Annual Production by Caddisflies and Mayflies in a Western Minnesota Plains Stream[1]

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Annual production was estimated for five species of caddisflies and mayflies, comprising major components of the insect community, in the Redwood River, a second- to third-order plains stream in western Minnesota. Estmates were made at two sites, one above and one below an impoundment. At the upstream site, annual production ($g \cdot m^{-2}$, wet weight) and annual P/B ratios (in parentheses) were *Hydropsyche bifida*, 8.3 (6.9); *Cheumatopsyche pettiti*, 5.5 (7.0); *Stenonema nepotellum*, 3.4 (5.7); *Stenacron interpunctatum canadense*, 0.8 (7.0); and *Caenis simulans*, 4.7 (4.2); with total annual production of 22.7 $g \cdot m^{-2}$. At the downstream site, annual production and P/B ratios were *H. bifida*, 34.3 (4.4); *C. pettiti*, 68.5 (4.4); *S. interpunctatum canadense*, 24.1 (6.1); and *C. simulans*, 2.8 (4.4); with total annual production of 129.7 $g \cdot m^{-2}$. These species comprised 27.5% of the total insect standing stock at the upstream site and 75.9% downstream. The hydropsychid production at the downstream site was apparently sustained by the drift of zooplankton from the impoundment, resulting in considerably higher production by hydropsychids than reported in woodland streams.

Key words: production, Trichoptera, Ephemeroptera, plains stream, benthos, size – frequency method

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Nous avons estimé la production annuelle pour cinq espèces de phryganes et d'éphémères, principales composantes de la communauté d'insectes de la rivière Redwood, un cours d'eau de plaine de second à troisième ordre du Minnesota occidental. Ces estimations ont été faites à deux endroits, l'un en amont et l'autre en aval d'un réservoir de retenue. Au site d'amont, la production annuelle ($g \cdot m^{-2}$, poids humide) et les rapports P/B annuels (entre parenthèses) sont: *Hydropsyche bifida*, 8,3 (6,9); *Cheumatopsyche pettiti*, 5,5 (7,0); *Stenonema nepotellum*, 3,4 (5,7); *Stenacron interpunctatum canadense*, 0,8 (7,0); et *Caenis simulans*, 4,7 (4,2); avec production annuelle totale de 22,7 $g \cdot m^{-2}$. Au site d'aval, la production et les rapports P/B annuels sont: *H. bifida*, 34,3 (4,4); *C. pettiti*, 68,5 (4,4); *S. interpunctatum canadense*, 24,1 (6,1); et *C. simulans*, 2,8 (4,4); avec production annuelle totale de 129,7 $g \cdot m^{-2}$. Ces espèces représentent 27,5% de la biomasse totale d'insectes au site d'amont et 75,9% au site d'aval. La production d'hydropsychide au site d'amont semble dépendre de la dérive du zooplancton du réservoir de retenue, avec, comme résultat, une proportion de ces organismes beaucoup plus forte que celle mentionnée pour les cours d'eau de pays boisé.

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There is growing interest among aquatic ecologists in the production biology of benthic invertebrates and in the use of production estimates to quantify energy flow through various components of aquatic ecosystems. Until recently, estimates of production by stream invertebrates have been scarce; however, at present, a sizable literature exists, having been published largely in the last decade (Waters 1977). Almost all data available have been obtained from small, low-order streams, particularly trout streams, where lack of turbidity, shallow depths, and easily sampled riffles apparently have facilitated bottom sampling. There are virtually no data available from the numerous prairie and plains streams of north

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central North America, many of which are affected by modern agricultural practices, characteristically have a high seston content from soil erosion, and are frequently turbid. Yet these often contain a rich benthic fauna dominated by immature insects classified as filterers or gatherers by Merritt and Cummins (1978), apparently using fine particulate organic matter (FPOM) as food.

