

## Macroinvertebrate secondary production in 3 forested streams of the upper Midwest, USA

Sally A. Entrekin<sup>1</sup>, Emma J. Rosi-Marshall<sup>2</sup>, Jennifer L. Tank<sup>3</sup>,  
Timothy J. Hoellein<sup>4</sup>, AND Gary A. Lamberti<sup>5</sup>

*Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556-0369 USA*

**Abstract.** Macroinvertebrate secondary production was estimated for 2 reaches in each of 3 adjacent forested headwater streams. We had 3 objectives: 1) to compare macroinvertebrate secondary production and community structure both within and among streams to examine the spatial extent of variability, 2) to explore important habitat variables related to secondary production, and 3) to compare our secondary production values to values from other headwater streams in deciduous forests. Principal components analysis separated study streams on the basis of small differences in substrate composition, organic-matter standing crops, and instream wood, but geology, riparian tree species composition, and fine benthic organic-matter standing crops were similar among streams. Secondary production varied among streams (range ~1.2 to 3.3 g ash-free dry mass m<sup>-2</sup> y<sup>-1</sup>) and was low compared to estimates from other streams draining deciduous forest. Macroinvertebrate communities had relatively higher production of scrapers, predators, and collector-filterers and lower production of shredders and collector-gatherers as compared to other perennial eastern deciduous headwater streams. We expected differences in secondary production among streams to be related to leaf-litter standing crops; however, differences among streams were positively related to % cover of gravel and cobble and chlorophyll *a* concentrations on gravel ( $R^2 = 0.87$ ,  $p = 0.01$ ). Total secondary production was negatively related to the number of large pieces of wood, leaf-litter standing crop, and % cover of sand. A similar, positive relationship between % cover of gravel and cobble and chlorophyll *a* concentrations was found for primary consumers ( $R^2 = 0.89$ ,  $p = 0.03$ ), collector-filterers ( $R^2 = 0.76$ ,  $p = 0.02$ ), and scrapers ( $R^2 = 0.67$ ,  $p = 0.04$ ). Low amounts and patchy distributions of coarse benthic organic matter, leaf litter, and large wood probably resulted in more variable secondary production of predators and shredders within these streams than among all streams. Inorganic substrate composition, primary production, and water temperature probably were key factors regulating secondary production of the other functional feeding groups and total secondary production among streams.

**Key words:** macroinvertebrate secondary production, headwater streams, leaf litter, functional feeding groups, Midwestern streams.

In streams, secondary production reflects population-, community-, and ecosystem-level dynamics of macroinvertebrates and incorporates survivorship, density, and individual growth (Benke 1993, Huryn and Wallace 2000). Secondary production is the total tissue mass produced for each taxon during a given period of time regardless of its fate (see Waters 1979, Benke and Huryn 2006). Production estimates require

collection of community-structure metrics, such as taxonomic composition and diversity, and ecosystem-level measurements, such as production of secondary and tertiary consumers in a stream. Therefore, macroinvertebrate secondary production is an excellent indicator of ecosystem change resulting from natural (e.g., Leeper and Taylor 1998, Hauer and Benke 1991) or anthropogenic disturbances (e.g., Wallace et al. 1982, Carlisle and Clements 2005, Pretty et al. 2005).

Macroinvertebrate taxa have been categorized into morpho-behavioral groups or functional feeding groups to draw inferences about ecosystem characteristics (Cummins 1974, Merritt and Cummins 2006). For example, a high ratio of scrapers to shredders in a forested headwater stream might indicate little organic matter retention and relatively high rates of primary

<sup>1</sup> E-mail addresses: sally.a.entrekin.2@nd.edu

<sup>2</sup> Present address: Department of Biology, Loyola University of Chicago, Chicago, Illinois 60626 USA.

E-mail: erosi@luc.edu

<sup>3</sup> jennifer.l.tank.1@nd.edu

<sup>4</sup> timothy.j.hoellein.1@nd.edu

<sup>5</sup> glambert@nd.edu

production. The relative proportion of each functional feeding group, coupled with estimates of resources consumed, can be used to determine whether resources or habitats are limiting the macroinvertebrate community (Benke and Wallace 1980, Iversen 1988, Stagliano and Whiles 2002).

In forested headwater streams, macroinvertebrate secondary production and community structure have been linked to the standing crop of allochthonous organic matter (i.e., leaf litter) (Wallace et al. 1999, Hall et al. 2001, Chadwick and Huryn 2005, Cross et al. 2006). As a consequence, macroinvertebrate production in such streams typically is dominated by shredding and collector-gathering macroinvertebrates (Fisher and Likens 1973, Grubaugh and Wallace 1995, Whiles and Wallace 1997). In low-gradient sand-bottom streams, shredders typically are more productive where debris dams retain allochthonous food resources, whereas collector-gatherers are productive in dams and in the sandy benthos (Roeding and Smock 1989, Tillman et al. 2003). Conversely, production of collector-filterers and scrapers often is regulated by available stable substrates, such as snags and boulders (Smock et al. 1989).

Instream structures (e.g., large wood, boulders) in low-order forested streams retain large amounts of coarse (CPOM) and fine (FPOM) particulate organic matter (Lamberti and Berg 1995, Wallace et al. 1995). This organic matter is then consumed by a predictable community of organisms with specific mouthparts, enzymes, or gut fauna adapted to processing material with high lignin and cellulose content (Cummins 1974, Cummins and Klug 1979, Sinsabaugh et al. 1993). However, if the organic matter is exported downstream in an unprocessed state, it is in a form too large and unpalatable for filtering, scraping, or collector-gathering invertebrates (Cummins 1974, Bilby and Likens 1980). Therefore, the extent of organic matter retention and processing in headwaters influences both local and downstream macroinvertebrate community structure.

Secondary production and community structure of macroinvertebrates also can vary among streams that differ in local geomorphology, wood snags, and debris accumulations (Huryn and Wallace 1987, Wohl et al. 1995, Chadwick and Huryn 2007). Streams with similar geomorphology, land use, and water chemistry often are assumed to have similar levels of production, but this assumption is rarely tested.

Secondary production of macroinvertebrate communities also can vary longitudinally and among discrete habitats within a stream (e.g., Smock et al. 1985, Huryn and Wallace 1987, Grubaugh and Wallace 1995, Buffagni and Comin 2000, Chadwick and Huryn

2007) and among streams draining adjacent watersheds (e.g., Wallace et al. 1999, Cross et al. 2006). Substrate distribution and stream-channel heterogeneity are important factors determining macroinvertebrate community composition (Huryn et al. 2005). However, few studies have explored the specific factors responsible for variation in secondary production among multiple streams (but see Krueger and Waters 1983, Huryn and Wallace 1987) and among stream reaches in a single watershed (but see Smock et al. 1985, Grubaugh and Wallace 1995, Chadwick and Huryn 2007).

We had 3 objectives: 1) to compare macroinvertebrate secondary production and community structure both within and among headwater streams in deciduous forested systems to examine the spatial extent of variability, 2) to explore important habitat variables related to secondary production, and 3) to compare our secondary production values to values in other headwater streams in deciduous forests. Our data are the pretreatment data collected for a larger experimental study of the effects of large wood addition to streams; therefore, each stream had an upstream control reach and downstream treatment reach to which wood was later added. Our study also provided novel data on macroinvertebrate secondary production for an understudied region in North America, the upper Midwest.

## Methods

### *Study area*

We studied three 1<sup>st</sup>-order streams (Shane Creek, State Creek, and Walton Creek) located in the 2<sup>nd</sup>-growth forest of the Ontonagan River watershed in the Upper Peninsula of Michigan (lat 46°28'N, long 89°1'W). All 3 streams are located in the Ottawa National Forest and drain small watersheds of young forest with intact riparian areas. The Shane Creek watershed is 83% forested, the State Creek watershed is 95% forested, and the Walton Creek watershed is 85% forested (<http://pasture.ecn.purdue.edu/~watergen>). The remainder of each watershed is predominantly wetland. Riparian trees include young hemlock (*Tsuga canadensis* L.), white pine (*Pinus alba* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and paper birch (*Betula papyfera* L.) typical of the region. Shane Creek resides on a lake plain of coarse-to-fine-texture materials and was last logged in 1967. State Creek has a surficial geology of coarse-texture terminal moraine and was last logged in 1967. Walton Creek drains recessional moraine of coarse-texture material and was last logged in 1915 (Miesbauer 2004). In each stream, we focused our

sampling on two 100-m study reaches separated by a 20- to 50-m buffer reach as an antecedent to the later large-wood addition.

#### *Secondary production*

We sampled benthic macroinvertebrates within the stream channel approximately monthly from May 2003 through April 2004 (9 intervals). Snow and ice cover prohibited sampling in December, January, and February. On each sampling date, we took 5 benthic samples using a 32-cm-diameter Hess sampler (500- $\mu$ m mesh) down to 10 cm in the streambed in each stream reach. Hess sampling excluded boulders and debris dams. We preserved macroinvertebrates in 6 to 8% formalin and sorted them from debris using a dissecting microscope (15 $\times$  magnification). We identified macroinvertebrates to genus using keys in Merritt and Cummins (1996), Epler (2001), Hilsenhoff (1995), and Wiederholm (1983), counted them, and measured their body length (nearest 1 mm). One replicate sample was lost during processing. We estimated biomass using length–mass regressions in Benke et al. (1999). We estimated secondary production using the size–frequency method for common taxa with a correction for cohort production interval (CPI) using size–frequency histograms (Benke 1984, Benke and Huryn 2006). For rare taxa, we estimated secondary production using published production to biomass (P/B) ratios (Krueger and Waters 1983) or our own P/B ratios estimated from the study streams. We quantified chironomid production using the instantaneous growth method, where growth was estimated using temperature and size-specific growth rates in Walther et al. (2006). We assigned functional feeding groups using Merritt and Cummins (1996) and Wohl et al. (1995).

#### *Habitat variables*

We measured CBOM and FBOM standing crops from five 804-cm<sup>2</sup> cores (collected separately from the invertebrate samples) from each stream reach. We sampled both benthic organic matter fractions concurrently with macroinvertebrate sampling; however, FBOM was not sampled in July 2003. We separated CBOM, including leaf litter, using a 1-mm sieve. We oven-dried CBOM at 60°C, sorted it by organic matter type (leaves, moss, and wood), and weighed each component. We took a subsample of each organic matter type, combusted it at 550°C, and reweighed it to determine ash-free dry mass (AFDM) (Benfield 2006). We sampled FBOM after CBOM was removed from the corer. We made a slurry by mixing sediment in the corer and subsampled the slurry. We stored the

subsamples on ice. In the laboratory, we filtered the subsamples onto glass-fiber filters. We dried the filters at 60°C, weighed them, combusted them at 550°C, and reweighed them to determine AFDM.

