

## Effects of seasonality and resource limitation on organic matter turnover by Chironomidae (Diptera) in southern Appalachian headwater streams

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### *Abstract*

Despite their high abundance, secondary production, and known reliance on detrital material, the role of chironomids (Diptera) in fine particulate organic matter (FPOM) dynamics has not been well quantified. We conducted field trials using fluorescent pigment markers to estimate seasonal rates of consumption, annual secondary production, assimilation efficiency (AE), and FPOM turnover for non-Tanytopodinae chironomids in two similar, southern Appalachian, headwater streams. An ecosystem-level experimental manipulation of detrital inputs in one study stream allowed for a unique assessment of turnover in reference, resource-limited, and resource-recovery systems. Seasonality had a significant effect on larval gut-passage time (GPT), with faster GPT at higher temperatures. Mean GPT ranged from 39 min (summer) to 67 min (winter). Mean annual FPOM turnover was reduced in the resource-limited stream (5.5 kg ash-free dry weight per year; 12% of mean annual FPOM export) compared to the reference stream (46 kg yr<sup>-1</sup>; 74% of mean export). Following 4 yr of resource recovery, FPOM turnover increased to 24 kg ash-free dry wt yr<sup>-1</sup> (16% of export) but remained lower than levels measured in the reference stream (53 kg ash-free dry wt yr<sup>-1</sup>; 20% of export). Chironomid contribution to FPOM turnover was much higher in low vs. high discharge conditions (74% in low discharge vs. 20% in high discharge). Assimilation efficiency was estimated to be low in all systems (1.7–2.5%). Chironomids turned over a large portion of FPOM available to them, suggesting that turnover by the entire collector community in forested headwater systems may be much higher than expected.

Despite the importance of deposit-feeding invertebrate collectors in the processing and cycling of fine particulate organic matter (FPOM), few studies have compared FPOM turnover relative to the overall storage and export of organic matter. Turnover is defined here as the amount of FPOM that has passed through invertebrate guts per stream per unit time (Fisher and Gray 1983). In a previous study examining stream FPOM dynamics, Fisher and Gray (1983) reported very high rates of turnover for collectors in a U.S. southwestern desert stream, with daily ingestion exceeding gross primary production. These high rates suggested that collectors were largely responsible for the rapid turnover of FPOM in arid streams of the desert southwest.

Studies conducted in heterotrophic streams of the eastern deciduous forest biome also suggest the importance of collectors in FPOM dynamics. Using a computer-simulation model for a southeastern Appalachian stream, Webster (1983) predicted that, by transforming entrained organic matter from large particles into smaller particles, shredders and collectors were responsible for 27% of FPOM entering into transport. In a nearby headwater stream, the experimental reduction of macroinvertebrates via insecticide applications resulted in a pronounced reduction in FPOM export (Wallace et al. 1991). Although

the few studies to date have suggested the importance of collectors in the processing and cycling of organic matter in streams, more detailed studies are needed.

Chironomids dominate macroinvertebrate communities in headwater Appalachian streams, often contributing more than half of the benthic abundance (Lugthart et al. 1990; Wallace et al. 1999). Their rapid growth rates and short generation times result in high rates of secondary production (Lugthart et al. 1990; Entekin et al. 2007). Chironomids have also been shown to rely on terrestrially derived detritus (Wallace et al. 1997, 1999), providing an important link between basal food resources and higher trophic levels (Lugthart et al. 1990; Entekin et al. 2007). Thus chironomids show a significant potential contribution to FPOM turnover (Fisher and Gray 1983), but their contribution to turnover has not been well-quantified.

The main objective of this study was to evaluate the role of chironomids belonging to the collector functional-feeding group in FPOM turnover and to test several hypotheses about what factors control these rates of turnover. We measured seasonal rates of consumption and mean annual secondary production for chironomids in two similar headwater streams in four seasons and 2 yr, and we used these rates to estimate assimilation efficiency and FPOM turnover. An ecosystem-level experimental manipulation of detrital inputs in one study stream (Wallace et al. 1997, 1999) allowed for a unique evaluation of how turnover varied in reference, resource-limited, and resource-recovery systems. We predicted that feeding rates would vary seasonally with higher feeding rates at higher

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Table 1. Physical characteristics for reference (Catchment 53) and treatment (Catchment 55) streams, at Coweeta Hydrologic Laboratory, North Carolina.

Stream	C53	C55
Catchment		
Area (km <sup>2</sup> )	0.052	0.075
Elevation (m asl)	829	810
Aspect	south	south
Channel length (m)	135	170
Wetted area (m <sup>2</sup> )	207	247
Gradient (cm m <sup>-1</sup> )	27	20
Canopy cover (%)	88.9	91.7
Substrate (% composition)		
Mixed	73	87
Bedrock outcrop	27	13
Mean discharge (2000–2001, L s <sup>-1</sup> )	0.22	0.37
Mean discharge (2005, L s <sup>-1</sup> )	1.40	1.98
Mean annual water temp. (2000–2001, °C)	11.4	10.9
Mean annual water temp. (2005, °C)	12.3	12.3

temperatures. Although the chironomid contribution to FPOM turnover was expected to be high in both streams, we predicted that resource-limitation that resulted from litter exclusion would reduce rates of turnover in the experimental stream. We also expected that turnover rates in this stream would rebound in response to the addition of leaves (i.e., during resource recovery) but would remain low relative to the reference stream.

## Methods

**Study site description**—This study was conducted in two first order streams, Catchments (C) 53 and 55, at Coweeta Hydrologic Laboratory (USDA Forest Service) located in the Blue Ridge physiographic region in western North Carolina. The riparian canopy was similar in both streams and was composed primarily of tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), and dogwood (*Cornus florida*). A dense understory population of rhododendron (*Rhododendron maximum*) provided year-round shade. Elevation, area drained, thermal regime, discharge, and aspect (south-facing) were similar in both catchments (Table 1). Detailed descriptions of the Coweeta basin were given by Swank and Crossley (1988).

