackay 1972). Where larval densities are high, 4th instars may switch to mineral substrates prematurely (Mackay 1977). The ability to successfully construct cases is critical for caddisflies; cases aid respiration (Williams et al. 1987), provide protection from predators (Otto and Svensson 1980, Nislow and Molles 1993, Otto and Johansson 1995), provide ballast (Webster and Webster 1943), and prevent desiccation (Zamora-Muñoz and Svensson 1996).

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The experimental exclusion of particulate organic matter from a forested headwater stream at Coweeta Hydrologic Laboratory, North Carolina, reduced benthic leaf standing crops by 94%. Results from the first 4 y of litter exclusion suggested that all shredder taxa did not respond similarly to detrital resource reduction during the early years of the 8-y study (Wallace et al. 1999). Here we report *P. gentilis* production and resource supply for the entire 8-y study, which included an additional year of data following small wood removal and 2 y of data after large wood removal. Another objective of our study was to determine mechanisms responsible for changes in *P. gentilis* production that occurred as a result of litter exclusion. Low survivorship of this species could be the result of a lack of available food resources, higher predation rates, or respiratory stress caused by the absence of leaf litter as a material for case construction for 2nd to 4th instars. In the laboratory, we manipulated levels of leaf standing crop (low, intermediate, and high) and larval case type (field constructed case vs laboratory constructed case) to examine the role of leaf detritus as a food resource and as case-construction material for *P. gentilis*. Specifically, we observed case-building behavior to determine whether young *P. gentilis* larvae could adapt to the lack of leaf material and survive in cases constructed from substrate containing little leaf material. In addition, we measured differences in growth rates and mortality of larvae with normal leaf cases reared with various amounts of leaf litter to see whether differences in food availability could account for the decline in *P. gentilis* production in the field.

Methods

Study sites

Organic matter was excluded from Catchment (C) 55 at Coweeta Hydrologic Laboratory in Macon Co., North Carolina, USA, beginning in August 1993 using 1.2-cm mesh gillnet canopy to exclude direct litter fall and lateral fencing to prevent blow-in from the banks. The canopy began at the top of the catchment and was open along the sides for aerial insect colonization. Small woody debris (<10 cm diameter) was removed by hand from the litter exclusion stream in August 1996. Remaining large wood was removed in August 1998. An unmanipulated stream, C53, located within the same basin, served as a reference stream. Both catchments are similar with respect to aspect, elevation, discharge, water chemistry, and water temperature (Table 1).

TABLE 1. Physical characteristics of reference and litter exclusion streams at Coweeta Hydrologic Laboratory, North Carolina.

Variable	Reference	Litter exclusion
Catchment		
Area (ha)	5.2	7.5
Elevation (m asl)	829	810
Aspect	South	South
Channel length (m)	135	170
Wetted width (m)	0.7–1.2	1.2–1.6
Bankful channel area (m^2)	327	373
Gradient (cm/m)	27	20
Canopy cover (%)	88.9	91.7
Substrate (% composition)		
Mixed	73	87
Bedrock outcrop	27	13
Discharge (1985–2000, L/s)		
Average	0.73	1.35
Maximum	32.13	71.45
Water temperature (1992–2000, °C)		
Annual average	12.0	12.0
Annual degree days	4363	4363
Maximum	20.7	20.1
Minimum	0.7	0.6

Production and organic matter standing crop

Abundance and biomass of *P. gentilis* for mixed-substrate habitats (substratum consisting of mixed silt, sand, pebble, and cobble) was estimated in each stream using a 400-cm^2 corer. Four random samples were collected monthly from September 1992 to August 2000 from each stream. Organisms and organic matter were separated into a >1-mm fraction and <1-mm fraction using nested sieves. *Pycnopsyche gentilis* from both fractions were sorted from organic matter under 15× magnification and preserved in 7% formalin. Animals in the <1-mm fraction were subsampled if necessary (Waters 1969). All individuals were identified, counted, and measured to the nearest mm using a dissecting microscope and graduated stage. Biomass was calculated using length–mass regressions (Benke et al. 1999). Secondary production estimates for *P. gentilis* were calculated using the size-frequency method (Hamilton 1969) with a cohort production interval correction of 275 (Benke 1979, Huryn and Wallace 1988). Mean annual length and annual maximum length of *P. gentilis* were compared between streams over the 8-y study to determine whether litter exclusion influenced *P. gentilis* growth and survivorship to emergence. Coarse particulate organic matter in each sample was separated into categories (i.e., leaf, wood, seeds, roots), dried at 60°C, weighed, ashed at 500°C, and reweighed to obtain ash-free dry mass (AFDM).

