Macroinvertebrate production and trophic structure in a tallgrass prairie headwater stream

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Abstract. Research on North American prairie stream communities has lagged behind other regions. We examined the ecosystem significance of the macroinvertebrate community of riffle/run habitats in Kings Creek, a 2nd-order tallgrass prairie stream at Konza Prairie Biological Station (Kansas, USA), by estimating secondary production, benthic organic matter standing stocks, and resource consumption and egestion by functional groups. Annual mean standing stock macroinvertebrate biomass was 2.3 g ash-free dry mass (AFDM)/m², annual production was 19.7 g AFDM m^{-2} y^{-1}, and the annual community production/biomass (P/B) ratio was 8.6. Macroinvertebrate production was higher than published estimates for forested streams of similar size, but much lower than that of a Sonoran desert stream. Distribution of production among functional groups was 30% for collector-gatherers, 9% for collector-filterers, 20% for scrapers, 23% for shredders, and 18% for predators, resembling estimates from some forested streams with the exception of higher scraper production. Although detritivorous groups were productive in this prairie stream, they appeared food limited. Consumption estimates indicated shredders and collector-gatherers annually ingested ~80% and ~240% of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) standing stocks, respectively. Thus, re-ingestion and/or diet shifts may be common, particularly among collector-gatherers, and the FPOM pool must turn over rapidly. Invertebrate predators also consumed a sizeable portion (~52%) of prey, whereas scrapers (~21%) and filterers (<1%) consumed relatively small portions of their respective resources, suggesting top-down influences on these groups. This study indicates that, during a period of relatively stable flow in this prairie stream, macroinvertebrate production and functional structure were roughly intermediate between North American forested and desert systems. Our results underscore the value of secondary production estimates for examining invertebrate communities in an ecosystem context.

Key words: aquatic macroinvertebrates, secondary production, organic matter, energy flow, trophic structure, food web, prairie stream, Konza Prairie Biological Station.

Benthic invertebrate communities in North American prairie streams are poorly studied compared to those of other regions (e.g., forested streams, Matthews 1988). Studies have described prairie stream macroinvertebrate community composition and functional structure (e.g., Gray and Johnson 1988), and examined the influence of hydrologic disturbance (e.g., Miller and Golladay 1996, Hax and Golladay 1998) and even bison crossings (Fritz et al. 1999) on macroinvertebrate communities. More recently, N cycling was quantified through the biotic and abiotic compartments of a prairie stream, including macroinvertebrates (Dodds et al. 2000).

However, no studies have examined the flow of energy through or within macroinvertebrate communities in North American prairie streams. Energy flow through trophic levels is one measurable property that all ecosystems share, and on which meaningful comparisons can be based (Odum 1983). To quantify the role of a population in energy flow, an estimate of production is essential.

Secondary production is the ultimate measure of the success of a population because it integrates abundance, biomass, growth, reproduction, and survivorship (Benke 1993). Studies examining macroinvertebrate community production in streams have increased since Benke's (1993) review, and some studies have examined streams in regions that were previously poorly studied (e.g., Ramirez and Pringle 1998). An advantage of using production to examine macroinvertebrate communities is that production estimates allow for better characterization of community structure and function than either

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abundance or biomass estimates, and they link macroinvertebrate communities to ecosystem function (Gaines et al. 1992, Lugthart and Wallace 1992, Benke 1993, Whiles and Wallace 1995, Ramirez and Pringle 1998). Secondary production estimates have been used to quantify energy flow through aquatic consumers, and thus may provide insight into the trophic status and dynamics of a variety of streams (e.g., Benke and Wallace 1980, 1997, Jackson and Fisher 1986, Roell and Orth 1993, Huryn 1998). Classification of aquatic macroinvertebrates into functional feeding groups (Cummins 1973, Cummins and Merritt 1996) has also facilitated the study of trophic relationships and energy flow through consumer groups in streams (reviewed by Wallace and Webster 1996).

Macroinvertebrate functional structure in streams is intrinsically linked to energy inputs (Wallace et al. 1997). The river continuum concept (RCC, Vannote et al. 1980) predicts that invertebrate functional structure shifts longitudinally along a continuum as communities adjust to changing energy inputs. Prairie streams, such as those on the Konza Prairie Biological Station (KPBS), deviate considerably from predictions of the RCC because headwater reaches usually lack a forest canopy and are thus autotrophic rather than heterotrophic in nature (Dodds et al. 1996, Gray 1997). As a result, macroinvertebrate functional structure in headwater prairie streams should differ substantially from similar-sized forested streams. Gray and Johnson (1988) found that macroinvertebrate functional structure, based on biomass estimates, in a headwater tallgrass prairie stream resembled that of a desert stream (i.e., dominated by collectors, with low shredder and scraper biomass, Fisher and Gray 1983). However, Gray and Johnson (1988) also reported that functional structure ~1 km downstream in a reach of the same stream with a riparian forest was most similar to patterns reported for some forested systems. This longitudinal pattern suggests that, in the context of the RCC, prairie streams are reversed.

Given the current lack of information on prairie stream communities, and that studies of secondary production remain a major shortcoming in stream ecosystem research (Benke and Wallace 1997), our main objective was to characterize and quantify the structure and function of the macroinvertebrate community in a headwater prairie stream by estimating secondary production. With these estimates, we quantified organic matter resource utilization, and used this information to construct a food web for this system. We hypothesized that macroinvertebrate production and functional structure in this prairie stream would be intermediate to similar-sized forested and desert streams, and would most closely resemble RCC predictions for mid-reaches rather than headwaters.

Study Site

The Kings Creek watershed (lat 39°05'N, long 96°35'W) encompasses 1637 ha within the boundaries of the KPBS and includes stream orders 1 to 5 (Fig. 1). Kings Creek is a US Geological Survey benchmark site for tallgrass prairie streams, and has been part of the National Science Foundation (NSF) Long-Term Ecological Research (LTER) network since 1980. KPBS is a preserved tract of tallgrass prairie (3487 ha) within the Flint Hills ecoregion, ~10 km south of Manhattan, Kansas. Knapp et al. (1998) provide a detailed description of KPBS.

The 150-m study area selected on Kings Creek is a headwater reach located in upland prairie in the N04D research treatment (grazed by bison with a 4-y burn regime). Stream gradient is 0.038 m/m and morphology consists of riffles and runs (86% of reach) dominated by chert and flint-bearing limestone cobbles separated by occasional silt/clay pools. There is very little coarse woody debris in the stream channel, and most allochthonous material originates from leaves of riparian shrubs and small trees (mostly *Ulmus* spp. and *Cornus drummondii*). A smaller portion of allochthonous inputs is from riparian grasses (Gurtz et al. 1982). Shading of the channel is limited, with ~75% of the reach unshaded at peak foliage (DMS, unpublished data).

