

The response of Chironomidae (Diptera) to a long-term exclusion of terrestrial organic matter

Sally A. Entrekin · J. Bruce Wallace ·
Susan L. Eggert

Received: 28 February 2006 / Revised: 14 August 2006 / Accepted: 17 August 2006 / Published online: 24 October 2006
© Springer Science+Business Media B.V. 2006

Abstract We examined the effects of a seven-year detrital exclusion on chironomid assemblages in an Appalachian headwater stream. We hypothesized that litter exclusion would lead to a reduction in all chironomids at both the subfamily and generic levels because organic matter serves as both food and habitat in these headwater streams. Tanytarsini total abundance and biomass significantly declined after litter exclusion. Before litter exclusion, Tanytarsini average abundance was 4271 ± 1135 S.E. m^{-2} and 625 ± 98 after litter exclusion. Biomass was 3.57 ± 0.96 mg AFDM m^{-2} before litter exclusion and 1.03 ± 0.9 after exclusion. In contrast, Orthocladiinae abundance and biomass did not change because a psammophilic chironomid, *Lopescladius* sp., and other Orthocladiinae genera did not decline significantly. Overall chironomid taxa richness and

diversity did not change as a result of litter exclusion. However, Canonical Correspondence Analysis (CCA) of genus-level biomass did show a clear separation between the litter exclusion stream and a reference stream. Separation of taxa between the two streams was due to differences in fine ($r^2 = 0.39$) and coarse ($r^2 = 0.36$) organic matter standing stocks and the proportion of small inorganic substrates ($r^2 = 0.39$) present within a sample. As organic matter declined in the litter exclusion stream, overall chironomid biomass declined and the chironomid community assemblage changed. Tanytarsini were replaced by Orthocladiinae in the litter exclusion stream because they were better able to live and feed on biofilm associated with inorganic substrates.

Keywords Benthos · Chironomidae · Detritus · Resource limitation · Bottom-up regulation

Handling editor: K. Martens

S. A. Entrekin (✉)
Department of Biological Sciences, University of
Notre Dame, Notre Dame, IN 46556, USA
e-mail: sentreki@nd

J. B. Wallace · S. L. Eggert
Department of Entomology and Institute of Ecology,
University of Georgia, Athens, GA 30602, USA

S. L. Eggert
USDA Forest Service, North Central Research
Station, Grand Rapids, MN 55744, USA

Introduction

Chironomidae are often the most productive primary consumers in an ecosystem; they represent an important link between basal food resources (e.g., algae, fungi, and leaf litter) and predators in freshwater habitats (Stites & Benke, 1989; Leeper & Taylor, 1998; Ramirez & Pringle, 1998). The success of chironomids is a result of their diverse physiological adaptations that allow

them to live in hot, cold, and low-oxygen environments. Chironomidae often have high densities, fast growth, and small size resulting in high colonization rates and production (Berg & Helenthal, 1992; Tokeshi, 1995; Huryn & Wallace, 2000).

Studies have shown that Chironomidae in forested streams depend on terrestrially derived detritus in the form of coarse (CPOM) and fine particulate organic matter (FPOM) as habitat and food (Huryn, 1990; Richardson, 1991; Grubbs & Cummins, 1994; Berg, 1995), in addition to dissolved organic matter taken up by microbes on organic and inorganic substrates (Hall & Meyer, 1998; Benke, 1998). But other studies have also shown Chironomidae production to be limited by food and habitat. For example, Johnson et al. (2003) found that growth rates of collector-gathering chironomids significantly declined in response to litter exclusion in a temperate headwater stream. Chironomids were also limited by nutrients in other aquatic ecosystems. For example, Chaloner et al. (2004) found that chironomid biomass increased, indirectly, in response to nutrients delivered from the ocean to nutrient-limited freshwater streams by salmon spawning upstream. However, these ecosystem studies placed chironomids into two groups based on their general feeding modes, the predaceous Tanypodinae and non-Tanypodinae collector-gatherers.

Other studies have evaluated mechanisms controlling chironomid assemblages at the generic and species levels (Wiley, 1981; Ladle et al., 1984; Ruse & Davidson, 2000; Silver et al., 2004) and they showed that important ecological information may be lost by using broad groupings. For example, Wiley (1981) experimentally determined that both habitat stability and competition among psammanophilic chironomids determined the benthic community structure. Furthermore, Hershey (1985) described the Chironomidae community in an Arctic lake and identified stratification of specific genera based on distribution of macrophytes and soft sediments. Our goal was to evaluate possible changes in the chironomid community assemblage in response to an ecosystem-level exclusion of leaf litter and wood that

decoupled the riparian and stream ecosystems without altering the riparian habitat.

We hypothesized that the exclusion of allochthonous organic matter could lead to a change in the Chironomidae assemblage. In a previous litter exclusion study, Wallace et al. (1997, 1999) found that long-term litter exclusion (i.e., 4 years) from a headwater stream resulted in a significant decline in biomass and abundance of most non-Tanypodinae chironomids (76% decline). We expanded on this study by looking at chironomids at a finer taxonomic level and through three additional years of litter exclusion. We examined the chironomid change in assemblage to a long-term litter exclusion and subsequent removal and exclusion of small and large wood in a headwater stream. Our objectives were to describe changes in taxa assemblage at the subfamily and generic levels before and after litter exclusion and to identify temporal changes in chironomid assemblage and biomass as a result of litter exclusion.

Methods

Study sites

A seven-year litter exclusion experiment (LE) was conducted in a first-order forested, headwater stream (C55) at Coweeta Hydrologic Laboratory (Macon Co., N.C.) in the southern Appalachians. For more information about the study sites see Wallace et al. (1999). A similar stream nearby was used as a reference (C53). The riparian canopy was similar in both streams and was composed primarily of tulip poplar (*Liriodendron tulipifera* L.), white oak (*Quercus rubra* L.), and dogwood (*Cornus florida* L.). Rhododendron (*Rhododendron maximum* L.) was the primary understory species and provided dense shade all year, which reduced in-stream primary production to very low levels. Both streams were similar with respect to their climate and physical parameters (Table 1); however, the litter exclusion stream had a higher percentage of pebble and sand. In August 1993, a 2.5-cm gill mesh net was built over the first 170 m of stream to exclude direct leaf fall and a 20-cm high fence of plastic mesh was erected on the

Table 1 Study site description of the litter exclusion (C55) and reference stream (C53) at Coweeta Hydrologic Laboratory, NC

Site description	Litter excluded	Reference
Catchment area (ha)	7.5	5.2
Elevation (m asl)	810.0	829.0
Channel length (m)	170.0	135.0
Canopy cover	91.7	88.9
<i>Mixed substrate (%)</i>		
Boulder	3.0	7.0
Cobble	29.0	19.0
Pebble and Sand	49.0	14.0
Silt	6.0	33.0
<i>Water temperature</i> (1992–2000°C)		
Annual average	12.0	12.0
Discharge (1992–2000 l s ⁻¹)	1.5	0.7

stream banks to exclude lateral litter blow-in. After three years of litter exclusion, small and large wood was removed and excluded (LE + WR, see Wallace et al., 2001). As a result of the litter exclusions, organic matter standing stock was reduced in the stream by ~95% compared to pre-litter exclusion values (Wallace et al., 1997, 1999; Eggert & Wallace, 2003b).

