

## Effects of stream regulation on density, growth, and emergence of two mayflies (Ephemeroptera: Ephemerellidae) and a caddisfly (Trichoptera: Hydropsychidae) in two Rocky Mountain rivers (U.S.A.)

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The influence of altered temperature and food regimes on the life histories of three univoltine species of aquatic insects were compared in two regulated river systems in northwestern Montana, U.S.A. Temperatures in both regulated rivers were more moderate than below many deep-release dams as a result of the operation of a selective withdrawal system on the dam on the Kootenai River and of major input of waters from unregulated forks in the Flathead River. Population densities of these species were generally highest in the regulated Kootenai River where the greatest biomass of periphyton and seston were measured. Differences in growth rates between regulated and reference stations were observed for *Drunella flavilinea* and *Hydropsyche oslari* but not for *Serratella tibialis*. Temperature had little effect upon total developmental time for *H. oslari* but altered growth rates and time spent in late instars. Peak emergence times were 2 to 4 weeks later in regulated areas where summer water temperatures were cooler, and the duration of emergence periods was extended in regulated areas.

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L'influence de la modification du régime de température et du régime alimentaire sur le cycle biologique de trois espèces univoltines d'insectes aquatiques a été comparée dans deux systèmes hydrographiques contrôlés du nord-ouest du Montana, États-Unis. Les températures des deux rivières contrôlées étaient plus fraîches qu'elles ne l'étaient en aval de plusieurs barrages importants, et cette diminution était attribuable à l'existence d'un système de retrait sélectif au barrage de la rivière Kootenai, et à l'arrivée considérable d'eaux de branches non contrôlées de la rivière Flathead. Les densités de population des espèces étudiées étaient généralement plus élevées dans la rivière Kootenai contrôlée où existaient aussi les biomasses de périphton et de seston les plus considérables. Des différences de taux de croissance ont été enregistrées entre les stations contrôlées et des stations témoins chez *Drunella flavilinea* et *Hydropsyche oslari*, mais pas chez *Serratella tibialis*. La température n'avait que peu d'effet sur la durée totale du développement d'*H. oslari*, mais elle a modifié les taux de croissance et la durée des derniers stades. Les densités maximales d'adultes à l'émergence se sont produites 2 à 4 semaines plus tard dans les zones contrôlées où la température de l'eau l'été était plus froide, et la durée de la période d'émergence y était aussi plus étendue.

[Traduit par la Revue]

### Introduction

Alterations in temperature can affect life histories of aquatic insects by direct effects on larval growth and by indirect influences on the quantity and quality of available food material (see reviews by Anderson and Cummins 1979; Ward and Stanford 1982; Sweeney 1984). River regulation is generally manifested by substantial alteration of diel and annual temperature regimes. Regulation also may alter autochthonous and allochthonous carbon loading, which implies a change in food resources for zoobenthos (Ward and Stanford 1979). Therefore, analyses of insect growth and abundance in regulated rivers should provide insight into the subtleties of nonlethal disturbances on life-history parameters (see Lehmkühl 1979) and the relative success of a species in terms of population densities. The life cycles and emergence times of certain species of insects have been studied in regulated rivers (e.g., Radford and Hartland-Rowe 1971; Vaught and Stewart 1974; McClure and Stewart 1976; Rhame and Stewart 1976; Hauer and Stanford 1981, 1982a, 1982b; Kondratieff and Voshell 1981; Parker and Voshell 1982), but few attempts have been made to relate growth rates and developmental times of insects to environmental changes.

In this study we compared the effects of differences in temperature on the growth rates, developmental times, and the

timing and duration of the emergence periods of three species of insects growing under different thermal regimes as a result of river regulation. Two ephemereid mayflies (*Drunella flavilinea* McDunnough and *Serratella tibialis* McDunnough) and a hydropsychid caddisfly (*Hydropsyche oslari* Banks) were studied because they were relatively abundant in most river segments and represent both hemi- and holo-metabolous growth patterns. Differences in the quantity and quality of the food base were also quantified to help resolve questions about food constraints on growth, relative size, and densities.

### Study areas

This study was conducted on the Flathead and Kootenai river systems in northwestern Montana (Fig. 1). Three different regulation scenarios were investigated in these two river systems: (i) unregulated, (ii) partially regulated by a deep-release dam, and (iii) regulated by a selective withdrawal system. The two rivers are similar in size and geography, and the substrate at all sample stations was composed of glacial cobble of similar ranges in size.

Hungry Horse Dam, which has a hypolimnial release, is located on the South Fork Flathead River 11 km east of Columbia Falls, Montana (latitude 48°20'28"). The South Fork flows into the mainstem Flathead River 8 km from the dam. The effect of regulation is greatly moderated in the mainstem Flathead River, because 63% of the average flow (mean annual discharge, 233 m<sup>3</sup>/s during the year of this study) is derived from unregulated tributaries (United States Geological Survey 1981). Because the ameliorative effect imposed by unregulated segments is much greater than in most other regulated rivers, we refer

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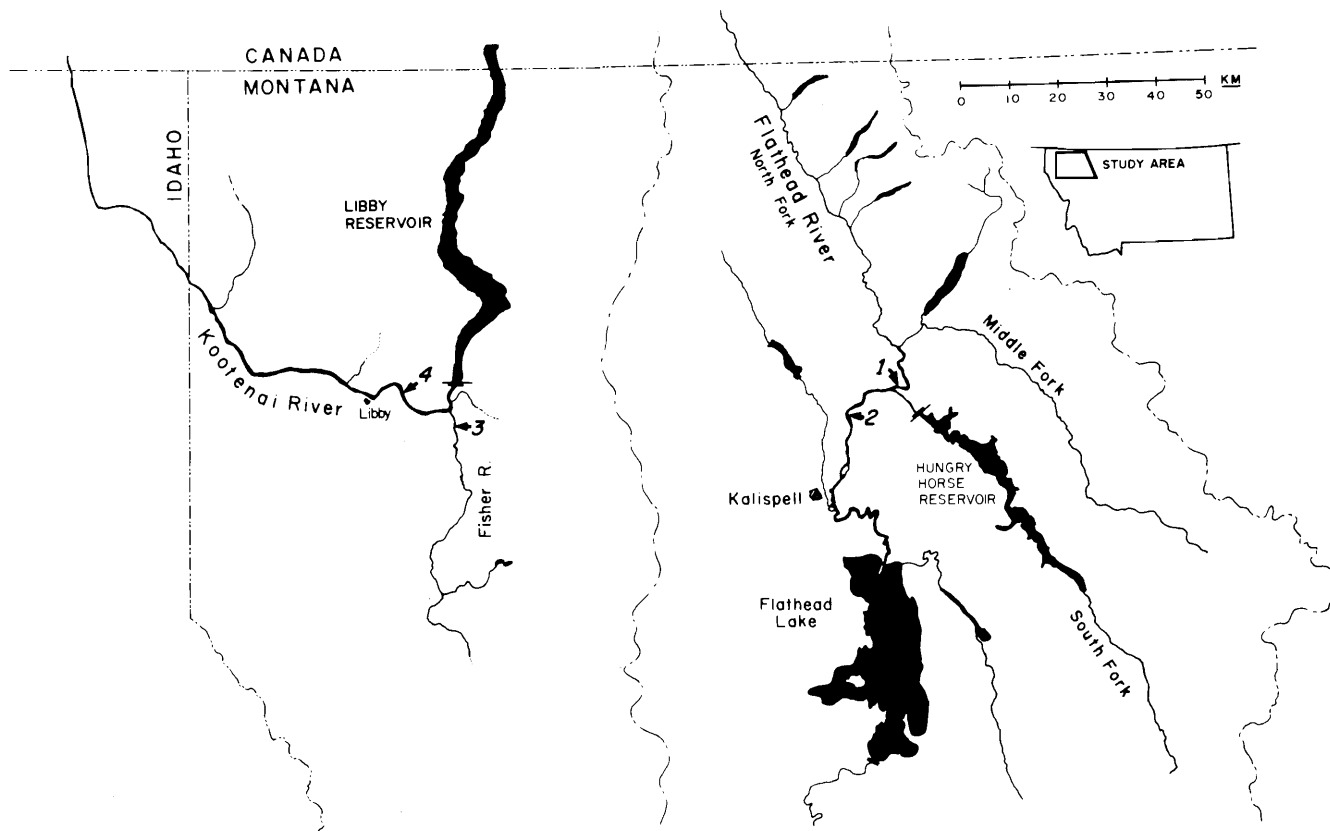