Much of the Kings Creek system is intermittent, and drying of most reaches generally occurs by late summer. However, most of the study reach has maintained perennial flow since 1992 because of above-normal precipitation. Peak flows in Kings Creek usually occur in spring and summer during flash flooding from thunderstorms (Gray et al. 1998). However, spates occurred in late summer and fall during this study, and were not as intense as previous periods (Dodds et al. 1996, Gray et al. 1998). Detailed descriptions of the hydrology and ecol-
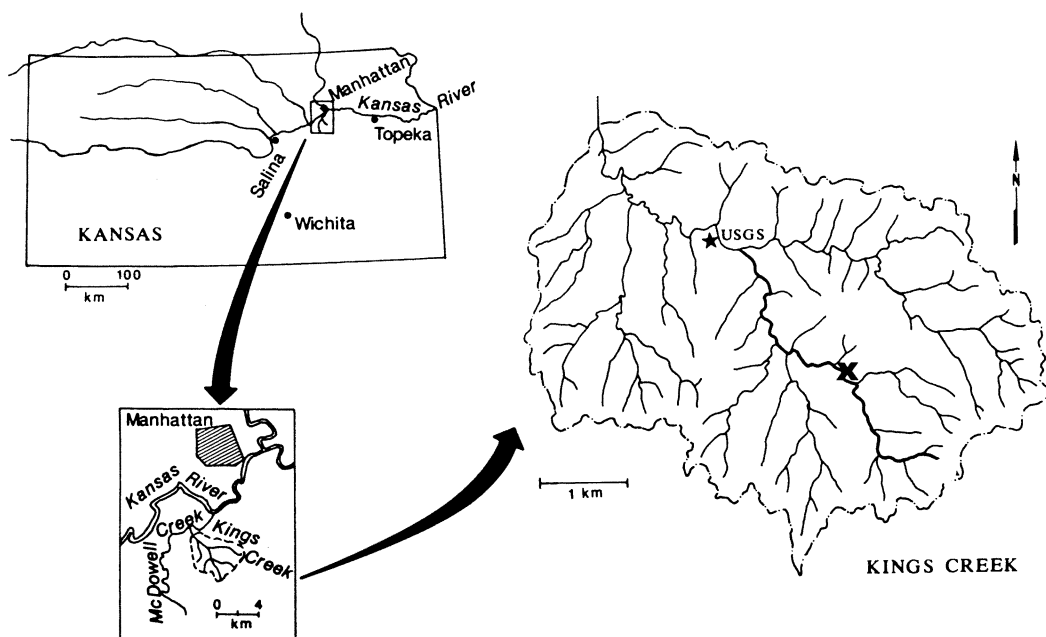
FIG. 1.   Study reach (x) in the south branch Kings Creek watershed on the Konza Prairie Biological Station. US Geological Survey (USGS) star indicates the benchmark gauging station. (Reprinted from Gurtz et al. 1988. Canadian Journal of Fisheries and Aquatic Sciences 45:655–665, by permission of the Canadian Journal of Fisheries and Aquatic Sciences.)

TABLE 1.   Physical and chemical characteristics of the Kings Creek study reach measured from 1998 to 1999.

Characteristic	Value
Stream order	2
Watershed area (ha)	134
Gradient (m/m)	0.038
Mean wetted width (m)	1.6
Mean surface area (m²)	240
% riffle/run	86
% pool	14
% riparian shading of reach	24
Inorganic substrates (%)	
Boulder/bedrock	10
Cobble/pebble/gravel	75
Fine (sand, silt, clay)	15
Discharge (m³/s)	
Mean annual	0.014
Maximum	0.35
Minimum	0.002
Mean annual water temperature (°C)	13.9
Mean annual pH	8.2
Mean annual specific conductance (μS/cm)	540

ogy of Kings Creek are provided by Gray et al. (1998) and Gray and Dodds (1998).

Methods

Physical and chemical characteristics

Physical and chemical characteristics measured during this study are summarized in Table 1. Stream habitats, inorganic substrates, and wetted width and area were quantified in spring and fall of 1998. For these analyses, transects were established every 10 m along the entire length of the study reach. Linear meters of each major habitat type (pool, riffle/run) were estimated for each 10-m section of the stream and summed to calculate the proportion of each in the study reach. Inorganic substrates were analyzed by measuring substrate particle sizes at 5 to 10 points across each transect using a modified Wentworth scale (Cummins 1962). Wetted width was also measured at each transect, and the product of average wetted width and stream length (150 m) was used as an estimate of total wetted area. Canopy cover was quantified at each transect with a spherical den-

siometer during May 1998 and June 1999. Specific conductance and pH were measured monthly at each site where invertebrate samples were collected. An estimate of stream gradient was obtained from Gray (1997). Temperature and discharge were recorded continuously during this study at a gauging weir equipped with a CR-21X data-logger (Campbell Scientific, Logan, Utah) ~200 m downstream of the study reach.

Organic matter

Benthic organic matter standing stocks were estimated from material collected in monthly stovepipe cores (total $n = 48$). Organic material was separated into coarse benthic particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, <1 mm) using nested sieves. CPOM was further separated into nongrass leaves, grass, woody debris, and miscellaneous categories before drying. To estimate ash-free dry mass (AFDM), samples were placed in a drying oven (55°C) for 2 to 3 d, transferred to a desiccator for 24 h, and then weighed to obtain dry mass (DM). Samples were then ashed in a muffle furnace (500°C) for ~4 h and reweighed to obtain ash mass. Ash mass was subtracted from DM to obtain AFDM. Large CPOM samples were subsampled before combustion, and % AFDM estimates from subsamples were applied to total masses. FPOM values were adjusted by adding an additional 65% as a correction factor. This value was based on the % of FPOM from Kings Creek samples that passed through a 250-μm sieve (DMS, unpublished data, Minshall et al. 1982). We also estimated suspended particulate organic matter (SPOM) for the study reach, based on sampling during 1999 (Dodds et al. 2000).

Primary production

Annual primary production was estimated from values generated during previous studies on prairie reaches of Kings Creek (Gurtz et al. 1982, Dodds et al. 1996). Although >10 y apart, these 2 studies generated similar annual primary production estimates (111 and 129 g AFDM m^{-2} y^{-1}, respectively). Thus, we used an average of these 2 values for our estimate (120.5 g AFDM m^{-2} y^{-1}). Daily primary production estimates from the downstream end of our study

reach during 1999 (Dodds et al. 2000) were in agreement with the value we used, indicating that our estimate was reasonable for the study year.

Macroinvertebrates and secondary production estimates

Benthic macroinvertebrate samples were collected monthly (February 1998–January 1999) with a stovepipe corer (313 cm^2 sampling area), from 4 randomly selected riffle/run areas within the study reach. We did not sample pools in the study area because they composed only ~14% of the reach. All material enclosed by the corer was removed to a depth of ~10 cm or until bedrock was contacted. Sediments were placed into a bucket and cobbles were scrubbed clean with a stiff brush. Organic materials were elutriated from mineral portions and collected on a 250-μm sieve. Samples were then placed in plastic bags and preserved in 8 to 10% formalin solution containing Phloxine B stain to facilitate sorting.