Chironomidae sampling

Samples were collected monthly from 1992 through October 2001. For each sample date, a 400-cm² stovepipe corer was used to collect four benthic samples, composed primarily of mixed substrate (sand, silt, cobble, pebble, gravel). All material was collected, placed on ice, and taken back to the laboratory for processing. At the time of collection, a visual assessment of the benthic substrate was also recorded as percent sand, gravel, pebble, silt and cobble. In the laboratory, organic matter was separated into two size fractions: >1 mm and <1 mm >250 µm. Individual size fractions were placed in plastic bags, dyed with Phloxin B, and preserved with 6–8% formalin. The formalin fixed samples were picked for invertebrates under a 15× dissecting microscope. All invertebrates were picked from the >1-mm samples. If more than 100 individual invertebrates were present in the 250-µm samples, they were subsampled using a sample splitter (Waters, 1969; Lugthart & Wallace, 1992).

Chironomid larvae were separated from the other invertebrate taxa, identified to genus, body lengths measured to the nearest 1 mm, and counted. Length–mass regressions were then applied to estimate biomass (Benke et al., 1999). Chironomids were identified from January, April, July, and October samples, each month representing the winter, spring, summer, or autumn season, respectively. We examined chironomids from 1992, 1993, 1995, 1998, and 2000. Chironomids were sorted under a dissecting microscope into like-groups and all individuals were mounted, unless the totals were >20, then 50% were mounted and identified. If different taxa were found mounted within like-groups, taxa were further separated and mounted. All chironomids were mounted using CMC-10 and identified to genus using Wiederholm (1983), Coffman & Ferrington (1996), and Epler (2001).

Data analysis

All abundance and biomass data were log₁₀ transformed to meet the assumptions of ANOVA. We compared total differences in Chironomidae abundance and biomass over time by subtracting the mean of the reference (C53) from the mean of the Litter Exclusion (C55) stream for each sampling date. Zero indicated no difference in abundance or biomass of chironomids between the two streams. Positive numbers indicated higher chironomid abundance or biomass in the LE stream. Negative numbers indicated higher chironomid abundance or biomass in the reference stream. Least-squares regression was used to examine the change in treatment versus control.

We used a Before-After-Control-Intervention-Paired (BACIP) design (Osenberg et al., 1994; Smith, 2002) to detect litter exclusion effects, and to compare changes in chironomid abundance and biomass between the reference and litter exclusion streams. A two-way ANOVA with litter exclusion effects (i.e., pre-litter exclusion (P), litter excluded (LE), and litter and wood excluded (LE + WR)) plus control (C53) versus Intervention (C55) represented our class level variables. Because there were an uneven number of observations for each litter exclusion period (i.e., P: $n = 4$, LE: $n = 7$, and LE + WR: $n = 10$),

a General Linear Model was used (SAS v. 8.02, SAS Institute Inc., Cary, North Carolina). Only if a significant interaction between the Before-After and Control-Intervention occurred was a litter exclusion effect inferred.

Shannon–Weiner Index (SWI) values, represented as $H' = -\sum p_i \log p_i$ where p_i represents proportion of total number of individuals in the i th species, values were compared using BACIP design and differences were detected using Tukey's multiple comparison test. Generic differences in abundance and biomass were examined using the BACIP factorial ANOVA. Least square means percent differences were used to detect paired differences in litter exclusion periods and stream, but a Tukey–Kramer correction was used to correct for multiple comparisons.

Genus-level biomass dynamics for each sampling period were explored using Canonical Correspondence Analysis (CCA, PC-ORD Version 4, MJM Software Design, Glenden Beach, OR, USA: <http://home.centurytel.net/~mjm/pcordwin.htm>). CCA was used to relate measured environmental variables to the seasonal distribution of chironomid biomass at the genus level (PC-ORD, McCune, 1997). We used ordination to graphically explore the changes in chironomid community biomass in response to LE. Log₁₀ transformed generic mean biomass was used to create a matrix for all taxa represented in at least 5% of the total samples. A secondary matrix of environmental variables (e.g., CPOM, FBOM, and % sand, gravel, and pebble, maximum stream discharge, and mean water temperature) were correlated with each axis and graphed as vectors. The closer a vector was to an axis, the greater the correlation to that axis. A longer vector represented a stronger correlation between that environmental variable and chironomid biomass within a stream and season.

Results

Chironomidae abundance, biomass, and diversity

Total chironomid abundance (Fig. 1a) and biomass (Fig. 1b) became progressively lower in the