FIG. 1. Location of the study stations in northwestern Montana, U.S.A. 1, unregulated Flathead River; 2, partially regulated Flathead River; 3, unregulated Fisher River; 4, regulated Kootenai River.

to the Flathead River downstream from the mouth of the South Fork as partially regulated. Collections for life-history studies were made in riffle areas at an unregulated (reference) site 1.2 km upstream of the mouth of the South Fork and at a partially regulated site 12 km downstream of the mouth of the South Fork in the mainstem Flathead River (Fig. 1). An intervening stretch of slow water between the two stations lessened the possibility that insects from unregulated areas might drift downstream to the station in the partially regulated Flathead River.

Libby Dam on the Kootenai River is 18 km east of Libby, Montana (latitude 48°24'03"). A selective withdrawal system on Libby Dam controls the release depth. Releases from higher levels in the reservoir moderate the temperature regime and increase the input of limnoplankton from the reservoir compared to deep-release dams. The Kootenai River below the dam had an annual mean discharge of 290 m<sup>3</sup>/s during the time of this study. Insects for the study were collected from a riffle area 18 km downstream from the dam (Fig. 1). A station on the Fisher River, a tributary stream which enters the Kootenai River four km below Libby Dam, was used as an unregulated reference site. The Fisher River (5th order) is smaller than the Kootenai River (7th order), but it was chosen because of its geographical proximity and the fact that the Kootenai River above Libby Reservoir has been altered by industrial discharges.

### Methods and materials

Continuous recording thermograph data, collected by the United States Geological Survey (1981), were obtained for the unregulated and partially regulated Flathead River and for the Fisher River. Similar data for the Kootenai River below Libby Dam were obtained from the United States Army Corps of Engineers.

Analyses of the periphyton standing crops (chlorophyll *a*, ash-free dry weight, C:N), community metabolism, and seston carbon (POC) were used to characterize the food resources in the study segments. The periphyton standing crop was quantified at the sampling stations on a

seasonal basis (August, October, and January). Ash-free dry weight (AFDW) and chlorophyll  $\alpha$  were measured on material collected from a known area on natural substrates. Methanol was used as the extraction solvent for chlorophyll  $\alpha$  analyses (Holm-Hansen and Riemann 1978). Calculations for chlorophyll  $\alpha$  (Lorenzen 1967) were made using empirical absorption coefficients (Riemann 1978). C:N ratios were obtained by drying samples of periphyton at 50°C for 24 h and storing them in a desiccator until analysed. Analyses were conducted in duplicate using a Perkin Elmer model 316 CHN analyzer.

Benthic community metabolism was measured at the four study areas in September 1981. Rocks from the riverbed were placed in four recirculating chambers *in situ* at each site, and changes in oxygen evolution over a 24-h period were recorded with a YSI oxygen meter. Metabolic parameters were measured by the diel oxygen method (Bott et al. 1978; Naiman and Sedell 1980), with care taken to avoid gas supersaturation in the closed chambers.

Grab samples for particulate organic carbon (POC) analyses were collected monthly during conditions of minimum discharge from the dams. Seston was concentrated by filtering river water through pre-ashed (500°C, 8 h) glass-fiber filters. Particulate organic carbon on the filters was quantified by a CO<sub>2</sub> liberation procedure (Menzel and Vaccaro 1964) with the use of an Oceanography International carbon analyser.

Particulate organic matter (POM) >355  $\mu$ m was collected using insect drift nets with a rectangular opening measuring 46 by 30 cm. The nets were set in place for a 30-min interval, and the flow rate was monitored with a flow meter to quantify the volume filtered. All insects and any debris larger than 1 cm were removed before analysis. Concentrations of this sestonic source of POM were determined by mass after ashing at 550°C.

Monthly sampling of benthic insects at the stations on the Flathead River was begun in July 1979. Eight to ten quantitative samples were collected at each station each month through September 1980. In the Kootenai River system, six to nine samples were taken each month

(except December and February) from October 1979 through September 1980. The two samplers used in the study enclosed a sample area of 0.33 m<sup>2</sup> and had a mesh size of 150 µm (Perry 1984). Adults were collected with sweep nets, by hand, in drift nets, and in light traps, which were operated nightly from June to October 1980 at the four sample stations.

Total head capsule width was measured for the two mayfly species, while the interocular distance was used for the hydropsychid caddisfly. The genus name *Hydropsyche*, as opposed to *Symphitopsyche*, (Ross and Unzicker 1977) or *Ceratopsyche* (Morse and Holzenthal 1984) was retained for *H. oslari*, since its taxonomic status has not been resolved (G. Wiggins, personal communication). The earliest instars of *H. oslari* could not always be separated from those of *H. occidentalis*, so specimens were used only when a positive identification could be made. Larval instar determinations were established using the Mackay (1978) method.

Means of head capsule widths of individuals collected at each station on each sample date were used to estimate growth rates. The regression statistics for head capsule widths on sample dates were calculated using the General Linear Models procedure of SAS (SAS Institute, Inc. 1982). The data for the two mayfly species were log transformed to obtain significant ( $p < 0.05$ ) linear regressions, and then slopes of the regression lines were compared using analysis of covariance. A semilog, linear model was not appropriate for *H. oslari*, because growth was not continuous for all individuals throughout the year; consequently a good linear regression could not be obtained for site comparisons. Instead, an analysis of variance of head capsule sizes was conducted for *H. oslari* to detect significant differences in sizes between sites.

## Results

### Physical environmental factors

Discharge from Hungry Horse Dam on the Flathead River varied between a minimum flow of 4.1 m<sup>3</sup>/s and a peak discharge of 323 m<sup>3</sup>/s. The hydrograph of the mainstem Flathead River reflected the composite discharge from the three forks and thus showed the effect of the runoff period from mid-April through mid-July. Discharge during the winter of 1980 was atypical, because minimum flows from the regulated South Fork were generally maintained from mid-December through mid-May. This flow regime minimized differences between the partially regulated and unregulated areas during that period of time.

Both rivers were characterized by reduced annual thermal amplitude as a result of regulated releases. The details of the discharge-temperature interaction and history have been given elsewhere (Perry 1984). Although the Flathead River was only partially regulated at Station 2 and the temperature regime in the Kootenai River was moderated by the selective withdrawal system, summer temperatures were still lower and late fall and winter temperatures were higher at these stations than at the reference stations (Fig. 2). Diurnal temperature variations were minimal in the regulated Kootenai River; release temperatures frequently varied only 1°C in 24 h. Diurnal temperature fluctuations were much greater in the partially regulated Flathead River due to lower volume discharge and the ameliorating effect of the unregulated tributaries. The thermal impact of cold releases from Hungry Horse Dam in the partially regulated Flathead River was reduced during the summer months by the diurnal temperature increases which occurred when flows from the South Fork were reduced to minimum levels for part of the day.