Laboratory experiment

Survivorship and growth of *P. gentilis* reared with high, intermediate, and low amounts (see below) of leaf litter were measured in the laboratory from December 1999 to February 2000 for 1st and 3rd instars. Organisms were collected from lower reaches of C53. First instars grew to the 3rd-instar stage between December and January. Newly collected 3rd-instar individuals grew to the 4th-instar stage from January to February. For each size class, 50 individuals (25 in original field cases and 25 removed from field cases) were incubated individually in tea infusers (Toby TeaBoy Ltd., Aldridge, England) for 4 to 6 wk. Toby Teaboys, 56 × 43-mm plastic barrels lined with 244-μm mesh netting, have been used to measure insect growth rates in other studies (Benke and Jacobi 1986, Rosemond et al. 2001). The bottoms of tea infusers for each treatment were filled with substrate (silt, sand, and pebbles) from the reference or litter exclusion stream. Naturally conditioned leaves of each breakdown-rate category (see following) from the reference stream were added to substrate in the tea infusers according to mean proportions of each breakdown category in previously measured leaf litter inputs to C53 and C55 (fast [e.g., dogwood] = 3%, medium [e.g., red maple] = 30%, slow [e.g., white oak] = 47%, very slow [e.g., rhododendron] = 20%; Cuffney et al. 1990). Our high leaf treatment (268 g AFDM/m^2) simulated mean leaf standing crop naturally found in the reference stream from December to February. The low leaf treatment (0.4 g AFDM/m^2) represented the actual leaf standing crop in the litter exclusion stream at the time our experiment was run. An intermediate leaf treatment of 13 g AFDM/m^2 was also included, which simulated the amount of leaf litter present during the winter months of year 1 in the litter exclusion stream, when the decline in *P. gentilis* production was first observed.

Teaboys were randomly placed in 32-L tubs of aerated stream water, which was replaced weekly. Water temperature was maintained at 12.5°C. Timers controlled the light:dark cycle at 12 h light:12 h dark. Additional conditioned leaves collected from the reference stream were added to each teaboy as needed to maintain constant leaf standing crops in each treatment. At the beginning of the experiment, individuals removed from their field cases were observed on a daily basis, to record case-building activities. Case-building behavior of additional individuals was videotaped using a video camera equipped with a macro lens. Survivorship was recorded weekly. Initial mass was estimated by measuring head capsule widths (HCW) at the start of the experiment using an ocular micrometer. Initial wet masses were not measured because of the reluctance of larvae to voluntarily return to their cases (i.e., head capsule widths could be measured while larvae were in their cases). HCWs were converted to initial AFDM using a HCW–AFDM regression equation developed from individuals collected in the reference stream: AFDM (g) = 0.0008128x HCW (mm)− 0.000203 ($r^2 = 0.67$, $p < 0.001$, $n = 35$). AFDM was measured for each individual at the end of the experiment. Individual instantaneous growth rates (IGR) were calculated using the equation:

$$\mathrm{IGR} = (\ln W_t - \ln W_o)/t$$

where W_t is the individual AFDM (mg) at time t (d), and W_o is the initial estimate of individual AFDM (mg).

Differences in survivorship between organic matter levels and case treatments were determined using 2-way repeated measures ANOVA of arcsine-transformed % survival values (Sigma Stat, version 2.0, SPSS, Chicago). Differences in individual growth rates between organic matter level and case treatment were examined for each size class using 2-way ANCOVA (JMP, version 4.0.4, SAS, Cary, North Carolina) with initial HCW as the covariate because smaller larvae tend to grow faster than larger larvae (Perry et al. 1987). Differences in mean survivorship and