In the laboratory, samples were washed through nested 1-mm and 250-μm sieves to separate large (>1 mm) and fine materials (<1 mm >250 μm). Large fractions were processed in their entirety, whereas fine fractions were often subsampled ($^1/_2$ to $^1/_8$ of total) using sectioned petri dishes prior to invertebrate removal. Invertebrates were sorted from other organic material under a dissecting microscope (10–40×), identified to the lowest possible taxonomic level, measured for total body length (carapace length for crayfish) to the nearest mm, and counted. Most macroinvertebrates were identified to genus or species using Merritt and Cummins (1996) and Huggins et al. (1985), except for some noninsect groups, which were identified to class or order. Chironomids identified and measured for production (tribe or subfamily level) were wet-mounted, whereas those identified to genus were permanently mounted (see methods in Epler 1995). Specimens collected during this study have been deposited in the Museum for Prairie Arthropod Research, Department of Entomology, Kansas State University (voucher lot #127).

Size-specific AFDM of some taxa was estimated using published length-mass relationships (Benke et al. 1999). For others, formalin-preserved individuals of each size class were

used to obtain estimates of AFDM using the same methods described above for organic matter. Ash mass and DM of individuals were weighed to the nearest μg on a Cahn 26® electrobalance. Natural log-transformed length-mass regressions were then used to generate predictive equations for estimating AFDM from body length. Mean monthly biomass values of individual taxa were summed and divided by the number of sampling periods ($n = 12$) to estimate mean annual biomass. This value was used to estimate annual production/biomass (P/B) ratios.

Annual secondary production was estimated for most taxa using the size-frequency method (Hamilton 1969, Benke 1984), and corrected for the cohort production interval (CPI, Benke 1979). CPIs were derived by examining size-frequency plots of individual taxa. The size-frequency method is appropriate when development is asynchronous and clear cohorts cannot be followed. Empirical studies have shown that the size-frequency method and the CPI correction yield production estimates similar to those of other methods (Benke 1993). For taxa with synchronous cohorts, the increment-summation method was used (Waters 1977).

Production of Chironomidae was estimated at the family, subfamily, and tribe levels using 3 different methods in an attempt to yield the most reliable estimate. First, we used the instantaneous growth method (Benke 1984) to estimate chironomid production at the family level and for the tribe Tanytarsini, using a temperature-dependent growth equation derived by Huryn and Wallace (1986). Although originally developed for streams in the southern Appalachian Mountains, size classes of midges in this study were similar to the range used by Huryn and Wallace (1986), and our average monthly stream temperatures only slightly exceeded theirs. Further, Stites and Benke (1989) reported comparable results when extrapolating this same equation to higher temperatures. Second, we used the size-frequency method, with conservative CPIs based on size-frequency plots, to estimate production at the family level, for individual subfamilies Tanypodinae and Orthocladiinae, and for the tribe Chironomini. Third, we estimated production by summing values for the subfamilies and tribes generated with methods described above into a total family-level estimate. Because the estimate from the 3rd meth-

od was intermediate to the other 2, we chose it for community and functional-group calculations.

Production values for rare taxa and most non-insects were estimated by applying annual P/B ratios to mean annual biomass. Published P/B values of 18, 10, and 10 were used for Copepoda, Cladocera, and Ostracoda, respectively (O'Doherty 1988). A P/B of 2 was used for the crayfish *Orconectes neglectus* (Faxon), based on recent life-history studies in Kings Creek (M. A. Evans-White, Kansas State University, Manhattan, Kansas, unpublished data). Theoretical P/B values of 5 or 10 were used to estimate production of infrequently encountered univoltine and bivoltine taxa, respectively (Waters 1977, see Appendix).

Production values of individual taxa were summed into their respective functional feeding groups, based on assignments by Merritt and Cummins (1996), or results from a recent N[15] tracer experiment in Kings Creek (Dodds et al. 2000). Because crayfish feed on a variety of resources (Creed 1994, Lamberti 1996), their production was divided evenly among shredder, collector-gatherer, scraper, and predator functional groups.

Macroinvertebrate consumption and egestion

Food resource ingestion by functional groups was estimated by dividing annual production values by the product of assimilation efficiency (AE) and net production efficiency (NPE, Benke and Wallace 1980) taken from the literature. Respectively, AE and NPE were 13% and 38% for shredders (Perry et al. 1987), 70% and 50% for predators (Lawton 1970), 10% and 33% for collectors, and 30% and 50% for scrapers (Benke and Wallace 1980). Egestion by functional groups was estimated as the product of ingestion and $1 - $ AE.

Results

Organic matter

Benthic organic matter standing stocks showed a seasonal pattern typical of forested streams, with largest amounts of CPOM in the autumn and lowest values in summer (Fig. 2). Leaves (not including grasses) composed ~90% of the total CPOM during the fall peak, and con-
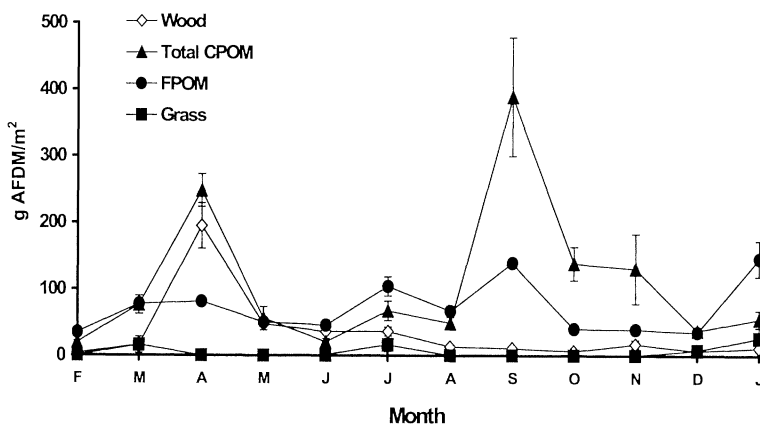
FIG. 2. Mean (±1 SE) monthly organic matter standing stocks (g ash-free dry mass [AFDM]/m²) in the Kings Creek study reach, 1998 to 1999. Terrestrial grasses and wood were separated from coarse particulate organic matter (CPOM) estimates (primarily leaves and leaf fragments). FPOM = fine particulate organic matter.

tributed 62% to the mean annual nonwoody CPOM standing stock of 112.9 g AFDM/m² (Table 2). Other contributors to CPOM included senesced algae, mosses, aquatic macrophytes, and grasses (listed as miscellaneous CPOM in Table 2). Woody debris represented a small component of total CPOM during most of the year (<25%, Fig. 2), except for a peak in April that appeared related to high winds, which increased lateral inputs (DMS, personal observation). Corrected mean annual standing stock of

TABLE 2. Primary production and organic matter values for the Kings Creek study reach from 1998 to 1999. AFDM = ash-free dry mass, CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, SPOM = suspended particulate organic matter.