The regulated Kootenai River was warmer than the partially regulated Flathead River; similarly, the reference Fisher River was warmer than the unregulated station on the Flathead River in both the summer and winter (Fig. 2). The Kootenai River is regulated through selective depth withdrawal to provide

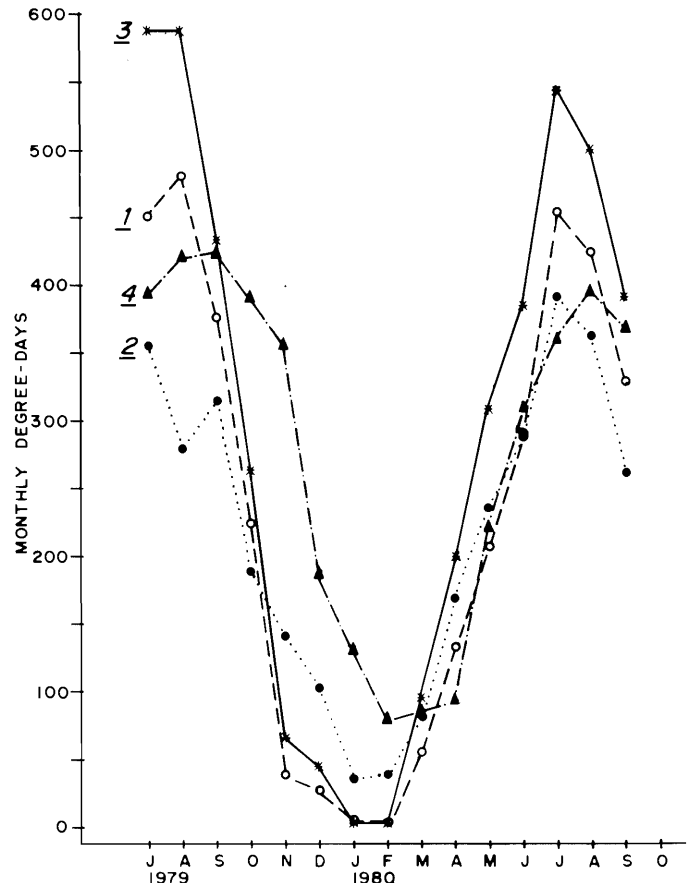


FIG. 2. Comparative temperature regimes at the study sites. 1, unregulated Flathead River; 2, partially regulated Flathead River; 3, unregulated Fisher River; 4, regulated Kootenai River. The points represent the sum of the mean daily temperatures each month.

warm fall temperatures. As a result, the station on the Kootenai River was substantially warmer than the other study areas from October through February.

The mean annual river temperatures were not greatly modified by impoundment, despite seasonal modification of the thermal regime. During the 1980 Water Year (October 1979 – September 1980) the annual mean degree-day accumulation for the regulated Kootenai River was only about 2.9% higher than the reference Fisher River, and the partially regulated Flathead River was 5.7% higher than the unregulated North Fork.

### Available food resources

There were differences in the periphytic and sestonic food base between reference and regulated areas and between the two river systems. Both species of ephemeropterid mayflies studied are characterized as collector-gatherers, with *S. tibialis* consuming large amounts of detritus and *D. flavilinea* consuming some animal matter (Hawkins 1982). *Hydropsyche oslari* was characterized as a large-particle herbivore-detrivore that exhibited carnivory in late instars in a stream in Colorado (Gray and Ward 1979).

Community metabolism was measured in September when biomass of periphyton was at a maximum. Net daily metabolism of the periphytic community was about 1.5 times higher in the two regulated than in the respective free-flowing rivers, and net daily metabolism was 3.7 times higher in the regulated Kootenai River than in the partially regulated Flathead River (Fig. 3). Similarly, estimates of periphyton biomass were higher in

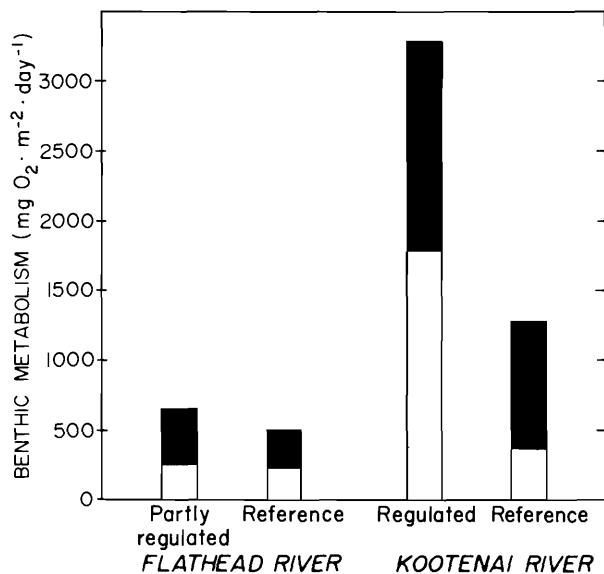


FIG. 3. Periphyton community metabolism measured during September in the partially regulated and unregulated Flathead River, regulated Kootenai River, and unregulated Fisher River. The entire bar represents gross productivity; the black area is net daily metabolism, and the white area represents 24-h respiration.

regulated than reference areas, reflecting greater autotrophy as a result of regulation. AFDW and chlorophyll *a* values were generally an order of magnitude higher in the regulated Kootenai River than in the partially regulated Flathead River (Table 1). Seasonal means for C:N ratios in the periphyton were not markedly different between the stations; they ranged from 16:1 to 18:1 in the reference Flathead River, from 13:1 to 19:1 in the partially regulated Flathead River, from 8:1 to 11:1 in the Fisher River, and from 8:1 to 14:1 in the regulated Kootenai River.

The sestonic food base was compared in the regulated Kootenai River and reference Flathead River where the filter-feeding caddisfly, *H. oslari*, was most abundant. The differences in autotrophy in the Kootenai and Flathead Rivers, as well as the effects of the selective withdrawal system, were reflected in the results of seston analyses. Mean annual total particulate organic carbon (POC) measured in grab samples collected during conditions of minimum discharge from the dams were lower at the reference Flathead River station ( $0.14 \pm 0.18$ ; 95% CI) than at the regulated Kootenai River station ( $0.19 \pm 0.28$ ). Mean values of net seston ( $350 \mu\text{m}$  to  $1 \text{ cm}$ ) during July and October were three times higher for the regulated Kootenai than the reference Flathead River. Even greater differences would be expected if samples had been taken during high or changing discharges instead of at minimum flow.

#### Density and life history

There were marked differences in the densities of benthic populations of *H. oslari* and *S. tibialis* at reference and regulated stations but not for populations of *D. flavilinea* (Table 2). Higher annual mean densities were measured for *S. tibialis* at the partially regulated Flathead and the regulated Kootenai River station than at the reference stations. *Hydropsyche oslari* was most abundant in the reference Flathead River and in the regulated Kootenai River.