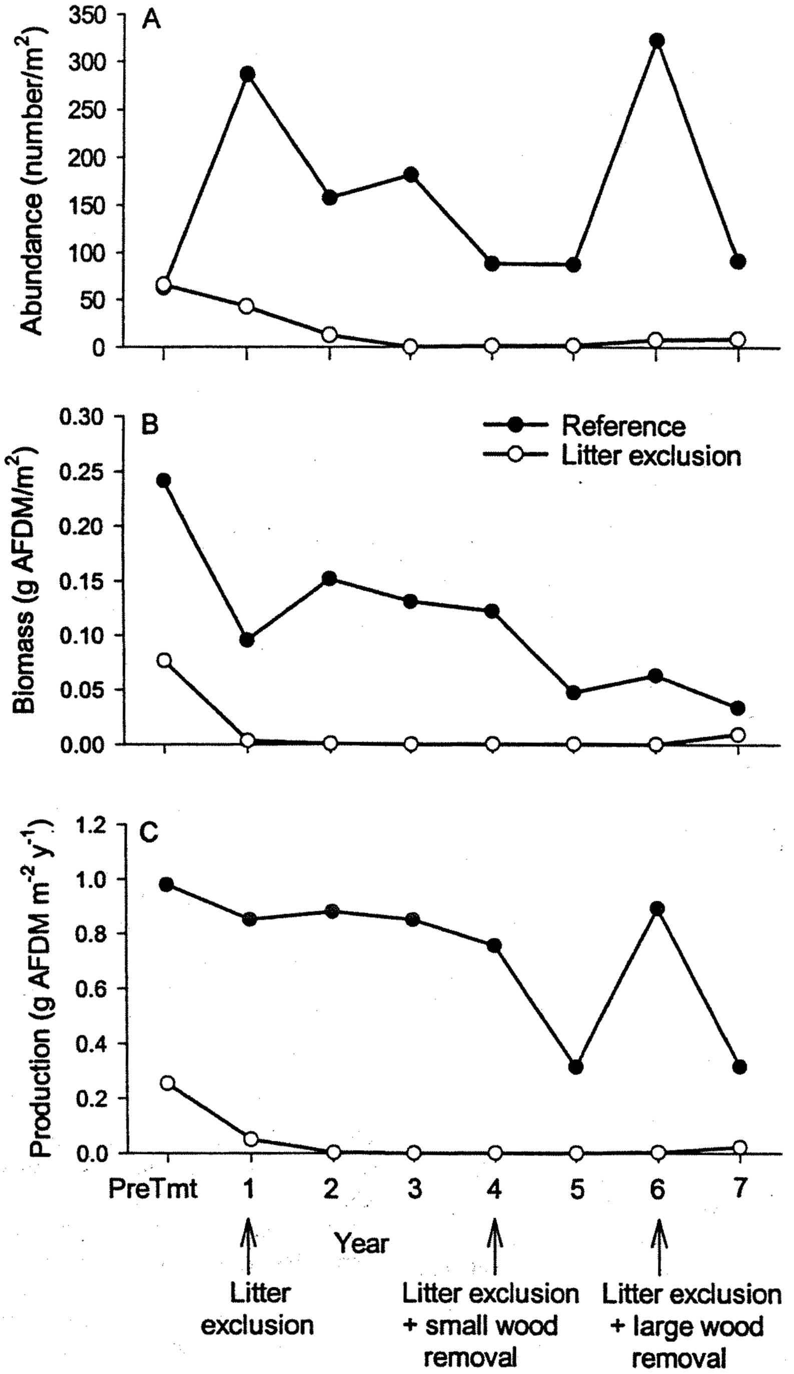

FIG. 1. Mean annual abundance (A), biomass (B), and production (C) of *Pycnopsyche gentilis* in mixed substrates of reference and litter exclusion streams from 1992 to 2000. Arrows indicate start of treatment periods. Pretmt = pretreatment year. Years 1, 2, and 3 = first 3 y of litter exclusion in Catchment (C) 55. Years 4 and 5 = small wood removal with ongoing litter exclusion in C55. Years 6 and 7 = large wood removal with ongoing litter exclusion in C55.

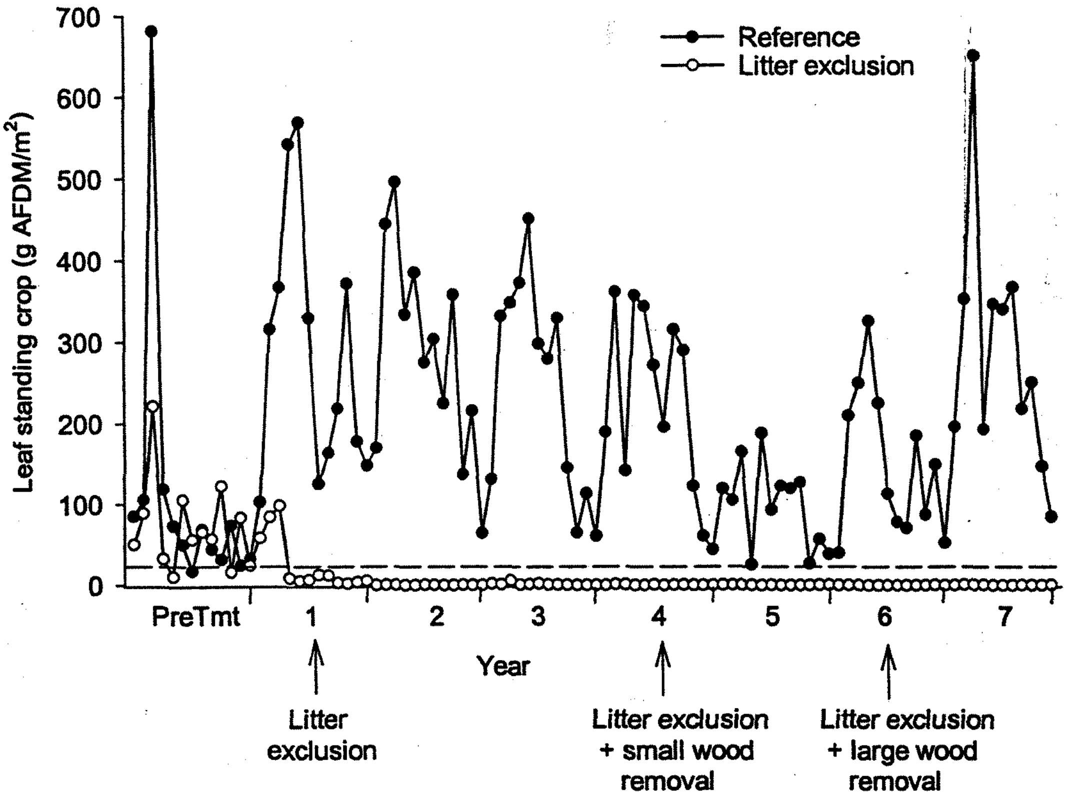

FIG. 2. Mean monthly leaf standing crop in mixed substrate of reference and litter exclusion streams from 1992 to 2000. Dashed line indicates 25 g AFDM/m². Years as explained in Fig. 1.

growth rates between treatments were compared using Tukey's multiple comparison tests.