Variable	Value
Net primary production (g AFDM m⁻² y⁻¹)[a]	120.5
Organic matter standing stocks (g AFDM/m²)	
Total CPOM (>1 mm)	146.2
Leaves (nongrass)	69.9
Wood >1 mm	33.3
Miscellaneous CPOM >1 mm	43.0
FPOM <1 mm	77.6
Organic matter fluxes (g AFDM m⁻² y⁻¹)	
SPOM <1 mm[b]	6899.0

[a] Averaged from values reported in Gurtz et al. (1982) and Dodds et al. (1996)
[b] Based on measurements from April to June 1999 by Dodds et al. (2000)

FPOM was 77.6 g AFDM/m² (Table 2). FPOM exceeded CPOM during only 3 mo of the study year (Fig. 2).

Macroinvertebrate abundance, biomass, and production

Approximately 50 taxa, including 13 chironomid genera, were collected during the study year (Appendix). Mean annual abundance and standing stock of macroinvertebrates were 23,843 individuals/m², and 2.3 g AFDM/m², respectively. Non-Tanypodinae midges dominated abundance (annual average = 10,097 individuals/m²). *Tipula abdominalis* (Say) had the highest annual average biomass of any single taxon (~0.5 g AFDM/m²), with highest values during the fall and winter months.

Collector-gatherers composed 64% of total abundance, whereas predators and shredders each accounted for ~⅓ of total biomass (Fig. 3). Seasonally, dominance based on biomass shifted from predators for much of the year (March, April, and June–September), to shredders during autumn and winter months (October–February).

Total macroinvertebrate community production was 19.7 g AFDM m⁻² y⁻¹, with production being dominated by aquatic insects (~85%, Table 3). Diptera alone accounted for 64% of insect production, and >56% (10.8 g AFDM m⁻² y⁻¹) of total production. The most productive dipteran family was the Tipulidae (~4.7 g AFDM m⁻² y⁻¹), 86% of which was attributable to *T.*
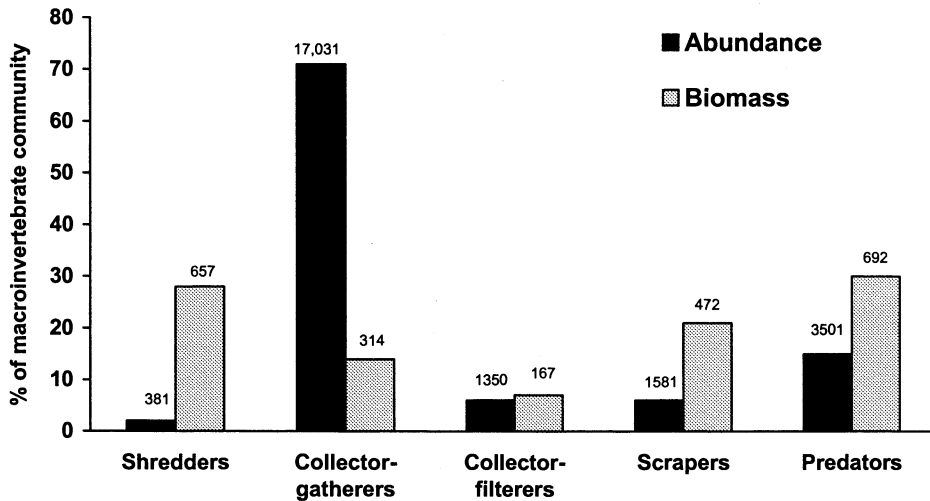
FIG. 3.   Functional-group contributions to total benthic macroinvertebrate abundance (individuals/m²) and biomass (mg ash-free dry mass/m²) in the Kings Creek study reach, 1998 to 1999. Percentages are based on annual means. Numbers above bars are actual values.

abdominalis (Appendix). Chironomidae was the 2nd most productive family of dipterans (4.4 g AFDM m^{-2} y^{-1}). Predaceous Tanypodinae contributed 0.54 g AFDM m^{-2} y^{-1}, whereas 88% of chironomid production (3.86 g AFDM m^{-2} y^{-1}) was contributed by non-Tanypodinae chironomids (Table 4). The Orthocladiinae was the most productive chironomid subfamily, followed by the tribes Tanytarsini and Chironomini (Table 4). Ceratopogonidae also contributed significantly to dipteran production (~1.4 g AFDM m^{-2} y^{-1}), 76% of which was the predaceous *Bezzia/Palpomyia* group (Table 5).

Other important contributors to macroinvertebrate production were the ephemeropterans *Stenonema femoratum* (Say) and *Fallceon quilleri* (Dodds), with ~1 and 1.6 g AFDM m^{-2} y^{-1}, respectively (Table 5, Appendix). *Cheumatopsyche* spp. was the dominant trichopteran (~1.5 g AFDM m^{-2} y^{-1}). Oligocheata was the most productive noninsect taxon, contributing 1.6 g AFDM m^{-2} y^{-1}, or ~8% of total stream production (Table 3). Most other noninsect taxa contributed minimally to both biomass and production (Table 3, Appendix).

Annual P/B ratio for the entire macroinvertebrate assemblage was ~8.6, with P/B values for individual taxa ranging from 0.7 for *Sialis* sp. (Appendix) to 46 for Orthocladiinae (Table 4).

TABLE 3.   Macroinvertebrate production (mg ash-free dry mass m^{-2} y^{-1}) in the Kings Creek study reach from 1998 to 1999. % = % contribution of each taxonomic group to total macroinvertebrate production. See Appendix for production of individual taxa.

	Production	%		Production	%
Insects			**Noninsects**		
Ephemeroptera	3065.7	16	Turbellaria	84.3	<1
Odonata	182.2	1	Nematoda	4.1	<1
Plecoptera	449.4	2	Oligochaeta	1587.0	8
Trichoptera	1585.4	8	Copepoda	38.8	<1
Megaloptera	189.7	1	Cladocera	1.5	<1
Coleoptera	492.6	3	Ostracoda	18.7	<1
Diptera	10,805.5	55	Decapoda	958.0	5
			Mollusca	228.0	1
Total	16,779.6	86	**Total**	2920.4	14

TABLE 4. Collector-gatherer chironomid biomass, production, and P/B ratios. Details of production methods are described in the text. Biomass is reported as mean annual standing stock (mg ash-free dry mass [AFDM]/ m²) and annual production is mg AFDM m^{-2} y^{-1}. See Appendix for taxa included within Chironomidae.

Taxon	Biomass	Production method	Production	P/B
Orthocladiinae	56.25	Size frequency	2585.0	46
Chironomini	11.56	Size frequency	241.5	21
Tanytarsini	24.24	Instantaneous growth	1032.5	43
Chironomidae	92.05	Sum of subfamilies	3859.0[a]	42
		Size frequency	4713.6	51
		Instantaneous growth	2636.8	29

[a] Value used for annual collector-gatherer chironomid production

Functional-group production and consumption

Distribution of annual production among functional groups was 23% for shredders, 30% for collector-gatherers, 20% for scrapers, 9% for collector-filterers, and 18% for predators. Dom-

TABLE 5. Production (mg ash-free dry mass m^{-2} y^{-1}) of the top 4 dominant macroinvertebrate taxa in each functional group and % contribution to production of each group in the Kings Creek study reach, 1998 to 1999.