The two species of ephemereid mayflies and the hydro-psyche caddisfly were univoltine in the Flathead and Kootenai rivers. *Drunella flavilinea* emerged from mid-July through

TABLE 1. Ranges of mean seasonal (August, October, January) ash-free dry weight and chlorophyll *a* in the periphyton in the Flathead and Kootenai river systems

	AFDW ( $\text{g}/\text{m}^2$ )	Chlorophyll <i>a</i> ( $\text{g}/\text{m}^2$ )
Flathead River		
Unregulated	1.9–9.3	0.019–0.039
Partially regulated	2.0–13.0	0.009–0.032
Kootenai River		
Reference	2.5–21.0	0.011–0.065
Regulated	20.0–79.0	0.085–0.331

TABLE 2. Annual mean densities (annual mean number/ $\text{m}^2$ ) of two ephemereid mayfly species and a hydro-psyche caddisfly species in the Flathead and Kootenai river systems

Station	<i>D. flavilinea</i>	<i>S. tibialis</i>	<i>H. oslari</i>
Flathead River			
Unregulated	24	80	130
Partially regulated	16	204	20
Kootenai River			
Reference Fisher R.	127	118	5
Regulated Kootenai R.	117	890	227

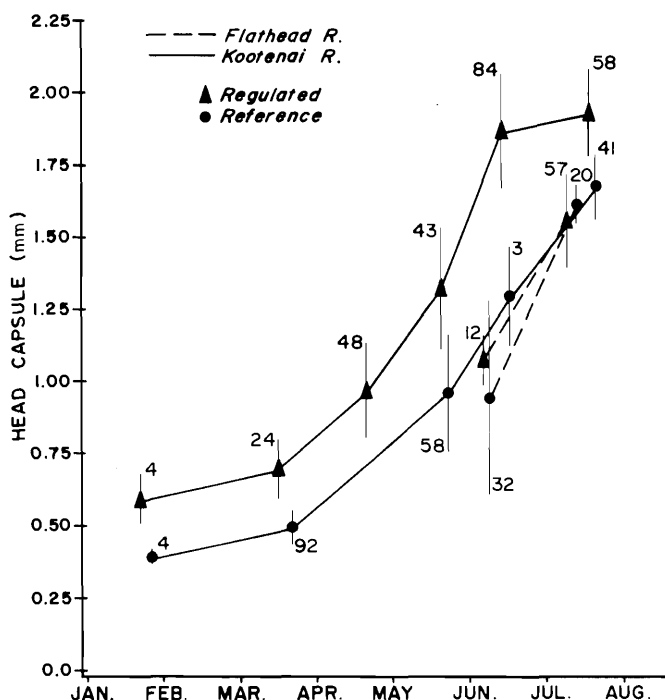


FIG. 4. Nymphal growth (mean head capsule width and 1 SD) of *Drunella flavilinea* at regulated, partially regulated, and reference stations in the Flathead Kootenai river systems. The number of head capsules measured are shown.

August and small nymphs were first collected in January in the Kootenai and Fisher Rivers (Fig. 4). It is probable that hatching of eggs occurred earlier in the regulated Kootenai River than in the reference Fisher River. The earliest instar nymphs, which were collected in January, were significantly larger at two Kootenai River stations ( $0.59 \pm 0.09 \text{ mm}$ ,  $0.51 \pm 0.06 \text{ mm}$ ) than in the Fisher River ( $0.39 \pm 0.03 \text{ mm}$ ). The earliest instars

TABLE 3. Comparison of growth and emergence data for *Drunella flavilinea* and *Serratella tibialis* between sites in the Flathead and Kootenai rivers

Comparison	Head capsule (mm) of mature nymphs		Growth rate	Peak emergence	
<i>Drunella flavilinea</i>					
Within river Flathead R.	Unregulated	Regulated	***	Unregulated July	Regulated August
	1.62 (0.07)	1.55 (0.16)			
Kootenai R.	Unregulated	Regulated	****	July	July
	1.67 (0.11)	1.93 (0.15)			
Between river Unregulated sites	Flathead	Kootenai	****	Flathead July	Kootenai July
	1.62 (0.07)	1.67 (0.11)			
Regulated sites	Flathead	Kootenai	NS	August	July
	1.55 (0.16)	1.93 (0.15)			
<i>Serratella tibialis</i>					
Within river Flathead R.	Unregulated	Regulated	NS	Unregulated August	Regulated September
	1.19 (0.16)	1.37 (0.14)			
Kootenai R.	Unregulated	Regulated	NS	August	September
	1.20 (0.15)	1.43 (0.12)			
Between river Unregulated sites	Flathead	Kootenai	****	Flathead August	Kootenai August
	1.19 (0.16)	1.20 (0.15)			
Regulated sites	Flathead	Kootenai	****	September	September
	1.37 (0.14)	1.43 (0.12)			

NOTE: Numbers within parentheses are standard deviations. \*\*\*,  $p < 0.001$ ; \*\*\*\*,  $p < 0.0001$ ; NS, not significant.

of this species were not collected in the Flathead River, despite extensive sampling of riffle areas with a small-meshed net. They may not have been present until the runoff period in the Flathead River, or they may have been present in slower-moving, deeper water that was not sampled. Nymphs of *D. flavilinea* were consistently larger at the Kootenai River station than in either the Flathead or Fisher rivers (Table 3, Fig. 4). An analysis of the slopes of the regression lines for *D. flavilinea* at each station showed significant differences in growth rates between the reference and regulated stations within each river system and between the reference stations for the two river systems (Table 3). However, the growth rates in the partially regulated Flathead River were not significantly different ( $p < 0.05$ ) from those in the regulated Kootenai River, despite differences in size.

*Serratella tibialis* has a fast seasonal type of life cycle (Hynes 1961). Small instars were first collected in April, and this species generally emerged in August and September (Fig. 5). *Serratella tibialis* may also have hatched approximately 1 month earlier in the Kootenai and Fisher rivers. The smallest individuals that were collected in large numbers were present 1 month earlier in the Kootenai River system. *Serratella tibialis* emerged in September at the station in the partially regulated Flathead River and in August at the reference station on the Flathead River. *Serratella tibialis* was smaller at the time of emergence at the reference stations than at the regulated stations, where peak emergence was a month later (Table 3).

*Serratella tibialis*, like *D. flavilinea*, was largest in the regulated Kootenai River (Table 3, Fig. 5). An analysis of growth rates for this species at each station showed no significant differences ( $0.10 > p > 0.05$ ) between the unregulated and

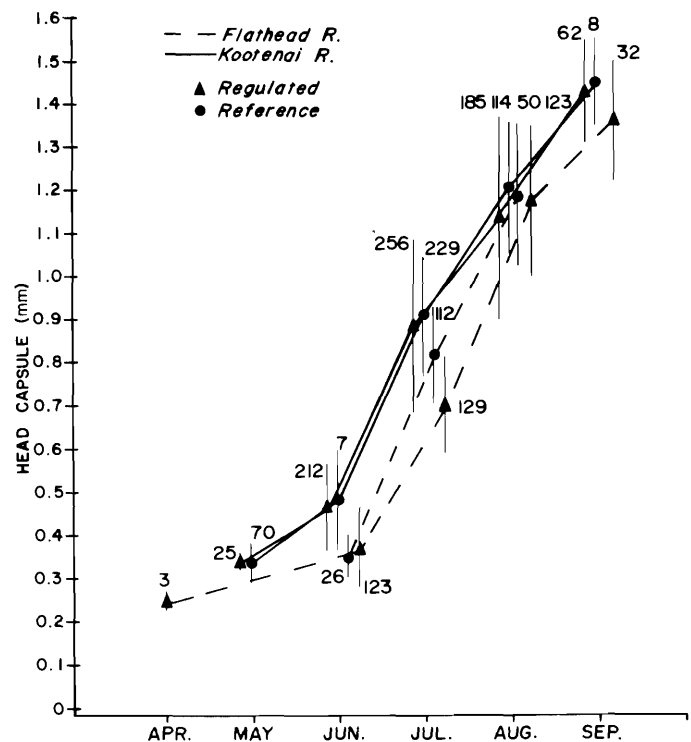


FIG. 5. Nymphal growth (mean head capsule width and 1 SD) of *Serratella tibialis* at regulated, partially regulated, and reference stations in the Flathead Kootenai river systems. The number of head capsules measured are shown.