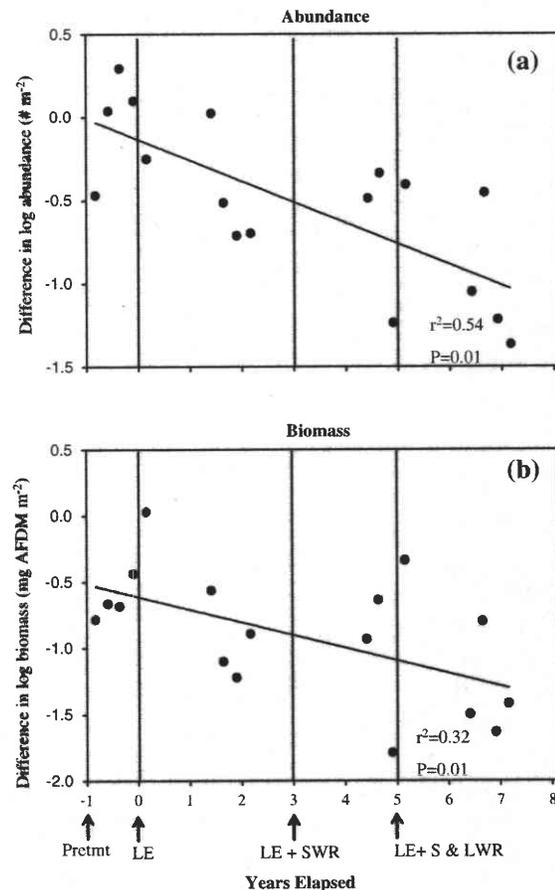


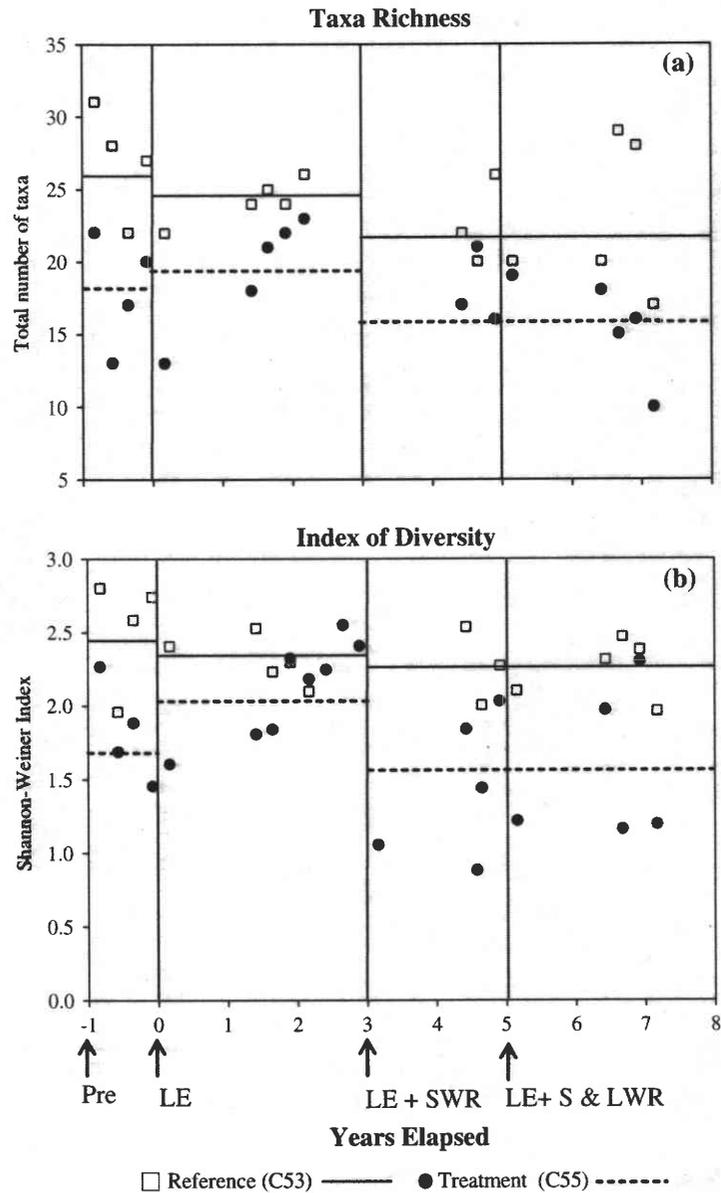
Fig. 1 Linear regression analyses of differences in the mean Chironomidae abundance (a) and biomass (b) in treatment versus reference streams (i.e., treatment minus reference)

LE compared to the reference streams over the study period. Taxon richness and Shannon–Weiner Index values did not decline in response to LE or LE + WR (Fig. 2a, b). A total of 35 genera were identified in the litter exclusion stream before and 43 genera were identified after LE + WR. In the reference stream, 43 genera were identified. Chironominae, Orthocladiinae, Tanytopodinae, Diamesinae, and Podinomyiinae were identified, but because Diamesinae and Podinomyiinae were so rare, their responses are not discussed.

Chironomidae response

Chironominae were neither abundant nor dominant in either stream (Fig. 3, Table 2). In the litter exclusion stream, Chironominae (predominantly *Polypedilum* sp., *Dicortendipes* sp., and *Steno-*

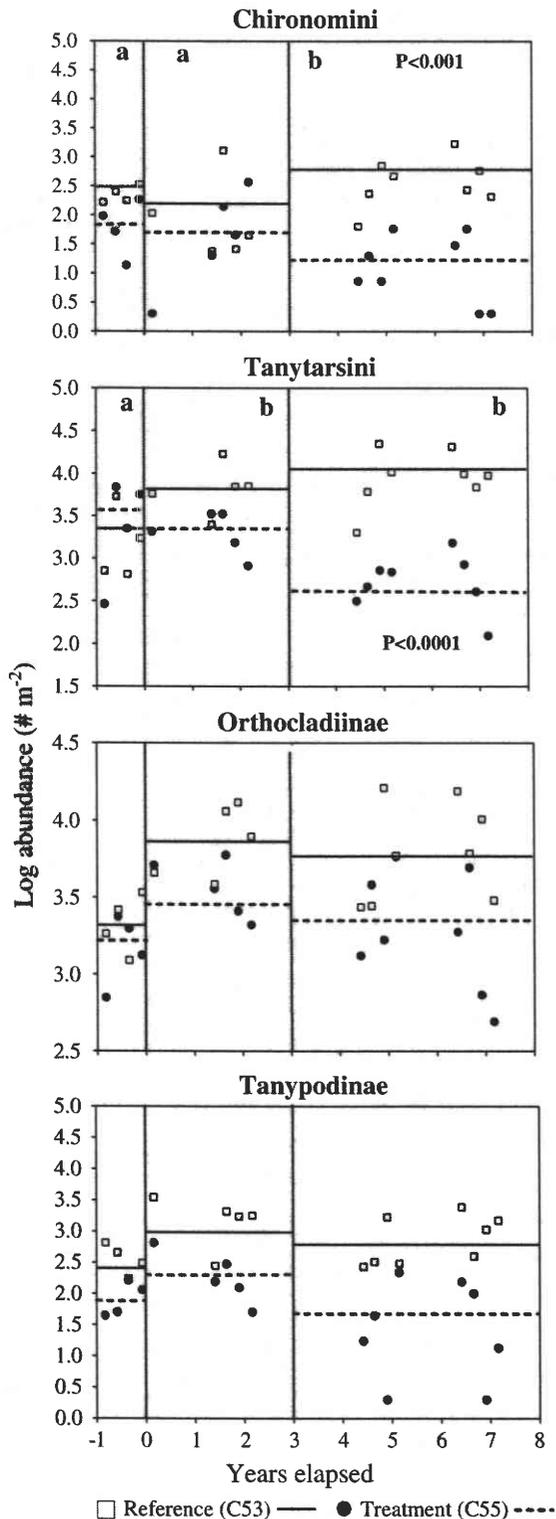
Fig. 2 Species richness (a) over the study period and (b) Shannon Weiner Index of Diversity of the chironomid assemblages in the treatment and reference streams. Lines (solid = reference and dashed = treatment) represent the average for each treatment period (PRE pretreatment, LE litter exclusion, LE + WR wood removal)



chironomus sp.) abundance significantly declined following LE + WR ($F = 5.17$, $P < 0.001$, Fig. 3), but not LE alone ($P > 0.05$). This decline could not be attributed to litter exclusion as Chironomini abundance also declined in the reference stream (i.e., no significant interaction). There was also no significant decline of Chironomini biomass after LE or LE + WR and variability among seasons was high within the tribe and among genera.