Furthermore, there are still few data available for many quantitatively important taxa, for which methodological difficulties have been related to their type of life history. Earlier methods for production estimation have been generally limited to species with readily separated cohorts. However, the more recent size–frequency (Hynes) method does not require the separation of cohorts, thus circumventing this major problem (Hynes 1961; Hynes and Coleman 1968; Hamilton 1969; Benke 1979). Whereas the size–frequency method was originally proposed for gaining approximations of production by whole faunas or groups of combined species, most use of the method has been for single species, particularly for those that have extended periods of hatching and where separation of cohorts is difficult or impossible (Waters 1979). The diverse and widely distributed caddisfly family, Hydropsychidae, and several genera of mayflies fall into this category.

Many authors have conducted methodological studies, comparing the size–frequency method with earlier methods, almost always with similar results (Waters and Crawford 1973; Resh 1977; Cushman et al. 1978; Welton 1979), and the method has now been generally accepted as a valid procedure yielding accurate estimates (Benke and Waide 1977; Benke 1979; Waters 1979). Krueger and Martin (1980) have recently developed a method to compute confidence intervals about annual production estimates by the size–frequency method, and early applications of the method have resulted in remarkably good precision (Waters and Hokenstrom 1980).

The present study was conducted in the Redwood River, a western Minnesota plains stream, in which two widely distributed species of hydropsychid caddisflies and three species of mayflies constituted major components of the stream insect benthos. The study addressed two main objectives: first, to estimate production rates for these benthic insects common in a plains stream, and, second, to compare production between two communities, above and below an impoundment, having different quantities and qualities of particulate organic food resources.

Study Sites

The Redwood River is a tributary to the Minnesota River in southwestern Minnesota and is a plains stream now draining mostly agricultural cropland. Its watershed is divided into two distinct regions. From its headwaters in the southwest, the river crosses a gently rolling upland plain, the Coteau des Prairies, a prominent topographic feature cutting diagonally across southwestern Minnesota. The river drops from the Coteau into a lowland plain, also gently rolling but with lower relief, and continues in a northeasterly direction to the Minnesota River Valley. Before entering the Minnesota Valley, the Redwood flows through an impoundment, Lake Redwood, which formerly served a hydroelectric facility.

Sampling sites were selected from two quite different reaches of the river. An upstream site (Camden) was located on the slope off the Coteau in a wooded valley (second order). A downstream site (Ramsey) was located on the slope into the Minnesota River Valley, a short distance below Lake Redwood (third order). Both sites have coarse substrates and steep gradients, habitats not uncommon to plains streams (Jewell 1927), particularly where they fall over glacial lake beaches, the Coteau, or slopes into receiving streams.

Both sites had abundant populations of two species of hydropsychid caddisflies, *Cheumatopsyche pettiti* (Banks) and *Hydropsyche bifida* (Banks), as well as the mayflies *Stenonema nepotellum* (McDunnough) and *Stenacron interpunctatum canadense* (Walker) (both in Heptageniidae), and *Caenis simulans* McDunnough (Caenidae). The hydropsychids are classified trophically as filterers and all three mayflies as gatherers and/or scrapers (Merritt and Cummins 1978). As a group, these five species constituted an important component of the stream communities. While no work was conducted in the present study on the fishes of the Redwood River, or on their use of these insects as food, studies in other small streams in southwestern Minnesota indicated these and similar stream insects to be important in the diet of common stream fishes such as minnows, including the creek chub, blacknose dace, bigmouth shiner, and common shiner, and darters (Luey 1978).

Water temperatures ranged from 0°C in winter at both sites to ~22°C at Camden and 26°C at Ramsey in summer.

Methods

SESTON DRIFT

Drift samples were collected to compare organic seston loads above and below the reservoir. Two nets as replicates were staked into the stream bottom, and samples were taken over 24-h periods on December 12–13, 1974, and June 17–18 and July 26–27, 1975.

Nets of 253-μm mesh were used for the December sampling, mainly as part of an invertebrate drift study, but the results are included here because of their relevance to seston drift. Nets of 100-μm mesh were used in the June and July sampling specifically for measuring seston. Material in all samples was screened through a 1000-μm mesh sieve to remove larger particles of detritus and macroinvertebrates. Thus, the remainder consisted of material between 253 and 1000 μm from the December samples and between 100 and 1000 μm from the June and July samples; the latter is a range that includes the mesh size of catch nets of most hydropsychids, at least in later instars (Wallace 1975; Wallace et al. 1977; Wallace and Merritt 1980). Small amounts of sand were removed by decantation. Organic material was dried to a constant weight at 60°C.

