

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 55

31 JANUARY 1995

No. 1

Great Basin Naturalist 55(1), © 1995, pp. 1–18

LIFE HISTORIES OF STONEFLIES (PLECOPTERA) IN THE RIO CONEJOS OF SOUTHERN COLORADO

R. Edward DeWalt^{1,2} and Kenneth W. Stewart¹

ABSTRACT.—Thirty-one stonefly species representing eight families were collected during the March 1987 to May 1990 study period. Genera represented by more than one species included *Capnia*, *Utacapnia*, *Taenionema*, *Suwallia*, *Triznaka*, *Isogenoides*, and *Isoperla*. Peak species richness was recorded on or near the summer solstice in 1988 and 1989. Climatic differences between years were reflected in nymphal development and emergence phenology of most species. New or important corroborative life history data are presented for 11 stonefly species of this assemblage. The hyporheic nymphal development of most chloroperlid species limited the number of early instars sampled and our capacity to interpret voltinism. Limited nymphal data suggested a univoltine-slow cycle for *Plumiperla diversa* (Frison). Adults of *Suwallia pallidula* (Banks) and *S. wardi* (Banks) were present for an extended summer period, but the bulk of their respective emergence times was temporally separated. *Isogenoides zionensis* Hanson, *Pteronarcella badia* (Hagen), and *Pteronarcys californica* Newport were all shown for the first time to have a 9–10-mo egg diapause, and all three species have a semivoltine life cycle. *Skwala americana* (Klapálek) and *Isoperla fulva* Claassen were further confirmed to have univoltine-slow cycles. Univoltine-fast and univoltine-slow life cycles are reported for the first time in *I. phalerata* and *I. quinquepunctata*, respectively. Regression analysis revealed that six of the eight abundant species had extended emergence patterns (slopes of <5%/d), while only two had synchronous patterns. Warmer spring and summer temperatures in 1989 increased the slopes for five of the eight species studied, but did not change their synchrony designation. Nine of 11 abundant species advanced their median emergence date in 1989 over 1988. This and the higher slope values are consistent with a hurried nymphal development and narrower emergence period due to the warmer thermal regime of 1989.

Key words: Plecoptera, life history, biodiversity, life cycle, Rocky Mountains.

Stoneflies (Plecoptera) are one of the integral and often dominant insect orders in stream ecosystems; therefore, they are important as biological indicators, as fish food, and as part of the energy and nutrient economy of streams (Stewart and Stark 1988). Taxonomy of the North American fauna is now well known; however, information on their life histories, local species richness, and ecology is still poorly

understood (Sheldon and Jewett 1967, Stewart and Stark 1988). Precise life histories are known for <5% of the more than 575 North American species, and knowledge of stonefly life histories and ecology in southern Rocky Mountain streams is sparse. This has limited our ability to increase understanding of ecological relationships between cohabiting stonefly species in this region.

¹Department of Biological Sciences, University of North Texas, Denton, TX 76203.

²Present address: Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803.

One objective of this study was to determine richness of the stonefly assemblage of the Rio Conejos of southern Colorado, a large drainage that has not been previously studied. Second, we documented the important life history events of its dominant species for which sufficient individuals and observations could be gathered by intensive monthly sampling and by living streamside during spring and summer.

Research was patterned after the classic studies of Harper (1973a, 1973b) and Harper and Hynes (1972), who studied a substantial portion of the eastern Canadian fauna and addressed critical aspects of life histories such as egg development, diapause, and adult behaviors that are often overlooked. H. B. N. Hynes, in an address to the International Plecoptera Symposium (1992), emphasized the need for more attention to these aspects to support the eventual development of a paradigm of life history evolution within the Plecoptera. We have also adopted the approaches of Knight and Gaufin (1966), Harper and Magnin (1969), Sheldon (1972), Barton (1980), Ernst and Stewart (1985a, 1985b), and Hassage and Stewart (1990) in comparatively studying an assemblage of species. This report is the first to address, on a large scale, such an assemblage in a western North American stream since the works of Knight and Gaufin (1966), Sheldon (1972), and Stanford (1975).

METHODS

Study Stream

The Rio Conejos is located in the southern Rocky Mountains of south central Colorado. The river flows east to west for 145 km from its headwaters in the Rio Grande National Forest of the San Juan range to the Rio Grande 32 km northeast of Antonito, CO. Three sampling sites were established along the Rio Conejos to ensure access to at least one of them during the winter and to enhance collection of stonefly species that were not abundant at all sites. These were located at elevations between 2400 and 2600 m above sea level. The primary site (106°15'W longitude, 37°03'N latitude) consisted of a 1-km stretch located 24 km west of Antonito, Conejos County, CO, off Colorado highway 17. Sites two and three were located 22.5 km west of Antonito, also on

highway 17, and 4 km north of Antonito at the Colorado highway 285 bridge, respectively.

Stream temperatures varied from below freezing during the winter months to near 20°C in August. Ice cover was common from December through March. Snowmelt began in April, usually leading to peak flows in June. Base flows were attained by late August and continued through the winter. Water released from Platoro Reservoir, 48 km upstream, augmented river flow during summer low-flow periods. Bottom substrates were characterized by large boulders, cobble, gravel, and sand. These were covered by a thin layer of silt in quiet water. Important organic substrates included the flooded coppices of willows and cottonwoods and their entrained leaf packs. Willow (*Salix* spp.), cottonwoods and aspens (*Populus* spp.), and alder (*Alnus* sp.) contributed to the riparian corridor.

Physical Conditions

Stream temperature was monitored at site one from June through August 1988 using a Ryan™ continuous recording thermograph. High, low, and mean daily stream temperatures were calculated from temperatures recorded at 0400, 0800, 1200, 1600, 2000, and 2400 h. Water temperatures were not recorded during 1989 due to equipment failure. However, summer air temperature highs and lows and rainfall were recorded (1300 h daily, mountain time) for both 1988 and 1989 at the Conejos Peak U.S. Weather Service reporting station at site one. Flow data for site two were gathered from Petsch (1987–90).

Nymphal Growth

Nymphs were collected monthly (except December due to poor weather conditions) at all sites from March 1987 to May 1988. Additional collections were made at irregular intervals until March 1990. Samples were collected by disturbing the substrate (mineral and organic) upstream of a BioQuip rectangular dipnet until debris clogged the net. The net was composed of a coarse, 1-mm mesh first stage, modified by the addition of a conical second stage of 153- μ m mesh size. The latter collected even the smallest instars. A plankton bucket was attached to the second stage to facilitate sample removal. Contents of the plankton bucket and the coarse stage constituted a sampling unit and were stored in

70% isopropyl alcohol. The number of sampling units per month varied with the effort necessary to secure approximately 50 nymphs of all abundant species.