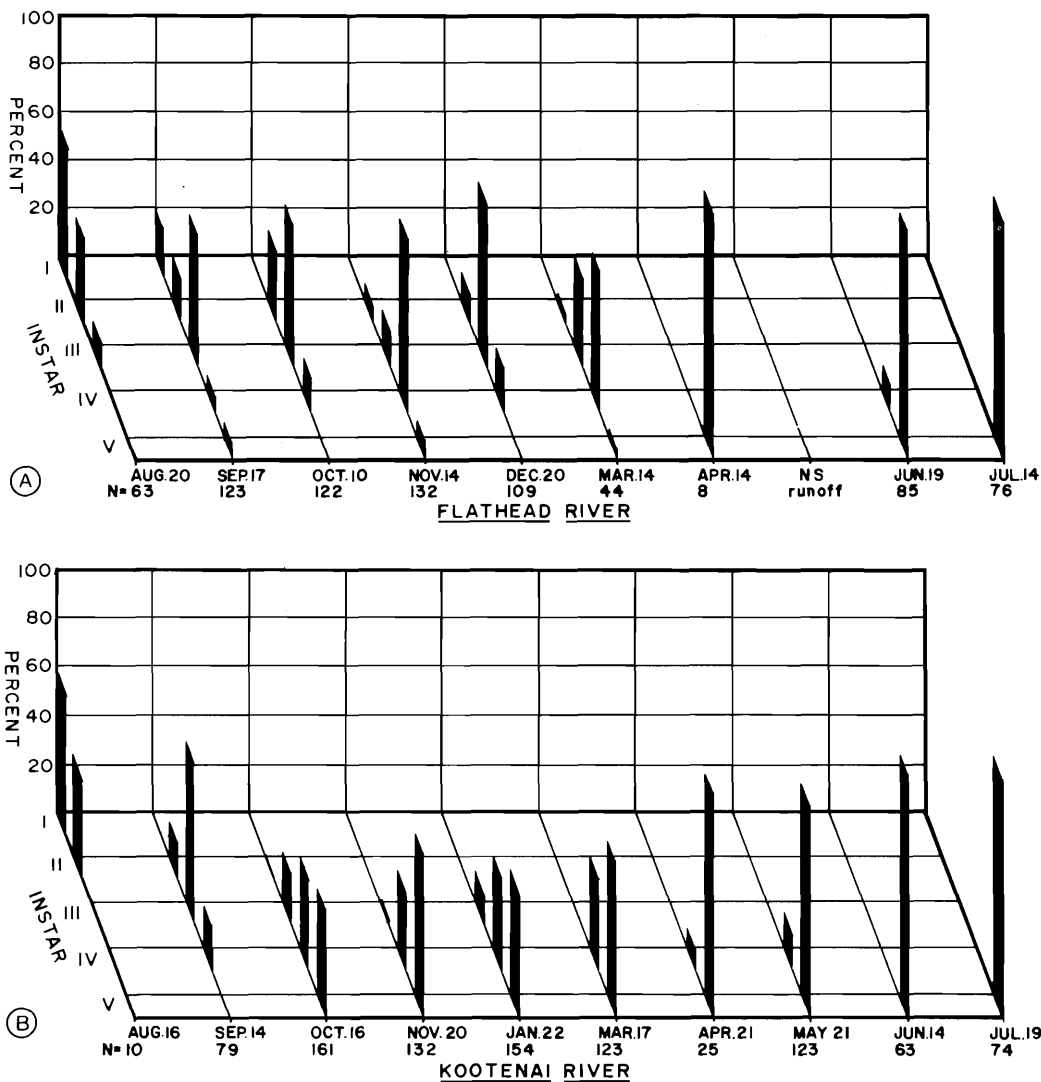


FIG. 6. Larval population structure by instar for *Hydropsyche oslari* in (A) the unregulated Flathead River and (B) regulated Kootenai River on each sampling date.

regulated stations within each river system (Table 3). However, there were significant differences between river systems.

Growth of *H. oslari* in the unregulated Flathead River was compared with growth in the regulated Kootenai River. These were the only two sites where densities of this species were high enough throughout the year for comparisons of the life cycle. Analysis of variance (ANOVA) showed a significant difference in head capsule sizes between the two sites. Pairwise *t*-tests of head capsule size at the two stations showed significant differences between sites during every month of the year. Mean head capsule widths were consistently larger in the regulated Kootenai River than in the unregulated Flathead River until June and July, when 90% or more of the total were in the fifth instar in the unregulated Flathead River and 100% were in the final instar in the regulated Kootenai River (Fig. 6). The smallest instars were first collected in August at both stations. During September most individuals were in the third instar at both stations (55% of the total at the unregulated Flathead River station and 67% of the total at the Kootenai River station). *Hydropsyche oslari* overwintered in the third and fourth instars in the unregulated Flathead River and only by June were 89% present as fifth instars. In contrast, this species overwintered in fourth

and fifth instar stages in the regulated Kootenai River where fall and winter water temperatures were warmer; by April 92% were in the fifth instar.

Mean head capsule sizes at pupation were relatively constant for *H. oslari*. It is probable that there were differences in body weights of fifth instar larvae at the various stations, but these were not measured. *Hydropsyche oslari* emerged from early July to late August in the unregulated Flathead River. In the regulated Kootenai River adults were collected primarily from mid-July through mid-August, but the emergence period extended through mid-September.

*Hydropsyche oslari* was present in low densities in the partially regulated Flathead River, and very few were collected after November. During late fall *H. oslari* was present in smaller instars at the partially regulated station than at the reference station (Table 4). Because of their low numbers in later collections, comparisons cannot easily be made, except to say that the population of *H. oslari* at the partially regulated site was comparatively unsuccessful after the fall season.

#### Temperature and growth

In these three species there was no close relationship between

TABLE 4. Percent composition by instar of *Hydropsyche oslari* at the Flathead and Kootenai river stations during October and November 1979

	Instar			
	2nd	3rd	4th	5th
October 1979				
Unregulated Flathead River ( <i>n</i> = 122)	0	27.0	59.8	13.1
Partially regulated Flathead ( <i>n</i> = 15)	53.3	13.3	6.7	26.7
Regulated Kootenai River ( <i>n</i> = 161)	0.6	19.9	38.5	41.0
November 1979				
Unregulated Flathead River ( <i>n</i> = 132)	5.3	14.4	74.2	6.1
Partially regulated Flathead ( <i>n</i> = 50)	44.0	48.0	2.0	6.0
Regulated Kootenai River ( <i>n</i> = 132)	1.5	0	31.1	67.4

mean specific growth rates (percent head capsule width increase per day) and mean temperatures. The correlation coefficients between mean specific growth rates and the mean temperature between sample intervals at the sample stations were not significant for any of these species. Highest mean specific growth rates for *S. tibialis* were from June to July, followed by May to June at all four stations (Table 5). *Drunella flavilinea* had the highest mean specific growth rates during March–May at both stations in the Kootenai River system. Highest mean specific growth rates for *D. flavilinea* at the two Flathead River stations were measured during June–July. *Hydropsyche oslari* had the highest mean specific growth rates during August–September when it was in the earliest instars at both the unregulated Flathead River and regulated Kootenai River stations.

The degree-day accumulations for these three species were calculated for the period from the appearance of the smallest instars in collections until emergence. A threshold temperature of 0°C was used for degree-day calculations. Degree-day requirements for *D. flavilinea* could not be evaluated in the Flathead River, since the earliest instars were not collected. Estimates for *D. flavilinea* were almost identical in the regulated Kootenai River (1413) and reference Fisher River (1398). The degree-day requirements for *S. tibialis* were also similar in the regulated Kootenai River (1503) and the reference Fisher River (1590). However, fewer degree-days were calculated for the life cycle of *S. tibialis* in the unregulated Flathead River (1189). The total degree days to emergence for *H. oslari* in the unregulated Flathead River (1724) were only 68% of those in the regulated Kootenai River (2524). The degree-day accumulation up to the month in which 90% or more of the individuals were in the final instar in the unregulated Flathead River was within 75% of the same determination in the regulated Kootenai River. Hauer and Stanford (1982a) found that total accumulated degree-days for *H. oslari* were similar in the North (1650) and Middle Forks (1680) of the Flathead River.