We estimated discharge monthly in each stream reach, except from November through February because of ice cover. We estimated discharge using the midsection method described by Gore (2006). We measured water velocity using a Marsh–McBirney flow meter.

We recorded water temperature at the bottom of each stream reach hourly from May 2003 through April 2004 using HOBO® data loggers (Onset Computer Corporation, Bourne, Massachusetts). We experienced logger failure in some months; therefore, temperatures from both loggers were used to measure within-stream temperature. We checked reach-level differences in temperature by comparing values between the 2 reaches when both loggers were collecting data. Temperature differences between reaches were  $\leq 0.5^\circ\text{C}$ . We calculated cumulative annual degree days as the sum of mean daily temperature during the study period (Minshall and Rugenski 2006), and we assigned mean daily temperatures to seasons (summer = July–September, autumn = October–November, winter = December–March, spring = April–June).

We conducted benthic habitat surveys using lateral transects spaced every 5 m (perpendicular to flow) in each stream in May and August 2003 ( $n = 21$  transects per date in each reach). For each transect, we categorized substrates using the Wentworth scale (Minshall 1984). Inorganic substrates were classified as boulders, gravel and cobble, and sand. We classified organic substrates as moss, CBOM (<1 mm), silt, small wood (<10 cm), and large wood (>10 cm) measured every 10 cm across the channel. We calculated % cover for each substrate category at each transect. Reach-level substrate % cover values were the means of each category across all transects.

We collected 5 replicate 28.7-cm<sup>2</sup> cores from predominantly gravel habitat each month, except for January, in each reach from May 2004 to May 2005 (11 intervals). We assumed that mean annual chlorophyll *a* on gravel was representative of standing crops in streams for 2003. We froze gravel samples and extracted chlorophyll *a* from them in the laboratory using the hot ethanol method (modified from Sartory and Grobbelaar 1984). We quantified chlorophyll *a* with a fluorometer and converted the values to an areal basis by weighting chlorophyll *a* concentration by the proportion of gravel in each reach. The estimate is conservative because it assumes no chlorophyll *a* on any other substrate within the reaches.

### *Food consumption by selected functional feeding groups*

We determined the proportions of different food resources consumed by functional feeding groups by estimating consumption as annual production (P) of each selected feeding group divided by gross production efficiency (GPE), where GPE equals assimilation efficiency multiplied by net production efficiency. We obtained assimilation and net production efficiencies from Stagliano and Whiles (2002). This estimate enabled us to calculate the proportion of measured organic matter and prey consumed by the macroinvertebrate community in each reach during the study period. We measured the best available estimates of the amount of available food for shredders as mean leaf-litter standing crop, for collector-gatherers as FPOM standing crop, and for predators as total secondary production (as in Benke and Wallace 1980, Stagliano and Whiles 2002). Food resource data were not available for calculating scraper or filterer consumption.

### *Data analysis*

*Habitat variables.*—We evaluated mean annual differences in habitat variables among streams and between reaches within streams using a nested analysis of variance (ANOVA). We evaluated significant differences among means using Tukey's multiple comparison tests. We transformed variables to meet the assumptions of ANOVA. We included chlorophyll *a* on gravel ( $n = 66$ ), % gravel and cobble cover ( $n = 12$ ), % sand cover ( $n = 12$ ), leaf-litter standing crop ( $n = 54$ ), FBOM standing crop ( $n = 48$ ), and total CBOM standing crop ( $n = 54$ ) in the analysis. We transformed data, if necessary, to meet ANOVA assumptions.

*Macroinvertebrate density and biomass.*—We evaluated mean annual differences in benthic macroinvertebrate density and biomass among streams, between reaches within streams, and among months using a nested 2-factor repeated measures ANOVA (rmANOVA) ( $n = 269$ ). We evaluated significant differences among means using least squares means with a Tukey's correction for multiple comparisons. Macroinvertebrate density and biomass were log transformed to meet the assumptions of ANOVA.

*Macroinvertebrate secondary production.*—We evaluated differences in mean annual total secondary production and functional feeding group production among streams using 1-way ANOVA followed by Tukey's test.

We used principal components analysis ([PCA] PC-ORD, version 4; MjM Software Design, Glenden Beach, Oregon) to separate streams and reaches based on differences in habitat variables. We included chlorophyll *a* on gravel, % gravel and cobble cover, % sand

cover, leaf-litter standing crop, number of large wood pieces/100 m of stream length, FBOM standing crop, and total CBOM standing crop as habitat variables. We used PCA to reduce these variables to principal components (PC) that could be used as explanatory variables in linear regressions. We used multiple linear regressions ( $\alpha = 0.05$ , maximum  $R^2$ ) with PC 1 and PC 2 as explanatory variables to explore relationships among habitat variables and variation in total macroinvertebrate secondary production among and within streams (3 streams  $\times$  2 reaches/stream;  $n = 6$ ). Assumptions of independence required for linear regression were violated by considering each stream reach independently. However, because of the absence of replication, we believe this method was the best way to explore relationships between secondary production and environmental variables. We used SAS (version 9.1; SAS Institute, Cary, North Carolina) to run all analyses except the ordination.

## Results

### *Habitat variables*

Habitat variables did not differ between reaches within streams. However, several habitat variables differed among streams. Mean annual CBOM standing crop was higher in Shane Creek and Walton Creek than in State Creek ( $F_{2,51} = 4.47$ ,  $p = 0.016$ ; Table 1). Percent gravel and cobble cover ( $F_{2,9} = 8.70$ ,  $p = 0.01$ ; Table 2) and chlorophyll *a* on gravel ( $F_{2,63} = 3.97$ ,  $p = 0.02$ ; Table 1) were higher in State Creek than in Shane Creek and Walton Creek. Percent sand cover was lower in State Creek than in Shane Creek and Walton Creek ( $F_{2,9} = 7.42$ ,  $p = 0.02$ ; Table 2).

### *Macroinvertebrate density and biomass*

Mean annual macroinvertebrate density did not differ among streams (Fig. 1A) or between reaches (data not shown). Monthly mean densities were higher in July than in May, August, and September ( $F_{9,259} = 2.80$ ,  $p = 0.003$ ) with no significant month  $\times$  stream (or reach) interaction (Fig. 2A; reach data not shown). Mean annual macroinvertebrate biomass was greater in State Creek than in Shane Creek ( $F_{2,266} = 7.41$ ,  $p = 0.008$ ; Fig. 1B), but did not differ between reaches (data not shown). Overall monthly mean biomass was greater in October than June and July ( $F_{9,259} = 2.84$ ,  $p = 0.003$ ) with no significant month  $\times$  stream (or reach) interaction (Fig. 2B; reach data not shown).

### *Total and functional feeding group secondary production*

Total macroinvertebrate secondary production was significantly higher in State Creek than in the other 2

TABLE 1. Mean ( $\pm 1$  SE) values of habitat variables in the upstream and downstream reaches of the 3 deciduous forested streams in the upper Midwest, USA. All data were collected during May 2003 to May 2004 unless otherwise noted. CBOM = coarse benthic organic matter, AFDM = ash-free dry mass, FBOM = fine benthic organic matter, Chl *a* = chlorophyll *a*.

| Habitat variable   | Shane Creek   |              | State Creek    |               | Walton Creek |               |
|--|---------------|--------------|----------------|---------------|--------------|---------------|
|  | Upstream      | Downstream   | Upstream       | Downstream    | Upstream     | Downstream    |
| Discharge (L/s)  | 35 $\pm$ 5    | 33 $\pm$ 5   | 63 $\pm$ 6     | 56 $\pm$ 6    | 44 $\pm$ 16  | 43 $\pm$ 16   |
| Bankful width (m)  | 2.3           | 2.5          | 2.7            | 2.9           | 1.9          | 2.6           |
| Slope (%)  | 1.0           | 0.8          | 2.4            | 1.2           | 0.8          | 1.2           |
| Specific conductance ( $\mu$ S/cm)                                 | 85 $\pm$ 9.4  | 82 $\pm$ 9.9 | 142 $\pm$ 10.3 | 140 $\pm$ 9.3 | 71 $\pm$ 8.5 | 71 $\pm$ 8.6  |
| CBOM (g AFDM/m <sup>2</sup> )                                      | 153 $\pm$ 58  | 87 $\pm$ 37  | 90 $\pm$ 35    | 203 $\pm$ 89  | 149 $\pm$ 62 | 266 $\pm$ 115 |
| FBOM (g AFDM/m <sup>2</sup> )                                      | 245 $\pm$ 113 | 111 $\pm$ 50 | 137 $\pm$ 69   | 114 $\pm$ 70  | 113 $\pm$ 58 | 183 $\pm$ 113 |
| Pieces of large wood (no./100 m stream length) <sup>a</sup>        | 20            | 17           | 12             | 11            | 16           | 16            |
| Chl <i>a</i> on gravel (weighted for % cover gravel in the stream) | 12            | 7            | 43             | 70            | 10           | 11            |
| Mean daily temperature ( $^{\circ}$ C) <sup>b</sup>                | 7.4           |              | 6.8            |               | 6.8          |               |
| Mean spring temperature ( $^{\circ}$ C) <sup>b</sup>               | 12.1          |              | 7.4            |               | 8.1          |               |
| Mean autumn temperature ( $^{\circ}$ C) <sup>b</sup>               | 10.7          |              | 11.3           |               | 12.9         |               |
| Mean summer temperature ( $^{\circ}$ C) <sup>b</sup>               | 13.9          |              | 10.9           |               | 10.8         |               |
| Mean winter temperature ( $^{\circ}$ C) <sup>b</sup>               | 1.2           |              | 2.0            |               | 0.9          |               |

<sup>a</sup> Data from Cordova et al. 2007

<sup>b</sup> Values are means of temperatures in upstream and downstream reaches

streams ( $F_{2,3} = 13.57$ ,  $p = 0.03$ ; Fig. 3). Scraper and total primary consumer production was also higher in State Creek than in the other 2 streams ( $F_{2,3} = 48.77$ ,  $p = 0.005$ ;  $F_{2,3} = 43.62$ ,  $p = 0.006$ ; respectively). *Baetis* spp. and *Glossosoma* sp. were the most productive scrapers in all stream reaches except in the upstream reach of Shane Creek where *Optioservus* sp. had the highest production (Appendix). Collector-gatherer production was low in all stream reaches, but significantly lower in Walton Creek than in the other 2 streams ( $F_{2,3} = 27.20$ ,  $p = 0.012$ ). Chironomids were the primary collector-gatherers in all stream reaches, except that *Hesperoconopa* sp. was the primary collector-gatherer in the downstream reach of State Creek (Appendix). Collector-filterer production and taxonomic composition varied both within and among streams, whereas predator and shredder production varied more within streams than among streams (Appendix).