Before litter exclusion, Tanytarsini (predominantly *Cladotanytarsus*, sp., *Constempellina* sp., *Microspectra* sp., *Rheotanytarsus* sp., *Stempellinella* sp., and *Tanytarsus* sp.) composed over 60%

of the chironomid assemblage in the litter exclusion stream (Table 2). Following LE and LE + WR, Tanytarsini abundance ($F = 5.17$, $P = 0.0002$) and biomass declined significantly ($F = 33.9$, $P < 0.0001$, Fig. 3). Overall, Tanytarsini abundance and biomass declined by 85% after litter exclusion and wood removal. However, at the genus level, only *Constempellina* sp. biomass declined significantly following both litter and wood exclusion ($F = 12.76$, $P < 0.001$). *Cladotanytarsus*, sp., *Constempellina* sp., *Microspectra* sp., *Rheotanytarsus* sp., *Stempellinella* sp., and *Tanytarsus* sp. were also most abundant in the



reference stream. Abundance, biomass, and relative abundance either increased or did not change significantly through time in the reference stream (Fig. 3).

Fig. 3 Log mean abundance and biomass of major Chironomidae tribes Chironominae and Tanytarsini, and subfamilies Orthoclaadiinae and Tanypodinae in the treatment and reference streams. Lines represent the average for each treatment period (PRE pretreatment, LE litter exclusion, and LE + WR wood removal). Different letters indicate significant differences between treatment periods, taking into account the difference in the values in the reference stream using BACIP

In contrast to Tanytarsini, Orthoclaadiinae abundance and biomass did not significantly change in the litter exclusion stream (Fig. 3). Before litter exclusion, Orthoclaadiinae (predominantly *Lopescladius* sp., *Parachaetocladius* sp., and *Synorthoclaadius* sp.) were 24% of the chironomid assemblage (Table 2). Following LE and WR, Orthoclaadiinae were 73% of the total assemblage but total abundance and biomass did not show a significant increase. Abundance was 1817 ± 1135 before litter exclusion and 3271 ± 221 following LE + WR. Biomass was 6.67 ± 1.54 before litter exclusion and 11.54 ± 3.15 after LE and WR. Genus level abundance and biomass did not change and the Orthoclaadiinae assemblage showed less seasonal variation in the reference stream.

Predaceous Tanypodinae represented 4% of the taxa in the litter exclusion stream, with no change in relative abundance, absolute abundance, or biomass in either the litter exclusion or reference streams over time (Fig. 3, Table 2).

Ordination results: organic matter dynamics and seasonal changes in chironomid community assemblage and biomass

Ordination of mean generic biomass of the most abundant taxa in each year, over seven years, showed a clear separation between the reference and litter exclusion streams (Fig. 4). Axis 1 described 42% and axis 2 described 16% of the variation among samples. Fine ($r^2 = 0.36$) and coarse ($r^2 = 0.39$) organic matter was positively related to axis 1. The proportion of sand, gravel, and pebbles ($r^2 = 0.39$) was negatively related to axis 1. Axis 2 accounted for little variation among samples (16%). Mean monthly temperature ($r^2 = 0.17$) and mean monthly discharge ($r^2 = 0.15$) were weakly related to axis 2 (Table 3). Separation between the two streams corresponded to changes in the

Table 2 Average biomass (mg AFDM m⁻², ±standard error) of most abundant (>5% of total abundance) chironomid taxa within each stream and treatment period

Taxa	Reference			Litter exclusion		
	Pre	LE	LE + WR	Pre	LE	LE + WR
Chironomini						
<i>Demicryptochironomus</i>	0.05 ± 0.02	0.70 ± 0.65	0.41 ± 0.20	0.07 ± 0.05	0.02 ± 0.01	0.01 ± 0.01
<i>Microtendipes</i>	0.55 ± 0.47	0.34 ± 0.34	15.53 ± 14.73	0.13 ± 0.12	0.17 ± 0.16	0.00 ± 0.00
<i>Polypedilium</i>	1.34 ± 0.98	1.04 ± 0.95	0.74 ± 0.22	0.14 ± 0.13	0.06 ± 0.03	0.06 ± 0.03
<i>Stenochironomus</i>	1.31 ± 1.31	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.14	0.92 ± 0.66	0.04 ± 0.04
Tanytarsini						
<i>Cladotanytarsus</i>	0.69 ± 0.29	0.16 ± 0.11	6.39 ± 2.92	0.69 ± 0.26	0.44 ± 0.17	0.46 ± 0.28
<i>Constempellina</i>	1.21 ± 0.92	11.04 ± 6.27	6.42 ± 1.74	0.72 ± 0.54	0.72 ± 0.23	0.11 ± 0.04
<i>Micropsectra</i>	6.69 ± 1.56	29.91 ± 13.26	26.27 ± 11.18	1.3 ± 10.79	0.59 ± 0.13	0.42 ± 0.12
<i>Rheotanytarsus</i>	0.89 ± 0.41	0.15 ± 0.13	0.02 ± 0.02	0.23 ± 0.22	0.32 ± 0.30	0.01 ± 0.01
<i>Stempellinella</i>	0.16 ± 0.15	2.75 ± 2.49	1.07 ± 0.75	0.01 ± 0.01 ^a	0.01 ± 0.01 ^a	0.01 ± 0.00 ^b
<i>Tanytarsus</i>	1.38 ± 1.07	0.11 ± 0.09	0.05 ± 0.04	0.15 ± 0.13	0.33 ± 0.20	0.02 ± 0.01
Orthoclaadiinae						
<i>Corynoneura</i>	0.07 ± 0.05	0.43 ± 0.33	0.63 ± 0.25	0.03 ± 0.02	0.08 ± 0.02	0.08 ± 0.03
<i>Brillia</i>	1.67 ± 0.44	1.07 ± 0.63	2.41 ± 1.30	0.50 ± 0.45	0.16 ± 0.12	0.06 ± 0.04
<i>Helleniella</i>	1.55 ± 0.85	20.11 ± 17.42	11.52 ± 3.27	0.03 ± 0.02	0.10 ± 0.08	0.15 ± 0.05
<i>Hydrobaenus</i>	0.04 ± 0.02	0.24 ± 0.17	0.28 ± 0.20	0.02 ± 0.01	0.20 ± 0.09	0.05 ± 0.03
<i>Krenosmittia</i>	0.70 ± 0.31	6.39 ± 3.86	2.24 ± 0.60	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Lopescladius</i>	0.36 ± 0.20	0.41 ± 0.32	0.03 ± 0.03	3.17 ± 1.58	10.70 ± 3.35	7.52 ± 2.86
<i>Parachaetocladius</i>	8.72 ± 3.90	19.24 ± 7.66	13.78 ± 3.75	1.08 ± 0.61	0.44 ± 0.21	0.15 ± 0.08
<i>Parametriocnemus</i>	8.16 ± 1.48	8.02 ± 5.02	14.75 ± 6.14	0.12 ± 0.09	0.02 ± 0.01	0.20 ± 0.07
<i>Rheocricotopus</i>	0.42 ± 0.35	2.07 ± 1.79	0.70 ± 0.32	0.07 ± 0.06	0.02 ± 0.01	0.04 ± 0.02
<i>Rheosmittia</i>	0.12 ± 0.12	0.00 ± 0.00	0.06 ± 0.04	0.01 ± 0.01	0.07 ± 0.04	0.11 ± 0.06
<i>Stilocladius</i>	0.32 ± 0.13	4.05 ± 3.27	0.81 ± 0.29	0.01 ± 0.01	0.17 ± 0.12	0.01 ± 0.01
<i>Synorthocladius</i>	1.55 ± 0.68	2.06 ± 1.20	0.99 ± 0.37	0.21 ± 0.21	0.02 ± 0.02	0.02 ± 0.02
<i>Thienemaniella</i>	0.01 ± 0.01	0.00 ± 1.00	0.00 ± 0.00	0.01 ± 0.01	0.01 ± 0.01	0.03 ± 0.02
<i>Tvetenia</i>	0.09 ± 0.06	0.02 ± 1.02	0.15 ± 0.10	0.00 ± 0.00	0.08 ± 0.07	0.08 ± 0.03
Tanypodinae						
<i>Krenopelopia</i>	0.97 ± 0.43	8.79 ± 4.88	3.40 ± 1.37	0.13 ± 0.03	0.10 ± 0.04	0.11 ± 0.04
<i>Monopelopia</i>	0.25 ± 0.17	0.42 ± 0.37	0.28 ± 0.28	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00
<i>Natarsia</i>	1.55 ± 0.87	1.37 ± 0.74	0.27 ± 0.27	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
<i>Nilotanypus</i>	0.00 ± 0.00	0.05 ± 0.05	0.01 ± 0.01	0.02 ± 0.01	0.13 ± 0.08	0.02 ± 0.01