## Discussion

### *Relationships between temperature and growth rates*

The results of a number of studies suggest that temperature may be the single most important factor influencing growth of aquatic insects (Mackey 1977; Humpesch 1979; Markarian 1980; Vannote and Sweeney 1980; Brittain 1983). Thus, it was expected that intraspecific variation in growth patterns would be

found among sites with different thermal regimes. However, in this study there was not always a simple relationship between temperature and growth, as evidenced by the lack of significant correlations between the mean temperature between sample intervals at the various sites and mean specific growth rates for these three species. Specific growth rates are greater for a small individual than for a larger one (Brody 1945), and mean specific growth rates were higher for the early instars of all three species. Thus, growth rates appeared to be more related to life-cycle stage than to temperature differences at the various stations. If measurements of insect growth had been made at more frequent intervals and water temperature had been measured at the specific microhabitat level, the correlation may have been higher. Correlation coefficients between cumulative degree days at each sample date and mean head capsule widths were significant ( $p < 0.01$ ) for each species at the sample sites. However, this measure of correlating temperature effects and growth was considered to be insensitive, as a result of the necessarily progressive nature of cumulative degree-days through time.

Sweeney (1978) reported faster developmental rates of nymphs of *Isonychia bicolor* with increased amplitude of the diel temperature pulse. A low diel amplitude in the regulated Kootenai River may have been a factor contributing to delayed maturation in the ephemereid mayflies. On the other hand, in the partially regulated Flathead River developmental processes were slowed and emergence was 1 month later than in the unregulated Flathead River, even though the magnitude of diel variation was greater. The daily amplitudes in temperature, summed for July 1980, totalled 117.5°C for the partially regulated Flathead River and 78.5°C for the unregulated Flathead River.

Few researchers have measured degree-day accumulations for a given species in rivers having different thermal regimes or in habitats with approximately the same total number of degree-days per year but differing in the seasonal distribution and annual range of temperatures (Sweeney 1984). These comparisons were made in the Flathead and Kootenai river systems, where differences in annual degree-days between reference and regulated areas within each river system were small, despite marked changes in the seasonal distribution of temperatures. Differences between river systems were comparatively larger. Degree-day accumulations during the 1980 Water Year totalled 2220 for the reference Flathead River, 2291 for the partially regulated Flathead River, 2797 for the reference Fisher River, and 2880 for the regulated Kootenai River. A similar pattern was found when the cumulative degree-days at emergence for the three species were compared at the various sites. In general, there were no major differences in degree-day summations calculated for these species between reference and regulated stations within the same river system. Differences between the river systems were often of a larger magnitude. A minimum number of degree-days to emergence is thought to be a requirement for most insect species. An excess number of temperature units may not lead to earlier emergence if other conditions are not suitable. For example, a temperature threshold is required in many insects to cue the onset of maturation or actual emergence timing. The results from this study suggest that the degree-day concept may be more valid within than between river systems, in part because of the probability that there are fewer differences in other factors (e.g., food resources) within one area than between rivers.

TABLE 5. Mean specific growth rates (percent increase in head capsule width per day) of two ephemereid mayflies and a hydropsychid caddisfly in regulated and unregulated areas of the Flathead and Kootenai river systems during 1980. Water temperature consists of the mean and the range in temperatures for each interval between sample periods

	Water temperature		n	Mean growth (%/day)
	Mean	Range		
<i>Drunella flavilinea</i>				
Flathead River				
Partially regulated				
15 Apr. – 07 Jun.	7.6	5.5–9.5	13	1.1
08 Jun. – 10 Jul.	10.8	8.5–13.5	69	1.4
11 Jul. – 11 Aug.	12.9	10.0–17.5	59	0.002
Unregulated				
10 Jun. – 14 Jul.	11.9	8.0–15.5	52	2.1
15 Jul. – 11 Aug.	15.1	12.0–17.5	21	1.6
Kootenai River				
Regulated				
22 Jan. – 16 Mar.	3.0	2.8–3.9	29	0.3
17 Mar. – 20 Apr.	2.8	2.8–2.8	72	1.2
21 Apr. – 21 May	5.3	2.8–7.8	90	1.2
22 May – 13 Jun.	9.8	7.8–11.1	134	1.3
14 Jun. – 19 Jul.	11.6	10.0–12.2	150	0.2
Unregulated				
25 Jan. – 19 Mar.	2.4	0.0–4.5	96	0.5
20 Mar. – 20 May	7.2	3.5–12.0	150	1.5
21 May – 14 Jun.	10.8	8.5–14.0	61	1.1
15 Jun. – 19 Jul.	15.1	13.0–18.5	44	1.1
<i>Serratella tibialis</i>				
Flathead River				
Partially regulated				
15 Apr. – 7 Jun.	7.6	5.5–9.5	127	1.0
8 Jun. – 10 Jul.	10.8	8.5–13.5	251	2.7
11 Jul. – 11 Aug.	12.9	10.0–17.5	251	2.1
12 Aug. – 11 Sep.	10.2	8.5–14.5	156	0.6
Unregulated				
10 Jun. – 14 Jul.	11.9	8.0–15.5	138	3.8
15 Jul. – 11 Aug.	15.1	12.0–17.5	162	1.7
Kootenai River				
Regulated				
22 May – 13 Jun.	9.8	7.8–11.1	237	1.2
14 Jun. – 18 Jul.	11.6	10.0–12.2	468	3.3
19 Jul. – 15 Aug.	13.5	12.8–15.6	441	1.0
16 Aug. – 12 Sep.	12.2	11.1–13.9	247	0.9
Unregulated				
21 May – 14 Jun.	10.8	8.5–14.0	77	1.8
15 Jun. – 19 Jul.	15.1	13.0–18.5	236	2.6
20 Jul. – 16 Aug.	18.5	16.0–21.0	343	1.1
17 Aug. – 13 Sep.	14.5	12.0–16.5	122	0.9
<i>Hydropsyche oslari</i>				
Regulated Kootenai River				
16 Aug. – 12 Sep.	12.2	11.1–13.9	53	2.4
16 Oct. – 19 Nov.	10.2	7.8–13.3	293	0.5
20 Nov. – 21 Jan.	5.7	3.9–7.8	286	0.0
22 Jan. – 16 Mar.	3.0	2.8–3.9	277	0.2
17 Mar. – 20 Apr.	2.8	2.8–2.8	148	0.4
21 Apr. – 21 May	5.3	2.8–7.8	148	0.0
22 May – 13 Jun.	9.8	7.8–11.1	164	0.1
14 Jun. – 18 Jul.	11.6	10.0–12.2	92	0.0

TABLE 5. (concluded)

	Water temperature		n	Mean growth (%/day)
	Mean	Range		
Unregulated Flathead River				
20 Aug. – 16 Sep.	14.1	11.5–17.0	186	2.4
17 Sep. – 10 Oct.	10.4	7.0–12.5	245	2.1
11 Oct. – 13 Nov.	4.8	1.0–9.0	254	0.0
14 Nov. – 20 Dec.	0.5	0.0–3.0	241	0.0
21 Dec. – 14 Mar.	0.4	0.0–2.0	153	0.4
15 Mar. – 14 Apr.	3.2	1.0–6.0	52	0.0
15 Apr. – 9 Jun.	6.2	4.5–9.5	93	1.4
10 Jun. – 14 Jul.	11.9	8.0–15.5	161	0.2
15 Jul. – 11 Aug.	15.1	12.0–17.5	87	0.0

#### Relationships between food, population density, and growth rates

The standing crop and productivity of both periphytic and sestonic food resources appeared to have a marked effect upon the total densities of macroinvertebrates within the two river systems (Perry 1984). Total densities of all macroinvertebrates were three to six times higher at the regulated stations on the Kootenai River than in the partially regulated Flathead River. The highest densities of each of the three species examined in the present study were found in the Kootenai River system and were probably a result of the available food resources.