Nymphs were separated from sample debris with the aid of 4–10X magnification on a stereo-dissecting microscope, sorted to species when possible, and stored in 80% ethanol until measurement. Head capsule width (HCW, greatest distance across the eyes) was measured with a calibrated ocular micrometer fitted to a stereo-dissection microscope. Nymphs from all sites for the 3-yr sampling period were pooled by species and month of collection to increase the number of nymphs per month and to allow construction of more robust growth histograms. Gender of nymphs was assessed by a gap in the posterior setal margin of the eighth sternum of females (Stewart and Stark 1988) and by developing external genitalia of females. Sex-specific kite diagrams were constructed by placing male and female nymphs into 0.1- or 0.2-mm size classes. The frequency of these classes was converted to a percentage of the total number of nymphs (males + females + unsexed nymphs) collected for that month. Polygons were constructed for each month depicting the relative proportion of all nymphs at that size class.

Adult Emergence

Adults of winter- and early spring-emerging stoneflies were collected from bridge abutments, from shoreline debris, and under the cobble at streamside to provide a general emergence period for each species. Adults were also reared from preemergent nymphs.

A combination of sampling methods and observational procedures was used during the summers of 1988 and 1989 to evaluate emergence, duration of adult presence, and behavior of these species. Adult traps and methods included a 2.25-m² basal area BioQuip malaise trap, two 0.25-m² basal area floating emergence traps, pitfall traps, sweepnetting of streamside vegetation, exuviae collection, and day and night transect walks. Pitfall traps were emptied on alternate days, and the others were emptied daily between 0900 and 1100 h. All of these methods were used at site one; sweepnetting was employed at site three on several occasions.

The malaise trap was deployed among willow and cottonwood coppices, where its olive-drab coloration mimicked the surrounding vegetation. Flying, or crawling, adults intercepted by the trap ascended the screening into a dry apical collection chamber. Additionally, all adults on the trap mesh were collected using an aspirator.

Emergence traps were anchored over shallow riffles during the 1988 field season. Natural diurnal changes in water level and erratic discharges due to water release from Platoro Reservoir rendered these ineffective at times; therefore, their use was discontinued in 1989.

Pitfall traps consisted of 28.3-cm² modified aluminum soda cans that were buried flush in streamside substrates. A mixture of 70% ethanol and ethylene glycol (the latter to retard evaporation) was used as a preservative. In 1988, 12 traps were installed 1 m from the stream at 1-m intervals on an open beach with nearby vegetation. This was expanded in 1989 to three transects, each consisting of 30 cans set 1 m apart in transects 1 m, 5 m, and 8 m from the initial shoreline. These traps monitored not only adult presence of ground-traversing, brachypterous stoneflies, but also their potential to move laterally from the stream.

Sweepnetting was conducted over a 15 × 2-m willow and cottonwood riparian zone. The entire area was methodically swept, working from the base of each clump of vegetation upward. Exuviae removal was the only method used to assess emergence of *Claassenia sabulosa* (Banks) and was used for no other species. In 1988 exuviae were removed daily from the same 15 × 1-m area of cobble shoreline, and the frequency of each sex was noted. In 1989 the removal area was expanded to 30 × 1 m of shoreline area and up to 5 m into the water for collecting exuviae from emergent substrates.

Year and sex-specific kite diagrams of adult presence were produced for all abundant summer stoneflies by pooling all methods and expressing daily catches as a percentage of the total catch. Duration of emergence of *Pteronarcys californica* Newport would be greatly overestimated by including pitfall trap collections due to its synchronous emergence and since pitfall traps were emptied on alternate days.

Dates of first capture, 50% cumulative catch, and last collection, plus total duration of adult presence, were determined for the 11 most abundant species collected in the summers of 1988 and 1989. Emergence synchrony was estimated using linear regression of the cumulative percentage catch (all methods pooled) versus days since first capture. Slopes generated for each species were used as an index of synchrony. Steeper slopes indicated a more synchronous emergence. Slopes $\geq 5\%/d$ were chosen to be indicative of synchronous emergence since species with these slopes emerged their entire population within a few days and had steep, j-shaped, cumulative emergence curves. Differences between slopes for 1988 and 1989 were tested using a modified *t* test (Zar 1984). Common slopes were calculated if no differences between years were noted. This was a purely descriptive approach designed to detect and compare patterns; therefore, it is not our aim to model emergence for the purpose of prediction, but only to describe patterns of emergence.

Since most adult collection methods employed in this study collected adults of unknown age, results reflected adult presence rather than, in the strictest sense, emergence. No attempt was made to discard old males and females using any index of age. However, patterns of adult presence should follow that of a true emergence pattern, and since longevity of most adults approached only 1 wk in the laboratory, we believe these results to be useful.

Behavioral observations were made from 0800 to 1300 h and from 2000 to 2300 h for several days during emergence of each species. Observations made during intervening hours produced little adult behavior. Timing of adult activities, their relative distance from the stream, and substrates on which activities took place were monitored by walking the stream margin, turning logs and rocks, and exposing leaf-entrained bases of marginal vegetation. Details of these observations have been narratively described for each species in this paper.

Fecundity and Egg Incubation

Eggs of several species were incubated in the laboratory to confirm proposed voltinism based on growth histograms. Eggs were placed into 1-cm-diameter dialysis tubing bags and reared in a Frigid Units Living StreamTM, or they were stored in 100 × 15-

mm plastic petri dishes in an environmental chamber. In both instances these were incubated at approximate stream temperature and light regime.

Fecundity was estimated from number of egg batches deposited, number of eggs per batch, and, for *Skwala americana* (Klapálek) only, total number of eggs remaining in the ovarioles. Females were housed at streamside in screened, glass containers and provided with moist cotton balls as a source of water. Alternatively, some species were reared in Denton and held under simulated streamside conditions in large cotton-stoppered shell vials.