Group/taxon	Production	% Of group total
Predators		
Bezzia/Palpomyia spp.	1127	33
Pseudolimnophila sp.	565	16
Tanypodinae	541	16
Culicoides spp.	316	9
Shredders		
Tipula abdominalis (Say)	4029	89
Orconectes neglectus (Faxon)	240	5
Zealeuctra claasseni (Frison)	166	4
Gonomyia sp.	103	2
Collector-gatherers		
Chironomidae	3859	64
Oligochaeta	1587	26
Orconectes neglectus (Faxon)	240	4
Leptophlebia sp.	140	2
Collector-filterers		
Cheumatopsyche spp.	1457	87
Simulium spp.	89	5
Chimarra sp.	66	4
Pisidium sp.	48	3
Scrapers		
Fallceon quilleri (Dodds)	1601	42
Stenonema femoratum (Say)	1034	27
Stenelmis crenata (Say)	493	13
Stenacron interpunctatum (Say)	261	7

inant taxa within functional groups followed patterns seen at the ordinal level, with *T. abdominalis* (shredder), detritivorous chironomids (collector-gatherer), *F. quilleri* (scraper), *Cheumatopsyche* spp. (collector-filterer), and *Bezzia/Palpomyia* spp. (predator) composing most of the production within their respective groups (Table 5). *Cheumatopsyche* spp. and *T. abdominalis* accounted for 87% and 89% of collector-filterer and shredder production, respectively. Relative to other functional groups, production among predator taxa was more evenly distributed, with 5 of 14 taxa constituting ~80% of production (Table 5, Appendix).

Consumption estimates indicated that most functional groups ingested a sizeable portion of available food resources (Table 6). Collector-gatherers consumed >200% of the mean standing stock of FPOM, and shredders consumed 81% of available CPOM. Predators ingested 52% of total benthic invertebrate production. In contrast, scrapers consumed only 21% of annual primary production, and collector-filterers consumed a very small portion (<1%) of the available annual SPOM (Table 6).

Estimates generated during this study and Dodds et al. (2000) were used to construct a quantitative food web for the study reach (Fig. 4). Detritivore pathways (CPOM to shredders, FPOM to [collector-] gatherers) were the dominant energy flow pathways, and FPOM was the major resource supporting collector-gatherers, the most productive functional group. The primary production pathway was less important, but unconsumed primary production was presumably an important input to the FPOM pool. Invertebrate predators (including a portion of crayfish production) removed 52% (10.3 g

TABLE 6. Functional-group production and consumption (g ash-free dry mass [AFDM] m^{-2} y^{-1}) in the Kings Creek study reach, 1998 to 1999. Assimilation efficiency (AE) and net production efficiency (NPE) are based on literature values; see Methods. GPE = gross production efficiency. Food resource availability values are mean annual standing stocks (g $AFDM/m^2$), except for filterers and scrapers where suspended particulate organic matter (SPOM) and primary production are g AFDM m^{-2} y^{-1}.

Functional group[a]	Production	Gross production efficiency (AE × NPE)	Consumption (Production ÷ GPE)	Available food resource	% Consumed
Shredders	4.5	0.049	91.9	112.9	81
Collector-gatherers	6.0	0.033	183.0	77.6	236
Scrapers	3.8	0.15	25.5	120.5	21
Collector-filterers	1.7	0.05	33.6	6899.0	<1
Predators	3.6	0.35	10.3	19.7	52

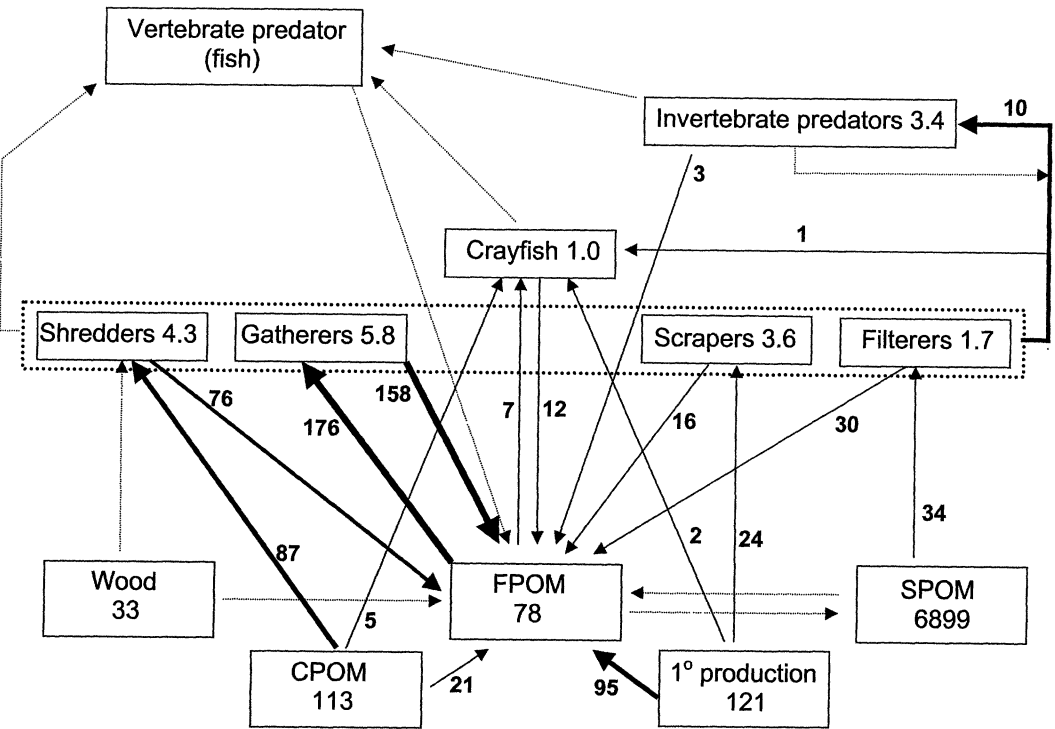[a] See Appendix for individual taxa

FIG. 4. Community food web and energy flow pathways for the Kings Creek study reach. Functional group and taxa values represent annual production (g ash-free dry mass [AFDM] m^{-2} y^{-1}). Resource pool values are mean standing stocks (g $AFDM/m^2$), except primary production and suspended particulate organic matter (SPOM) (g AFDM m^{-2} y^{-1}). Arrows entering consumer boxes indicate consumption (g AFDM m^{-2} y^{-1}), and those entering organic matter pools indicate estimated replenishment of the pool. Arrows exiting boxes indicate losses or, in the case of consumers, egestion (g AFDM m^{-2} y^{-1}). Arrows with dotted lines and no numbers were not quantified. Arrow widths represent the proportion of the flux relative to the respective resource pool. FPOM = fine particulate organic matter. SPOM value is calculated from Dodds et al. (2000), and annual primary production is based on Gurtz et al. (1982) and Dodds et al. (1996).