An ecosystem-level experimental exclusion of allochthonous inputs was conducted in C55 from 1993 to 2001. Consequently, organic-matter values of standing crops were reduced to ~ 5% of pre-litter exclusion values (Wallace et al. 1997, 1999; Eggert and Wallace 2003). In year 2001, a resource-limited year, all leaf-litter and small and large woody debris were excluded from the stream (Table 2), and plastic tree branches and polyvinyl chloride (PVC) pipes were used to simulate the structural component provided by wood. In 2002, resource-recovery was initiated via the addition of leaf-litter back into C55 at a rate similar to natural inputs (230 ash-free dry weight m<sup>-2</sup> yr<sup>-1</sup>) while maintaining the litter exclusion canopy. A different functional combination of leaf-litter was added to C55 each year from 2002 to 2006

Table 2. Summary of the ecosystem-level manipulation of allochthonous detrital inputs in Catchment 55 at Coweeta Hydrologic Laboratory. Treatment years are listed for the resource-recovery experiment. During resource-recovery, different functional combinations of leaf-litter were added to the stream at a rate of 230 g AF dry wt m<sup>-2</sup> yr<sup>-1</sup> in order to simulate natural annual litter inputs. Rapidly decomposing leaf species were added during years 1 and 2: Tulip Poplar, Dogwood, and Sycamore; slowly decomposing leaf species were added during years 3 and 4: Rhododendron, Northern Red Oak, and White Pine; and a combination of leaves with mixed decomposition rates were added during year 5: Tulip Poplar, Red Maple, and Rhododendron. (\*) indicates years used to estimate FPOM turnover.

Year	Treatment yr	Treatment
1993–2006		canopy exclusion of leaf-litter
1996–1998		small woody debris removed
1998–2000		large woody debris removed
2001*	year 0	PVC pipe+plastic branches added
2002	year 1	3 fast leaf species added: 33.3% by weight
2003	year 2	3 fast leaf species added: 33.3% by weight
2004	year 3	3 slow leaf species added: 33.3% by weight
2005*	year 4	3 slow leaf species added: 33.3% by weight
2006	year 5	1 fast, 1 medium, 1 slow species: 33.3% by weight

(Table 2), with fast, slow, and mixed breakdown rates represented during different time periods. In 2005, a resource-recovery year, FPOM standing crop was a reflection of the breakdown of the prior 3 yr of leaf addition.

**Gut passage time**—A fluorescent pigment marker was used to measure larval chironomid GPT in field studies during 2005 in February, May, July, and November. P-1600 (pink) Radiant Fluorescent Pigment (Radiant Color, Richmond, CA) was used to make a slurry composed of 4 g of pigment, 60 mL of water, and 0.4 mL of Kodak Photoflo (Kodak, www.kodak.com) as a wetting agent. The pigment slurry was pipetted slowly onto groups of submerged leaves and detritus, where non-Tanypodinae (non-predaceous) chironomids are usually abundant. Groups of leaves and attached substrate were removed and placed into bags following 10-min, 20-min, and 30-min exposure periods in each stream. Carbonated water was added to each bag to prevent regurgitation of gut contents (Davies and McCauley 1970) followed immediately by 7% formalin preservation. Chironomid larvae were removed using forceps with the aid of a dissecting microscope, mounted using CMC-10 mounting media (Masters Chemical Company, Inc., Elk Grove, IL), and identified to genus using the methods outlined by Epler (2001). A digital camera (JVC America Corp., model KY-F70BU, www.jvc.com) mounted on an Olympus BX60 microscope (www.olympus.com) interfaced with Auto-Montage Pro Software (Synoptics Ltd., version 5.01.0005, 2004, www.synoptics.co.uk) was used to digitize total gut length, fore-, mid-, and hindgut diameters, and a dark-field approach with ultra-violet illumination was used to measure the length from mouth to most posterior edge of the fluorescent pigment marker for each individual. Percent posterior displacement of pigment in the gut was calculated for each time treatment (T<sub>10</sub>, T<sub>20</sub>, T<sub>30</sub>) as the proportion of

the gut traveled by the fluorescent pigment relative to the total gut length. GPT was extrapolated as the time it took the fluorescent pigment marker to travel 100% of the gut length. Larvae that failed to consume pigment were excluded from the analysis because it was not possible to determine whether they had access to pigment at the site of release (e.g., individuals that were deep in sediments and leaf packs).

**Benthic sampling**—Four samples for chironomids and benthic organic matter were collected monthly from mixed substrate (mixed sand, gravel, pebble, and cobble) habitats in each stream using a 400 cm<sup>2</sup> corer (Wallace et al. 1997, 1999). Invertebrates and benthic organic matter were elutriated from inorganic materials by passing them through 1-mm and 250- $\mu$ m sieves and were preserved in 7% formalin (Wallace et al. 1999). Animals, including chironomids, were removed from substrates under 15 $\times$  magnification, and midges were identified as either Tanypodinae or non-Tanypodinae. Tanypodinae chironomids, which are considered to be primarily predaceous (Coffman and Ferrington 1984), did not contain dye in their guts and were excluded from this study. Body lengths of non-Tanypodinae chironomids were measured using an ocular micrometer, and lengths were converted to ash-free dry weight (AF dry wt) using length–weight regressions derived from chironomids in nearby Coweeta streams (Huryñ 1990). FPOM in samples was processed, weighed, ashed, and re-weighed following the procedures of Lugthart and Wallace (1992). Continuous export of seston was measured as described by Wallace et al. (1991).