Pre = pretreatment, LE = litter exclusion, LE + WR = litter and wood exclusion. Different letters indicate significant differences from BACI analysis (i.e., Before-After differences between the reference and treatment streams)

amount of organic matter and the proportion of inorganic substrates over time.

The taxonomic assemblage differed between the streams. At the genus level, Tanytarsini were positively associated with higher organic matter standing stocks in the reference stream. Tanytarsini genera associated with higher amounts of organic matter included *Micropsectra* sp. and *Constempellina* sp. Some Orthoclaadiinae were also positively associated with axis 1, such as *Parachaetocladius* sp., *Brillia* sp., and *Parametriocnemus* sp. (Table 4). The Orthoclaadiinae, *Lopescladius* sp., was associated with low organic matter standing stocks and higher proportions of inorganic substrates in the litter

exclusion stream. The Chironomini, *Stenochironomus* sp. and Tanytarsini, *Rheotanytarsus* sp., were associated with Axis 2. A decline in chironomid biomass corresponded with the decline in organic matter. For example, chironomid biomass in the LE stream was much closer to the chironomid biomass in the reference stream in autumn and summer prior to litter exclusion. Organic matter standing stocks and chironomid biomass and assemblage structure did not change appreciably in the reference stream by season or year, evidenced by the tight clustering of sampling points among years. Much more seasonal variability occurred in the litter exclusion stream (Fig. 4).

Table 3 Pearson and Kendall correlations of independent variables (CPOM, FPOM, and % Sand, Gravel, and Pebble) with CCA axes

	Axis	Pearson correlation		Independent variables
		r	r^2	
Biomass	Axis 1	0.60	0.36	FPOM
		0.59	0.39	CPOM
		-0.62	0.39	% Sand, Gravel, Pebble
	Axis 2	-0.42	0.17	Mean monthly temperature
		-0.39	0.15	Maximum monthly discharge

Discussion

Spatial and temporal differences in abundance and biomass

Chironomids are often bivoltine, fast colonizers found in high densities in disturbed habitats. These attributes allow them to be among the few

taxa able to exploit patchy, ephemeral food resources (Palmer et al., 2000). In this study, chironomid abundance and biomass declined at the family level, resulting from seven years of litter exclusion, but it did not consistently decline at the subfamily and generic levels. However, our results did show a clear decline of Tanytarsini at the tribe-level following both leaf litter and leaf litter and wood exclusion. The most abundant genera within the tribe Tanytarsini: *Cladotanytarsus* sp., *Constempellina* sp., and *Micropsectra* sp., were expected to decline significantly but only one genus did, *Constempellina* sp. Conversely, Orthocladiinae abundance and biomass did not change and seasonal variation was high. This spatial and temporal variation can be attributed to seasonal fluctuations in available food resources coupled with the phenology of different taxa.

Other studies have shown that high quality organic matter patches attract invertebrates when

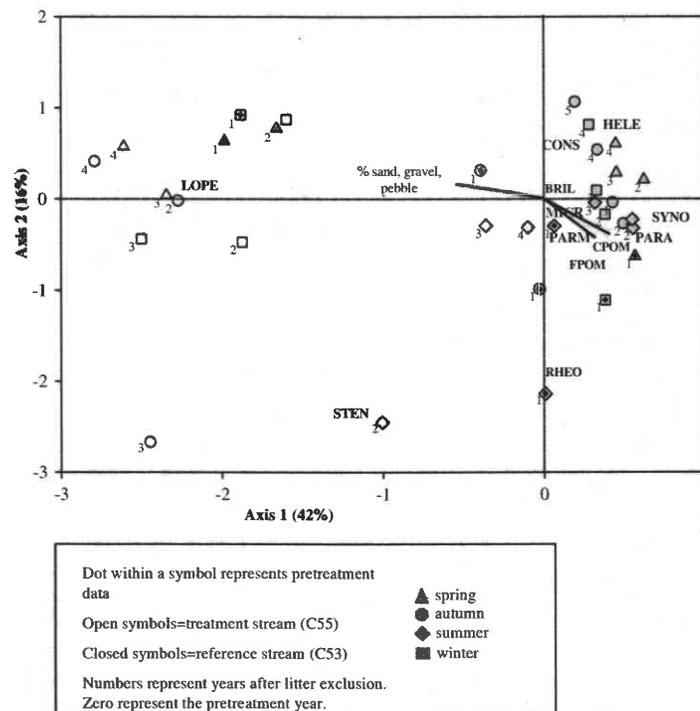


Fig. 4 Canonical correspondence analysis ordination of mean biomass for all taxa. Taxa representing < 5% in total samples were omitted in each stream from 1992 through 2000. Taxon names are abbreviated with *BRIL* = *Brillia*, *CONS* = *Constempellina* sp., *HELE* = *Heleniella* sp., *LOPE* = *Lopescladius* sp., *MICR* = *Micropsectra* sp.,