RESULTS

Physical Conditions

Mean daily stream temperatures in 1988 increased from near 10°C in early June to 15°C in mid-July (Fig. 1). The stream cooled dramatically between 8 and 12 July. This coincided with cool, damp weather conditions (Fig. 2). Summer air temperature highs rarely exceeded 30°C in 1988, and rainfall occurred at regular intervals throughout the summer (Fig. 2). However, 1989 was marked by many days above 30°C with rainfall relegated to late July and August (Fig. 2). The mean monthly discharge of the Rio Conejos during 1987–1989 fluctuated predictably. Peak discharge occurred typically in June but occurred in May during the warm, windy spring of 1989 (Fig. 3).

Species Richness

More than 13,000 nymphs and adults were studied over the 3-yr period. Among these

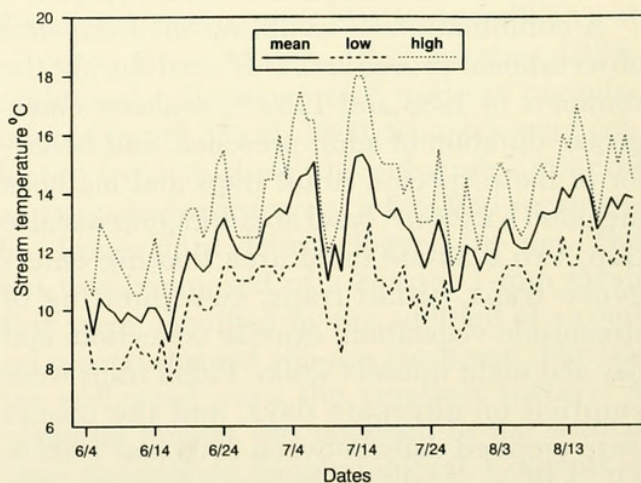


Fig. 1. Daily mean, high, and low stream temperatures in the Rio Conejos, summer 1988.

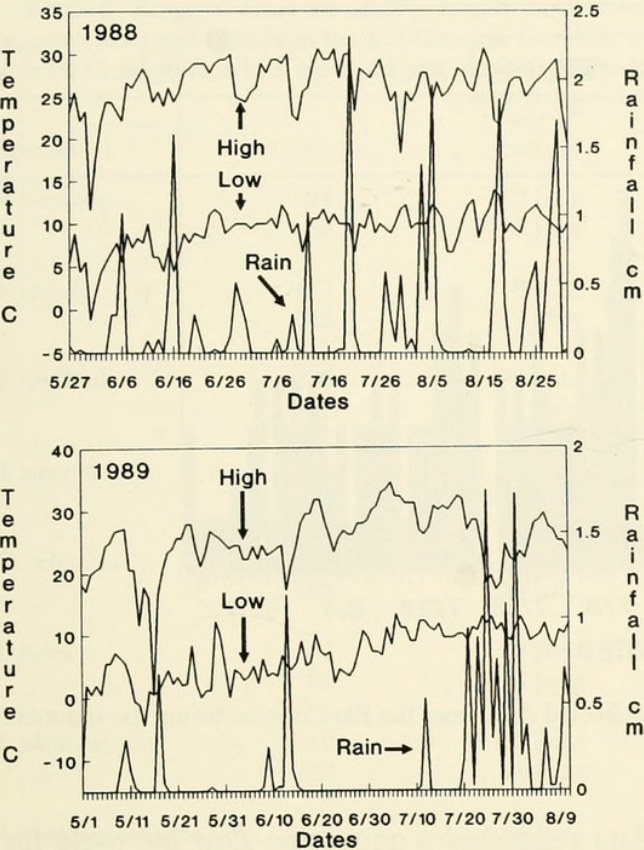


Fig. 2. Daily high and low air temperatures and rainfall for summer 1988 and 1989.

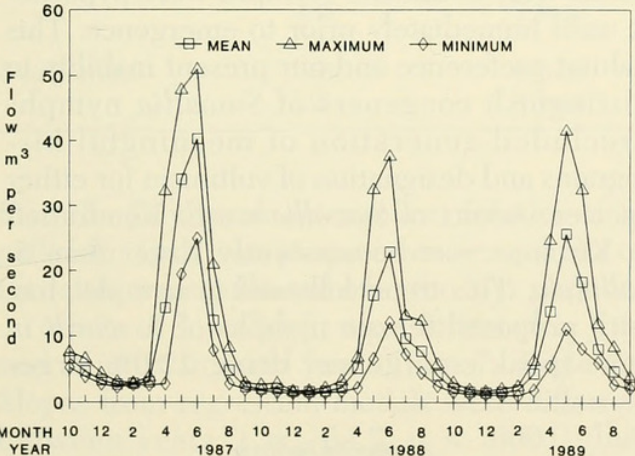


Fig. 3. Mean, minimum, and maximum monthly stream discharge of the Rio Conejos during the study period.

were 31 species (Table 1) in eight families. The Chloroperlidae, Perlodidae, and Capniidae were the most speciose families with six, seven, and seven species, respectively. Seven genera were represented by more than one species: *Capnia*, *Utacapnia*, *Taenionema*, *Suwallia*, *Triznaka*, *Isogenoides*, and *Isopterla* (Table 1). Peak species richness occurred on or near the summer solstice in both years (Fig. 4). Pattern differences existed between years,

including an early waning and a more peaked distribution of species richness in 1989.

Leuctridae

Paraleuctra vershina Gaufin and Ricker. This was the only leuctrid found at our sites. No nymphs were recovered from the stream, indicating a probable hyporheic existence. Adults were abundant in riparian vegetation during June and July (Fig. 5). No variation in adult presence parameters was noted for *P. vershina* (Table 2). Emergence was classified as extended in both years, although slopes of these cumulative emergence curves were significantly different over the 2 yr (Table 3).

TABLE 1. Stoneflies collected from the Rio Conejos, Colorado, March 1987 through March 1990.