The percentage of secondary production contributed by each functional feeding group differed among

streams and between reaches within a stream (Fig. 4). Generally, predators (20–45% of total production), collector-filterers (16–42%), and scrapers (17–45%) constituted the largest percentages of macroinvertebrate production, whereas collector-gatherers and shredders contributed less to production (2–10%; Fig. 4). The greatest upstream vs downstream differences were in the percentages of scrapers in Walton Creek (upstream: 23%, downstream: 42%) and collector-filterers in State Creek (upstream: 42%, downstream: 25%).

#### Variables influencing macroinvertebrate secondary production

PCA of habitat variables illustrated clear separation among all 3 streams; however, reaches in Walton Creek showed the greatest within-stream differences (Fig. 5). PC 1 explained 61% of the variation among habitat variables in the stream reaches and had an eigenvalue of 4.2, (broken-stick value of 2.6), whereas PC 2

TABLE 2. Mean (May and August 2003) % habitat cover in each stream reach. Values do not add to 100. Organic matter is the sum of small and large wood, leaf litter, and silt % cover.

| Substrate         | Shane Creek |            | State Creek |            | Walton Creek |            |
|-------------------|-------------|------------|-------------|------------|--------------|------------|
|                   | Upstream    | Downstream | Upstream    | Downstream | Upstream     | Downstream |
| Boulder           | 0           | 0          | 1           | 0          | 1            | 5          |
| Cobble and gravel | 35          | 24         | 52          | 53         | 37           | 37         |
| Moss              | 0           | 0          | 16          | 5          | 1            | 1          |
| Organic matter    | 41          | 48         | 19          | 30         | 43           | 28         |
| Sand              | 30          | 35         | 12          | 21         | 22           | 35         |

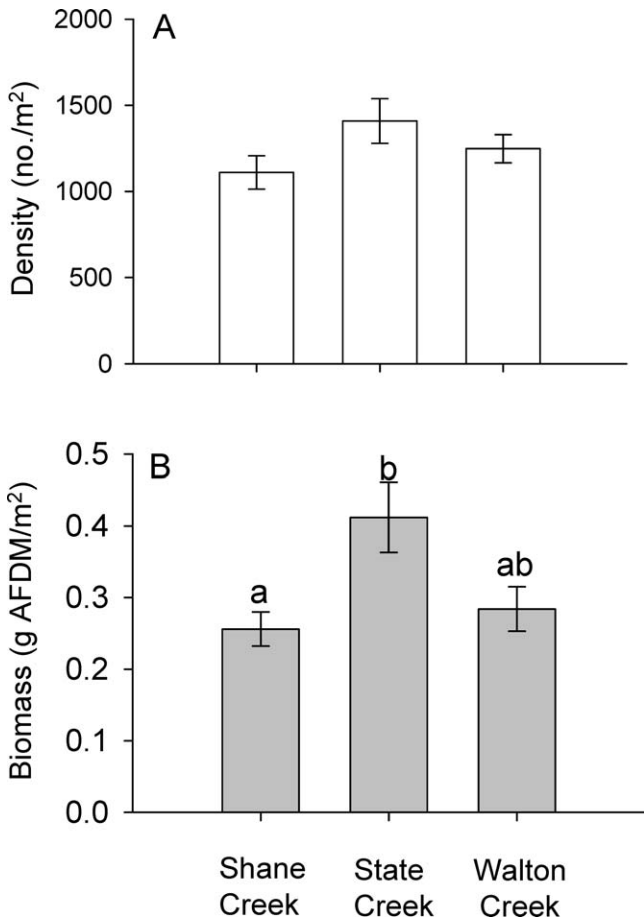


FIG. 1. Mean ( $\pm 1$  SE) annual density (A) and biomass (B) of benthic macroinvertebrates in each study stream. Bars with different letters are significantly different (Tukey's post-hoc test,  $p < 0.05$ ). AFDM = ash-free dry mass.

explained only 19% of the variation among the stream reaches and had an eigenvalue of 1.4 (broken-stick value of 1.6). Upstream and downstream reaches in State Creek were associated with greater % cover of gravel and cobble and higher concentrations of chlorophyll *a* on gravel. Stream reaches in Shane Creek and Walton Creek were distinct from reaches in State Creek in having a higher % cover of sand, more pieces of large wood, and higher leaf-litter standing stock (Table 3, Fig. 5), all of which were highly correlated with one another. CBOM standing crops were positively correlated with PC 2, which separated the downstream reaches of State Creek and Walton Creek from the other stream reaches despite explaining little of the variation in the data.

Total, primary consumer, scraper, and collector-filterer secondary production were positively correlated with PC 1 and were associated with greater % cover of gravel and cobble substrate and higher concentrations of chlorophyll *a* on gravel, which were highly

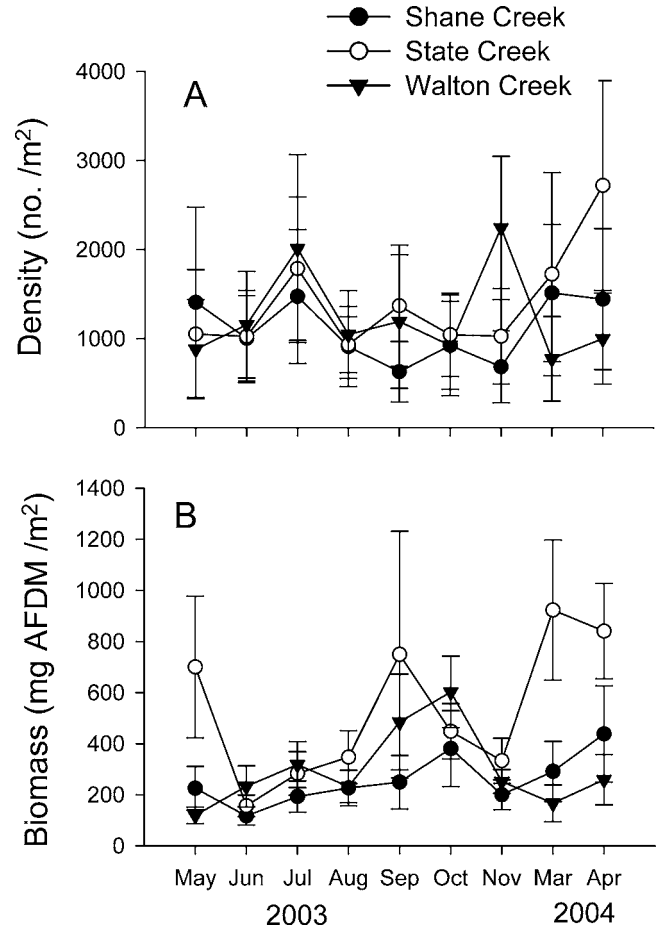


FIG. 2. Mean ( $\pm 1$  SE) monthly density (A) and biomass (B) of benthic macroinvertebrates in each study stream. AFDM = ash-free dry mass.

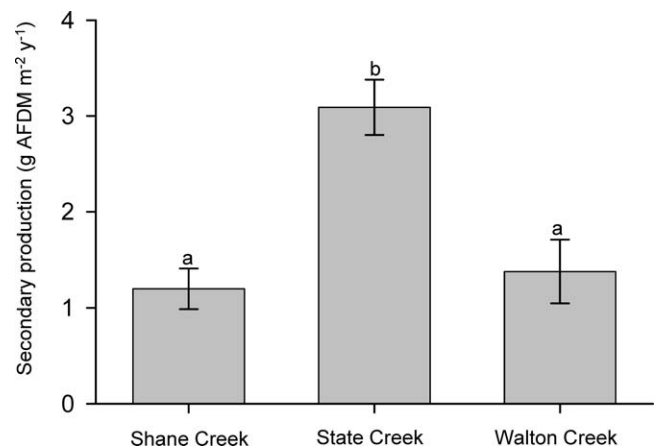


FIG. 3. Mean ( $\pm 1$  SE) annual secondary production of benthic macroinvertebrates in each study stream for the period May 2003 to May 2004. Bars with different letters are significantly different (Tukey's post-hoc test,  $p < 0.05$ ). AFDM = ash-free dry mass.

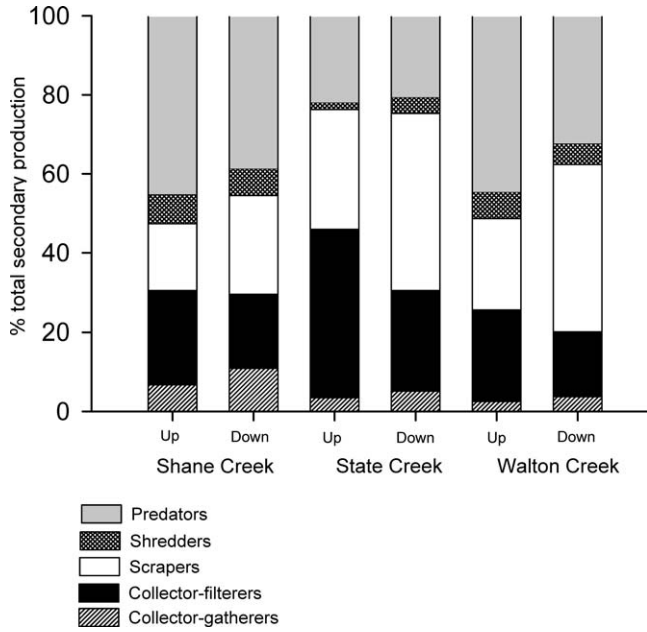


FIG. 4. Secondary production of each functional feeding group as % total secondary production in the upstream (Up) and downstream (Down) reaches of the study streams. AFDM = ash-free dry mass.

correlated with each other. Furthermore, Axis 2, which incorporated differences in CBOM (positive relationship), explained additional variation in total, scraper, and primary consumer production. Collector-gatherer,

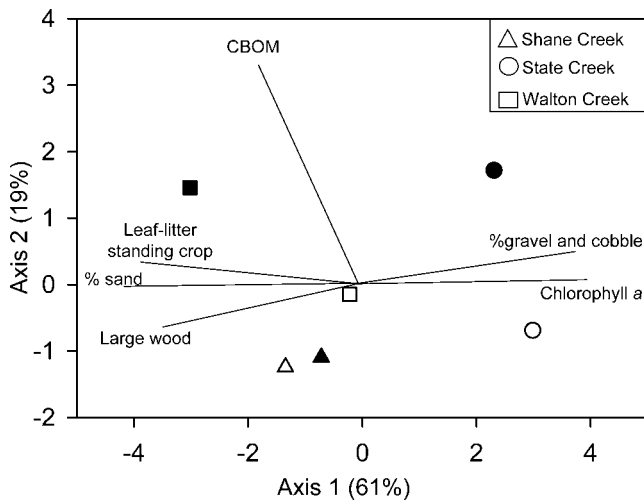


FIG. 5. Principal components analysis of habitat variables in the study streams. Habitat variables are represented as vectors, with longer vectors indicating a higher correlation with the closest axis. See Table 1 for variables and their units. Mean annual leaf-litter standing crop, coarse benthic organic matter (CBOM), and fine benthic organic matter (FBOM) were  $\log_{10}(x)$  transformed. Open symbols represent upstream reaches, and shaded symbols represent downstream reaches. Large wood = number of pieces of large wood.