Food quantity and quality also affects insect growth rates (Ward and Cummins 1979; Fuller and Mackay 1981). It is possible that lower food reserves slowed the winter growth rates of *D. flavilinea* in the reference Fisher River or the fall and winter growth rates of *H. oslari* in the reference Flathead River. However, in both these cases winter temperatures were cooler at the reference stations than in the regulated Kootenai River, so it was not possible to sort out the effects of the two factors. An abundant supply of seston in the regulated Kootenai River (due in part to the operation of the selective withdrawal system on Libby Dam) probably contributed to the faster growth rates of *H. oslari*. Much higher insect drift densities in the Kootenai River than in the free-flowing Flathead River (Perry and Perry 1985) also added to seston quantity and quality; Carlsson et al. (1977) reported that in lake outlet streams in Sweden, blackfly larvae had faster growth rates at stations near the outlet where fine particulate matter from the lake was more abundant than at downstream stations. Similarly, Richardson and Clifford (1983) found that growth rates of a polycentropodid caddisfly that fed on lake-derived zooplankton were more than an order of magnitude higher at a station below a lake outlet than at a site 17 km downstream from the lake.

*Hydropsyche oslari* retained a univoltine life cycle in the Kootenai River. Other investigators have reported increased voltinism of filter-feeding caddisflies for populations downstream from lake outlets (Mackay 1979; Richardson and Clifford 1983) and below dams (Rhame and Stewart 1976; Parker and Voshell 1982). Cooler summer temperatures, which were a result of regulation, may have prevented the development of a second generation during the summer. Also, the supply of seston from Libby Reservoir is probably less abundant and dependable than that from many natural lakes or reservoirs with a surface release.

Greater food availability probably resulted in generally larger



nymphal sizes of the mayflies in the regulated Kootenai River. These species were present in higher densities in the Kootenai than in the Flathead River, so their larger size in the Kootenai River was probably not a result of less intraspecific competition for food. Larger nymphal sizes of *D. flavilinea* in the Kootenai River may have been a result of a more abundant and (or) a higher quality food resource during the winter and spring or of warmer winter temperatures. However, *S. tibialis* was not present in the larval stage during the winter. Summer temperatures were cooler in the regulated Kootenai River than at the two reference stations, while mean sizes of the two mayfly species were larger. Mean sizes of these two mayflies were not as large in the partially regulated Flathead River where summer temperatures were also cooler, but where food resources were lower. An alternate explanation is that smaller larval sizes in the reference and partially regulated areas were a result of suboptimal thermal conditions for those species at those stations (see Vannote and Sweeney 1980).

#### *Effects of river regulation on growth rates, development, and emergence times*

Differences in growth rates between regulated and reference stations within each river system were evident for *D. flavilinea* but not for *S. tibialis*. Thus, *D. flavilinea* appeared to be responding to factors (i.e., seasonal alterations in temperature and periphyton biomass) that were a result of river regulation. The growth of *S. tibialis*, on the other hand, appeared to be more related to differences between the two river systems (i.e., total heat load, periphyton biomass) than to changes which were a direct result of regulation. *Serratella tibialis* is present in the larval stage for only 4 to 5 months of the year and therefore is subjected to regulated conditions for a shorter period. Further, during 4 of these months (April to July) differences between the two Flathead River stations were minimal, because of runoff conditions in both the free-flowing reference and partially regulated areas. *Drunella flavilinea* was present in the larval stage during the winter in the Kootenai River system and was thus exposed to environmental conditions imposed by regulation for a longer period of time.

Emergence of *D. flavilinea* averaged 1 or 2 weeks earlier in unregulated areas where summer temperatures were warmer. Similarly, emergence of *S. tibialis* was 1 month earlier at the reference stations than at the cooler regulated stations. For example, *S. tibialis* emerged in September at the station in the partially regulated Flathead River and in August at the reference station on the Flathead River. This was probably because colder summer temperatures in the partially regulated Flathead River (84% of the summer season degree-day accumulation at the reference station) delayed maturation. Emergence of *S. tibialis* was in August in the free-flowing Fisher River, as well as in unregulated streams in Alberta (Clifford et al. 1973). The emergence period extended from mid-July through mid-September in the regulated Kootenai River. An extended emergence period in the regulated Kootenai River was demonstrated for *S. tibialis* and *H. oslari*, as well as for other species of insects (Perry 1984). Extensions of the period of emergence have frequently been found in warm winter habitats and in streams below deep-release dams (Ward and Stanford 1982).

*Hydropsyche oslari* overwintered in the third and fourth instars in the unregulated Flathead River and in the fourth and fifth instar stages in the regulated Kootenai River where fall and winter water temperatures were warmer. Hauer and Stanford

(1982a) found that most *H. oslari* overwintered in the first two instars in the North and Middle Forks of the Flathead River. Oswald (1976) found that *H. oslari* overwintered as third and fourth instars in the downstream reaches of Owl Creek, a lake outlet stream in Northwest Montana. Alstad (1980) collected predominantly third and fourth instar larvae during February in the Weber River, northern Utah. Data from the stations at higher altitudes in that study are similar to data collected during October from the unregulated Flathead River (920 m), while there were more fifth instars present in the unregulated Kootenai River (625 m) than Alstad recorded at the station at his lowest elevation.

The emergence period for *H. oslari* began earlier in the unregulated Flathead River (early July) and continued later in the regulated Kootenai River (mid-September), although adults were collected primarily from mid-July through mid-August in both rivers. Emergence of *H. oslari* was somewhat earlier in the Flathead River, despite the fact that over 40% of the population had reached the final instar by the previous October in the regulated Kootenai River, while in the unregulated Flathead River few individuals reached the 5th instar until June. Warmer fall and winter temperatures, therefore, had no effect on the duration of the total larval period for this species. The effect of temperature was on the relative time spent in each of the later instar stages.

Temperature differences between regulated and reference sites during the period when these species were in late developmental stages appeared to exert a marked influence on maturation. Growth rates and developmental time for *H. oslari* were clearly affected differently by temperature. Growth rates were faster at stations where temperatures were warmer, but developmental time was much more constant at all study sites. Thus, factors resulting from regulation in the Kootenai River had the effect of uncoupling growth (tissue elaboration) and development (maturation).

In summary, stream regulation in the Flathead and Kootenai rivers had different effects on growth of the two hemimetabolous species. *Drunella flavilinea* responded to within-river differences and appeared sensitive to the effects of river regulation. *Serratella tibialis* was present as a nymph during months when changes resulting from regulation were less marked; it therefore showed a greater response to the wider differences between river systems. For the holometabolous species, *H. oslari*, regulation appeared to either affect the population's ability to sustain itself (as in the partially regulated Flathead River) or to accelerate growth rates, resulting in an extended period of time spent in later instars. For all three species, emergence was later in regulated areas where summer water temperatures were lower. Under the thermal regimes encountered during the study, food appeared to be a factor in constraining population densities in the Flathead River system. Despite alterations in life history (i.e., asynchrony between growth and development, delayed emergence, extended emergence periods), densities of all three species were high in the regulated Kootenai River.