Euholognatha	
CAPNIIDAE	
<i>Capnia coloradensis</i>	Claassen ¹
<i>Capnia confusa</i>	Claassen
<i>Capnia vernalis</i>	(Newport)
<i>Isocapnia crinita</i>	(Needham & Claassen) ¹
<i>Utacapnia logana</i>	(Nebeker & Gaufin) ¹
<i>Utacapnia poda</i>	(Nebeker & Gaufin) ¹
LEUCTRIDAE	
<i>Paraleuctra vershina</i>	Gaufin & Ricker ¹
NEMOURIDAE	
<i>Amphinemura banksi</i>	Baumann & Gaufin ¹
<i>Prostoia besemetsa</i>	(Ricker) ¹
<i>Zapada frigida</i>	(Claassen) ¹
TAENIOPTERYGIDAE	
<i>Taenionema pallidum</i>	(Banks) ¹
<i>Taenionema pacificum</i>	(Banks) ¹
<i>Doddsia occidentalis</i>	(Banks) ¹
Systellognatha	
CHLOROPERLIDAE	
<i>Paraperla frontalis</i>	(Banks) ¹
<i>Plumiperla diversa</i>	(Frison) ¹
<i>Suwallia lineosa</i>	(Banks) ¹
<i>Suwallia pallidula</i>	(Banks) ¹
<i>Suwallia wardi</i>	Kondratieff & Kirchner ¹
<i>Triznaka pintada</i>	(Ricker) ¹
<i>Triznaka signata</i>	(Banks) ¹
PERLIDAE	
<i>Claassenia sabulosa</i>	(Banks) ¹
<i>Hesperoperla pacifica</i>	(Banks) ¹
PERLODIDAE	
<i>Isogenoides zionensis</i>	Hanson ¹
<i>Isogenoides prob. colubrinus</i>	(Hagen) ¹
<i>Isopterla fulva</i>	Claassen
<i>Isopterla mormona</i>	Banks ¹
<i>Isopterla phalerata</i>	(Smith) ¹
<i>Isopterla quinquepunctata</i>	(Banks)
<i>Skwala americana</i>	(Klapálek)
PTERONARCYIDAE	
<i>Pteronarcella badia</i>	(Hagen)
<i>Pteronarcys californica</i>	Newport ¹

¹New drainage and county records.

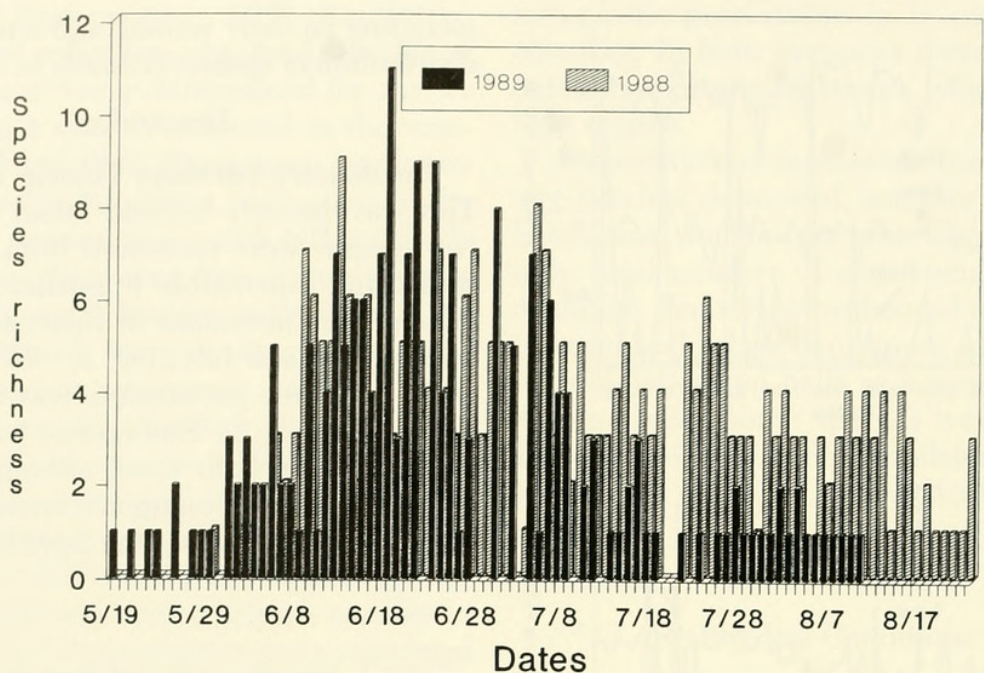


Fig. 4. Temporal species richness pattern of adult stoneflies collected daily from the Rio Conejos during the summers of 1988 and 1989.

Chloroperlidae

Representatives from two subfamilies inhabited the stream. The early- and mid-instar nymphs of the Chloroperlinae genera could not be reliably identified to genus. This necessitated the illustration of a portion of the nymphal growth of *Plumiperla diversa* (Frison) and *Triznaka signata* (Banks) as Chloroperlinae spp. (Fig. 6). Growth of reliably identified mid- to late-instar nymphs was illustrated separately.

***Paraperla frontalis* (Banks) (Paraperlinae).** Nymphs were collected infrequently among marginal substrates during the colder months of the year. All were pale, very thin, and had eyes set far forward as described for mature nymphs (Stewart and Stark 1988). These limited data are presented for the first year of the presumed semivoltine growth pattern of this large chloroperlid (Fig. 6). Less than 10 adults were collected in early June during the 3-yr study.

***Plumiperla diversa* (Chloroperlinae).** No adults were collected on which to base specific identity; however, nymphs of this genus are distinctive, and only *P. diversa* has been collected in this region (Baumann et al. 1977). Nymphs were identifiable to genus by March. Females were readily distinguished from males at this time. Growth continued through May when females attained a median HCW 9.6% larger than males. The limited nymphal

data suggested a univoltine-slow life cycle for this species.

***Suwallia pallidula* (Banks) (Chloroperlinae).** Only 59 nymphs of *Suwallia* spp. were collected from the Rio Conejos, even though adults were abundant. Nymphs were hyporheic until immediately prior to emergence. This habitat preference and our present inability to distinguish congeners of *Suwallia* nymphs precluded generation of meaningful histograms and designation of voltinism for either species. Adults of *Suwallia wardi* Kondratieff & Kirchner were consistently larger than *S. pallidula*. This trend followed in nymphs, too, with proposed female nymphs of *S. wardi* in June (peak emergence) being 22.0% larger

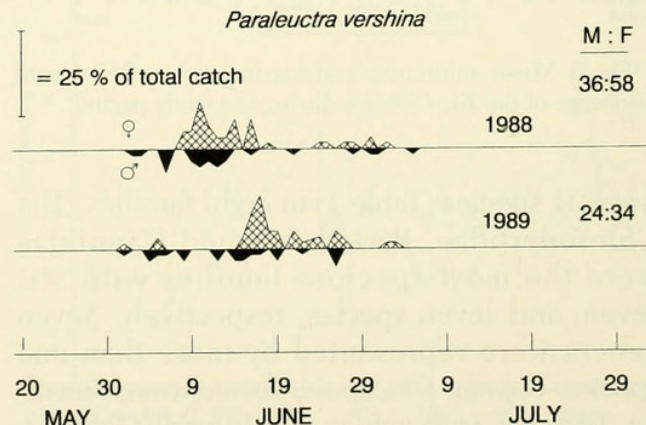


Fig. 5. Emergence of *Paraleuctra vershina* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

TABLE 2. Range of dates for adult presence parameters for 11 summer-emerging stonefly species collected in 1988 (appears first) and 1989 from the Rio Conejos. Duration is mean \pm SD of the number of days. All parameters not available for *C. sabulosa*, which emerged past our study period.