Table 7. Comparison of annual macroinvertebrate community production among similar-sized streams (arranged by increasing discharge) in the US and Europe. Values reported as dry mass were converted to ash-free dry mass (AFDM) by multiplying by 0.9. Discharge and temperature values are annual means.

Stream	Location	Production (g AFDM m^{-2} y^{-1})	Discharge (m^3/s)	Temperature (°C)	Reference
Coweeta (C53)	North Carolina	13.9	1×10^{-3}	12.9	Lugthart and Wallace 1992
Coweeta (C54)	North Carolina	11.5	1×10^{-3}	12.4	Lugthart and Wallace 1992
Coweeta (C55)	North Carolina	9.5	1×10^{-3}	12.7	Lugthart and Wallace 1992
Rold Kilde Stream	Denmark	7.9	3×10^{-3}	7.4	Iverson 1988
Kings Creek	Kansas	19.7	1×10^{-2}	13.9	This study
Bear Brook	New Hampshire	4.1	2×10^{-2}	7.0	Fisher and Likens 1973
Snively Springs	Washington	12.7	4×10^{-2}	10.8	Gaines et al. 1992
Sycamore Creek	Arizona	135.0	5×10^{-2}	17.0	Fisher and Gray 1983[a]
Sycamore Creek	Arizona	120.9	5×10^{-2}	17.0	Jackson and Fisher 1986

[a] Study did not include predators

AFDM m^{-2} y^{-1}) of total invertebrate production annually (Fig. 4).

Discussion

Macroinvertebrate community production

Total macroinvertebrate production in this headwater prairie stream was higher than most values reported for similar-sized forested streams, but much less (<15%) of that reported for a similar-sized Sonoran desert stream, Sycamore Creek (Fisher and Gray 1983, Jackson and Fisher 1986) (Table 7). Macroinvertebrate production in this headwater reach of Kings Creek also approached or exceeded production estimates for some substantially larger streams (Benke 1993). Temperature may influence patterns of macroinvertebrate production in different regions. For example, mean annual temperature in Kings Creek during our study was ~14°C, which is ~1°C higher than that reported for Coweeta, similar-sized forested streams in the Appalachian Mountains (Lugthart and Wallace 1992), and ~3°C cooler than Sycamore Creek (Fisher and Gray 1983, Jackson and Fisher 1986). Our macroinvertebrate community production estimate was intermediate between values for Coweeta and Sycamore Creek (Table 7), suggesting a positive relationship between temperature and production. However, a recent study of a neotropical stream in Costa Rica provides a contradiction to this apparent relationship. Despite mean annual temperatures of 24 to 26°C, Ramirez and Pringle (1998) estimated

macroinvertebrate production was <1 g AFDM m^{-2} y^{-1}. Further, Benke (1993) compared production estimates from ~40 streams and found no significant relationships with temperature.

Although relationships between temperature and macroinvertebrate production are unclear, generally higher production estimates have been reported for unshaded versus shaded stream reaches (Benke 1993). Relatively higher production of *Baetis* mayflies (Wallace and Gurtz 1986) and for all benthic macroinvertebrates (Behmer and Hawkins 1986) has been reported from unshaded versus shaded stream reaches. The prairie stream we examined is largely open-canopied, with ~75% of the reach unshaded at peak foliage. Because macroinvertebrate production has not been estimated for forested downstream reaches of Kings Creek, we could not directly compare shaded and open reaches. However, if we apply our community P/B value (8.6) to the mean standing stock biomass of the Kings Creek stream macroinvertebrate community in gallery forest reported by Gray and Johnson (1988, 1.01 g AFDM/m^2), we arrive at a production estimate of ~8.7 g AFDM m^{-2} y^{-1}. This estimate is 44% of the prairie community production reported in our study, and this difference was surprisingly similar to shaded vs open-stream macroinvertebrate production comparisons (43–57%) reported for the Horokiwi River in New Zealand (Hopkins 1976). Thus, our results provide additional evidence that invertebrate communities in open-stream reaches are more productive than those in shaded reaches.
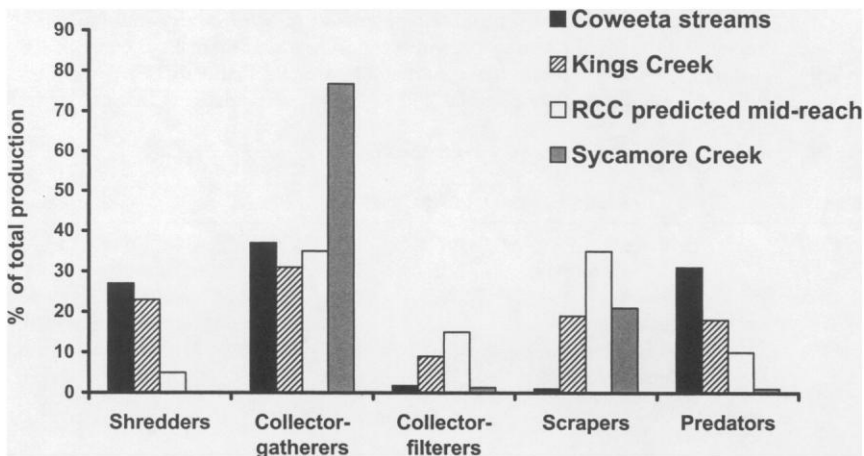
FIG. 5. Comparison of functional-group production in a forested headwater stream (based on averages of 3 streams at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains, Lugthart and Wallace 1992), a headwater prairie stream (this study), a Sonoran desert stream (Sycamore Creek, Jackson and Fisher 1986), and our interpretation of river continuum concept (RCC) predictions for mid-reaches (Vannote et al. 1980).

Macroinvertebrate functional structure

According to the RCC, open-canopied stream reaches are autotrophic, which is reflected in the dominance of scraper and collector invertebrate functional groups (Vannote et al. 1980). Instream primary production is the dominant energy source in KPBS prairie streams, which thus are considered primarily autotrophic (Dodds et al. 1996). Accordingly, scraper production in this stream reach was much higher than in Coweeta streams (Fig. 5). Contrary to the RCC, however, results of our study showed that scrapers did not dominate either biomass or production, and they consumed only ~20% of available instream primary production. Algae–grazer interactions in streams have been described as tightly coupled (Richardson 1993), but scraper production in our study reach appeared decoupled from the high primary production. Scraper production in autotrophic Sycamore Creek was limited by the availability of stable substrate (Fisher and Gray 1983). However, stable substrates were abundant in our study reach, suggesting other factors, such as predation, may have limited scraper production. In particular, *Physa* is one of the dominant scrapers in KPBS streams (Gray and Dodds 1998), but *Physa* abundance and production was relatively low during our study, and this may have been a result of predation by crayfish. Gray and Dodds (1998) noted that var-

iability in *Physa* populations on KPBS is apparently linked to predation by crayfish, and relatively stable, perennial flow prior to and during our study likely favored crayfish populations. In a related study from New Zealand grassland streams, Huryn (1998) reported that top-down control by an introduced vertebrate predator (*Salmo trutta* Linnaeus) decoupled scrapers and primary production, and that scrapers in a stream with trout consumed only ~21% of annual net primary production compared to ~75% in a stream without trout.