Results

Production and leaf standing crop

At the start of the study, *P. gentilis* abundance in mixed substrate was similar between streams (Fig. 1A). A greater proportion of large instars in the reference stream compared to the litter exclusion stream accounted for higher biomass and production in the reference stream during the pretreatment year (Fig. 1B, C). Production of *P. gentilis* in the litter exclusion stream declined to <1% of the pretreatment level by the end of the 2nd year of litter exclusion, and was reduced to 0 within 3 y (Fig. 1C). In the reference stream, *P. gentilis* production ranged from 0.32 to 0.98 g m^{-2} y^{-1} over the 8-y period. Leaf standing crops in the mixed substrate of the reference stream increased each autumn and declined during spring and summer (Fig. 2). Five months after the start of litter exclusion, leaf standing crop in the treatment stream declined to <25 g AFDM/m² and remained at least that low for the next 7 y.

Regression analyses suggested that mean annual leaf standing crop was an important determinant of *P. gentilis* production. C55 data from 1985 and 1986 (Lugthart and Wallace 1992) and 1989 and 1990 (Whiles and Wallace 1995) were included with C55 data collected in our study and strong positive relationships were found between leaf standing crop and mean annual abundance, biomass, and production of *P. gentilis*. The data included leaf standing crops that ranged over 2 orders of magnitude (Fig. 3). Maximum individual length of *P. gentilis* was dramatically reduced at mean annual leaf standing crops below 25 to 50 g AFDM/m² (Fig. 4). Maximum individual length of individuals collected in the reference stream and in the litter exclusion stream before treatment ranged from 16 to 18 mm (Fig. 5A). After litter exclusion,

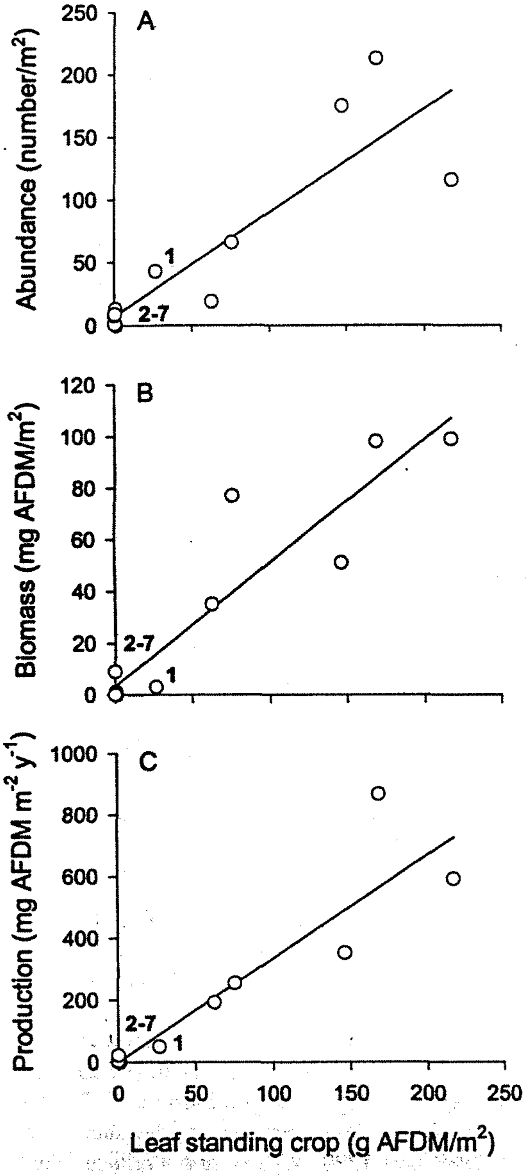

FIG. 3. Long-term relationships between mean annual abundance (A), ash-free dry mass (AFDM) (B), and production (C), and mean annual leaf standing crop in Catchment 55 for 1985, 1986, 1989, 1990, and 1992 to 1999. $n = 12$ for each regression. Data points labeled 1–7 designate litter exclusion years. Abundance = 6.864 + 0.831x (leaf standing crop), $r^2 = 0.77$, $p < 0.001$; biomass = 3.200 + 0.478x (leaf standing crop), $r^2 = 0.86$, $p < 0.001$; production = −0.0747 + 3.345x (leaf standing crop), $r^2 = 0.85$, $p < 0.001$.

maximum individual length in the treatment stream declined to 1–3 mm. The difference between streams for mean annual individual length was similar in both streams over the 8-y study (Fig. 5B).

Case building and survivorship

Pycnopsyche gentilis larvae reared in high leaf substrate followed the typical progression of case-building activity reported by Mackay (1972) and Mackay and Kalff (1973). First instars constructed cases of fine sand grains before converting to 3-sided leaf disk cases 1 to 2 wk later. Videotapes showed that young *P. gentilis* used mostly flakes of pyrite, which they carefully selected, fit in place, and attached with silk. The selection, fitting, and attachment process required ~5 min per particle. Larvae completely rebuilt cases within 4 to 8 h. All 2nd to 4th instars maintained their leaf cases until the 5th instar, when they gradually switched to large sand grain cases. In contrast, all of the larvae reared in substrate lacking leaf litter initially built fine sand grain cases and did not switch to the leaf disk cases. These larvae continued adding larger sand grains to the tops of cylindrical cases, and they used bits of wood and seeds if these materials were present in the substrate.