BENTHIC INVERTEBRATES

A set of 10 samples of benthic invertebrates was collected from each of the two sites, at approximately monthly intervals from November 1974 through October 1975, using a 0.1-m^2 Surber sampler with a 471-μm mesh netting. Samples were preserved in the field with 10% Formalin and sorted in the

TABLE 1. Type of organic particles and percent composition (number) and total concentration (dry wt) (mean of two samples).

Date	Percent composition					Concn., mg·L^{-1}
	Detritus	Copepoda	Cladocera	Rotifera	Eggs[a]	
Camden						
Dec. 12–13, 1974	85.3	7.0	7.7	0.0	0.0	0.001
June 17–18, 1975	99.7	0.2	0.0	0.1	0.0	0.057
July 26–27, 1975	98.8	0.0	0.0	1.2	0.0	0.001
Ramsey						
Dec. 12–13, 1974	3.9	10.4	85.7	0.0	0.0	0.012
June 17–18, 1975	27.5	0.1	1.2	20.3	50.9	0.102
July 26–27, 1975	99.9	0.1	0.0	0.0	0.0	0.027

[a] Small particles presumed to be eggs, but identity unknown.

laboratory. Mean wet weights were determined for each instar (hydropsychids) and for each size group (mayflies) by weighing a group of specimens after centrifuging in a screen cone to remove external liquids.

SPECIES IDENTIFICATIONS

Hydropsychid larvae and adults were identified using keys from Ross (1944) and later descriptions. Early instars were distinguished by head capsule width and coloration, using the methods of Mackay (1978). Head capsule widths were measured with an eyepiece micrometer, and the frequencies of these measurements were used to define a range in head capsule width for each instar of each species whereby the separate instars could be identified. *Hydropsyche bifida* larvae had slightly larger head capsule widths than *Cheumatopsyche pettiti* larvae in equivalent instars. Head capsule widths increased through instars by a factor of ~1.5 for both species as was true for the several species studied by Mackay (1978). All larvae from each month's collections were sorted into instars on the basis of the head capsule width ranges established for each species.

Mayfly nymphs were identified to genus with Edmunds et al. (1976) or Lewis (1974); subimagoes and imagoes were collected at the sampling sites at times of emergence or oviposition, identified to species with Burks (1953) or Lewis (1974), and presumed to correspond with nymphs as no other adults of the same genera were observed. Nymphs were sorted into size categories measuring head capsule widths of all specimens with an eyepiece micrometer.

PRODUCTION ESTIMATION

The size–frequency (Hynes) method was used for production estimation. Losses between successive size groups were multiplied by the number of size groups ("times loss" factor = *I* of Hamilton (1969) and Menzie (1980)) and summed algebraically for total annual production; however, negative values, when occurring in the early size groups, were considered to be zero, because these negative values were probably due to incomplete sampling of small specimens (Benke and Wallace 1980). The method of Krueger and Martin (1980) was used to calculate confidence intervals.

Benke's (1979) correction for cohort production interval (CPI) was used to account for periods in the life history when no aquatic production occurs, by multiplying by a ratio of 365/CPI in days. Based on data of Fremling (1960) and general ranges reported by Wiggins (1977), the egg stage of the hydropsychids was presumed to last about 15 d, the pupal stage about 7 d, and time between emergence and oviposition about 3 d. Thus a CPI of 340 d was used for estimates of production by univoltine hydropsychids. Hydropsychids were grouped into the five instars as size groups, and a "times loss" factor of 5 was used. Data reviewed by Edmunds et al. (1976) were used to estimate CPI for the mayflies. For the heptageniids, hatching was considered to occur about 20 d after oviposition, for *Caenis simulans* about 8 d. The time between emergence and oviposition was presumed negligible for all species. A CPI of 345 d was used for the heptageniids and 357 d for *C. simulans*.