TABLE 3. Correlation coefficients for habitat variables and principal components (PC) 1 and 2. CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter, AFDM = ash-free dry mass, Chl *a* = chlorophyll *a*.

| Habitat variable   | PC 1  | PC 2  |
|--|-------|-------|
| % sand   | -0.93 | 0.19  |
| Leaf-litter standing crop (g AFDM/m <sup>2</sup> )                 | -0.88 | 0.39  |
| Pieces of large wood (no./100 m)                                   | -0.82 | -0.55 |
| FBOM (g AFDM/m <sup>2</sup> )                                      | -0.51 | -0.17 |
| CBOM (g AFDM/ m <sup>2</sup> )                                     | -0.44 | 0.80  |
| Chl <i>a</i> on gravel (weighted for % cover gravel in the stream) | 0.86  | 0.48  |
| % cobble and gravel  | 0.89  | -0.08 |

predator, and shredder production were not related to habitat differences among streams represented by either PC (Table 4).

*Percentage of food consumed by selected functional feeding groups*

Shredders and collector-gatherers consumed only a small fraction of quantified food resources in all stream reaches (ranging from 0.4–3.8%; Table 5). The proportion of macroinvertebrate total secondary production consumed by predators varied among streams. For example, in State Creek, predators consumed ~62 to ~62% of total macroinvertebrate production, whereas predators in Shane Creek and Walton Creek consumed ~92 to ~129% of the total production (Table 5).

**Discussion**

Total macroinvertebrate secondary production in these upper Midwestern streams was low compared to other streams in eastern deciduous forests of the USA

TABLE 4. Results of multiple linear regressions relating macroinvertebrate secondary production across study reaches (*n* = 6) to habitat variables summarized as principal components (PC) 1 and 2. Primary consumers are the combination of all functional feeding groups except predators. All significant responses were positive. Bold font indicates statistical significance (*p* < 0.05). *R*<sup>2</sup> for PC 2 is cumulative.

| Macroinvertebrate group | PC 1        |                       | PC 2        |                       |
|-------------------------|-------------|-----------------------|-------------|-----------------------|
|                         | <i>p</i>    | <i>R</i> <sup>2</sup> | <i>p</i>    | <i>R</i> <sup>2</sup> |
| Total                   | <b>0.01</b> | <b>0.87</b>           | <b>0.03</b> | <b>0.89</b>           |
| Primary consumers       | <b>0.01</b> | <b>0.85</b>           | <b>0.03</b> | <b>0.90</b>           |
| Collector-gatherers     | 0.09        | 0.54                  | 0.30        | 0.54                  |
| Collector-filterers     | <b>0.02</b> | <b>0.76</b>           | 0.11        | 0.76                  |
| Scrapers                | <b>0.04</b> | <b>0.67</b>           | <b>0.01</b> | <b>0.96</b>           |
| Shredders               | 0.69        | 0.04                  | 0.93        | 0.05                  |
| Predators               | 0.21        | 0.35                  | 0.41        | 0.45                  |

TABLE 5. Percent consumption of resources measured in our study by selected functional feeding groups (FFG). GPE = gross production efficiency.

| FFG                 | GPE  | Stream | Consumption (production/GPE) |            | % consumed |            |
|---------------------|------|--------|------------------------------|------------|------------|------------|
|                     |      |        | Upstream                     | Downstream | Upstream   | Downstream |
| Shredders           | 0.05 | Shane  | 2.2                          | 1.4        | 1.4        | 1.6        |
|                     |      | State  | 1.2                          | 2.4        | 1.4        | 1.2        |
|                     |      | Walton | 2.4                          | 1.1        | 1.6        | 0.4        |
| Collector-gatherers | 0.03 | Shane  | 2.9                          | 3.2        | 1.2        | 2.9        |
|                     |      | State  | 3.5                          | 4.4        | 2.6        | 3.8        |
|                     |      | Walton | 1.3                          | 1.2        | 1.2        | 0.6        |
| Predators           | 0.35 | Shane  | 1.8                          | 1.1        | 128.8      | 110.2      |
|                     |      | State  | 2.1                          | 1.6        | 62.2       | 58.7       |
|                     |      | Walton | 2.2                          | 1.0        | 127.2      | 92.3       |

(Fig. 6). We also found significant variation in total and functional feeding group secondary production among our study streams, despite their close geographic proximity and similarity in gross physical characteristics. Among-stream differences in secondary production were related to variation in stream substrate composition, primary production, and water temperature. However, variation in shredder and predator production was greater within than among streams and probably was related to the patchy distribution of leaf litter and macroinvertebrates.

#### Factors influencing total secondary production

As we predicted, differences in total, scraper, and collector-gatherer secondary production were greater among the 3 study streams than within streams. In contrast, filterer production was equally variable within and among streams, and predator and shredder productions were more variable within than among streams. Much of the variation in filterer production was explained by differences in substrate composition and organic-matter standing crop. However, those variables did not explain variation in predator or shredder production. It is possible that the high within-stream variability of predators and shredders was caused by the patchy distribution of their resources. Heterogeneity of the stream benthic environment often results in a spatial and temporal mosaic of invertebrate distributions (Pringle et al. 1988, Malmqvist 2002). In general, predator and shredder taxa might be more likely to vary spatially and temporally because they are mobile and long-lived. For example, their mobility enables them to track patchy resources, and their univoltine life cycle usually means they have 1 cohort that develops across a relatively short period when resources are the most abundant. Other studies have shown that macroinvertebrates and leaf litter are patchily distributed within

streams, resulting in the aggregation of predators and shredders and, consequently, increasing within-stream variation (Lowe and Richardson 2001, Abós et al. 2006). In our study, the low amount and high variation in macroinvertebrates and leaf litter were probably responsible for the substantial within-stream variation in predator and shredder secondary production.

We expected leaf-litter standing crop to be the most important variable corresponding to the level and variation in secondary production (Fisher and Likens 1973, Wallace et al. 1999). Other studies in deciduous forests have shown a positive relationship between

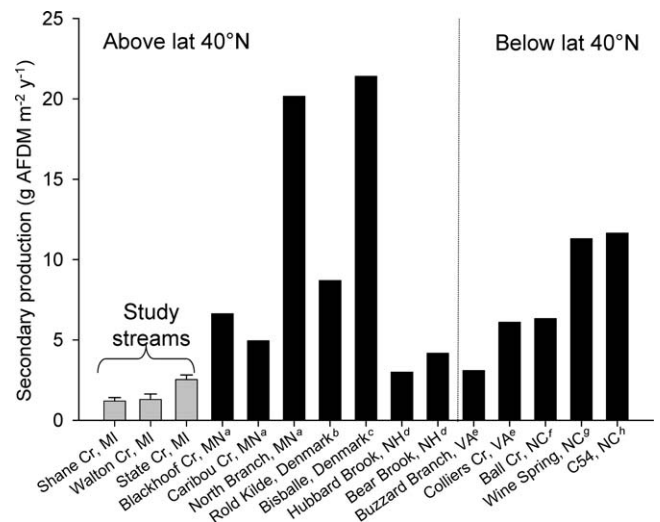


FIG. 6. Secondary production of benthic macroinvertebrates in our study streams and in other streams in deciduous forests. The boundary between climate types occurs at lat 40°N. Letters next to stream names indicate references. <sup>a</sup> = Krueger and Waters (1983), <sup>b</sup> = Iversen (1988), <sup>c</sup> = Mortensen and Simonsen (1983, consumers only), <sup>d</sup> = Hall et al. (2001), <sup>e</sup> = Smock et al. (1985), <sup>f</sup> = Hury and Wallace (1987), <sup>g</sup> = Wohl et al. (1995), <sup>h</sup> = Wallace et al. (1999). MI = Michigan, MN = Minnesota, NC = North Carolina, NH = New Hampshire, VA = Virginia. AFDM = ash-free dry mass.

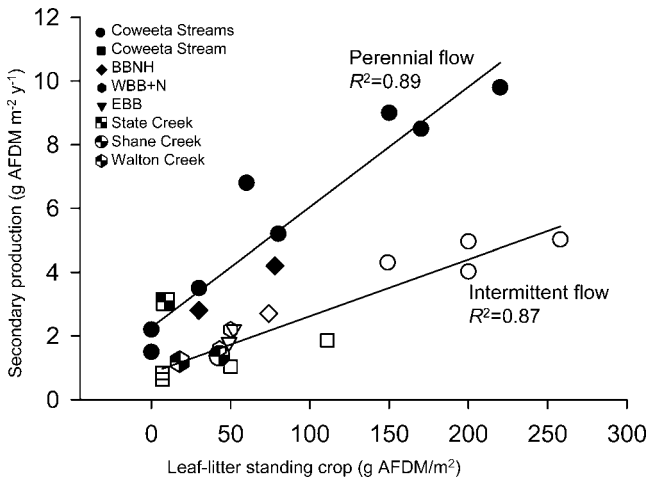


FIG. 7. Relationship between macroinvertebrate secondary production rates and annual leaf-litter standing crop in perennial forested headwater streams (data from Wallace et al. 1999, Hall et al. 2001) (solid symbols). In the lower regression line, secondary production estimates were corrected to include taxa able to persist in intermittent streams (data from Chadwick and Huryń 2005) (open symbols). Our estimates of total secondary production are plotted, but our data were not included in regression calculations. BBNH = Bear Brook, New Hampshire, WBB+N = west Bear Brook (+N treatment), and EBB = east Bear Brook. AFDM = ash-free dry mass.

total macroinvertebrate secondary production and leaf-litter standing crops (Wallace et al. 1999, Hall et al. 2001, Chadwick and Huryń 2005, Cross et al. 2006). We compared our data to published values for macroinvertebrate secondary production and leaf-litter standing crop in perennial and intermittent forested headwater streams (Fig. 7). In the combined data set, only 1 of our study streams, State Creek, fit the relationship for perennial streams, and values were at the low end for both leaf litter and secondary production. In fact, leaf-litter standing crops in these streams were similar to amounts in an experimental stream from which litter was excluded for several years (Wallace et al. 1999).