Survivorship of larvae kept in high leaf standing crops ranged from 84 to 95% during the experiment (Fig. 6). Only 28 to 32% of 1st instars survived through wk 6 in the intermediate level of leaf substrate (Fig. 6A). Ninety to 95% of 3rd instars were still alive through the end of wk 4 in the intermediate leaf substrate (Fig. 6B). Results from repeated measures ANOVA indicated that survival of 1st instars was greatest for larvae growing at high followed by intermediate and low leaf standing crops regardless of case type (ANOVA, $p < 0.001$, Tukey test, $p < 0.05$) (Table 2, Fig. 6A). For 3rd instars, the effect of leaf standing crop depended on case type (Table 2, Fig. 6B). More larvae with rebuilt cases survived at high leaf standing crops relative to larvae with field cases (Tukey test, $p = 0.02$) (Fig. 6B). At low leaf standing crops, survivorship over the 4-wk experiment was significantly greater for larvae with field cases than those with rebuilt cases (Tukey test, $p = 0.04$) (Fig. 6B).

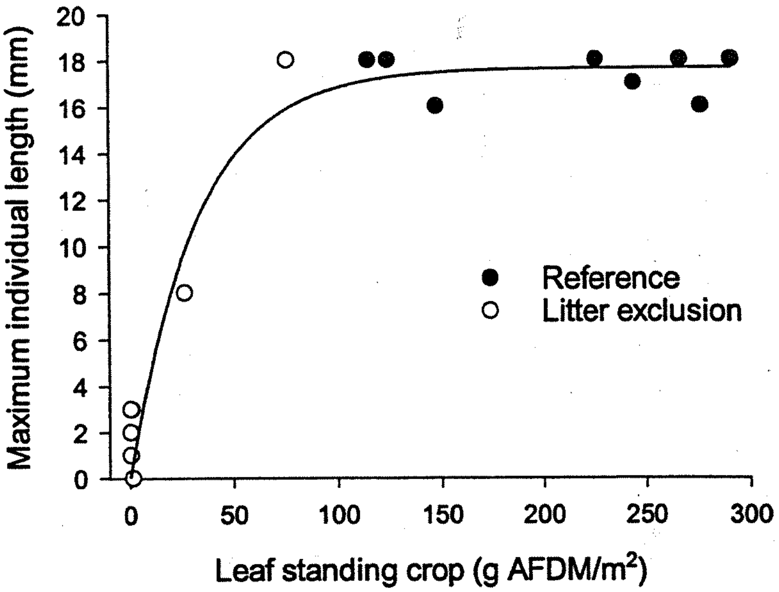

FIG. 4. Relationship between leaf standing crop and maximum individual body length ($y = 17.642\ (1 - 0.97^x)$; $r^2 = 0.96$, $p < 0.0001$) for *Pycnopsyche gentilis* collected in mixed substrates of reference and litter exclusion streams from 1992 to 2000. $n = 16$.

Larval growth

First instars grew to 3rd instars, and 3rd instars grew to 4th instars during the growth experiments. IGRs of 1st instars with field cases in the high leaf treatment were 1.5× greater than in the intermediate leaf treatment (Fig. 7, ANCOVA followed by Tukey test, $p < 0.05$). For 1st instars forced to rebuild cases, there was a 2.4× difference in growth rates between high and intermediate treatments (Fig. 7, Tukey test, $p < 0.05$). Differences in IGR between high and intermediate leaf standing crops for 3rd instar *P. gentilis* were 1.5× for organisms with field cases (Tukey test, $p > 0.05$) and 1.6× for those with rebuilt cases (Fig. 7, Tukey test, $p > 0.05$). Growth rates were significantly lower for 1st and 3rd instars in low leaf standing crops than in intermediate or high leaf standing crops (Fig. 7, Tukey test, $p < 0.05$). The laboratory data corroborated results observed from field data. As with the maximum individual length data from the field (Fig. 4), a decline in laboratory growth rates of *P. gentilis* occurred when leaf standing crop declined to <25 to 50 g AFDM/m² (Fig. 7).

Discussion

Response to reduced leaf inputs

Production of other shredders (e.g., Peltoperlidae, *Leuctra* spp., *Lepidostoma* spp., *Tipula* spp.) in the litter exclusion stream declined following the start of the experiment, but not as quickly as observed for *P. gentilis* (Wallace et al. 1999). *Pycnopsyche gentilis* production (0.255 g AFDM $m^{-2}\ y^{-1}$) composed 14% of total shredder production in the litter exclusion stream before the start of the manipulation. Production of *P. gentilis* averaged 0.011 g AFDM $m^{-2}\ y^{-1}$ during the 7-y exclusion period, representing 2% of total shredder production. *Pycnopsyche gentilis* production in the reference stream made up 21% of total shredder production (average production over 8 y = 0.731 g AFDM $m^{-2}\ y^{-1}$) and was similar to that reported by Stout et al. (1993) and Stone and Wallace (1998) for other 1st-order reference streams at Coweeta Hydrologic Laboratory.