Results

SESTON DRIFT

Drifting seston was consistently in higher concentrations at the Ramsey site (downstream from Lake Redwood) than at the Camden site (upstream), for all three dates, ranging from a low of 0.001 mg·L^{-1} at Camden (December and July) to a high of 0.102 mg·L^{-1} at Ramsey (June) (Table 1). The impoundment above Ramsey apparently was also responsible for greater proportions of animal materials in the seston, with higher amounts of Copepoda and Cladocera in December, and Rotifera and eggs (unknown identity) in June. Seston in late July was almost entirely of detritus at both sites. The concentrations reported here are low compared to other reported data, e.g. up to 8.2 mg·L^{-1} ash-free dry weight (AFDW) (Gurtz et al. 1980) and 3.68 mg·L^{-1} AFDW (Wallace et al. 1982); however, particles <100 μm (which frequently constitute the major portion of organic seston) were not collected in the present study.

LIFE HISTORIES

Life history patterns for all species were similar at the two sites. All appeared to be univoltine; however, there remained the possibility that *Cheumatopsyche pettiti* was bivoltine, es-

TABLE 2. Example of size–frequency calculation of annual production by *Cheumatopsyche pettiti* (wet wt).

Instar	$N \cdot m^{-2}$	Mean wt (mg)	Biomass ($g \cdot m^{-2}$)	$N \cdot m^{-2}$/ lost $\cdot m^{-2}$	Mean wt loss (mg)	Wt loss ($g \cdot m^{-2}$)	×5 ($g \cdot m^{-2}$)
			Camden				
I	90	0.13	0.01				
				−113	0.17	−0.02	0.00
II	203	0.24	0.05				
				11	0.39	0.00	0.00
III	192	0.61	0.12				
				31	1.15	0.04	0.20
IV	161	2.22	0.36				
				142	5.20	0.74	3.70
V	19	12.78	0.24				
				19	12.78	0.24	1.20
Total							5.10
Corrected annual production = 5.10 × 365/340 = 5.46							
			Ramsey				
I	31	0.13	0.01				
				−446	0.17	−0.08	0.00
II	477	0.24	0.11				
				−679	0.39	−0.26	0.00
III	1156	0.61	0.71				
				178	1.15	0.20	1.00
IV	978	2.22	2.17				
				−8	5.20	−0.04	−0.21
V	986	12.78	12.60				
				986	12.78	12.60	63.00
Total							63.79
Corrected annual production = 63.79 × 365/340 = 68.48							

pecially at the Ramsey site, where summer water temperatures were slightly higher. Pupation by hydropsychids began in May and extended through August or September. Hatching and recruitment of first instar larvae into the population began immediately in May or June and extended at least into September. Maximum overlap between cohorts occurred in June and July, and in the third and fourth instars, respectively. Larvae overwintered mainly in the second through fifth instars and a few in the first instar. No pupae were found during the winter.

The two heptageniid mayflies had emergence peaks in May or June, somewhat earlier than *Caenis simulans* which peaked in June and July. Maximum recruitment for all mayflies occurred shortly after the peak emergence, in June or July for the heptageniids and in July or August for *C. simulans*. All species had extended periods of recruitment and were broadly distributed among size groups throughout the entire year.

PRODUCTION

The size–frequency calculations of annual production by species are exemplified for a hydropsychid (*Cheumatopsyche pettiti*) in Table 2 and for a mayfly (*Caenis simulans*) in Table 3. The use of head capsule widths to place individual specimens into instars or size groups probably reduces the error mentioned by Waters and Crawford (1973) wherein the "times loss" factor may be inaccurately high because of the presence of one or a few unusual individuals in the largest size group when length is used to categorize groups.