In the other 2 streams, the relationship between leaf litter and total secondary production aligned with that predicted for intermittent streams (data from Chadwick and Huryń 2005). Furthermore, the ordination separating stream reaches by habitat variables showed that secondary production was lowest in streams with more large wood, greater leaf-litter standing crop, and higher % sand cover. Organic-matter standing crops varied among streams, but values for leaf litter and wood were low as compared to other forested streams (Webster and Meyer 1997, Cordova et al. 2007). In addition, all habitat variables were highly correlated;

therefore, it was not possible to determine the variables most important in driving among-stream differences in secondary production.

Differences in mean seasonal temperatures might explain why macroinvertebrate secondary production–leaf-litter relationships fell along the predicted line for intermittent streams. Stream water in Shane Creek had the most accumulated annual degree days and was warmer than in the other streams in spring and summer, but stream water in State Creek was warmer than in the other streams in winter. The average water temperature from January through March was 2°C in State Creek, 1.2°C in Shane Creek, and 0.9°C in Walton Creek. The stream with the highest macroinvertebrate biomass and secondary production, State Creek, also accumulated  $\geq 200$  more degree days in the winter than the other 2 streams and had less extensive ice cover (SAE, unpublished data). The streams never froze completely, but in February and March 2006, State Creek had, on average, 5% ice cover, whereas the other 2 streams had 50 to 60% ice cover (A. Fowler, University of Notre Dame, unpublished data). The difference in % ice cover also might have contributed to the higher chlorophyll *a* concentrations in State Creek relative to the other 2 streams.

Differences in substrate composition also probably contributed to within- and among-stream variation in secondary production. For example, State Creek had the highest % cover of cobble and gravel and highest total secondary production, whereas Shane Creek had the lowest total secondary production and greatest % sand. Local geomorphology is important in explaining spatial variation in the secondary production of specific functional feeding groups. For example, in a headwater forested stream in North Carolina, bedrock had a higher proportion of filtering macroinvertebrate secondary production, whereas pools had more shredder and collector-gatherer production (Huryń and Wallace 1987, Wohl et al. 1995). In a southeastern Coastal Plain stream, differences in total secondary production between an upstream reach, a swampy reach, and a downstream reach were attributed to differences in available habitat (Smock et al. 1989).

Measured differences in % cover of cobble and gravel and chlorophyll *a* concentration on gravel might be an indication of differences in substrate stability among streams. Other studies have demonstrated the importance of stable substrate to macroinvertebrate communities (Minshall 1984, Parker and Huryń 2006). For example, Parker and Huryń (2006) found higher macroinvertebrate taxon richness and biomass on more stable substrates in an arctic spring-fed stream than in a flashy arctic mountain stream. In our study, PCA indicated a correlation among % cover gravel and

TABLE 6. Percentage of secondary production contributed by each functional feeding group in forested, 1<sup>st</sup>-order streams.

| Study streams                          | Filterers | Gatherers | Predators | Scrapers | Shredders | Reference               |
|--|-----------|-----------|-----------|----------|-----------|-------------------------|
| Bear Brook, Massachusetts <sup>a</sup> | 10        | 12        | 32        | <1       | 46        | Chadwick and Huryn 2005 |
| Black Hoof River, Minnesota            | 48        | 17        | 15        | 5        | 14        | Krueger and Waters 1983 |
| Cedar Creek (upper reach), Virginia    | 34        | 26        | 30        | 5        | 5         | Smock et al. 1985       |
| North Branch Creek, Minnesota          | 24        | 54        | 10        | 9        | 3         | Krueger and Waters 1983 |
| Ontonagon River tributaries, Michigan  | 25        | 5         | 34        | 30       | 5         | Our study               |
| Rold Kilde, Denmark                    | ≤1        | 30        | NA        | 2        | 69        | Iversen 1988            |
| Upper Ball Creek, North Carolina       | 7         | 38        | 23        | 9        | 23        | Huryn and Wallace 1987  |

<sup>a</sup> Reference stream (EBB) from 1998–1999

cobble and chlorophyll *a* concentration on gravel, a result that might be attributable to the larger and more stable substrate and less flashy hydrology of State Creek (SAE, personal observation).

#### *Factors influencing secondary production of functional feeding groups*

**Shredders.**—Shredders had the lowest secondary production rates in the macroinvertebrate community despite the forested riparian zones of the streams. Few other studies of macroinvertebrate secondary production in forested streams have reported such low values for shredders (but see Smock et al. 1985). However, based on the estimate of presumed available food (i.e., leaf litter), shredders consumed ≤1.6% of the total available resources. This discrepancy might have arisen because much of the organic matter in the streams was highly transient during periods of high flow; therefore, leaves were less available to shredders as a food resource in these streams than in other forested streams (Smith and Lake 1993). Retention of organic matter by more stable wood and boulders is essential to support a productive shredder community in many stream types (Cummins et al. 1989, Reice 1980). Such retention structures were not abundant in our study streams, and standing crop averages were extremely variable. We suggest that the absence of retention structures was another reason that shredder secondary production was unrelated to organic-matter standing crops and showed high within-stream variation.

**Collector-gatherers.**—Secondary production of collector-gatherers, particularly Chironomidae, was much lower than expected for forested headwater streams (Lugthart et al. 1990, Hall et al. 2001). This result might be related to our decision to sample the dominant mixed substrate rather than shallow depositional areas and debris dams where many collector-gatherers reside (Yamamuro 2004, Merritt and Cummins 2006). However, depositional areas constituted a small proportion of the total stream area. In addition, our 500- $\mu$ m mesh sampler might not have retained all early-instar collector-gatherers. Collector-gatherers

contributed only 5% of the total production, but ~10% of the total individuals collected were ≤1 mm in body length.

Collector-gatherer production in our streams was highest in May, when the canopy was open, water was warming, and periphyton was most abundant (data not shown). Other studies have shown that many collector-gatherer taxa eat biofilm associated with inorganic substrates (Lamberti and Moore 1984, Tavares-Cromar and Williams 1996, Tank et al. 2000), and some of the most productive collector-gatherer taxa in our study streams often rely on cobble and gravel as habitat (Pinder 1986, Berg and Hellenthal 1992, Entekin et al. 2007). It might be that low chironomid secondary production in our study streams is related to low standing crops of CBOM and the omission of debris dam sampling in our study.

**Collector-filterers.**—Filterers contributed 15 to 50% of total secondary production, a range higher than estimates from other small forested streams (Table 6) and more typical of mid-order streams (Hawkins and Sedell 1981, Grubaugh and Wallace 1995). We found a positive relationship between collector-filterer production and % cover of gravel and cobble and chlorophyll *a* on gravel. Food consumption of filterers could not be determined because seston was not measured; however, stable substrate might have limited filterer abundance. Filterers need stable substrate for attachment and fast-flowing water for capturing food (Merritt and Cummins 1996, Wallace and Webster 1996). In a concurrent study in these streams, we added 10 cobbles to the sandiest stream (Shane Creek), and the cobbles were colonized by filtering *Brachycentrus* sp. caddisflies within 1 mo.

**Scrapers.**—Scraper production was highest in State Creek, the stream with the highest % cover of cobble and gravel and highest chlorophyll *a* on gravel concentrations. In addition, a small amount of variation (29%) in scraper production was related to CBOM standing crop. Overall, scraper production was higher than expected for a 1<sup>st</sup>-order forested stream (Hawkins and Sedell 1981) (Table 6), or even for an open-canopy

prairie stream (Stagliano and Whiles 2002). High scraper production was a result of the high density of *Baetis* sp. collected from both inorganic and organic substrates in all streams. *Baetis* biomass peaked in late winter and again in late spring when the canopy was open before leafout and after ice-breakup, coinciding with a diatom bloom (SAE, personal observation).

**Predators.**—Overall predator production was high in all 3 streams, but was lower in the stream reaches with more sand and was more variable within streams than among streams. Predators consumed the largest proportion of total prey in the most sandy stream reaches, perhaps because prey had fewer refuges from predators in those simple habitats (cf. Huffaker 1958). Macroinvertebrate predators consumed ~58 to ~129% of the estimated total secondary production as prey. Other studies have found similarly high predator production and prey consumption estimates in small streams. For example, Smock et al. (1985) found that macroinvertebrate predators consumed ~94% of the total prey in sand-bottom coastal plain streams. As in previous studies (Allen 1951, Edwards and Huryn 1995, Huryn 1996), the high percentages of prey consumption in our study could be attributable to errors in macroinvertebrate secondary production estimates and unmeasured subsidies of terrestrial invertebrates as a food source. In addition, we could have underestimated production of chironomids, oligochaetes, and other small invertebrates (e.g., meiofauna) by using a 500- $\mu$ m mesh. We probably further underestimated secondary production in the sandy reaches because prey taxa tended to be smaller in sandy reaches and the dominant predator in the sandier streams was a large odonate predator, *Cordulegaster maculata*.

**Accounting for errors in secondary production estimates.**—To account for possible underestimates in production, we recalculated the amount of production in each reach by assuming that  $\leq 95\%$  of the total production was actually consumed as prey (as in Smock et al. 1989, Wallace et al. 1999). We then added that presumed amount of unaccounted production to the total production and recalculated our regressions. Following this correction, we still saw a strong positive relationship between total macroinvertebrate secondary production and both % cover cobble and gravel and chlorophyll *a* concentrations on gravel, giving us confidence in our results despite possible estimation errors.