Estimating gut mass via dissection and weighing is problematic due to the small size of larval chironomids. Thus, mass of FPOM in midge guts was estimated using a volume-to-mass conversion factor (0.191 g FPOM mL<sup>-1</sup>) derived by drying and weighing samples of FPOM from study streams to estimate ash-free dry weights of FPOM ( $n = 10$ ). Gut-volume calculations were based on the assumption that midge guts are cylindrical; calculations used measures of gut length and average gut diameter ( $n = 30$ ).

**Production and assimilation efficiency**—Production of non-Tanypodinae chironomids was estimated in C53 and C55 for both study years using the community-level method of Huryñ (1990). Using values for production (J. B. Wallace and S. L. Eggert unpubl.), net production efficiency (NPE) for collector macroinvertebrates (NPE = 33%, Stagliano and Whiles 2002), and our measures of turnover (consumption), we estimated the assimilation efficiency (AE) of chironomids using methods of Benke and Wallace (1980):

$$\text{AE(\%)} = \frac{\text{annual secondary production}}{\text{(consumption} \times \text{NPE)}} \quad (1)$$

**Statistical methods and turnover calculations**—Multilevel models were used to test for differences in gut-passage time among seasons, midge taxon, body length, and three time treatments. Models were fit using a Bayesian framework because significance tests for fixed effects in mixed models can be problematic (Pinheiro and Bates 2000). The Bayesian framework is particularly useful for estimating variance components of complex multilevel models that include fixed

and random effects (Gelman and Hill 2007), and is increasingly being used to study a variety of ecological problems (McMahon and Diez 2007). In this study, we were primarily interested in testing for fixed seasonal effects on GPT, but wanted to account for the relationship with midge size as nested within the two focal genera. The Bayesian framework also facilitated the incorporation of multiple sources of variability into estimates of overall organic matter turnover. Midge consumption rates were modeled using a mixed model that allowed for time, taxa, and seasonal differences, while also accounting for effects of individual body lengths. The percent posterior displacement of pigment in midge guts was modeled as normally distributed (confirmed using the Shapiro-Wilk Normality test;  $W = 0.9356$ ,  $p < 2.2e - 16$ ) (Royston 1995), with mean

$$\mu_i = \alpha_{t,g,s} + \beta_{t,g} \times \text{size}_i \quad (2)$$

where  $\mu$  is the mean GPT of midge  $i$ ,  $\alpha$  is an intercept allowing differences among time treatments  $t$ , genera  $g$ , and season  $s$ . The effect of midge size on GPT is estimated by a coefficient  $\beta$  that is allowed to vary with species and time treatment. There was no significant difference in GPT between watersheds ( $p > 0.05$ ), so all data were pooled for analyses.

The rate of FPOM turnover is complex and is influenced by a number of subprocesses that each may vary spatially and temporally. Reasonable estimates of turnover thus depend on properly propagating variability in underlying subprocesses into the estimation procedure. In this study, a major source of variability in estimates of turnover is the substantial spatial and temporal variability in midge densities. Although four benthic cores per month per catchment is a substantial monitoring effort, the inherent variability makes estimating chironomid densities difficult. Variability in density estimates may be particularly problematic in our focal taxon due to the considerable diversity of chironomid assemblages in these streams, with up to 43 representative genera exhibiting a wide range of voltinism and probable overlapping generations (Huryñ 1990; Entekin et al. 2007). We used the hierarchical model structure to estimate variability using all monthly data, within each size class.

GPT was estimated from the model (2) described above as follows:

$$\text{GPT}_{c,s} = (\text{time/\% displacement}) \times 100\% \quad (3)$$

where  $c$  and  $s$  indicate separate estimates for the two catchments and four seasons, respectively.

Another component of turnover is the mass of organic matter stored in the guts of the entire chironomid community. The mass of organic matter in guts was calculated as:

$$\begin{aligned} \text{gut mass density}_{c,s} = & \text{gut mass} \\ & \times \left( \sum \text{gut vol}_{\text{size}} \right) \\ & \times \text{chironomid density}_{c,s,\text{size}} \end{aligned} \quad (4)$$

where gut mass, or the mass of organic matter in individual guts, was estimated from dissections as the mean of a normal distribution with variance ( $n = 8$ ). We used a hierarchical model structure to calculate the variability in monthly

Table 3. Mean percent posterior pigment displacement and gut-passage time (GPT) from T<sub>30</sub> time treatments (ranges in parentheses). Standard deviations (SD) are included directly below each parameter. Larvae ranged in size from 0.05 mm to 5.4 mm.

	July	May	November	February
Temperature (°C)	16.1	12.7	8.8	8.1
% Posterior displacement	81.5 (42.4–100)	62.5 (27.4–100)	51.5 (24.2–100)	47.7 (20.2–77.8)
SD	17.8	14.6	14.2	13.0
GPT (min)	38.8	50.4	62.8	67.3
GPT range	(30–70.6)	(30–110)	(30–124)	(38.6–148.3)
SD	13.2	10.3	16.3	18.2
n	85	105	103	105

chironomid density estimates using all monthly data, within each size class, which better informed the variability around any given month’s estimate.

FPOM turnover was thus modeled as a function of GPT, chironomid density, and mixed-substrate weighted stream area (a catchment-specific constant). The catchment and season specific turnover (TO) values were calculated as

$$TO_{c,s} = GPT_{c,s}^{-1} \times \text{gut mass density}_{c,s} \times \text{stream area} \quad (5)$$

In a Bayesian framework, the model specified above describes a multivariate distribution of unknown parameters conditional on observed data. Markov-chain Monte Carlo simulation (MCMC) is an approach to estimating complex distributions that uses iterative simulation (Gelman et al. 2004). MCMC algorithms sample sequentially from the probability distribution of each random variable conditional on all current values of other variables in the model. This process ensures that variability in parameters of submodels (e.g., chironomid density) influence the uncertainty of final estimates of turnover. The resulting simulations explore the likelihood of a range of values, but emphasize those values with the highest probabilities, a process called convergence. To assess whether convergence has occurred, multiple independent sets of simulations (or chains) are run and compared. The resulting samples from this process characterize the posterior distributions of all variables of interest in the model and form the basis for all inference about the importance of different variables. Thus, no ‘test statistics’ are needed, and all reported p-values represent actual probabilities that the distributions characterizing parameters of interest overlap.