Production of *P. gentilis* in the reference stream varied annually. Based on the relationship between *P. gentilis* production and mean annual leaf standing crop, it appears that much of the variation in production was a result of

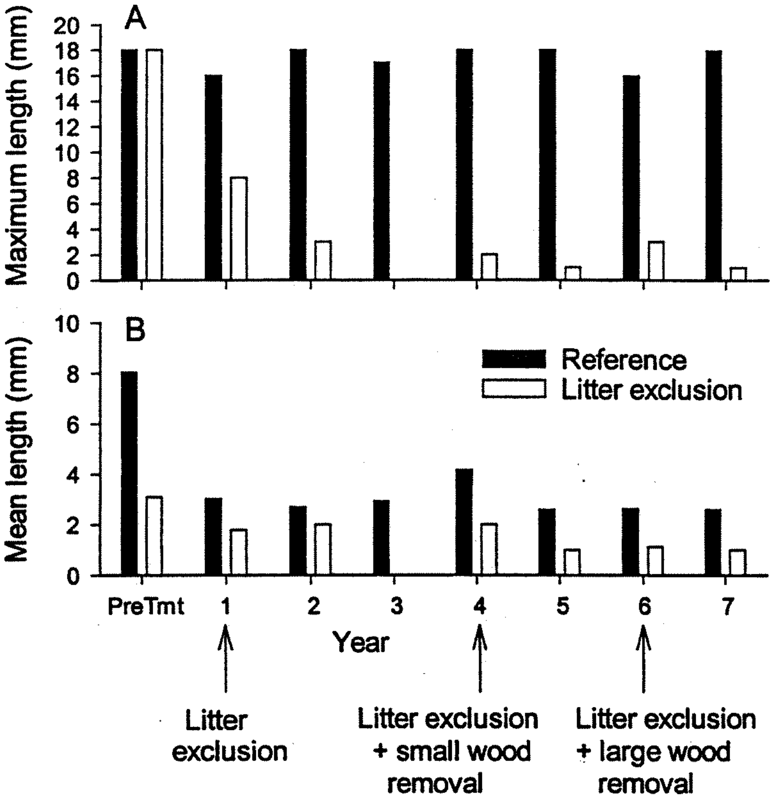

FIG. 5. Annual maximum body length (A) and mean annual body length (B) for *Pycnopsyche gentilis* in reference and litter exclusion streams from 1992 to 2000. Years as explained in Fig. 1.

annual differences in leaf standing crop. Annual leaf standing crop varies with the timing and frequency of storms; thus, it is not constant from one year to the next (Wallace et al. 1997). Mean monthly leaf standing crop in the reference stream was >25 g AFDM/m^2 for 94 of 96 mo in this study. *Pycnopsyche gentilis* larvae grow continuously from October to June, the period when leaf standing crops are >25 g AFDM/m^2. Leaf standing crop in the reference stream fell below 25 g AFDM/m^2 most often during the months of July, August, and September, after leaves with fast and medium breakdown rates had disappeared from the stream. *Pycnopsyche gentilis* larvae pupate in July and August, and, therefore, are not affected by the late-summer decline in leaf standing crop.

Average length of *P. gentilis* in both streams reflected an abundance of small instars relative to large instars, except for the pretreatment year in each stream. The 94% reduction in maximum individual lengths of exclusion stream larvae suggests that larvae in the detritus-limited stream were not completing larval development. Small instars appeared in the litter exclusion stream each year because of recolonization by aerial adults, but did not survive to emergence.

When leaf standing crops in the litter exclusion stream declined to <25 g AFDM/m^2, *P. gentilis* did not switch to alternate food resources such as wood, as did other shredder taxa in the stream (Hall et al. 2000, Eggert 2003). Hutchens et al. (1997) reported that leaf material made up 86 to 100% of the diet of *P. gentilis* in another Coweeta stream. Hutchens et al. (1997) found no evidence of *P. gentilis* switching to alternate food resources. Mackay (1972) found that *P. gentilis* in West Creek, Quebec, used only leaf material for case materials, food, and habitat. When offered twigs as food in the laboratory, *P. gentilis* preferred leaf material (Mackay and Kalff 1973). In contrast to the specialized behavior of *P. gentilis*, *P. luculenta* used twigs readily as a food and case-building resource (Mackay and Kalff 1973).