Unlike scrapers, the proportion of production attributable to collector-gatherers in Kings Creek was consistent with RCC predictions for an open-stream reach (Fig. 5). However, based on biomass, collector-gatherers represented a small fraction of the invertebrate community (12%), ~20% of that observed by Gray and Johnson (1988) in this same stream reach. Some of this disparity was a result of increased biomass of other groups during our study rather than lower values for collector-gatherers per se. Shredders made up a large % of production (22%) and biomass (29%) of our invertebrate community, whereas Gray and Johnson (1988) found that shredders accounted for only ~1% of total community biomass. The difference in the relative importance of shredders during 2 different studies in this stream may be related

Table 8. Mean annual standing stocks of benthic organic matter (g ash-free dry mass m²) in similar-sized streams in different regions of the US. Letters in parentheses indicate dominant land cover in the watershed: F = forested, P = prairie, D = desert. Total coarse particulate organic matter (CPOM) includes all organic material >1 mm, and CPOM excludes woody material. FPOM = fine particulate organic matter. na = no value reported.

Stream	Location	Total CPOM	CPOM	FPOM	Reference
Augusta Creek (F)	Michigan	na	126	440	Cummins et al. 1981
Coweeta C53 (F)	North Carolina	1206	451	704	Lugthart and Wallace 1992
Devil's Club Creek (F)	Oregon	24,762	1012	538	Naiman and Sedell 1979
Kings Creek (F)	Kansas	567	238	na	Gurtz et al. 1988
Bear Brook (F)	New Hampshire	1140	610	53	Fisher and Likens 1973
Kings Creek (P)	Kansas	146	113	78	This study
Kings Creek (P)	Kansas	129	38	na	Gurtz et al. 1988
Sycamore Creek (D)	Arizona	~1	~1	~50	Fisher and Gray 1983

to long-term hydrologic patterns. Prairie streams are characterized by having highly variable annual discharge and frequent spates and droughts (Matthews 1988), and this is also true for Kings Creek (Gray et al. 1998). However, above average-precipitation on KPBS in years preceding and during our study resulted in more stable, prolonged flow compared to prior periods (i.e., during the Gray and Johnson 1988 study), and may have favored relatively long-lived shredder species. In addition, spates that generally account for most export of CPOM from Kings Creek (Gurtz et al. 1982, Dodds et al. 1996) were less frequent and intense than normal during our study year, which may also have favored shredders. Studies that have examined functional-group production in forested headwater streams (e.g., Lugthart and Wallace 1992, Whiles and Wallace 1995) suggest that shredders account for 19 to 36% of community production. Thus, our estimate for shredders was surprisingly similar to those of similar-sized forested streams. However, our consumption estimates indicate this group may be resource limited, and comparisons with prior studies on the same stream reach suggest shredder populations exhibit high temporal variability.

Based on contributions of functional groups to total production and relatively high primary production, this prairie stream fits most closely with the RCC predictions for an open-canopied, mid-order stream (Vannote et al. 1980). However, the relatively productive shredder component also indicates that this prairie stream shares similarities with forested heterotrophic systems.

Detritivores and organic matter

Although CPOM seasonal dynamics in Kings Creek followed patterns within forested systems (e.g., highest values during autumn and winter), annual average standing stocks were considerably lower (Table 8). According to our estimates, shredders consumed ~81% of the annual average standing stock of CPOM. This % is quite high, considering that shredders in forested streams consumed ~38% of annual average standing stocks (Lugthart and Wallace 1992). Further, unlike other food sources in streams (e.g., algae) turnover rates for CPOM can be relatively low. For example, during a concurrent investigation downstream from our study reach, Dodds et al. (2000) estimated that N turnover in leaf litter was 0.0002/d, the lowest rate for all ecosystem compartments examined. It is unlikely that we underestimated CPOM during this study because our values compare favorably with previous estimates from this same stream (Gurtz et al. 1988, Dodds et al. 1996). In fact, our values for nonwoody CPOM were somewhat higher than previous investigations, probably related to the relatively stable flows and lack of scouring floods during the study period.

Shredders can be food-limited in streams (e.g., Dobson and Hildrew 1992), which has been partly attributed to low CPOM retention. Retentive structures (e.g., large woody debris

and roots in the stream channel) were scarce in Kings Creek. Previous studies in Kings Creek have reported low CPOM retention, with transport enhanced during frequent spates (Gurtz et al. 1988, Gray 1997, Gray and Dodds 1998). However, the combination of low allochthonous inputs and poor retention apparently does not preclude development of a productive shredder assemblage in this prairie stream during favorable hydrologic periods.

The highest FPOM standing stocks in forested headwater streams are often associated with pools and debris dams (Bilby and Likens 1980, Smock et al. 1985, Wallace et al. 1995). Our study reach contained only 14% pool area and little woody debris, so opportunities for CPOM and FPOM retention were rare. As with CPOM, FPOM values in our study reach were at least an order of magnitude less than those reported for similar-sized forested streams (e.g., Bilby and Likens 1980, Whiles and Wallace 1995). This pattern, combined with relatively high collector-gatherer production, suggests the FPOM standing stock was insufficient to support the collector-gatherer group. However, high FPOM turnover rates may account for this apparent inequity. For example, in Sycamore Creek, which has a highly productive collector-gatherer community, Fisher and Gray (1983) estimated that collectors feeding on FPOM ingested $>4\times$ their mass per day, the FPOM pool turned over every 2 to 3 d, and collectors exhibited a high rate of fecal reingestion. Our results suggest that high turnover of the FPOM pool, reingestion, and/or diet shifts among collector-gatherers are likely in Kings Creek. In agreement, a concurrent investigation downstream of our study reach indicated the fine benthic organic N pool turned over quickly (up to 0.05/d, Dodds et al. 2000). When we apply this turnover rate to our estimated FPOM pool, we arrive at a flux of $\sim$3.9 g AFDM m^{-2} d^{-1} to the FPOM standing stock, and a complete replenishment of the FPOM pool in 20 d ($\sim$18 times per y). This estimate assumes a steady state FPOM standing stock and a constant flux rate, but it reconciles the apparent imbalance we measured between collector-gatherer production and available FPOM resources, and demonstrates the significance of addressing energy flow rather than relying on static measures. Potential pathways for replenishment of the FPOM pool in this stream include egestion from all consumers including

vertebrates, senescence of primary production, settling of SPOM from upstream reaches, and CPOM breakdown (Fig. 4).