Annual production by all five species totaled 22.7 $g \cdot m^{-2}$ (wet) at the Camden site and 129.7 $g \cdot m^{-2}$ at Ramsey (Table 4). The latter, below Lake Redwood, was nearly sixfold higher than at the upstream Camden site, probably reflecting the influence of the greater seston quantities below the impoundment. Total annual production by the two hydropsychids *H. bifida* and *C. pettiti* was 13.8 $g \cdot m^{-2}$ at Camden and 102.8 $g \cdot m^{-2}$ at Ramsey; for the mayflies, total annual production was 8.9 $g \cdot m^{-2}$ at Camden and 26.9 $g \cdot m^{-2}$ at Ramsey.

Annual production by individual species shows other differences between sites (Table 4). With the exception of the mayflies *C. simulans* and *Stenonema nepotellum*, all production rates were higher at the Ramsey site below Lake Redwood. Annual production by *C. simulans* was nearly twice as high at the upstream site, Camden (4.7 $g \cdot m^{-2}$), than at Ramsey (2.8 $g \cdot m^{-2}$), suggesting that this species was not benefiting from the greater seston at Ramsey, but rather that it was functioning more as a scraper than a gatherer in its trophic habits. A similar situation may apply for *S. nepotellum*; annual production was 3.4 $g \cdot m^{-2}$ at Camden, but negligible at Ramsey.

TABLE 3. Example of size–frequency calculation of annual production by *Caenis simulans* (wet wt).

Head width (µm)	$N \cdot m^{-2}$	Mean wt (mg)	Biomass ($g \cdot m^{-2}$)	$N \cdot m^{-2}$/ lost $\cdot m^{-2}$	Mean wt loss (mg)	Wt loss ($g \cdot m^{-2}$)	×10 ($g \cdot m^{-2}$)
			Camden				
0.38	13	0.34	0.004				
				−66	0.36	−0.024	0.00
0.39–0.50	79	0.42	0.033				
				−145	0.49	−0.071	0.00
0.51–0.62	224	0.57	0.128				
				−7	0.66	−0.005	0.00
0.63–0.74	231	0.76	0.176				
				1	0.86	0.001	0.01
0.75–0.86	230	0.98	0.225				
				42	1.16	0.049	0.49
0.87–0.98	188	1.38	0.259				
				129	1.66	0.214	2.14
0.99–1.10	59	2.00	0.118				
				39	2.49	0.097	0.97
1.11–1.22	20	3.11	0.062				
				6	3.74	0.022	0.22
1.23–1.34	14	4.49	0.063				
				6	5.09	0.031	0.31
1.35	8	5.78	0.046				
				8	5.78	0.046	0.46
Total							4.60
Corrected annual production = 4.60 × 365/357 = 4.69							
			Ramsey				
0.38	1	0.34	0.000				
				−40	0.36	−0.014	0.00
0.39–0.50	41	0.42	0.017				
				−96	0.49	−0.047	0.00
0.51–0.62	137	0.57	0.078				
				−5	0.66	−0.003	0.00
0.63–0.74	142	0.76	0.108				
				27	0.86	0.023	0.23
0.75–0.86	115	0.98	0.113				
				15	1.16	0.017	0.17
0.87–0.98	100	1.38	0.138				
				48	1.66	0.080	0.80
0.99–1.10	52	2.00	0.104				
				39	2.49	0.097	0.97
1.11–1.22	13	3.11	0.040				
				7	3.74	0.026	0.26
1.23–1.34	6	4.49	0.027				
				3	5.09	0.015	0.15
1.35	3	5.78	0.017				
				3	5.78	0.017	0.17
Total							2.75
Corrected annual production = 2.75 × 365/357 = 2.81							

Annual P/B ratios fell approximately in the range reported elsewhere for univoltine benthic invertebrates (Waters 1977), ranging from 4.2 to 7.0 (Table 4). For the hydropsychids, P/B ratios were higher at the Camden site (6.9–7.0) than at Ramsey (4.4). For the mayflies, no such difference between sites was found.

Discussion

Total hydropsychid production at Ramsey at 102.8 $g \cdot m^{-2}$ (wet) (~17.1 $g \cdot m^{-2}$ (dry)) is high relative to most hydropsychid estimates of production in the literature, although some are higher, e.g. 26.0 $g \cdot m^{-2}$ (dry) (Floessner 1976). Even higher production rates have been reported on the basis of snag surface area (Benke et al. 1979; Cudney and Wallace 1980).