### Summary

Despite the close geographic proximity of the study streams, we found significant differences in total and

functional feeding group secondary production among the 3 study streams and a large variation in predator and shredder production within streams. Furthermore, we observed different relationships between controlling factors and production values across streams. Differences in total secondary production were positively related to differences in substrate composition and the amount of chlorophyll *a* on gravel and negatively related to % cover sand, leaf-litter standing crop, and number of large wood pieces, whereas patchy distribution of resources was the likely driver of high within-stream variation. Total production in State Creek could be predicted from annual leaf-litter standing crops with a regression incorporating data from other studies in deciduous forests. The relationship between leaf litter and total macroinvertebrate secondary production in State Creek might have been a result of higher winter growth rates caused by warmer winter water temperatures and less ice cover. In contrast, total secondary production in the other 2 streams was related to a leaf litter–secondary production relationship estimated for intermittent streams (Chadwick and Huryn 2005). We hypothesize that this relationship was driven by cold winter water temperatures and ice cover that inhibited macroinvertebrate growth. This effect might be similar to the effect of annual drying in intermittent streams (Chadwick and Huryn 2007). Furthermore, differences in substrate composition and chlorophyll *a* influenced both total secondary production and functional composition of the macroinvertebrate community in 3 adjacent streams.

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APPENDIX. Macroinvertebrate biomass (B; mg ash-free dry mass [AFDM]/m<sup>2</sup>), secondary production (P; mg AFDM m<sup>-2</sup> y<sup>-1</sup>), and P/B. IGR = instantaneous growth rate method, SF = size-frequency method, P/B our data = secondary production calculated using P/B data from our study, P/B estimate = secondary production was calculated assuming P/B = 5, and P/B KW = secondary production calculated using P/B published in Krueger and Waters (1983).

| Functional feeding group/taxon     | Family or genus         | B     | P     | P/B  | Method       |
|------------------------------------|-------------------------|-------|-------|------|--------------|
| <b>Shane Creek: upstream reach</b> |                         |       |       |      |              |
| Collector-gatherers                |                         |       |       |      |              |
| Diptera                            | Chironomidae            | 3.3   | 52.2  | 15.8 | IGR          |
|                                    | <i>Hesperoconopa</i>    | 0.2   | 1.1   | 6.0  | P/B our data |
| Ephemeroptera                      | <i>Ephemerella</i>      | 2.1   | 9.5   | 4.6  | SF           |
|                                    | <i>Paraleptophlebia</i> | 5.5   | 26.4  | 4.8  | SF           |
| Oligochaeta                        |                         | 1.2   | 5.9   | 5.0  | P/B KW       |
|                                    | Total                   | 12.3  | 95.1  |      |              |
| Collector-filterers                |                         |       |       |      |              |
| Diptera                            | <i>Prosimulium</i>      | 0.5   | 6.2   | 12.9 | SF           |
|                                    | <i>Simulium</i>         | 5.4   | 69.5  | 12.8 | SF           |
| Trichoptera                        | <i>Brachycentrus</i>    | 36.6  | 233.1 | 6.4  | SF           |
|                                    | <i>Dolophiloides</i>    | 4.5   | 22.3  | 5.0  | SF           |
|                                    | <i>Hydropsyche</i>      | 1.2   | 5.0   | 4.1  | P/B KW       |
|                                    | Total                   | 48.2  | 336.1 |      |              |
| Predators                          |                         |       |       |      |              |
| Diptera                            | <i>Atherix</i>          | 18.3  | 91.5  | 5.0  | P/B estimate |
|                                    | Ceratopogonidae         | 0.7   | 3.7   | 5.3  | P/B KW       |
|                                    | <i>Dicranota</i>        | 13.5  | 80.2  | 5.9  | SF           |
|                                    | <i>Hexatoma</i>         | 35.7  | 184.1 | 5.2  | SF           |
|                                    | Muscidae                | 1.5   | 7.4   | 5.0  | P/B KW       |
| Megaloptera                        | <i>Nigronia</i>         | 1.0   | 5.2   | 5.0  | P/B estimate |
| Odonata                            | <i>Cordulegaster</i>    | 49.4  | 177.9 | 3.6  | P/B KW       |
|                                    | <i>Ophiogomphus</i>     | 2.1   | 7.4   | 3.5  | P/B KW       |
| Plecoptera                         | <i>Isogenoides</i>      | 15.4  | 66.3  | 4.3  | P/B KW       |
|                                    | <i>Isoperla</i>         | 2.8   | 15.0  | 5.5  | SF           |
| Trichoptera                        | <i>Rhyacophila</i>      | 0.0   | 0.0   | 3.5  | SF           |
|                                    | Total                   | 140.4 | 638.7 |      |              |
| Scrapers                           |                         |       |       |      |              |
| Coleoptera                         | <i>Optioservus</i>      | 11.7  | 58.3  | 5.0  | P/B KW       |

## APPENDIX. Continued.

| Functional feeding group/taxon       | Family or genus         | B     | P      | P/B  | Method       |
|--------------------------------------|-------------------------|-------|--------|------|--------------|
| Ephemeroptera                        | <i>Baetis</i>           | 6.4   | 71.4   | 11.1 | SF           |
|                                      | <i>Drunella</i>         | 3.0   | 17.0   | 5.6  | SF           |
|                                      | <i>Heptagenia</i>       | 4.4   | 17.4   | 4.0  | P/B KW       |
|                                      | <i>Rhithrogena</i>      | 3.0   | 15.5   | 5.1  | SF           |
|                                      | <i>Stenonema</i>        | 2.6   | 9.5    | 3.7  | P/B KW       |
| Trichoptera                          | <i>Glossosoma</i>       | 5.2   | 28.5   | 5.5  | SF           |
|                                      | <i>Goera</i>            | 1.9   | 9.5    | 5.0  | P/B estimate |
|                                      | <i>Neophylax</i>        | 2.0   | 12.2   | 6.2  | SF           |
|                                      | Total                   | 40.2  | 239.3  |      |              |
| <b>Shredders</b>                     |                         |       |        |      |              |
| Diptera                              | <i>Tipula</i>           | 2.5   | 14.9   | 6.0  | SF           |
| Plecoptera                           | <i>Allocapnia</i>       | 2.3   | 13.9   | 6.1  | SF           |
|                                      | <i>Amphinemura</i>      | 0.7   | 3.6    | 5.0  | P/B KW       |
|                                      | <i>Leuctra</i>          | 3.2   | 15.8   | 5.0  | P/B estimate |
|                                      | <i>Nemoura</i>          | 0.6   | 2.9    | 5.0  | P/B estimate |
|                                      | <i>Taeniopteryx</i>     | 0.0   | 0.0    | 5.0  | P/B KW       |
| Trichoptera                          | <i>Lepidostoma</i>      | 9.2   | 55.0   | 6.0  | SF           |
|                                      | Total                   | 18.5  | 106.1  |      |              |
| Grand total                          |                         | 259.5 | 1415.3 |      |              |
| <b>Shane Creek: downstream reach</b> |                         |       |        |      |              |
| <b>Collector-gatherers</b>           |                         |       |        |      |              |
| Diptera                              | Chironomidae            | 3.2   | 76.3   | 23.8 | IGR          |
|                                      | <i>Hesperoconopa</i>    | 0.1   | 0.3    | 6.0  | P/B          |
| Ephemeroptera                        | <i>Ephemerella</i>      | 1.9   | 6.1    | 3.3  | SF           |
|                                      | <i>Paraleptophlebia</i> | 6.2   | 19.6   | 3.2  | SF           |
| Oligochaeta                          | Total                   | 1.0   | 5.2    | 5.0  | P/B KW       |
| Total                                |                         | 12.4  | 107.5  |      |              |
| <b>Collector-filterers</b>           |                         |       |        |      |              |
| Diptera                              | <i>Prosimulium</i>      | 0.4   | 3.6    | 9.9  | SF           |
|                                      | <i>Simulium</i>         | 2.5   | 40.9   | 16.3 | SF           |
| Trichoptera                          | <i>Brachycentrus</i>    | 20.6  | 114.5  | 5.6  | SF           |
|                                      | <i>Dolophiloides</i>    | 4.5   | 22.3   | 5.0  | SF           |
|                                      | <i>Hydropsyche</i>      | 0.7   | 2.9    | 4.1  | P/B KW       |
|                                      | Total                   | 28.7  | 184.2  |      |              |
| <b>Predators</b>                     |                         |       |        |      |              |
| Diptera                              | <i>Atherix</i>          | 6.3   | 31.3   | 5.0  | P/B estimate |
|                                      | Ceratopogonidae         | 1.3   | 6.7    | 5.3  | P/B KW       |
|                                      | <i>Dicranota</i>        | 11.7  | 36.9   | 3.1  | SF           |
|                                      | <i>Hexatoma</i>         | 3.0   | 15.4   | 5.1  | SF           |
|                                      | Muscidae                | 0.9   | 4.5    | 5.0  | P/B KW       |
| Megaloptera                          | <i>Nigronia</i>         | 1.3   | 6.7    | 5.0  | P/B estimate |
| Odonata                              | <i>Cordulegaster</i>    | 42.8  | 153.9  | 3.6  | P/B KW       |
|                                      | <i>Ophiogomphus</i>     | 17.0  | 59.4   | 3.5  | P/B KW       |
| Plecoptera                           | <i>Isogenoides</i>      | 12.2  | 52.5   | 4.3  | SF           |
|                                      | <i>Isoperla</i>         | 2.7   | 14.6   | 5.3  | SF           |
| Trichoptera                          | <i>Rhyacophila</i>      | 0.0   | 0.0    | 3.5  | SF           |
|                                      | Total                   | 99.2  | 381.9  |      |              |
| <b>Scrapers</b>                      |                         |       |        |      |              |
| Coleoptera                           | <i>Optioservus</i>      | 5.3   | 26.6   | 5.0  | P/B KW       |
| Ephemeroptera                        | <i>Baetis</i>           | 10.8  | 65.9   | 6.1  | SF           |
|                                      | <i>Drunella</i>         | 3.0   | 17.0   | 5.6  | SF           |
|                                      | <i>Heptagenia</i>       | 3.4   | 13.8   | 4.0  | P/B KW       |
|                                      | <i>Rhithrogena</i>      | 12.1  | 57.6   | 4.7  | SF           |
|                                      | <i>Stenonema</i>        | 2.1   | 7.9    | 3.7  | P/B KW       |
| Trichoptera                          | <i>Glossosoma</i>       | 9.0   | 54.8   | 6.1  | SF           |
|                                      | <i>Goera</i>            | 0.1   | 0.3    | 5.0  | P/B estimate |