All models were fit using the BRugs package (Thomas et al. 2006) in R version 2.7.1 (R Development Core Team 2006). Convergence of three independent MCMC chains was assessed using visual inspection and the Gelman-Rubin convergence statistic, which compares the variation within each chain to the variation among chains. After a burn-in period of 2000 iterations, an additional 5000 MCMC iterations were used to characterize posterior distributions.

Results

*Gut passage time*—Overall year-round mean GPT (watershed, taxa, season, and size combined; n = 1189)

was 55.6 minutes (Table 3). Percent posterior displacement of pigment in midge guts was greatest at T<sub>30</sub> > T<sub>20</sub> > T<sub>10</sub> (Table 4). We found a significant effect of season on GPT (p < 0.01; Fig. 1). Fastest GPTs were in July followed by May, while feeding rates were significantly slower in November and February (Fig. 1, Table 3) (p < 0.0001). Differences in GPT in February and November were not significant (p > 0.05). Seasonal effects became more pronounced in longer time treatments, with T<sub>10</sub> < T<sub>20</sub> < T<sub>30</sub> (Fig. 1). Seasonal differences in GPT correspond to changes in temperature, with shorter GPTs in warmer months (Table 3, Fig. 1). On average, midges cleared their guts in 38.8 min in July when water temperature was 16.1°C, while GPT took much longer with a mean of 67.3 min in February when water temperature was 8.1°C. Significant shifts in consumption rates corresponded to temperature changes of about 4°C; whereas, a relatively minor temperature change (8.8°C to 8.1°C) from November to February did not result in any detectable shift in GPT.

GPT did not differ significantly between *Micropsectra* and *Corynoneura*, despite large differences in taxa size (p > 0.05; Fig. 2). Most *Corynoneura* were smaller than *Micropsectra*, with a mean body length of 1.17 mm (range: 0.69–2.06 mm) vs. 2.81 mm (range: 0.81–5.37 mm) in *Micropsectra*. We found negative relationships between size and displacement in *Micropsectra* for all time treatments (p < 0.05 for T<sub>20</sub> and T<sub>30</sub>, and p = 0.06 for T<sub>10</sub>; Fig. 3). The relationships also tended to be negative for *Corynoneura* but were not significant (p > 0.05; Fig. 3).

*Chironomid density*—Mean monthly chironomid density (± SD) in 2001 was reduced in the resource-limited stream (C55) at 3709 ± 575 chironomids m<sup>-2</sup> vs. 32,061 ± 11,363 chironomids m<sup>-2</sup> in the reference stream (C53). Three years

Table 4. Mean percent posterior pigment displacement in larval chironomid guts after 10 min, 20 min, and 30 min in July 2005 and November 2005, for *Micropsectra* (ranges in parentheses).

	10 min	20 min	30 min
July	32.7	53.4	81.8
Posterior displacement	(16.6–55.7)	(25.5–100)	(46.9–100)
n	76	51	60
November	26.7	39.1	51.9
Posterior displacement	(14.8–41.2)	(16.3–68.4)	(24.2–100)
n	75	40	74

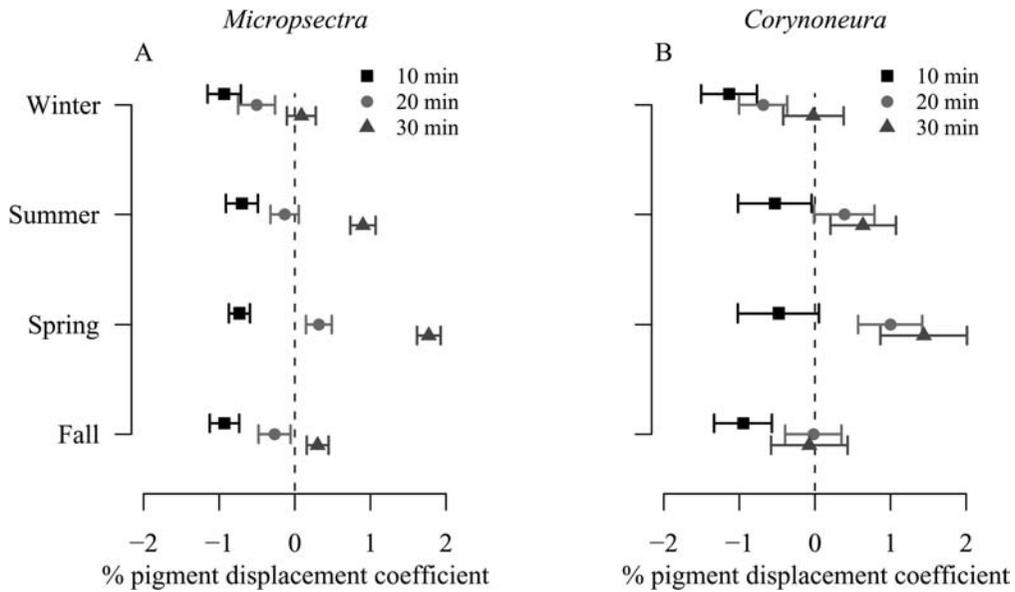


Fig. 1. Effects of season on % posterior pigment displacement for the two focal genera, (A) *Micropsectra* and (B) *Corynoneura*, across three time treatments. Plotted are 95% posterior credible intervals for the  $\alpha$  parameters (from Eq. 2) that describe the effects of season, taxa, and time treatment on % pigment displacement. The effect of season is best assessed by comparing intervals of the same time treatment (same shape). While patterns are consistent across time treatments (summer and spring are higher than winter and fall), the differences become more pronounced over time. Note that the wider intervals for *Corynoneura* reflect a smaller sample size for that genera.

after litter inputs resumed (2005), density in C55 recovered to 21,751 chironomids  $m^{-2}$  but remained below levels observed in C53 where mean density was 37,782 chironomids  $m^{-2}$  (Fig. 4A). Larval sizes of midges in both catchments were skewed toward the smaller size classes, with most individuals < 2 mm (Fig. 5). The proportion of individuals in size class one was greater in the resource-limited system than in the reference system (87% in C55 vs.