Species	<i>n</i>	Date 1 st capture	Date 50% catch	Last date capture	Duration (d)
<i>P. vershina</i>	94	2 June	12 June	5 July	35.0 \pm 0.0
	58	1 June	17 June	7 July	
<i>S. wardi</i>	467	6 June	10 July	15 August	66.0 \pm 7.1
	352	19 May	25 June	18 July	
<i>S. pallidula</i>	276	30 June	28 July	23 August	44.5 \pm 4.8
	162	1 July	14 July	4 August	
<i>T. signata</i>	662	9 June	28 June	23 August	59.0 \pm 24.0
	2697	2 June	19 June	12 July	
<i>C. sabulosa</i>	356	19 July	—	—	—
	1195	16 July	—	—	
<i>I. fulva</i>	19	9 June	22 June	7 July	24.5 \pm 7.8
	61	9 June	18 June	28 June	
<i>I. phalerata</i>	12	20 June	28 June	24 July	22.5 \pm 3.5
	20	18 June	25 June	8 July	
<i>I. quinquepunctata</i>	9	24 June	14 July	27 July	30.0 \pm 4.2
	12	19 June	5 July	15 July	
<i>I. zionensis</i>	200	8 June	19 June	28 June	15.5 \pm 4.9
	75	10 June	17 June	24 June	
<i>P. badia</i>	215	10 June	22 June	17 July	34.5 \pm 3.5
	480	7 June	20 June	7 July	
<i>P. californica</i>	55	6 June	8 June	12 June	6.0 \pm 2.8
	21	4 June	5 June	13 June	

than the July (peak emergence) females of *S. pallidula*. Only two proposed male nymphs of the latter were collected over the 3-yr period.

Adults of *S. pallidula* were collected in July and August in both years (Fig. 7, Table 2). Slopes from regression models were different between years ($t = -64.7$, $p < .0001$), but below the 5%/d criterion. We categorized this species as an extended emerger (Table 3). The median emergence date was advanced by 2 wk in 1989 over that of 1988 (Table 2). The adult sex ratio over the two seasons was 13 ♂: 415 ♀. Six field-collected and laboratory-maintained females produced only one egg batch (Table 4).

***Suwallia wardi* (Chloroperlinae).** This was the most abundant of the three *Suwallia* species collected from the Rio Conejos. Adults were first collected in late May or early June, reached 50% cumulative catch by mid-July, and disappeared from streamside by early

August (Table 2). It had the longest mean duration of presence (66 d) for any stonefly studied on the Rio Conejos (Table 2). Like its congener, *S. wardi*'s 1989 date of median catch was advanced by 2 wk over that of 1988 (Table 2, Fig. 7). Emergence of *S. wardi* was extended, and no significant slope differences were noted between years (Table 3). No egg data were collected for this species.

Riparian vegetation was used by this large, yellow-green chloroperlid as a staging ground for adult behaviors. *Suwallia wardi* was active throughout the morning on sunny days and again for 2–3 h before sunset if conditions were warm and dry. During cool, rainy days the low vegetation was devoid of *S. wardi* or any other stonefly species.

***Triznaka signata* (Banks) (Chloroperlinae).** Identifiable, late-instar nymphs were collected during a 5-mo period in the spring and summer. Nymphs of this univoltine-slow

TABLE 3. Synchrony and linear regression statistics for the years 1988 (appears first) and 1989. Slopes between years were tested: * = significance .05-.01, ** = <.001 level or lower probability, and NT = not tested.

Species	Slope	R ²	p	Synchrony
<i>P. vershina</i>	3.0	.85	.0001	extended
	3.5**	.90	.0001	extended
<i>T. signata</i>	1.5	.87	.0001	extended
	3.0**	.91	.0001	extended
<i>S. pallidula</i>	2.5	.96	.0001	extended
	3.5**	.90	.0001	extended
<i>S. wardi</i>	2.2	.84	.0001	extended
	2.2	.85	.0001	extended
<i>C. sabulosa</i>	2.8	.94	.0001	extended
	4.1**	.99	.0001	extended
<i>I. zionensis</i>	7.5	.92	.0001	synchronous
	7.9	.95	.0001	synchronous
<i>P. badia</i>	3.6	.81	.0001	extended
	4.4*	.92	.0001	extended
<i>P. californica</i>	13.3	.84	.004	synchronous
	18.9NT	.97	.103	synchronous

species were largely full grown by April (Fig. 6) with some degree of sexual dimorphism present at this time.

Adults first appeared in early June, reached 50% cumulative catch 2 wk later, and could no longer be collected by late August (Fig. 7, Table 2). Emergence was protandrous, but slightly female-skewed sex ratios dominated in both 1988 and 1989 (Fig. 7). *Triznaka signata* displayed the greatest variation in last date of capture and duration of presence of all stoneflies in the river (Table 2). It advanced its 1989 median emergence date by 9 d over that of 1988. Regression slopes indicated an extended emergence in both years (Table 3). Differences between slopes for 1988 and 1989 were significant ($t = -11.35, p < .0001$).

Attempts during the entire study to obtain eggs from laboratory-reared and -mated females were unsuccessful. The mean number of eggs from six females caught during oviposition flights was lower than any first batches for other stoneflies studied (Table 4). Although these females were held for a prolonged period of time, no additional egg batches were laid.