## APPENDIX. Continued.

| Functional feeding group/taxon     | Family or genus         | B     | P      | P/B  | Method       |
|------------------------------------|-------------------------|-------|--------|------|--------------|
|                                    | <i>Neophylax</i>        | 0.7   | 3.3    | 4.7  | SF           |
|                                    | Total                   | 46.5  | 247.2  |      |              |
| <b>Shredders</b>                   |                         |       |        |      |              |
| Diptera                            | <i>Tipula</i>           | 5.6   | 45.5   | 8.1  | SF           |
| Plecoptera                         | <i>Allocapnia</i>       | 1.5   | 8.4    | 5.6  | SF           |
|                                    | <i>Amphinemura</i>      | 0.1   | 0.4    | 5.0  | P/B KW       |
|                                    | <i>Leuctra</i>          | 1.3   | 6.3    | 5.0  | P/B estimate |
|                                    | <i>Nemoura</i>          | 0.1   | 0.3    | 5.0  | P/B estimate |
|                                    | <i>Taeniopteryx</i>     | 0.0   | 0.0    | 5.0  | P/B KW       |
| Trichoptera                        | <i>Lepidostoma</i>      | 2.1   | 6.6    | 3.2  | SF           |
|                                    | Total                   | 10.7  | 67.5   |      |              |
|                                    | Grand total             | 197.5 | 988.3  |      |              |
| <b>State Creek: upstream reach</b> |                         |       |        |      |              |
| <b>Collector-gatherers</b>         |                         |       |        |      |              |
| Diptera                            | Chironomidae            | 3.0   | 59.5   | 20.1 | IGR          |
|                                    | <i>Hesperoconopa</i>    | 4.6   | 28.6   | 6.2  | SF           |
| Ephemeroptera                      | <i>Ephemerella</i>      | 2.6   | 11.8   | 4.5  | SF           |
|                                    | <i>Paraleptophlebia</i> | 0.9   | 3.7    | 4.0  | P/B our data |
| Oligochaeta                        |                         | 2.7   | 13.3   | 5.0  | SF           |
|                                    | Total                   | 13.8  | 116.9  |      |              |
| <b>Collector-filterers</b>         |                         |       |        |      |              |
| Diptera                            | <i>Prosimulium</i>      | 102.1 | 755.1  | 7.4  | SF           |
|                                    | <i>Simulium</i>         | 32.1  | 469.6  | 14.6 | SF           |
| Trichoptera                        | <i>Brachycentrus</i>    | 0.6   | 2.6    | 4.8  | SF           |
|                                    | <i>Dolophiloides</i>    | 8.9   | 73.4   | 8.3  | SF           |
|                                    | <i>Parapsyche</i>       | 24.7  | 134.9  | 5.5  | SF           |
|                                    | Total                   | 168.4 | 1435.6 |      |              |
| <b>Predators</b>                   |                         |       |        |      |              |
| Diptera                            | <i>Atherix</i>          | 0.3   | 1.3    | 5.0  | P/B estimate |
|                                    | Ceratopogonidae         | 3.5   | 18.5   | 5.3  | P/B KW       |
|                                    | <i>Dicranota</i>        | 15.2  | 140.2  | 9.3  | SF           |
|                                    | <i>Hexatoma</i>         | 0.8   | 4.0    | 5.0  | P/B our data |
|                                    | Muscidae                | 5.7   | 28.6   | 5.0  | P/B KW       |
| Megaloptera                        | <i>Nigronia</i>         | 0.0   | 0.0    | 5.0  | P/B estimate |
| Odonata                            | <i>Cordulegaster</i>    | 0.5   | 2.0    | 3.6  | P/B KW       |
|                                    | <i>Ophiogomphus</i>     | 0.5   | 1.9    | 3.5  | P/B KW       |
| Plecoptera                         | <i>Isogenoides</i>      | 36.0  | 154.8  | 4.3  | P/B KW       |
|                                    | <i>Isoperla</i>         | 3.4   | 18.4   | 5.4  | P/B our data |
| Trichoptera                        | <i>Rhyacophila</i>      | 53.0  | 370.8  | 7.0  | P/B our data |
|                                    | Total                   | 118.9 | 740.5  |      |              |
| <b>Scrapers</b>                    |                         |       |        |      |              |
| Coleoptera                         | <i>Optioservus</i>      | 2.9   | 14.4   | 5.0  | P/B KW       |
| Ephemeroptera                      | <i>Baetis</i>           | 82.2  | 767.7  | 9.3  | SF           |
|                                    | <i>Drunella</i>         | 0.0   | 0.0    | 5.6  | P/B our data |
|                                    | <i>Heptagenia</i>       | 0.2   | 1.0    | 4.0  | P/B KW       |
|                                    | <i>Rhithrogena</i>      | 2.1   | 15.2   | 7.1  | SF           |
|                                    | <i>Stenonema</i>        | 0.0   | 0.0    | 3.7  | P/B KW       |
| Trichoptera                        | <i>Glossosoma</i>       | 63.9  | 206.6  | 3.2  | SF           |
|                                    | <i>Goera</i>            | 2.6   | 12.8   | 5.0  | P/B estimate |
|                                    | <i>Neophylax</i>        | 1.9   | 7.6    | 4.0  | SF           |
|                                    | Total                   | 155.8 | 1025.3 |      |              |
| <b>Shredders</b>                   |                         |       |        |      |              |
| Diptera                            | <i>Tipula</i>           | 1.2   | 5.8    | 5.0  | P/B our data |
| Plecoptera                         | <i>Allocapnia</i>       | 3.7   | 15.5   | 4.2  | SF           |
|                                    | <i>Amphinemura</i>      | 3.6   | 18.1   | 5.0  | P/B KW       |
|                                    | <i>Leuctra</i>          | 1.2   | 5.9    | 5.0  | P/B estimate |

## APPENDIX. Continued.

| Functional feeding group/taxon       | Family or genus         | B     | P      | P/B  | Method       |
|--------------------------------------|-------------------------|-------|--------|------|--------------|
| Trichoptera                          | <i>Nemoura</i>          | 1.0   | 5.2    | 5.0  | P/B estimate |
|                                      | <i>Taeniopteryx</i>     | 1.7   | 8.4    | 5.0  | P/B KW       |
|                                      | <i>Lepidostoma</i>      | 0.5   | 2.4    | 4.5  | P/B KW       |
|                                      | Total                   | 12.9  | 61.3   |      |              |
|                                      | Grand total             | 469.9 | 3379.9 |      |              |
| <b>State Creek: downstream reach</b> |                         |       |        |      |              |
| Collector-gatherers                  |                         |       |        |      |              |
| Diptera                              | Chironomidae            | 2.0   | 35.5   | 18.0 | IGR          |
|                                      | <i>Hesperoconopa</i>    | 12.6  | 82.2   | 6.5  | P/B KW       |
| Ephemeroptera                        | <i>Ephemerella</i>      | 2.6   | 15.7   | 6.0  | SF           |
|                                      | <i>Paraleptophlebia</i> | 1.8   | 7.0    | 4.0  | SF           |
| Oligochaeta                          |                         | 0.8   | 3.8    | 5.0  | P/B KW       |
|                                      | Total                   | 19.9  | 144.2  |      |              |
| Collector-filterers                  |                         |       |        |      |              |
| Diptera                              | <i>Prosimulium</i>      | 5.8   | 99.4   | 17.3 | SF           |
|                                      | <i>Simulium</i>         | 13.1  | 202.0  | 15.4 | SF           |
| Trichoptera                          | <i>Brachycentrus</i>    | 4.0   | 20.3   | 5.0  | SF           |
|                                      | <i>Dolophiloides</i>    | 5.7   | 25.5   | 4.5  | SF           |
|                                      | <i>Parapsyche</i>       | 45.0  | 362.4  | 8.1  | SF           |
|                                      | Total                   | 73.6  | 709.5  |      |              |
| Predators                            |                         |       |        |      |              |
| Diptera                              | <i>Atherix</i>          | 12.8  | 64.0   | 5.0  | P/B estimate |
|                                      | Ceratopogonidae         | 7.8   | 41.3   | 5.3  | P/B: KW      |
|                                      | <i>Dicranota</i>        | 16.4  | 122.4  | 7.5  | SF           |
|                                      | <i>Hexatoma</i>         | 0.3   | 1.7    | 5.0  | SF           |
|                                      | Muscidae                | 0.2   | 0.8    | 5.0  | P/B KW       |
| Megaloptera                          | <i>Nigronia</i>         | 0.0   | 0.0    | 5.0  | P/B estimate |
| Odonata                              | <i>Cordulegaster</i>    | 0.0   | 0.0    | 3.6  | P/B KW       |
|                                      | <i>Ophiogomphus</i>     | 0.0   | 0.0    | 3.5  | P/B KW       |
| Plecoptera                           | <i>Isogenoides</i>      | 34.9  | 82.9   | 4.3  | P/B KW       |
|                                      | <i>Isoperla</i>         | 0.4   | 2.1    | 5.4  | P/B our data |
| Trichoptera                          | <i>Rhyacophila</i>      | 35.2  | 261.5  | 7.4  | SF           |
|                                      | Total                   | 108.0 | 576.6  |      |              |
| Scrapers                             |                         |       |        |      |              |
| Coleoptera                           | <i>Optioserous</i>      | 0.5   | 2.7    | 5.0  | P/B KW       |
| Ephemeroptera                        | <i>Baetis</i>           | 89.3  | 764.7  | 8.6  | SF           |
|                                      | <i>Drunella</i>         | 4.2   | 23.2   | 5.6  | P/B KW       |
|                                      | <i>Heptagenia</i>       | 5.8   | 23.2   | 4.0  | P/B KW       |
|                                      | <i>Rhithrogena</i>      | 8.0   | 23.7   | 3.0  | SF           |
|                                      | <i>Stenonema</i>        | 0.3   | 1.0    | 3.7  | P/B KW       |
|                                      | <i>Glossosoma</i>       | 39.0  | 221.6  | 5.7  | SF           |
|                                      | <i>Goera</i>            | 0.4   | 2.2    | 5.0  | P/B estimate |
| Trichoptera                          | <i>Neophylax</i>        | 22.5  | 193.8  | 8.6  | SF           |
|                                      | Total                   | 170.0 | 1256.1 |      |              |
|                                      | Shredders               |       |        |      |              |
| Diptera                              | <i>Tipula</i>           | 3.4   | 17.0   | 5.0  | P/B          |
| Plecoptera                           | <i>Allocaenia</i>       | 1.1   | 4.5    | 4.2  | P/B our data |
|                                      | <i>Amphinemura</i>      | 1.3   | 6.5    | 5.0  | P/B KW       |
|                                      | <i>Leuctra</i>          | 2.1   | 10.3   | 5.0  | P/B estimate |
|                                      | <i>Nemoura</i>          | 13.6  | 68.2   | 5.0  | P/B estimate |
|                                      | <i>Taeniopteryx</i>     | 0.0   | 0.0    | 5.0  | P/B KW       |
| Trichoptera                          | <i>Lepidostoma</i>      | 2.3   | 10.2   | 4.5  | P/B KW       |
|                                      | Total                   | 23.8  | 116.7  |      |              |
|                                      | Grand total             | 395.3 | 2803.1 |      |              |