70% in C53; Fig. 5). This trend was not detected in the resource-recovery system.

**Organic matter**—Seasonal FPOM standing crops were consistently higher in the reference stream than in the treatment stream (Fig. 4B). The treatment stream exhibited no temporal changes in standing crop. In 2001, mean seasonal standing crop was 770.7 g AF dry wt  $m^{-2}$  in C53 vs. 318.9 g AF dry wt  $m^{-2}$  in C55. Mean standing crops in 2005 were 748.6 g AF dry wt  $m^{-2}$  and 346.7 g AF dry wt  $m^{-2}$  in C53 and C55 respectively. Storage exceeded export in both catchments in 2001, while export

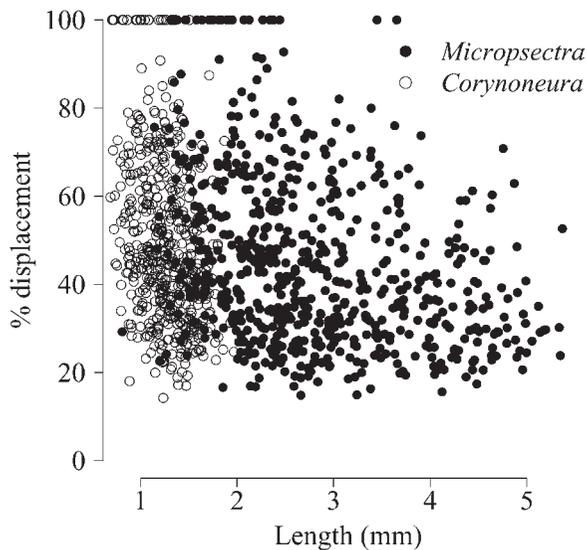


Fig. 2. Relationships between % posterior pigment displacement and midge length (mm) among two focal genera, *Micropsectra* and *Corynoneura*.

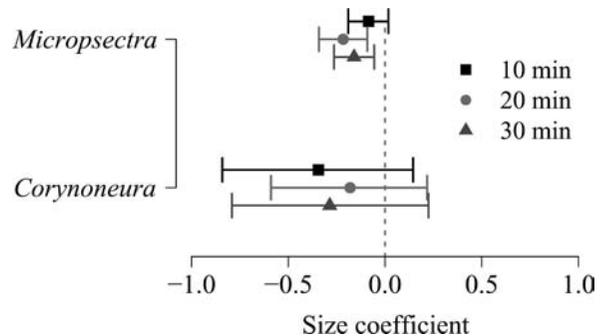


Fig. 3. The effect of midge size on percent posterior pigment displacement ( $\beta$  parameters from equations in text). Shown are 95% posterior credible intervals for the effect of size on displacement in each species and in each time treatment. Interval widths reflect the certainty of these estimates. Intervals not overlapping zero (vertical dashed line) can be considered significantly different from zero at the 95% level.