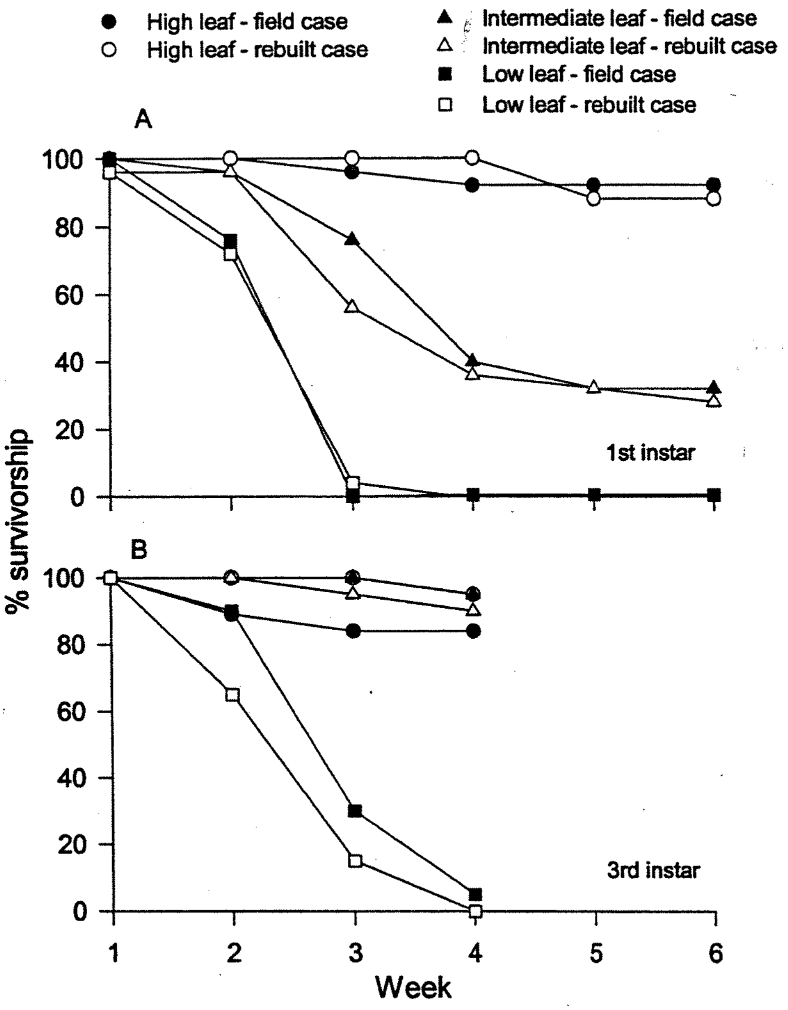

FIG. 6. Percent survival of *Pycnopsyche gentilis* 1st instars (A) and 3rd instars (B) reared with high (268 g AFDM/m^2), intermediate (13 g AFDM/m^2), and low (0.4 g AFDM/m^2) levels of leaves. "Field case" larvae had field-constructed cases. "Rebuilt case" larvae were removed from field cases before start of experiment and forced to rebuild cases.

Response to low leaf standing crop in the laboratory

Mortality as a result of predation was not a factor in our laboratory experiments. Larvae successfully rebuilt cases of inorganic materials in the absence of leaves and survived for up to 3 wk, which indicates that respiratory functions in the atypical cases were not impaired to the point of causing death by respiratory stress. Otto and Svensson (1980) showed that inorganic cases of the caddisfly *Potamophylax cingulatus* were energetically more expensive to build than leaf-disk cases because leaf-disk cases have fewer pieces to be assembled. A similar energetic cost may have contributed to the higher mortality rates and slower growth rates observed in our study for larvae that were forced to rebuild cases of mineral material instead of the usual leaf material.

First instars suffered higher mortality rates at low resource levels than did 3rd instars. Otto (1974) reported higher fat content (12–14%) in 3rd through 5th instars of *P. cingulatus* than in 1st instars (9%). In addition, fat and energy content of *P. cingulatus* larvae was related to the presence of preferred food resources in the stream (Otto 1974). In our study, higher fat con-

TABLE 2. Results of 2-way repeated measures ANOVAs for survivorship of 1st and 3rd instar *Pycnopsyche gentilis* reared at 3 levels of leaf standing crop (high, intermediate, and low) and 2 case types (field-constructed or laboratory-constructed) over the 4 to 6 wk laboratory study in winter 1999 to 2000. * = $p < 0.05$, *** = $p < 0.001$.

Source of variation	df	MS	*F*
1st instar			
Time	5	2945.6	
Leaf standing crop	2	9632.2	19.29***
Leaf standing crop × Time	10	499.4	
Case type	1	3.3	0.11
Case type × Time	5	29.7	
Leaf standing crop × Case type	2	49.9	2.01
Residual	10	24.8	
3rd instar			
Time	3	1740.6	
Leaf standing crop	2	3397.4	15.59*
Leaf standing crop × Time	6	607.9	
Case type	1	1.5	0.50
Case type × Time	3	3.0	
Leaf standing crop × Case type	2	306.1	6.22*
Residual	6	49.2	

tent accumulated by older instars may have served as an energy reserve for larvae reared with limited resources for food and case-building activities.

IGRs of 3rd instars were lower than those of 1st instars, regardless of resource level. Mackay (1972) reported a similar pattern of growth for *P. gentilis* in West Creek. Our 3rd-instar AFDM growth rates (0.0100/d) were lower than dry mass growth rates measured by Hutchens et al. (1997) for 3rd-instar *P. gentilis* reared on birch leaves (0.0174–0.0313/d), but were similar to those reared on a diet of white oak (0.0084–0.0233/d). Growth rates of 1st instars forced to rebuild a case were also lower than those left in their original case. Dudgeon (1987) also found that when *Polycentropus flavomaculatus* larvae were forced to rebuild nets, they lost more mass than undisturbed larvae. The difference in IGR for field case vs rebuilt case organisms was larger for 1st instars than for 3rd instars, again indicating that older larvae had more internal energy reserves available to them when resources were reduced.