Mayfly production generally was not high compared with others from the literature with the exception of the heptageniid *Stenacron interpunctatum canadense* at Ramsey. The highest

TABLE 4. Annual production (P, $g \cdot m^{-2}$, wet weight) and annual P/B ratios for insects in the Redwood River. Ninety-five percent confidence intervals are given in parentheses.

	Camden		Ramsey	
	P	P/B	P	P/B
Hydropsychidae				
Hydropsyche bifida	8.3 (7.47–9.11)	6.9	34.3 (31.88–36.72)	4.4
Cheumatopsyche pettiti	5.5 (4.65–6.27)	7.0	68.5 (64.96–72.00)	4.4
Total Hydropsychidae	13.8		102.8	
Ephemeroptera				
Stenonema nepotellum	3.4 (3.30–3.58)	5.7		
Stenacron interpunctatum canadense	0.8 (0.78–0.88)	7.0	24.1 (23.67–24.57)	6.1
Caenis simulans	4.7 (4.61–4.77)	4.2	2.8 (2.75–2.87)	4.4
Total Ephemeroptera	8.9		26.9	
Total	22.7		129.7	

production reported for Heptageniidae appears to be 2.08 $g \cdot m^{-2}$ (dry) for *Rhithrogena semicolorata* (Zelinka 1973). Although the estimate from Ramsey was considerably higher than this, it was still within the range for Ephemeroptera based on Waters's (1977) review and well below a recent estimate for *Tricorythodes atratus* (Hall et al. 1980). We are aware of no production estimates for species in the mayfly family Caenidae.

The five species selected for production estimates in this study represented 75.9% of the insect biomass at Ramsey and 27.5% at Camden, and of the total invertebrate biomass, 46.8% at Ramsey and 15.4% at Camden (calculated from data in MacFarlane 1978). Thus, total invertebrate production was much greater than the sum of these five insect species' production at either site, particularly at Camden. Two estimates of total insect production in streams are available for comparison, both from second-order, woodland streams. These estimates fall remarkably close together: 4.78 $g \cdot m^{-2}$ for Bear Brook (Fisher and Likens 1973); 4.80 and 4.32 $g \cdot m^{-2}$ (dry) for Factory Brook, 1974 and 1975 (Neves 1979). The five-species sum of production estimates at Camden, ~3.8 $g \cdot m^{-2}$ (dry), was near these values, and at Ramsey the sum was much greater, 21.6 $g \cdot m^{-2}$ (dry). Total insect production at both sites in this plains stream was apparently much greater than in the above woodland streams; this difference may be true for plains streams generally caused by abundant organic seston, particularly in regions of intensive agriculture where it apparently is derived from surrounding cropland soils.

Large production differences between the two sites were apparent. High hydropsychid production at Ramsey was presumably sustained by the higher sestonic drift at that site with its high proportion of zooplankton. High standing stocks of hydropsychids below lakes or reservoirs are common (Chutter 1963; Cushing 1963; Spence and Hynes 1971). The high proportion of animal food available in these habitats is a major factor; such animal food provides essential nutritional supplements to a diet mainly of detritus (Anderson 1976) and may account for the major share of hydropsychid production (Benke and Wallace 1980). Slightly coarser substrates at Ramsey presumably provided a greater quantity of optimal habitat for hydropsychids, also contributing to the difference.

Differences in mayfly production were more complicated but probably were also related to food and substrate combinations. Two species were more productive at Camden, *Stenonema nepotellum* and *Caenis simulans*. The coarser substrates at Ramsey provided abundant habitat for the heptageniids, and an abundant supply of FPOM was available in the sediments. *Stenacron interpunctatum canadense* was much more productive at Ramsey. *Stenonema nepotellum*, however, did not occur in significant numbers at Ramsey; perhaps this species and *C. simulans*, not benefiting from the larger quantities of FPOM at Ramsey, functioned more as scrapers in their trophic habits. Slightly finer substrates at Camden and some in-channel vegetation further improved the habitat for *C. simulans* at that site.