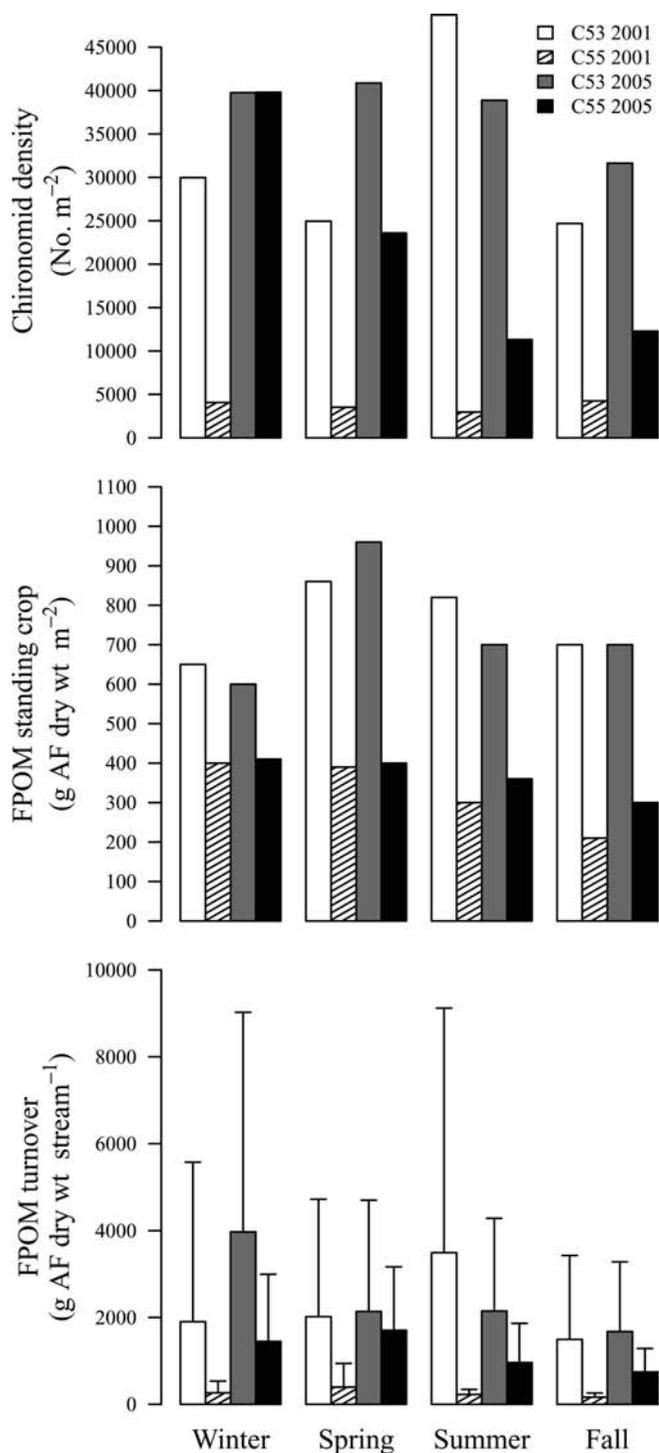


Fig. 4. (A) Seasonal averages of the number of chironomids per m<sup>2</sup>; (B) FPOM standing crops (g AF dry wt m<sup>-2</sup>), and (C) estimates of FPOM turnover in resource-limited (Catchment 55 during 2001), resource-recovery (Catchment 55 during 2005), and reference (Catchment 53 during 2001 and 2005) streams. Error bars represent upper 95% credible intervals in (C).

exceeded storage in both catchments in 2005 (Table 5). Higher export in 2005 corresponded to a higher mean annual discharge in 2005 (1.40–1.98 L s<sup>-1</sup> in 2005 vs. 0.22–0.37 L s<sup>-1</sup> in 2001).

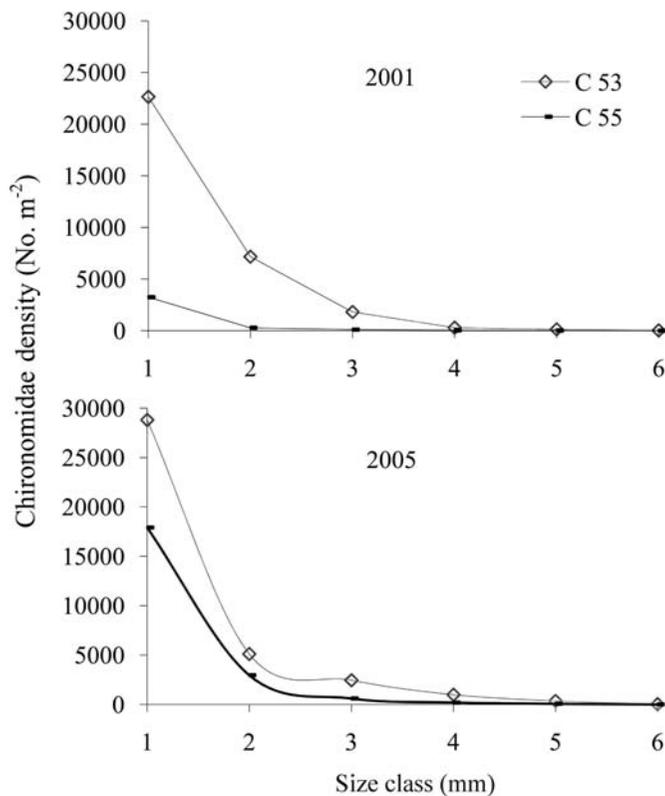


Fig. 5. Size frequency distributions of non-Tanypodinae chironomids from mixed substrate habitats in reference (Catchment 53) and resource-limited (Catchment 55) systems in 2001 and 2005.

**FPOM turnover**—Annual FPOM turnover in the resource-limited stream (5.5 kg stream<sup>-1</sup> yr<sup>-1</sup>, 12% of export) was lower than in the reference stream (46.2 kg stream<sup>-1</sup> yr<sup>-1</sup>, 74% of export) (Fig. 4C; Table 5). Turnover during resource-recovery (23.6 kg stream<sup>-1</sup> yr<sup>-1</sup>, 26% of export) was five times higher than in the resource-limited year but remained lower than levels observed in the reference stream (52.7 kg stream<sup>-1</sup> yr<sup>-1</sup>, 34%) (Fig. 4C; Table 5). We did not detect any seasonal trends in turnover (Fig. 4C).

**Secondary production and assimilation efficiency**—Annual secondary production of chironomids in the reference stream was 1.26 g AF dry wt m<sup>-2</sup> yr<sup>-1</sup> in 2001 and 1.88 g AF dry wt m<sup>-2</sup> yr<sup>-1</sup> in 2005. In the treatment stream annual secondary production rates were 0.134 g AF dry wt m<sup>-2</sup> yr<sup>-1</sup> and 0.783 g AF dry wt m<sup>-2</sup> yr<sup>-1</sup> in each year, respectively. Estimates of assimilation efficiency appeared to be very low in both streams and both years, ranging from 1.7% to 2.5% (Table 5).

## Discussion

The processing and cycling of organic matter is fundamental to the functioning of stream ecosystems. In detritus-based systems, significant attention has been paid to the processing of coarse particulate organic matter

Table 5. Assimilation efficiency, FPOM turnover, export, and storage by non-Tanypodinae chironomids in mixed-substrate habitats for reference (C53) and treatment (C55) streams at Coweeta Hydrologic Laboratory in 2001 (resource-limited year) and 2005 (resource-recovery year). Measures are in units of ash-free dry weight. Stream wetted area was a constant used to estimate catchment-level turnover (C53 = 207 m<sup>2</sup>; C55 = 247 m<sup>2</sup>).