PARA = *Parachaeotocladus* sp., *PARM* = *Parametrioctenus* sp., *RHEO* = *Rheotanytarsus* sp., and *STEN* = *Stenochironomus* sp. Independent variables shown are *FBOM* = fine benthic organic matter, *CBOM* = coarse benthic organic matter, and % sand, gravel, and pebble

Table 4 Pearson and Kendall correlations of taxa monthly biomass with CCA ordination axes

Taxa	Axis 1		Axis 2	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
<i>Brillia</i>	0.56	0.32	0.02	0.00
<i>Constempellina</i>	0.57	0.32	0.28	0.08
<i>Heleniella</i>	0.64	0.40	0.26	0.07
<i>Lopescladius</i>	-0.86	0.74	0.16	0.02
<i>Micropsectra</i>	0.73	0.53	0.05	0.00
<i>Parachaeocladius</i>	0.71	0.50	0.13	0.02
<i>Parametrioctenus</i>	0.67	0.44	0.10	0.01
<i>Rheotanytarsus</i>	0.27	0.07	-0.57	0.33
<i>Stenochironomus</i>	-0.14	0.02	-0.64	0.41
<i>Synorthocladius</i>	0.59	0.35	0.04	0.00

carbon is limited (e.g., Palmer et al., 2000; Eggert & Wallace, 2003b). Because some particulate organic matter was present within the litter exclusion stream, patches of fine particles created 'resource islands' for chironomids. Fine particulate organic matter did decline in the LE stream; however, concentrations may have been high enough, especially in spring, to support a small and spatially variable population of chironomids (Huryn, 1990; Berg, 1995). Tanytarsini, specifically, have been shown to be associated with organic matter (Oliver, 1971; Pinder, 1986) and were likely able to track organic matter even at low densities. For example, Eggert and Wallace (2003b) previously found that a shredding caddisfly, *Pycnopsyche gentilis*, was able to closely track leaf litter during litter exclusion until standing stocks declined below 25–50 g AFDM m⁻². Consequently, *Pycnopsyche gentilis* production declined significantly. Chironomids may be able to track even lower amounts of organic matter and this could have maintained a link in the detrital food web when other taxa were unable to persist (Wallace et al., 1999).

Life history differences among taxa helped to promote the success of Orthoclaadiinae in the LE stream. Orthoclaadiinae are often most abundant in winter and spring when temperatures are cool and algae and DOC are most abundant (Boerger, 1981; Berg & Hellenthal, 1992). Consequently, Orthoclaadiinae were able to maintain higher densities than other groups following litter exclusion. Conversely, Tanytarsini are often abundant in summer and have been shown to feed

on slow-breakdown leaf litter and fine particulates. The absence of summer leaf litter may exclude some Tanytarsini genera, while others would feed on FPOM (Grubbs & Cummins, 1994). Grubbs & Cummins (1994) found chironomids to be important especially important in processing organic matter in streams with low summer leaf standing stocks when few other shredders were present. These studies emphasize the importance of chironomids in processing organic matter in streams when standing stocks may be too low to support other larger organisms (i.e., shredding Plecoptera).

Taxonomic composition

Chironomid taxon richness and evenness did not change. Recruitment still occurred and our results are supported by those of Lughart et al. (1990) in a nearby Coweeta stream that was treated with insecticide. In their study, chironomid secondary production declined but continuous recruitment from aerial adults maintained benthic diversity. Baer et al. (2001) experimentally confirmed that the litter exclusion stream was continually colonized by aerial adults from downstream, but colonization was lower than before litter exclusion. Our results suggest that emergence and recruitment might have declined due to limited resources for hatched larvae or oviposition of less fecund adults from within the litter exclusion reach. Furthermore, individuals hatched in the litter exclusion stream experienced increased predation pressures (Hall et al., 2000; Wallace et al., 1999) and an elevated per capita drift of late-instars (Siler et al., 2001) in response to limited food and habitat in the litter exclusion stream.

Chironomidae response to habitat alteration

Tanytarsini responded most dramatically to litter exclusion. Several unique characteristics made them particularly vulnerable to litter and wood exclusion. First, Tanytarsini are small, rheophilic chironomids that depend on stable habitat for either case (e.g., *Constempellina* sp.) or tube (e.g., *Micropsectra* sp.) attachment (Oliver, 1971; Pinder, 1986; Coffman & Ferrington, 1996). The loss

of leaves and wood likely eliminated Tanytarsini habitat (Chaloner & Wotton, 1996) and created an environment less buffered from disturbances (Bilby & Likens, 1980; Smock et al., 1989). Food was also reduced and became more limited. Fine particulate organic matter (FPOM), a known food source for many Tanytarsini, declined from about 1500 g to 200 g AFDM m⁻² from the start of LE through the end of the seven-year study period (as cited in Wallace et al., 1999; Eggert & Wallace, 2003a). The temporal and spatial heterogeneity of FPOM would have contributed to the decline and variability found in Tanytarsini abundance and biomass.

The additional removal and exclusion of small and large wood had the largest impact on the chironomids due to the combined loss of habitat, retention structures, and the direct reduction of food resources. The physical attributes of wood in streams are well known, but less is known about the role it plays as a food resource (Bilby & Bisson, 2000). Wood provides critical habitat for biofilms, a complex matrix of algae, bacteria, and fungi (Golladay & Sinsabaugh, 1991; Couch & Meyer, 1992) and retains fine particles. Bacteria and algae on the wood provided a labile food source for chironomids in the LE stream (Hall & Meyer, 1998; Hart & Lovvorn, 2003). Some of the Orthocladiinae in the LE stream had scraping mouthparts able to feed on biofilms growing on wood and inorganic substrate (i.e., *Lopescladius* sp., *Parachaetocladius* sp., and *Rheosmittia* sp.). Furthermore, Meyer et al. (1998) found that overall, dissolved organic carbon (DOC) concentrations declined as leaf standing stock declined; however, DOC concentrations did not significantly decline in the spring and summer because leaves were not the primary DOC source. This DOC would have been an important nutrient source for bacteria and algae on FPOM, sand, and rocks in the litter exclusion stream during summer.

Many Orthocladiinae persisted in the litter exclusion stream after litter and wood exclusion, the genus *Lopescladius* sp. being most successful. *Lopescladius* sp. abundance and biomass increased during spring, autumn, and winter in the litter exclusion stream; however, their absence during summer confounded statistical analyses.