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- ALSTAD, D. N. 1980. Comparative biology of the common Utah Hydropsychidae (Trichoptera). *Am. Midl. Nat.* **103**: 7–174.
- ANDERSON, N. H., and K. W. CUMMINS. 1979. Influences of diet on the life histories of aquatic insects. *J. Fish. Res. Board Can.* **36**: 335–342.
- BOTT, T. L., J. T. BROCK, C. E. CUSHING, S. V. GREGORY, D. KING, and R. C. PETERSEN. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. *Hydrobiologia*, **60**: 3–12.
- BRITTAI, J. E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). *Ecology*, **64**: 440–446.
- BRODY, S. 1945. *Bioenergetics and growth*. Reinhold Publishing Corp., New York.
- CARLSSON, M., L. M. NILSSON, B. M. SVENSSON, S. ULFSTRAND, and R. S. WOTTON. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. *Oikos*, **29**: 229–238.
- CLIFFORD, H. F., M. R. ROBERTSON, and K. A. ZELT. 1973. Life cycle patterns of mayflies (Ephemeroptera) from some streams of Alberta, Canada. Proceedings of the 1st International Conference on Ephemeroptera, Florida A & M University, Tallahassee, FL, August 17–20, 1970. Edited by W. L. Peters and J. G. Peters. E. J. Brill, Leiden. pp. 122–131.
- FULLER, R. L., and R. L. MACKAY. 1981. Effects of food quality on the growth of three *Hydropsyche* species (Trichoptera: Hydropsychidae). *Can. J. Zool.* **59**: 1133–1140.
- GRAY, L. J., and J. V. WARD. 1979. Food habits of stream benthos at sites of different food availability. *Am. Midl. Nat.* **102**(1): 157–167.
- HAUER, F. R., and J. A. STANFORD. 1981. Larval specialization and phenotypic variation in *Arctopsyche grandis* (Trichoptera: Hydropsychidae). *Ecology*, **62**: 645–653.
- . 1982a. Ecology and life histories of three net-spinning caddisfly species (Hydropsychidae: *Hydropsyche*) in the Flathead River, Montana. *Freshwater Invert. Biol.* **1**: 18–29.
- . 1982b. Bionomics of *Dicosmoecus gilvipes* (Trichoptera: Limnephilidae) in a large western montane river. *Am. Midl. Nat.* **108**: 81–87.
- HAWKINS, C. P. 1982. Food habits of species of ephemereid mayflies (Ephemeroptera: Insecta) in streams of Oregon. *Am. Midl. Nat.* **113**: 343–352.
- HOLM-HANSEN, O., and B. RIEMANN. 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos*, **30**: 438–447.
- HUMPESCH, U. H. 1979. Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. *Freshwater Biol.* **9**: 467–479.
- HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* **57**: 344–388.
- KONDRAITIEFF, B. C., and J. R. VOSHELL, JR. 1981. Influence of a reservoir with surface release on the life history of the mayfly *Heterocloeon curiosum* (McDunnough) (Ephemeroptera: Baetidae). *Can. J. Zool.* **59**: 305–314.
- LEHMKUHL, D. M. 1979. Environmental disturbance and life histories: principles and examples. *J. Fish. Res. Board Can.* **36**: 329–334.
- LORENZEN, C. J. 1967. Determination of chlorophyll and pheopigments: Spectrophotometric equations. *Limnol. Oceanogr.* **12**: 343–346.
- MACKAY, R. J. 1978. Larval identification and instar association in some species of *Hydropsyche* and *Cheumatopsyche* (Trichoptera: Hydropsychidae). *Ann. Entomol. Soc. Am.* **71**: 499–509.
- . 1979. Life history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. *Can. J. Zool.* **57**: 963–975.
- MACKAY, A. P. 1977. Growth and development of larval Chironomidae. *Oikos*, **28**: 270–275.
- MARKARIAN, R. K. 1980. A study of the relationship between aquatic insect growth and water temperature in a small stream. *Hydrobiologia*, **75**: 81–95.
- MCCLURE, R. G., and K. W. STEWART. 1976. Life cycle and production of the mayfly *Choroterpes* (Neochoroterpes) *mexicanus* Allen (Ephemeroptera: Leptophlebiidae). *Ann. Entomol. Soc. Am.* **69**: 134–144.
- MENZEL, D. W., and R. F. VACCARO. 1964. The measurement of dissolved organic and particulate carbon in seawater. *Limnol. Oceanogr.* **9**: 138–142.
- MORSE, J. C., and R. W. HOLZENTHAL. 1984. Trichoptera genera. In *An introduction to the aquatic insects of North America*. 2nd ed. Edited by R. W. Merritt and K. W. Cummins. Kendall/Hunt, Dubuque, IA. pp. 312–347.
- NAIMAN, R. J., and J. R. SEDELL. 1980. Relationships between metabolic parameters and stream order in Oregon. *Can. J. Fish. Aquat. Sci.* **37**: 834–847.
- OSWOOD, M. W. 1976. Comparative life histories of the Hydropsychidae (Trichoptera) in a Montana lake outlet. *Am. Midl. Nat.* **96**: 493–497.
- PARKER, C. R., and J. R. VOSHELL, JR. 1982. Life histories of some filter-feeding Trichoptera in Virginia. *Can. J. Zool.* **60**: 1732–1742.
- PERRY, S. A. 1984. Comparative ecology of benthic communities in natural and regulated areas of the Flathead and Kootenai Rivers, Montana. Ph.D. dissertation. North Texas State University, Denton, TX.
- PERRY, S. A., and W. B. PERRY. 1986. Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, U.S.A. *Hydrobiologia*. In press.
- RADFORD, D. S., and R. HARTLAND-ROWE. 1971. Emergence patterns of some Plecoptera in two mountain streams in Alberta. *Can. J. Zool.* **49**: 657–662.
- RHAME, R. E., and K. W. STEWART. 1976. Life cycles and food habits of three Hydropsychidae (Trichoptera) species in the Brazos River, Texas. *Trans. Am. Entomol. Soc.* **102**: 65–99.
- RICHARDSON, J. S., and H. F. CLIFFORD. 1983. Life history and microdistribution of *Neureclipsis bimaculata* (Trichoptera: Polycentropodidae) in a lake outflow stream of Alberta, Canada. *Can. J. Zool.* **61**: 2434–2445.
- RIEMANN, B. 1978. Absorption coefficients for chlorophylls *a* and *b* in methanol and a comment on interference of chlorophyll *b* in determinations of chlorophyll *a*. *Vatten*, **3**: 187–194.
- ROSS, H. H., and J. D. UNZICKER. 1977. The relationships of the genera of American Hydropsychinae as indicated by phallic structures (Trichoptera, Hydropsychidae). *J. Ga. Entomol. Soc.* **12**: 298–312.
- SAS INSTITUTE, INC. 1982. *SAS User's guide: Statistics*, 1982 edition. Cary, NC.
- SWEENEY, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnol. Oceanogr.* **23**: 461–477.
- SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. In *The ecology of aquatic insects*. Edited by V. H. Resh and D. M. Rosenberg. Praeger Publishers, New York. pp. 56–100.
- SWEENEY, B. W., and R. L. VANNOTE. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science (Washington, D.C.)*, **200**: 444–446.
- UNITED STATES GEOLOGICAL SURVEY. 1981. Water resources data for Montana. Vol. 2. Upper Columbia River Basin. Water Year 1980. U.S. Geol. Surv. (Helena, MT), MT-80-2.
- VANNOTE, R. L., and B. W. SWEENEY. 1980. Geographic analysis of

- thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *Am. Nat.* **115**: 667–695.
- VAUGHT, G. L., and K. W. STEWART. 1974. The life history and ecology of the stonefly *Neoperla clymene* (Newman) (Plecoptera: Perlidae). *Ann. Entomol. Soc. Am.* **67**: 167–178.
- WARD, G. M., and K. W. CUMMINS. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). *Ecology*, **60**: 57–64.
- WARD, J. V., and J. A. STANFORD. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification in regulated streams. *In* The ecology of regulated streams. *Edited by* J. V. Ward and J. A. Stanford. Plenum Press, New York. pp. 35–55.
- . 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* **27**: 97–117.