Adults were never seen emerging in the field, despite many hours of observation along the shoreline, day and night, in habitats where

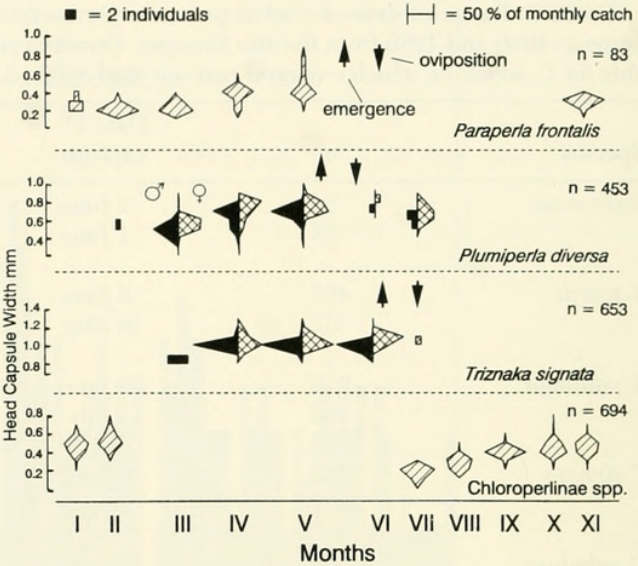


Fig. 6. Growth of Chloroperlidae nymphs collected from the Rio Conejos, 1987-1990.

they were collected in abundance during the day. Adults inhabited marginal vegetation, where males were observed actively searching willow stems and leaves for females. No drumming was observed during the two summers of intensive fieldwork. Large flights of adults of both sexes took place just before dark, at which time females were observed ovipositing. Egg masses were dropped from up to 4-5 m above the stream.

Perlidae

Claassenia sabulosa. Although two perlids were present in the Rio Conejos (Table 1), only *C. sabulosa* was sufficiently abundant for growth and emergence interpretation. Nymphs of this species were found among larger rubble of midstream. The life cycle was semivoltine and appeared to require 3 yr of nymphal growth (Fig. 8). Recruitment occurred throughout the fall with possibly some additional recruitment in March from overwintering eggs. Eggs containing eyespots were recovered from the stream in October and November. Sexual dimorphism in both size and external genitalia occurred when nymphal size reached 2.2 mm HCW. The size disparity increased until the third year of growth when little overlap between the sexes remained.

A protandrous emergence began in mid-July in both years (Fig. 9, Table 2). Exuviae of this species were abundant throughout August, possibly into September. Emergence of *C. sabulosa* was extended and slopes were significantly different between years ($t = -10.7, p < .0001$, Table 3).

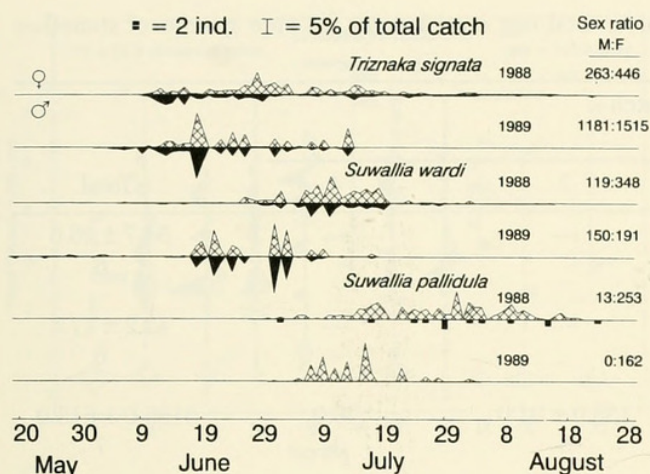


Fig. 7. Emergence of Chloroperlidae from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Claassenia sabulosa produced the greatest mean number of eggs of any stonefly species studied (Table 4), with females producing up to four batches. Longevity of seven females was 3.9 ± 1.9 d. Egg production lasted through 80% of the adult life. Several egg batches were incubated, but none hatched within 6 mo of observation.

Emergence occurred between 2000 and 2200 h. Nymphs crawled out of the water onto emergent cobble and boulders to transform, the entire molting process taking less than 5 min. Hardened and newly transformed males ran over all emergent substrates, searched for females in a circular pattern, and drummed mostly on large mineral substrates. Pitfall trap collections of 1989 caught a total of 115 male adults in transect 1 and only 12 in transects 2 and 3. Only two females were collected in the pitfall traps, presumably because of their less-intensive and unidirectional movement pattern. Therefore, excursions of great distance away from the water's edge for either sex were infrequent. Females were often found in the morning under dry cobble with abdomens devoid of eggs or with large egg masses suspended between the cerci. Several females were observed at night running over the surface of the water, but the cause of this behavior could not be determined. No females were actually observed ovipositing. Males were distinctly cursorial, which fits with their brachypterous morphology; however, females were never observed flying, nor did they inhabit tall substrates, even though they had full wings.

Perlodidae

Isogenoides zionensis Hanson (Perlodinae: Perlodini). The large range in size of nymphs from July samples (Fig. 10) could not be accounted for by nymphs hatching from eggs laid by June-mated females. June eggs reared at simulated stream conditions hatched in March and April, 9–10 mo after oviposition. Therefore, at least some individuals of this species have a semivoltine life cycle with eggs diapausing over their first summer and winter. Early-instar nymphs were missed in benthic samples during their second spring, possibly due to high water or their occurrence deep in the substratum. Sexual dimorphism in size and morphology was apparent by July of the second year when nymphs approached 1.8 mm HCW (Fig. 10). This disparity increased steadily throughout the rest of their growth. Little overlap in size of the sexes existed by May prior to emergence.

The adult presence parameters of *I. zionensis* showed little variation over the 2 yr studied (Table 2). Emergence was not protandrous, but the sex ratio was heavily skewed towards males (Fig. 11). This species was one of two that emerged synchronously (Table 3). No difference in slope was found between years ($t = 0.82$, $p > .2$); therefore, a common slope of 7.6%/d was calculated.

Laboratory-reared females put nearly 75% of their total egg complement into a first batch (Table 4). Only one of four females produced additional batches.

Transformation of *I. zionensis* took place from 2030 to about 2200 h. Nymphs crawled away from the stream until they reached willows or other vegetation, then ascended <1 m vertically where they molted. Daylight activity began by 0700–0800 h at the base of small willow coppices, where adults were often found in emergent leafpacks. Adults ascended stream-side willows as the sun rose. Drumming, mating, and egg batch formation took place from these perches. Females crawled to the tops of these willows and flew to the stream where they fluttered on the water to release their black egg masses. Most activity ceased by 1300–1400 h on days when air temperature reached near 25°C. On cloudy, cool days this ascendance did not occur. Most adults could then be found in the leaf-entrained bases of riparian vegetation. Drumming on willow stems

TABLE 4. Mean eggs per batch, number of batches, and mean total egg complement for nine species of stoneflies occurring in the Rio Conejos, Colorado.