Our experiment did not separate the use of leaf litter as a food resource and case material, but our results showed that growth rates of 1st- and 3rd-instars of *P. gentilis* that were not required to rebuild atypical cases were significantly lower at low leaf standing crops than at the high and intermediate levels. This reduction in growth was most apparent for young instars. In addition, the 95 to 100% mortality for individuals of both age classes that had field-built cases suggests that food was insufficient at the lowest leaf standing crop treatment (litter exclusion stream) for *P. gentilis* to survive.

Linkages between P. gentilis *and leaf inputs*

Results of our study showed that production, survivorship, and growth of *P. gentilis* were linked to leaf litter standing crop. *Pycnopsyche gentilis* tracks its primary food resource closely and does not switch to alternate energy sources in these streams. As a result, this species could not complete its life cycle in the stream lacking detrital inputs, thus lowering the overall diversity of the ecosystem. Researchers have hypothesized that limnephilid caddisfly diversity is related to resource availability (Flint 1960, Ross 1963, Wiggins and Mackay 1978, Mackay and Wiggins 1979). *Pycnopsyche* is limited to temperate deciduous forests of eastern North America (Flint 1960, Ross 1963). In southern Appalachians forested streams, *P. gentilis* is tightly linked to terrestrial leaf inputs and may be more specialized in its resource use than other shredders (Cummins 1964, Mackay 1972, Mackay and Kalff 1973).

Our field data suggest that at least 25 to 50 g AFDM/m^2 of leaf standing crop are required during larval development (October to June) for *P. gentilis* to survive and maintain its functional role in a stream. The energetic needs of other shredder taxa in these streams remain unknown, but additional shredder production will require even higher levels of organic matter standing crops. Because of differences in litter breakdown rates, the presence of fast, medium, and slow decaying leaf species all may be necessary to sustain production of obligate leaf shredders like *P. gentilis* throughout the year (Petersen and Cummins 1974, Webster and Benfield 1986, Cummins et al. 1989, Stout et al.

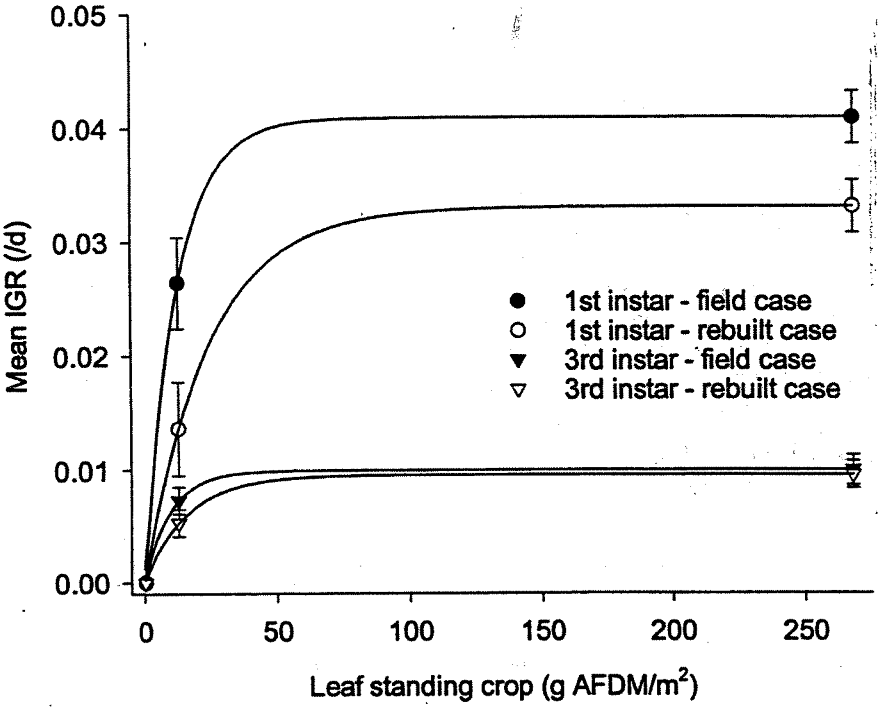

FIG. 7. Relationship between leaf standing crop and mean (±1 SE) instantaneous growth rates (IGR) of 1st- and 3rd-instar *Pycnopsyche gentilis* reared in substrate with high (268 g AFDM/m^2), intermediate (13 g AFDM/m^2), and low (0.4 g AFDM/m^2) levels of leaves. "Field case" larvae had field-constructed cases (1st instar $r^2 = 0.99, p = 0.03$; 3rd instar $r^2 = 0.99, p = 0.03$). "Rebuilt case" larvae were removed from field cases before start of experiment and forced to rebuild cases (1st instar $r^2 = 0.99, p = 0.01$; 3rd instar $r^2 = 0.99, p = 0.02$).

1993, Grubbs and Cummins 1996). We suggest that small stream restoration efforts consider the replacement of riparian vegetation in a manner that maintains both leaf litter diversity and total inputs to accommodate stream detritivores that depend on leaf litter as a food resource.

Acknowledgements

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