Confidence intervals calculated for these estimates ranged from 3.4 to 29.7% of production, seemingly low values when compared with the known high variance in stream bottom sampling. Krueger and Martin (1980) obtained intervals of 35.3–46.8% of production for their examples using data for two mayflies. Waters and Hokenstrom (1980) obtained smaller intervals, 11.1–15.6% of production by the amphipod *Gammarus pseudolimnaeus*, but took a larger number of samples (20) per day. Our confidence intervals were generally larger for the hydropsychids (10.3–29.7% of production) than for the mayflies (3.4–12.1% of production). Smaller confidence intervals were obtained for larger values of production by a given species. Spatial distributions appeared to exert an important influence on the size of the confidence interval. Although all species had contagious spatial distributions based on the Chi-squared variance to mean ratio (Elliott 1971), the mayflies appeared more evenly distributed than the hydropsychids, and the confidence intervals were smaller. Systematic errors, such as errors in determining CPI or voltinism, were probably small in view of the published data referred to in the Methods section.

Hydropsychid P/B ratios were substantially higher at Camden than at Ramsey (Table 4), but no comparable difference was apparent for the mayflies. Robertson (1979) in his review of marine P/B ratios points out that more older and larger individuals in a population reduces the P/B ratio, because these individuals increase mean population biomass but add relatively less to production. Hydropsychid survival into the last larval instar was much greater at Ramsey than at

Camden for both species and probably accounts for the higher P/B ratios at the Camden site (see data for *Cheumatopsyche pettiti* in Table 2; survival by *H. bifida* from IV to V instars was 158−22 m^{-2}, or 14%, at Camden, but was 357−344 m^{-2}, or 96%, at Ramsey). Greater survival at Ramsey may be due in part to more abundant space under cobbles at that site. At Camden, most cobbles were embedded in sand. At Ramsey, much of the larger interstitial space remained open; settling of coarser sands in the reservoir helps preserve these spaces where the larvae are better protected from scour during high water and from predation by fish. Greater survival to V instar at Ramsey might also be due to the greater abundance and higher quality of sestonic food at this downstream site.

The annual P/B ratios approximate cohort P/B ratios as all species were univoltine; however, cohort P/B ratios would in all cases be slightly lower, approximately in the proportion CPI/365, because the CPI for all species was slightly less than 365 d (Waters 1979).

Hynes (1980) cautions against the uncritical acceptance of confidence limits obtained from the method of Krueger and Martin (1980). Sampling problems, particularly on hard substrates, must keep us from feeling overly comfortable with narrow confidence limits; as studies of the hyporheic benthos clearly demonstrated (Coleman and Hynes 1970; Bishop 1973; Hynes 1974; Williams and Hynes 1974), systematic error in benthic sampling can be very large. However, as Benke et al. (1979) pointed out, samples from all dates through the year are dealt with as replicates in the size−frequency method, in effect increasing degrees of freedom and resulting in lower variance.

In this study, the smallest individuals of each species apparently were not sampled accurately, with the result being negative entries in the production tables for the first one or two size groups. These were treated as zero, as explained above, but this result still represents an error in the direction of an underestimate. The underrepresentation of smallest instars is probably due to several factors, including escapement through too large mesh in the sampler, rapid growth of early instars between sampling dates, and lack of detection in sample analysis because of their small size. The error is common in production studies and the degree of error unknown; however, in view of the extremely small size (i.e. weight) of the earliest instars, the error in terms of biomass may be small or even negligible.

The caddisfly and mayfly production estimates from the Redwood River provide data for a plains stream, a type of stream from which no previous production estimates have been available. Production apparently was influenced by the quantity and quality of organic seston loads, which probably were derived from cropland soils. Hydropsychids below the impoundment may have been particularly advantaged by the availability of animal food in the drift which increased their production.

Production by plains stream benthos appears high compared with available data on production in woodland streams. The high organic seston loads of plains streams, especially in regions of intensive agriculture, probably constitute a major factor increasing invertebrate production.

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