Year:	2001		2005		
	Catchments:	53	55	53	55
Assimilation efficiency (%)		1.7	1.8	2.2	2.5
FPOM turnover (kg stream <sup>-1</sup> yr <sup>-1</sup> )		46.2	5.5	52.7	23.6
FPOM export (kg stream <sup>-1</sup> yr <sup>-1</sup> )		62.4	45.1	258	145
FPOM storage (kg stream <sup>-1</sup> yr <sup>-1</sup> )		159.5	78.8	170.6	90.2
Turnover as a proportion of export (%)		74	12.1	20	16
Turnover as a proportion of storage (%)		28.9	6.9	34	26

(CPOM) by shredder invertebrates; however, the role of collector invertebrates in stream organic matter dynamics is not as well understood. In particular, despite the dominance of chironomids in freshwater systems, very little is known about their contribution to organic matter processing in streams. We have shown in this study that the chironomid contribution to organic matter turnover is likely to be substantial and also context-dependent, with significant variation across seasons and stream resource conditions.

*Gut passage time*—The observed mean GPTs, between 39 min and 67 min for midges *Micropsectra* and *Corynoneura* at Coweeta, were similar to feeding rates measured for other freshwater detritivores. The fastest reported feeding rates belong to the filter-feeding larval black fly, *Simulium tescorum*, which can clear its gut in as little as 10 min (Mulla and Lacey 1976). Other studies have found GPTs ranging from 20 min to 75 min for larval black flies (Wotton 1978b; Lacey and Lacey 1983; Schroder 1988), between 2 h and 3 h for deposit feeding mayflies (Mattingly 1987b), and between 0.5 h and 2 h for the freshwater amphipod, *Gammarus pulex*, and the eurythermal chironomid, *Pseudochironomus richardsoni* (Welton et al. 1983; Gresens 2001). In contrast to these relatively rapid GPTs, phantom crane fly larvae, *Ptychoptera townesi*, were shown to retain material in their guts for up to 26 h (Mattingly 1987a).

Variation in feeding rates may reflect generalized vs. specialized strategies of resource utilization (Mattingly 1987b). Detritivores exhibiting rapid GPTs pass high volumes of low-quality food through the gut very quickly, assimilating only a small portion of the most labile material. Midges in this study exhibited rapid feeding rates and low assimilation efficiencies, and thus are probably generalist consumers. In comparison, resource utilization by *P. townesi* involved the relatively slow handling of small volumes of food and selective consumption of high quality FPOM derived from flocculated dissolved organic matter (Mattingly 1987a).

Temperature is one major factor influencing the handling and processing of food by freshwater invertebrates. Our finding of more rapid gut-passage times at higher temperatures is consistent with other studies suggesting

faster food processing by aquatic invertebrates at warmer temperatures. For example, Mulla and Lacey (1976) reported that black fly feeding rates became two to three times more rapid when temperatures rose from 12.8°C to 30°C. In a temperature range similar to that of the present study, feeding rates in *Gammarus pulex* slowed considerably when temperatures dropped from 13.8°C to 7°C (Welton et al. 1983). This is comparable to what we found in larval chironomids, with the fastest mean GPT in the warmest month (July) and the slowest mean GPT in the coldest month (February).

Invertebrate responses to temperature are probably dependent on the thermal characteristics of their habitats. Ectothermic animals inhabiting stable thermal environments are generally more sensitive to shifts in ambient temperature (Huey and Kingsolver 1989; Gresens 2001) than those adapted to highly variable thermal regimes. In habitats with widely fluctuating temperature regimes, feeding rates that are less dependent on temperature may gain a selective advantage. For example, the eurythermal chironomid, *Pseudochironomus richardsoni*, consumed food more rapidly when exposed to an 8°C increase in temperature (13°C to 21°C), but a 3°C change in temperature (10°C to 13°C) did not have an effect on feeding rates (Gresens 2001). In contrast, we found that GPTs slowed significantly with a relatively small drop in temperature (12.7°C to 8.8°C) between May and July in our study midges. Heavy shading and groundwater inputs at Coweeta streams provide a relatively stable thermal environment compared to the highly variable thermal habitats of *P. richardsoni* (i.e., cold groundwater seeps to sunlit pools) (Gresens 2001).

The slight negative relationship between consumption rate and body size in *Micropsectra* is consistent with previous studies of freshwater detritivores (Cammen 1980). The more rapid feeding rate of small larvae may be a mechanism to offset the higher respiratory costs (Wotton 1978a). Due to their simple, tube-like guts, smaller chironomid larvae may have faster GPTs simply because food has less distance to travel in a short gut. On the other hand, the absence of a size effect in *Corynoneura* is probably attributed to its consistently small larval size. *Corynoneura* reaches a terminal size of ~1.5–2.5 mm and is multivoltine, exhibiting continuous emergence throughout

the year, whereas *Micropsectra* reaches a terminal size of  $\sim 5.5$  mm and is bivoltine (Huryn 1990). Despite these differences in taxa size and voltinism, *Micropsectra* and *Corynoneura* did not exhibit significantly different rates of consumption. This finding is similar to what has been observed for cohabitating black fly species (Ladle et al. 1972; Wotton 1978a).

The variability in chironomid feeding rates at Coweeta was much higher than that observed for suspension-feeding black flies (Ladle et al. 1972; Mulla and Lacey 1976; Lacey and Lacey 1983), but comparable to the freshwater amphipod *Gammarus pulex* (Welton et al. 1983). These differences in variability could partly reflect differences in research design that resulted from the different feeding strategies of target organisms. In studies of suspension-feeding black flies, food-labels were added to the water column where markers would encounter seston, thus giving label additions a pulsed nature. In our study, and that of Welton et al. (1983), the label was applied to benthic substrates such that deposit-feeding chironomids and amphipods probably encountered food-labels with less uniformity than did suspension-feeding black flies.