Predator production and consumption

The proportion of macroinvertebrate production attributable to predators in Kings Creek (19%) was intermediate among values reported for Coweeta streams and RCC predictions for unshaded, mid-order streams (Fig. 5). Lugthart and Wallace (1992) reported that predaceous invertebrates and salamander larvae in Coweeta streams consumed 67 to 79% of total macroinvertebrate production, with invertebrate predators composing 28 to 33% of total community production. Gray and Johnson (1988) previously noted an apparent predator-heavy trophic structure in Kings Creek, based on standing stock biomass. Results of our study suggest that invertebrate predators are productive in this prairie stream, but that the rapid turnover rates of 1° consumer groups are sufficient to support predator production. Based on our estimates, $\sim$50% of total macroinvertebrate production is consumed by macroinvertebrate predators. Other studies have also demonstrated that apparent trophic imbalances can often be explained by relatively high turnover rates of 1° consumers (Benke 1984, Huryn 1996).

Vertebrate predators in this prairie stream also consume macroinvertebrate production, but were not quantified. Orangethroat darters (*Etheostoma spectabile* (Agassiz)) are benthic insectivores (Cross and Collins 1995), and guts from specimens revealed chironomids and simuliids to be important prey items (DMS, unpublished data). The creek chub (*Semotilus atromaculatus* (Mitchill)) also was present in our reach, but they are more general in their feeding and do not concentrate entirely on benthos. Further, we concentrated on riffle/run habitats, and our benthic core sampling undoubtedly underestimated large crayfish, which can also be important predators on macroinvertebrates (e.g., Creed 1994, Lamberti 1996) and are most abundant in pools in Kings Creek (Loring 1987). Because we did not account for vertebrate predator consumption, and probably underestimated the impact of crayfish, we likely underestimated instream consumption of macroinvertebrate production. Nonetheless, our estimates suggest that, overall, bottom-up processes are at least as

important as top-down controls in this prairie stream, at least under conditions prevailing during our study.

Regarding the dynamic nature of prairie streams, Matthews (1988) stated, "you haven't been there, until you've been there a whole year, and this should probably be. . . . 5 or 10 years, or more". Thus, although we characterized the structure and function of the macroinvertebrate community in this prairie stream, our results may have differed greatly under more variable environmental circumstances (i.e., during drier conditions or years with more frequent and/or intense spates). Future studies that account for the inherent variability in prairie streams will further our understanding of these poorly studied ecosystems.

Acknowledgements

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APPENDIX. Annual mean abundance (individuals/m²), biomass (mg ash-free dry mass [AFDM]/m²), production (mg AFDM m⁻² y⁻¹), and P/B ratios of macroinvertebrate taxa in the Kings Creek study reach, 1998 to 1999.

Taxon	Order[a]	Abundance	Biomass	Production	P/B
Predators					
Argia spp.	O	56	30	152	5
Bezzia/Palpomyia spp.	D	723	99	1127	11
Calopteryx maculata (Beauvois)[b]	O	11	6	30	5
Chrysops sp.[b]	D	10	2	10	5
Culicoides spp.	D	567	27	316	12
Dolichopodidae[b]	D	48	3	29	10
Hemerodromia sp.[b]	D	162	8	79	10
Nematoda	–	545	<1	4	6
Orconectes neglectus (Faxon)	DE	3	120	240	2

APPENDIX. Continued.

Taxon	Order[a]	Abundance	Biomass	Production	P/B
Perlesta placida (Hagen) complex	P	71	35	284	8
Polycentropus sp.[b,c]	T	9	4	41	10
Pseudolimnophila sp.	D	92	60	565	9
Sialis sp.	M	54	278	190	<1
Tanypodinae[d]	D	1155	20	541	27
Total		**3501**	**692**	**3608**	**5**
Scrapers					
Stenonema femoratum (Say)	E	87	150	1034	7
Stenacron interpunctatum (Say)	E	236	30	261	9
Fallceon quilleri (Dodds)	E	891	62	1601	26
Hydroptilidae[e]	T	39	2	22	10
Stenelmis crenata (Say)	C	228	91	493	5
Physa sp.	L	99	17	180	11
Orconectes neglectus (Faxon)	DE	3	120	240	2
Total		**1581**	**472**	**3831**	**8**
Collector-gatherers					
Leptophlebia sp.	E	95	16	140	9
Caenis latipennis Banks	E	35	4	31	8
Chironomidae[f]	D	10,097	92	3859	42
Dasyhelea sp.	D	139	4	58	14
Oligochaeta	–	4705	66	1587	24
Turbellaria	–	98	10	84	8
Orconectes neglectus (Faxon)	DE	3	120	240	2
Copepoda[b]	–	1862	2	39	18
Total		**17,031**	**314**	**6038**	**19**
Collector-filterers					
Cheumatopsyche spp.[g]	T	350	143	1457	10
Pisidium sp.	H	46	5	48	10
Chimarra sp.[h]	T	22	9	66	7
Simulium spp.	D	65	9	89	10
Cladocera[b]		64	<1	2	10
Ostracoda[b]		803	2	19	10
Total		**1350**	**167**	**1681**	**10**
Shredders					
Tipula abdominalis (Say)	D	188	504	4029	8
Zealeuctra claasseni (Frison)	P	183	12	166	14
Gonomyia sp.[b]	D	7	21	103	5
Orconectes neglectus (Faxon)	DE	3	120	240	2
Total		**381**	**657**	**4538**	**7**
Total for all groups (average for P/B)		**23,843**	**2301**	**19,690**	**9**

[a] C = Coleoptera, D = Diptera, DE = Decapoda, E = Ephemeroptera, H = Heterodonta (Mollusca:Bivalvia), L = Limnophila (Mollusca:Gastropoda), M = Megaloptera, P = Plecoptera, T = Trichoptera

[b] Production estimated by applying P/B ratios to mean annual biomass (see Methods)

[c] *Polycentropus* sp. were probably all *Polycentropus centralis* Banks, based on adult collections

[d] Includes *Ablabesmyia* spp., *Larsia* sp., and *Thienemannimyia* sp.

[e] Hydroptilidae includes *Hydroptila consimilis* Morton and *Ochrotrichia arizonica* Denning and Blickle

[f] Includes Orthocladiinae genera: *Corynoneura* sp., *Cricotopus* spp., *Eukiefferiella* sp., *Parametriocnemus* sp., *Thienemanniella* sp.; Chironominae genera: *Cryptochironomus* sp., *Dicrotendipes* spp., *Stenochironomus* sp., and Tanytarsini (mostly *Rheotanytarsus* and *Cladotanytarsus*)

[g] *Cheumatopsyche* spp. were probably all *Cheumatopsyche pettiti* (Banks) based on adult collections

[h] *Chimarra* sp. were probably all *Chimarra obscura* (Walker), based on adult collections