Hurn (1990) found that the most abundant chironomid taxa in Coweeta streams were present throughout the year, but *Lopescladius* sp. was not abundant in his study. However, in this study, chironomid abundance and biomass declined, particularly *Lopescladius* sp., in summer when canopy was closed and fine organic matter export was low. The Orthocladiinae that persisted in the litter exclusion stream were small, bivoltine species, making them very fast colonizers. In fact, when leaves were added back in autumn to the stream, they were among the first to colonize (J.B. Wallace & S.L. Eggert, University of Georgia, unpublished data). They are also good swimmers, adapted to fast-flowing, cold water streams that often experience frequent hydrologic disturbance (Coffman & Ferrington, 1996; Lods-Crozet et al., 2001). Some researchers have found *Lopescladius* sp. and *Rheosmittia* sp. to be indicative of disturbance in southeastern U.S. streams and to dominate sandy, coastal plain blackwater rivers (see also Soluk, 1985; Benke, 1998; Rinella & Feminella, 2005).

Community response to resource reduction

A combination of parametric statistics and ordination proved to be an insightful approach for exploring generic-level community dynamics within the litter exclusion stream and between the reference and litter exclusion streams. Ordination analyses clearly illustrated differences in the chironomid community structure between the reference and litter exclusion streams. It also showed that the biomass and community assemblage in the litter exclusion stream was more closely related to the reference stream before litter exclusion, especially in autumn. Differences in chironomid biomass between the two streams increased with each passing year of litter exclusion. These differences were related to the amount of fine and coarse particulate organic matter in the streams and the amount of small inorganic substrates. Differences in inorganic substrate were more important in structuring the community before LE and seemed to become less important with the continued exclusion of leaf litter and wood.

Functional feeding

Macroinvertebrates are often classified into functional feeding groups (FFGs) to clarify their ecological significance (Cummins, 1974), but chironomids are typically grouped as predators (Tanytopodinae) or collector–gatherers (non-Tanytopodinae) in ecosystem-level manipulations (e.g., Wallace et al., 1999). The use of FFGs to categorize chironomid feeding habits is problematic because chironomids are often facultative feeders that shift their diet with the most abundant food available. The particles they ingest are so small it can only be identified as amorphous detritus (Berg, 1995; Tavares-Comar & Williams, 1996; Rosi-Marshall & Wallace, 2002; Henriques-Olivera et al., 2003). Our results show that categorizing chironomid feeding into a functional mode can lead to an oversimplification of their response to environmental change.

Chironomidae facultative feeding habits make categorization into functional feeding groups difficult. Out of 22 dominant chironomid genera in this study, 12 were classified as collector–gatherers, six had not been classified, and two were predators. However, categorizing chironomids by subfamily was informative and the additional classification of feeding modes and other life history attributes of subfamilies provided more insight into the overall chironomid response to litter exclusion. A few key genera were sensitive to changes in organic matter standing stocks (i.e., *Constempellina* sp. and *Lopescladius* sp.) and loss of wood (e.g., *Micropsectra* sp.). These taxa may be useful as indicator species in altered stream ecosystems.

Conclusions

The chironomid assemblage changed as a result of excluding terrestrial detrital inputs. Lowered standing stocks of CPOM, FPOM, and DOC concentrations negatively affected the Tanytarsini, but not Tanytopodinae or Orthocladiinae, in fact, Orthocladiinae abundance and biomass did not change over the course of litter exclusion. The coupled removal of litter and wood had the

largest affect on the chironomid community, due to a loss of habitat and stable retention structures, as well as the indirect reduction of food resources (e.g., biofilms, Golladay & Sinsabaugh, 1991; Couch & Meyer, 1992). Orthocladiinae were able to persist because of their habitat preferences, feeding strategies, and recolonization by aerial adults. From a management perspective, our results suggest a forested headwater stream community dominated by Orthocladiinae such as *Lopescladius* sp. and *Rheosmittia* sp. and a lack of common Tanytarsini could be indicative of an ecologically significant loss of detritus. This may occur in streams with disturbed riparian habitats or streams with increased inorganic sediments and loss of retention structures.

Acknowledgements We thank Randy Bernot, Dominic Chaloner, Wyatt Cross, Ashley Moerke, and Allison Roy for many helpful suggestions. Darold Batzer, Amy Braccia, Dominic Chaloner, Brent Johnson, and two anonymous reviewers provided helpful comments on early drafts that improved this paper. This project was funded by the National Science Foundation grant DEB-9207498 and DEB-962968.

References

- Baer, S. G., E. R. Siler, S. L. Eggert & J. B. Wallace, 2001. Colonization and production of macroinvertebrates on artificial substrate: upstream–downstream responses to a leaf litter exclusion manipulation. *Freshwater Biology* 46: 347–365.
- Benke, A. C., 1998. Production dynamics of riverine chironomids: extremely high biomass and turnover rates of primary consumers. *Ecology* 79: 899–910.
- Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to Southeastern United States. *Journal of the North American Benthological Society* 18: 308–343.
- Berg, M. B., 1995. Larval food and feeding behaviour. In Armitage P., P. S. Cranston & L. C. V Pinder (eds), *The Chironomidae: Biology and Ecology of Non-Biting Midges*. Chapman & Hall, Hartnolls Ltd., Bodmin, Cornwall, UK, 3–6.
- Berg, M. B. & R. A. Hellenthal, 1992. Life histories and growth of lotic chironomids (Diptera:Chironomidae). *Annals of the Entomological Society of America* 85: 578–589.
- Bilby, R. E. & P. A. Bisson, 2000. Function and distribution of large woody debris. In Naiman R. J. & R. E. Bilby (eds), *River Ecology and Management*, Springer, 324–338.