**Assimilation efficiency**—The ability of aquatic invertebrates to extract nutrition varies greatly with the quality and quantity of food consumed (Gresens 2001). For invertebrates consuming low-quality detritus, it may be energetically more efficient to feed continuously while assimilating microbes and exopolymers stripped easily from the surface, particularly when food is not limiting. Midges at Coweeta, which generally have access to copious amounts of relatively low-quality detritus, were estimated to have very low AEs ranging from 1.7% to 2.5%. Similarly, black flies feeding on detritus assimilated only 1.8% of material consumed (Wotton 1978a), and the deposit-feeding midge, *Chironomus riparius*, was found to assimilate 6% of food consumed. Conversely, invertebrates that consume relatively high-quality food may gain an energetic advantage from assimilating a greater fraction of ingested material. For example, larval midges fed on a relatively high-quality diet of diatoms exhibited AEs of  $\sim 32\%$  (Gresens 2001), likewise *Tricorythodes minutus* mayfly nymphs assimilated 33–57% of nutritionally rich diets comprised of cyanobacteria, diatoms, and algae (McCullough et al. 1979).

**FPOM turnover**—Our estimates for chironomid contribution to FPOM export (12–74%), which only represent a subset of the overall collector community, were much higher than the 5.2% predicted by Webster (1983) for the entire collector community in a nearby Appalachian stream. This difference is most probably due to Webster's use of a large, mesh Surber sampler to collect invertebrates which resulted in underestimates of abundance. Our estimates of turnover are similar to those measured for collector-macroinvertebrates in a warm, high-productivity desert stream, which consumed up to 30% of organic matter available to them per day (Fisher and Gray 1983).

When viewed as a proportion of export, FPOM turnover is dependent on both invertebrate processing of detritus

and stream discharge. The downstream transport of organic matter in our study streams is strongly related to discharge (Wallace et al. 1991). An experimental reduction of invertebrate abundances in these streams indicated that invertebrate contribution to FPOM export is comparable to that provided by discharge (Wallace et al. 1991). In the present study, FPOM export in both catchments was much lower in 2001 than in 2005 because of a six times greater discharge in 2005. During the low discharge year, chironomids turned over 74% of export vs. 20% during normal discharge. Thus, invertebrate contribution to FPOM turnover becomes more significant in times of low discharge or drought. Under normal discharge, export exceeded storage by up to 1.6 times, dictating the continual replacement and turnover of FPOM, whereas low discharge in 2001 suppressed this effect.

Mean annual FPOM turnover is expected to be related to midge density, which is ultimately dependent on the availability of resources. Considerably lower rates of turnover in the resource-limited catchment (C55) relative to the reference stream supported this hypothesis. Mean annual turnover of  $5.5 \text{ kg stream}^{-1}$  in the resource-limited system was more than eight times smaller than the  $46.2 \text{ kg stream}^{-1}$  in the reference stream. This difference can be attributed to extremely low midge densities in C55, especially in large size classes. Short-lived chironomid taxa, such as *Corynoneura*, complete more than seven generations per year and generally emerge before reaching 2 mm in length (Huryn 1990), while univoltine or bivoltine taxa (e.g., *Micropsectra*) must reach a larger terminal length to successfully pupate and emerge. Therefore, the greater proportion of small individuals in C55 may indicate that resource-limitation favors the success of small, multivoltine taxa as indicated by Entekin et al. (2007). However, this trend could instead indicate that chironomids in the resource-limited system did not reach terminal body size, probably due to insufficient food resources. For example, Wallace et al. (1999), suggested that resource limitation prevented taxa in these same streams from reaching mature size classes, even among individuals that were able to utilize alternate food resources.

Reduced midge densities could have also resulted from experimental exclusion of allochthonous litter if there were increased predation due to the removal of leaves which serve as prey cover. This appears not to be the case, however, as predators comprised a smaller proportion of the macroinvertebrate community in the resource limited stream (28.9% of community abundance) than in the reference stream (36% of community abundance) (S. L. Eggert and J. B. Wallace unpubl.).

The large contribution to turnover and low assimilation efficiencies of these abundant and ubiquitous invertebrates raises additional questions about midge resource utilization and general life-history strategies. Material egested by chironomids can either be exported downstream or redeposited onto benthic substrates where it remains available to midges or other headwater consumers as a food resource. Low AEs and rapid turnover of FPOM in these streams, along with no plausible mechanism to avoid reingestion, suggests chironomid reingestion of feces.

Indeed, coprophagy has been observed in midges, black flies, baetid mayflies, and oligochaetes (Wotton et al. 1998), and also probably supported high levels of secondary production observed in a desert stream (Fisher and Gray 1983). The economics of coprophagy suggest an enhancement of food quality that warrants the expense of re-collecting and reprocessing fecal material (Wotton 1980; Fisher and Gray 1983; Wotton and Malmqvist 2001). Bacterial colonization and conditioning of feces may improve its digestibility and nitrogen content (Fisher and Gray 1983). Feces may also provide an important homeostasis function in streams by providing a continuous supply of organic material once seasonal inputs of leaf litter are consumed (Shepherd and Minshall 1984; Joyce and Wotton 2008). Chironomids also incorporate fecal particles into sediments used to construct the tubes in which they live (Hirabayashi and Wotton 1998; Wotton and Malmqvist 2001).

In summary, rapid GPTs and low assimilation efficiencies suggest that detritivorous midges in this study rely on a particle-stripping method of resource utilization, in which microbes are assimilated rather than more recalcitrant substrate. Additionally, low AEs and rapid turnover suggest the reprocessing of particulate material via coprophagy. Chironomids turned over a large portion of FPOM available to them, demonstrating the importance of the chironomid contribution to FPOM turnover. The rate of FPOM turnover by the entire collector community in forested headwater streams is probably very large.

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