Species	Eggs / batch				Total
	1	2	3	4	
<i>S. pallidula</i>	54.7 ± 26.6 6	—	—	—	54.7 ± 26.6 6
<i>T. signata</i>	42.2 ± 17.4 6	—	—	—	42.2 ± 17.4 6
<i>C. sabulosa</i>	2166.0 ± 774.0 7	902.0 ± 246.2 5	158.0 ± 91.0 5	40.0 1	3188.0 ± 613.0 7
<i>I. zionensis</i>	588.0 ± 86.0 4	327.0 1	185.0 1	—	843.2 ± 141.4 4
<i>I. fulva</i>	231.5 ± 7.8 2	—	—	—	231.5 ± 7.8 2
<i>I. phalerata</i>	703.0 1	—	—	—	703.0 1
<i>S. americana</i>	884.7 ± 267.3 6	—	—	—	884.7 ± 267.3 ^a 6
<i>P. badia</i>	339.0 ± 86.0 30	58.4 ± 37.2 5	56.8 ± 39.7 4	—	351.0 ± 101.0 30
<i>P. californica</i>	393.0 ± 125.6 4	191.3 ± 130.2 4	94.3 ± 49.5 4	69.8 ± 24.7 4	
	5	6	7		
	51.3 ± 29.3 4	58.5 ± 23.3 2	57.0 1		

^aTotal fecundity includes those eggs remaining in ovarioles.

was observed at night, even when temperatures approached 10°C.

***Isoperla fulva* Claassen (Isoperlinae).** We collected this species in benthic samples only occasionally, but enough individuals were obtained to allow a tentative interpretation of voltinism. Recruitment of nymphs was first detected in August (Fig. 12). These measured 0.4–0.8 mm HCW and grew at a slow rate throughout the fall until a winter decrease in growth rate. Their size increased dramatically after February, until emergence in June and July. This species conformed to a univoltine-slow growth pattern.

Adults were collected for the first time on 9 June in both years (Fig. 11, Table 2). Sex ratios for the small number of 1988 adults were approximately equal, but heavily skewed towards males in 1989. Numbers of adults collected in both years were too small to warrant an analysis of synchrony.

Fecundity was difficult to assess since few mature nymphs were available for rearing. One egg batch from each of two field-ovipositing females was collected (Table 4). Longevity of three field-collected adult females was 5.7 ± 0.58 d.

***Isoperla phalerata* (Smith) (Isoperlinae).** Although the number of nymphs collected was small, no month supported more than one size class (Fig. 12). Therefore, we have tentatively proposed a univoltine-slow growth pattern for this species. Adults were taken from mid-June through mid-July (Table 2, Fig. 11). No assessment of synchrony was made for *I. phalerata* due to low numbers of adults captured. Females did not produce eggs in captivity. A single egg batch from a field-collected individual contained 703 eggs. Four field-caught females lived 11.3 ± 3.6 d past date of capture.

***Isoperla quinquepunctata* (Banks) (Isoperlinae).** This species was more common at site

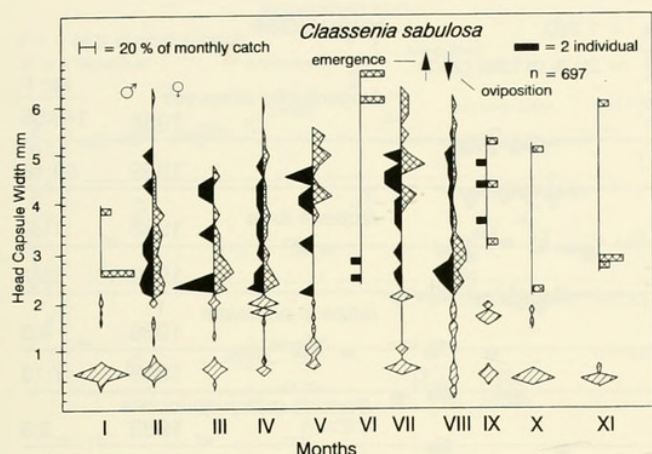


Fig. 8. Growth of *Claassenia sabulosa* nymphs collected from the Rio Conejos, 1987–1990.

three. The data suggested that *I. quinquepunctata* had a univoltine-fast growth pattern. Recruitment occurred in January and February (Fig. 12), and growth was rapid from March through May. Sexual dimorphism in nymphal size was not as evident in this species as in its congeners. Emergence began in mid-June and lasted through much of July (Table 2, Fig. 11). No eggs were collected.

***Skwala americana* (Klapálek) (Perlodinae).** This species displayed a univoltine-slow growth pattern and grew faster during summer and fall months than all other perlodids in the Rio Conejos (Fig. 13). Nymphs were recruited in June and increased their median HCW from 0.4 mm to about 2.8 mm by January. Growth was nearly completed by this time. Sexual dimorphism was apparent as early as August, and female nymphs reached a median HCW before emergence that was 21.4% greater than males. Female nymphs in April were found to contain fully sclerotized eggs in their oviducts; hence, this species is fully capable of mating and egg-laying immediately upon emergence.

Emergence was in April and early May when our sampling was still on a monthly basis; therefore, no detailed analysis of emergence phenology and synchrony can be offered. Adults were collected mainly from emergent logjam debris or under cobble at the stream margin.

Egg batches collected in mid-April from four laboratory-reared females hatched synchronously after a mean of 61.0 ± 7.3 d. This corroborates field collections of early-instar nymphs in June. Only a single egg batch was collected from each of six laboratory-reared females (Table 1).

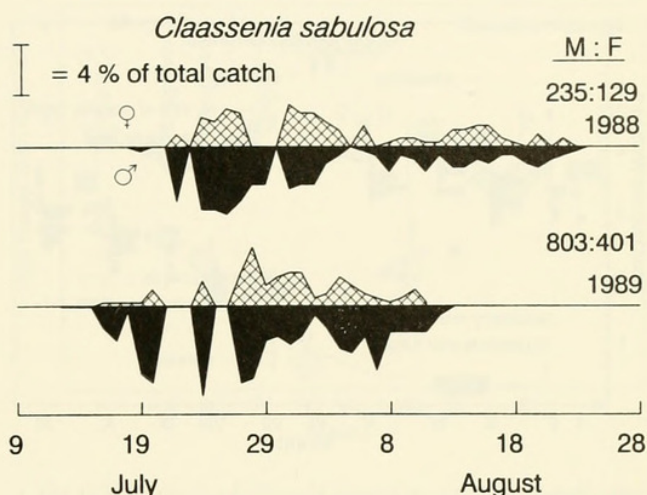


Fig. 9. Emergence of *Claassenia sabulosa* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Pteronarcyidae

***Pteronarcella badia* (Hagen).** This species was found to have a semivoltine growth pattern. Recruitment of nymphs began in March and April from eggs laid the previous June (Fig. 14). Many small nymphs were available in benthic samples by mid-April when they were at 0.2–0.4 mm HCW. This scenario was corroborated by laboratory incubation of several egg batches that hatched in March and April after a 9–10-mo diapause. Growth of nymphs was rapid throughout their first spring. Size differentiation among sexes was not apparent until August, a full 14 mo after oviposition. Median size of females just before emergence the following May was 21% greater than that of males.