- Bilby, R. E. & G. E. Likens, 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61: 1107–1113.
- Boerger, H., 1981. Species composition, abundance and emergence phenology of midges (Diptera: Chironomidae) in a brown-water stream of West-Central Alberta, Canada. *Hydrobiologia* 80: 7–30.
- Chaloner, D. T., G. A. Lamberti, R. W. Merritt, P. H. Ostrom & M. S. Wipfli, 2004. Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. *Freshwater Biology* 49: 587–599.
- Chaloner, D. T. & R. S. Wotton, 1996. Substratum preferences by larvae of three species of midge (Diptera: Chironomidae). *Hydrobiologia* 339: 93–99.
- Coffman, W. P. & L. C. Ferrington, 1996. Chironomidae. In Merritt R. W. & K. W. Cummins (eds), *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Publishing Co., Dubuque, Iowa, 635–754.
- Cummins, K. W., 1974. Structure and function of stream ecosystems. *Bioscience* 24: 631–641.
- Couch, C. A. & J. L. Meyer, 1992. Development and composition of the epixylic biofilm in a blackwater river. *Freshwater Biology* 27: 43–51.
- Eggert, S. L. & J. B. Wallace, 2003a. Litter breakdown and invertebrate detritivores in a resource-depleted Appalachian stream. *Hydrobiologia* 156: 315–338.
- Eggert, S. L. & J. B. Wallace, 2003b. Reduced detrital resources limit *Pycnopsyche gentilis* (Trichoptera: Limnephilidae) production and growth. *Journal of the North American Benthological Society* 22: 388–400.
- Epler, J. H., 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. North Carolina Department of Environment and Natural Resources Division of Water Quality. 526 pp.
- Golladay, S. W. & R. L. Sinsabaugh, 1991. Biofilm development on leaf and wood surfaces in a boreal river. *Freshwater Biology* 25: 437–455.
- Grubbs, S. A. & K. W. Cummins, 1994. Processing and macroinvertebrate colonization of Black Cherry (*Prunus serotina*) leaves in two streams differing in summer biota, thermal regime, and riparian vegetation. *American Midland Naturalist* 132: 284–293.
- Hall, R. O. & J. L. Meyer, 1998. The trophic significance of bacteria in a detritus-based stream food web. *Ecology* 79: 1995–2012.
- Hall, R. O., J. B. Wallace & S. L. Eggert, 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81: 3445–3463.
- Hart, E. A. & J. R. Lovvorn, 2003. Algal vs. macrophyte inputs to food webs of inland saline wetlands. *Ecology* 84: 3317–3326.
- Henriques-Oliveira, A. L., J. L. Nessimian & L. F. M. Dorvillé, 2003. Feeding habits of chironomid larvae (Insecta: Diptera) from a stream in the Floresta Da Tijuca, Rio De Janeiro, Brazil. *Brazil Journal of Biology* 63: 269–281.
- Hershey, A. E., 1985. Littoral chironomid communities in an arctic Alaskan lake. *Holarctic Ecology* 8: 39–48.
- 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. & J. B. Wallace, 2000. Life history and production of stream insects. *Annual Review of Entomology* 45: 83–100.
- Johnson, B. R., W. F. Cross & J. B. Wallace, 2003. Long-term resource limitation reduces insect detritivore growth in a headwater stream. *Journal of the North American Benthological Society* 22: 565–574.
- Ladle, M., J. S. Welton & J. A. B. Bass, 1984. Larval growth and production of three species of Chironomidae from an experimental recirculating stream. *Archiv für Hydrobiologie* 102: 201–214.
- Leeper, D. A. & B. E. Taylor, 1998. Insect emergence from a South Carolina (USA) temporary wetlands pond, with emphasis on the Chironomidae (Diptera). *Journal of the North American Benthological Society* 17: 45–72.
- Lods-Crozet, B., V. Lencioni, J. S. Olafsson, D. L. Snooks, G. Velle, J. E. Brittain, E. Castella & B. Rossaro, 2001. Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. *Freshwater Biology* 46: 1791–1809.
- Lugthart, G. J., J. B. Wallace & A. D. Huryn, 1990. Secondary production of chironomid communities in insecticide-treated and untreated headwater streams. *Freshwater Biology* 24: 417–427.
- Lugthart, G. J. & J. B. Wallace, 1992. Effects of disturbance on benthic functional structure and production in a mountain stream. *Journal of the North American Benthological Society* 11: 138–164.
- Meyer, J. L., J. B. Wallace & S. L. Eggert, 1998. Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems* 1: 240–249.
- Oliver, D. R., 1971. Life history of the Chironomidae. *Annual Review of Entomology* 12: 211–230.
- Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, K. E. Abu-Saba & A. R. Flegal, 1994. Detection of environmental impacts: natural variability, effect size, and power analysis. *Ecological Applications* 4: 16–30.
- Palmer, M. A., C. M. Swan, K. Nelson, P. Silver & R. Alvestad, 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecology* 15: 563–576.
- Pinder, L. V. C., 1986. Biology of freshwater Chironomidae. *Annual Review of Entomology* 31: 1–23.
- Ramirez, A. & C. M. Pringle, 1998. Structure and production of a benthic insect assemblage in a neotropical stream. *Journal of the North American Benthological Society* 17: 443–463.
- Richardson, J. S., 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72: 873–887.
- Rinella, D. J. & J. W. Feminella, 2005. Comparison of benthic macroinvertebrates colonizing sand, wood, and artificial substrates in a low-gradient stream. *Journal of Freshwater Ecology* 20: 209–219.
- Rosi-Marshall, E. J. & J. B. Wallace, 2002. Invertebrate food webs along a stream resource gradient. *Freshwater Biology* 47: 129–141.

- Ruse, L. & M. Davison, 2000. Long-term data assessment of chironomid taxa structure and function in the river Thames. *Regulated Rivers: Research and Management* 16: 113–126.
- SAS Institute, 2001. SAS/STAT user's guide, 8.04, SAS Institute, Cary, North Carolina.
- Siler, E. R., J. B. Wallace & S. L. Eggert, 2001. Long-term effects of resource limitation on stream invertebrate drift. *Canadian Journal of Fisheries and Aquatic Science* 58: 1624–1637.
- Silver, P., C. Brown-McCall & D. Wooster, 2004. Habitat partitioning by chironomid larvae in arrays of leaf patches in streams. *Journal of the North American Benthological Society* 23: 467–479.
- Smith, E. P., 2002. BACI design. In El-Shaarawi A. H., & W. W. Piegorsch (eds), *Encyclopedia of Environmetrics*. John Wiley & Sons, Ltd., Chichester, 1–7.
- Smock, L. A., G. M. Metzler & J. E. Gladden, 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70: 764–775.
- Soluk, D. A., 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1296–1302.
- Stites, D. L. & A. C. Benke, 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P:B ratios. *Limnology and Oceanography* 34: 1278–1289.
- Tavares-Cromar, A. F. & D. D. Williams, 1996. The importance of temporal resolution in food web analysis: evidence from a detritus based stream. *Ecological Monographs* 66: 91–113.
- Tokeshi, M., 1995. Life cycles and population dynamics. In Armitage P., P. S. Cranston & L. C. V Pinder (eds), *The Chironomidae: Biology and Ecology of Non-Biting Midges*. Chapman & Hall, Hartnolls Ltd, Bodmin, Cornwall, UK: 3–6.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & 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 & J. R. Webster, 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69: 409–442.
- Wallace, J. B., J. R. Webster, S. L. Eggert, J. L. Meyer & E. R. Siler, 2001. Large woody debris in a headwater stream: long-term legacies of forest disturbance. *Internationale Review of Hydrobiologie* 86: 501–513.
- Waters, T. F., 1969. Sub-sampler for dividing large samples of stream invertebrate drift. *Limnology and Oceanography* 14: 813–815.
- Wiederholm, T. (ed.), 1983. *Chironomidae (Diptera) of the Holarctic region. Keys and Diagnoses. Part I. Larvae*. Entomol. Scand. Suppl. No. 19. 457 pp.
- Wiley, M. J., 1981. Interacting influences of density and preference on the emigration rates of some lotic chironomid larvae (Diptera: Chironomidae). *Ecology* 62: 426–438.