APPENDIX. Continued.

| Functional feeding group/taxon        | Family or genus         | B     | P      | P/B  | Method       |
|---------------------------------------|-------------------------|-------|--------|------|--------------|
| <b>Walton Creek: upstream reach</b>   |                         |       |        |      |              |
| Collector-gatherers                   |                         |       |        |      |              |
| Diptera                               | Chironomidae            | 1.3   | 29.3   | 21.9 | IGR          |
|                                       | <i>Hesperoconopa</i>    | 0.2   | 0.9    | 6.0  | P/B our data |
| Ephemeroptera                         | <i>Ephemerella</i>      | 1.6   | 7.9    | 4.9  | SF           |
|                                       | <i>Paraleptophlebia</i> | 0.1   | 0.2    | 4.0  | P/B          |
| Oligochaeta                           |                         | 1.0   | 4.9    | 5.0  | SF           |
|                                       | Total                   | 4.2   | 43.2   |      |              |
| Collector-filterers                   |                         |       |        |      |              |
| Diptera                               | <i>Prosimulium</i>      | 1.1   | 13.8   | 13.0 | P/B KW       |
|                                       | <i>Simulium</i>         | 20.9  | 274.1  | 13.1 | SF           |
| Trichoptera                           | <i>Brachycentrus</i>    | 12.2  | 70.4   | 5.8  | SF           |
|                                       | <i>Dolophiloides</i>    | 9.3   | 23.3   | 2.5  | SF           |
|                                       | <i>Hydropsyche</i>      | 3.7   | 15.1   | 4.1  | P/B KW       |
|                                       | Total                   | 47.2  | 396.7  |      |              |
| Predators                             |                         |       |        |      |              |
| Diptera                               | <i>Atherix</i>          | 0.2   | 1.0    | 5.0  | P/B estimate |
|                                       | Ceratopogonidae         | 18.8  | 99.7   | 5.3  | P/B KW       |
|                                       | <i>Dicranota</i>        | 15.3  | 106.0  | 6.9  | SF           |
|                                       | <i>Hexatoma</i>         | 8.3   | 52.2   | 6.3  | SF           |
|                                       | Muscidae                | 0.3   | 1.7    | 5.0  | P/B KW       |
| Megaloptera                           | <i>Nigronia</i>         | 0.0   | 0.0    | 5.0  | P/B estimate |
| Odonata                               | <i>Cordulegaster</i>    | 48.6  | 170.1  | 3.5  | P/B KW       |
|                                       | <i>Ophiogomphus</i>     | 0.0   | 0.0    | 3.5  | P/B KW       |
| Plecoptera                            | <i>Isogenoides</i>      | 70.8  | 304.6  | 4.3  | P/B KW       |
|                                       | <i>Isoperla</i>         | 9.5   | 28.7   | 3.0  | SF           |
| Trichoptera                           | <i>Rhyacophila</i>      | 0.4   | 2.7    | 7.0  | P/B our data |
|                                       | Total                   | 172.2 | 766.7  |      |              |
| Scrapers                              |                         |       |        |      |              |
| Coleoptera                            | <i>Optioservus</i>      | 4.0   | 19.8   | 5.0  | P/B KW       |
| Ephemeroptera                         | <i>Baetis</i>           | 10.5  | 147.7  | 14.0 | SF           |
|                                       | <i>Drunella</i>         | 11.8  | 65.8   | 5.6  | SF           |
|                                       | <i>Heptagenia</i>       | 2.8   | 11.0   | 4.0  | P/B KW       |
|                                       | <i>Rhithrogena</i>      | 5.2   | 14.5   | 2.8  | SF           |
|                                       | <i>Stenonema</i>        | 0.1   | 0.3    | 3.7  | P/B KW       |
| Trichoptera                           | <i>Glossosoma</i>       | 24.6  | 111.8  | 4.6  | SF           |
|                                       | <i>Goera</i>            | 1.1   | 5.5    | 5.0  | P/B estimate |
|                                       | <i>Neophylax</i>        | 4.3   | 21.7   | 5.0  | SF           |
|                                       | Total                   | 64.4  | 398.1  |      |              |
| Shredders                             |                         |       |        |      |              |
| Diptera                               | <i>Tipula</i>           | 6.0   | 52.7   | 8.8  | SF           |
| Plecoptera                            | <i>Allocaenia</i>       | 4.9   | 26.8   | 5.4  | SF           |
|                                       | <i>Aphinemura</i>       | 0.5   | 2.7    | 5.0  | P/B KW       |
|                                       | <i>Leuctra</i>          | 0.3   | 1.7    | 5.0  | P/B estimate |
|                                       | <i>Nemoura</i>          | 0.4   | 2.2    | 5.0  | P/B estimate |
|                                       | <i>Taeniopteryx</i>     | 0.6   | 3.2    | 5.0  | P/B KW       |
| Trichoptera                           | <i>Lepidostoma</i>      | 3.7   | 26.8   | 7.2  | SF           |
|                                       | Total                   | 16.6  | 116.1  |      |              |
|                                       | Grand total             | 304.6 | 1720.8 |      |              |
| <b>Walton Creek: downstream reach</b> |                         |       |        |      |              |
| Collector-gatherers                   |                         |       |        |      |              |
| Diptera                               | Chironomidae            | 1.3   | 28.0   | 21.0 | IGR          |
|                                       | <i>Hesperoconopa</i>    | 0.3   | 1.9    | 6.0  | P/B our data |
| Ephemeroptera                         | <i>Ephemerella</i>      | 0.8   | 4.4    | 5.5  | SF           |
|                                       | <i>Paraleptophlebia</i> | 0.6   | 2.2    | 4.0  | SF           |
| Oligochaeta                           |                         | 0.5   | 2.6    | 5.0  | SF           |
|                                       | Total                   | 3.5   | 39.1   |      |              |

## APPENDIX. Continued.

| Functional feeding group/taxon | Family or genus      | B                  | P      | P/B  | Method       |
|--------------------------------|----------------------|--------------------|--------|------|--------------|
| Collector-filterers            |                      |                    |        |      |              |
| Diptera                        | <i>Prosimulium</i>   | 0.1                | 0.9    | 13.0 | P/B KW       |
|                                | <i>Simulium</i>      | 4.3                | 50.7   | 11.8 | SF           |
| Trichoptera                    | <i>Brachycentrus</i> | 18.9               | 91.4   | 4.8  | SF           |
|                                | <i>Dolophilodes</i>  | 2.7                | 26.8   | 10.0 | SF           |
|                                | <i>Hydropsyche</i>   | 0.8                | 3.1    | 4.1  | P/B KW       |
|                                | Total                | 26.8               | 172.9  |      |              |
| Predators                      |                      |                    |        |      |              |
| Diptera                        | <i>Atherix</i> sp.   | 1.0                | 5.1    | 5.0  | P/B estimate |
|                                | Ceratopogonidae      | 13.6               | 72.1   | 5.3  | P/B KW       |
|                                | <i>Dicranota</i>     | 17.9               | 55.8   | 3.1  | SF           |
|                                | <i>Hexatoma</i>      | 5.0                | 25.1   | 5.0  | SF           |
|                                | Muscidae             | 1.4                | 7.0    | 5.0  | P/B KW       |
| Megaloptera                    | <i>Nigronia</i>      | 0.0                | 0.0    | 5.0  | P/B estimate |
| Odonata                        | <i>Cordulegaster</i> | 14.1               | 9.8    | 0.7  | SF           |
|                                | <i>Ophiogomphus</i>  | 0.0                | 0.0    | 3.5  | P/B KW       |
| Plecoptera                     | <i>Isogenoides</i>   | 33.5               | 143.8  | 4.3  | P/B KW       |
|                                | <i>Isoperla</i>      | 0.7                | 3.5    | 5.1  | SF           |
| Trichoptera                    | <i>Rhyacophila</i>   | 2.6                | 18.1   | 7.0  | P/B our data |
|                                | Total                | 89.8               | 340.3  |      |              |
| Scrapers                       |                      |                    |        |      |              |
| Coleoptera                     | <i>Optioservus</i>   | 1.9                | 9.7    | 5.0  | P/B KW       |
| Ephemeroptera                  | <i>Baetis</i>        | 14.4               | 217.9  | 15.1 | SF           |
|                                | <i>Drunella</i>      | 9.1                | 50.0   | 5.5  | SF           |
|                                | <i>Heptagenia</i>    | 0.9                | 3.7    | 4.0  | P/B KW       |
|                                | <i>Rhithrogena</i>   | 1.8                | 5.3    | 3.0  | SF           |
|                                | <i>Stenonema</i>     | 1.7                | 6.3    | 3.7  | P/B KW       |
|                                | Trichoptera          | <i>Glossosoma</i>  | 17.4   | 93.9 | 5.4          |
|                                | <i>Goera</i>         | 0.1                | 0.3    | 5.0  | P/B estimate |
|                                | <i>Neophylax</i>     | 9.0                | 57.9   | 6.4  | SF           |
|                                | Total                | 56.3               | 445.0  |      |              |
| Shredders                      |                      |                    |        |      |              |
| Diptera                        | <i>Tipula</i>        | 1.7                | 9.4    | 5.4  | SF           |
| Plecoptera                     | <i>Allocapnia</i>    | 5.3                | 14.1   | 2.7  | SF           |
|                                | <i>Amphinemura</i>   | 0.2                | 0.8    | 5.0  | P/B KW       |
|                                | <i>Leuctra</i>       | 1.4                | 7.1    | 5.0  | P/B estimate |
|                                | <i>Nemoura</i>       | 1.0                | 4.8    | 5.0  | P/B estimate |
|                                | <i>Taeniopteryx</i>  | 1.2                | 6.1    | 5.0  | P/B KW       |
|                                | Trichoptera          | <i>Lepidostoma</i> | 2.0    | 14.1 | 7.1          |
|                                | Total                | 12.8               | 56.4   |      |              |
|                                | Grand total          | 189.2              | 1053.7 |      |              |