Emergence began by early June, with slight protandry and a preponderance of males being collected (Fig. 15). Median emergence occurred in the third week of June in both years (Table 2). Emergence was extended (Table 3) and slopes were significantly different between years ($t = -2.2, p < .05$).

Females generally laid only single egg batches, but a small number produced up to three egg batches (Table 4). Most females laid their first egg batch within 24 h of mating and often waited 2-d intervals before laying others. Longevity of seven females under simulated field conditions was 7.7 ± 4.2 d.

Pteronarcella badia emerged just after dusk and typically used willows, cottonwoods, and stream margin sedges as transformation sites. Males were observed actively searching the willows and drumming for females at night,

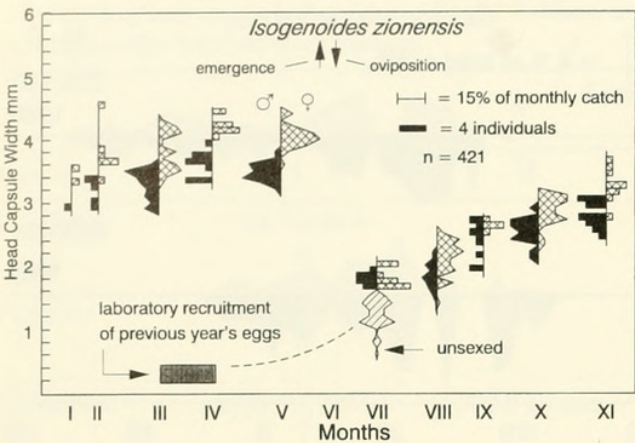


Fig. 10. Growth of *Isogenoides zionensis* nymphs collected from the Rio Conejos, 1987–1990.

even when air temperatures were near 10°C. Adults entered the leaf-choked bases of willows as the night progressed and were often found the next morning in large mating aggregations under these debris. These individuals ascended the willows as the sun warmed the air at streamside. Drumming, mate searching, mating, and egg batching took place in mid-morning hours, while most activity ceased by 1200 h when air temperatures reached 22–25°C. Females oviposited by launching themselves from the tips of tall riparian shrubs toward the stream, where they would jettison their white egg mass a few meters above the surface of fast-flowing water.

***Pteronarcys californica* Newport.** This species is commonly known as the salmonfly. Recruitment began in April (Fig. 16) after a 9–10-mo egg diapause. Nymphs grew to only about 1 mm HCW through their first year. Sexual differences in size and morphology were apparent by June of their second year, when they were nearly 1.5 mm HCW. Nymphs grew for two more years, by the end of which time preemergent females had attained a 20% larger median HCW than males. These data suggest a semivoltine life history of 4-yr duration for this species.

Adults were first found on 6 June during both years (Fig. 15, Table 2). Emergence was a highly synchronous event (Table 3). Slopes were not tested for significant differences due to small sample size.

Most laboratory-reared females produced five egg batches, but one individual produced seven (Table 4). Egg production lasted through 82% of the 15.0 ± 1.8 d (n = 4) average adult female life span.

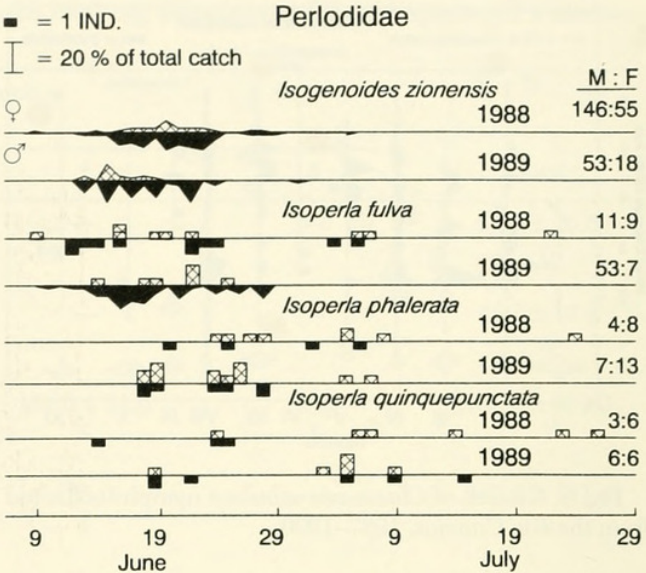


Fig. 11. Emergence of Perlodidae from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

Adults utilized marginal vegetation, much as did *P. badia*, as a staging ground for mating and ovipositing. However, they tended to select the taller cottonwoods and Engelmann spruce rather than the shorter willows for their activities. Salmonflies oviposited by flying over the stream and dropping their salmon-colored or bluish egg masses (dimorphism in egg color was observed) from as high as 10 m. Ovipositing adults were heavily fed upon by opportunistic Eastern Robins (*Turdus migratorius*) and Steller's Jays (*Cyanocitta stelleri*).

DISCUSSION

Species Richness

The Rio Conejos displayed a great diversity of Plecoptera. Twenty of the 31 species were evenly distributed among the Capniidae, the Chloroperlidae, and the Perlodidae. The only North American family not represented was the Peltoperlidae, which occurs transcontinentally, but not in latitudes below the northern Rocky Mountains (Baumann et al. 1977). Nearly all species collected were adapted for a montane existence and were characteristic of streams with high biotic integrity. Twenty-five species were both new drainage and county records (Baumann et al. 1977, Szczytko and Stewart 1979, Nelson and Baumann 1989; Table 1), though all of them had been previously reported from Colorado and neighboring New Mexico. This demonstrates that we have yet to adequately investigate the fine-scale diversity

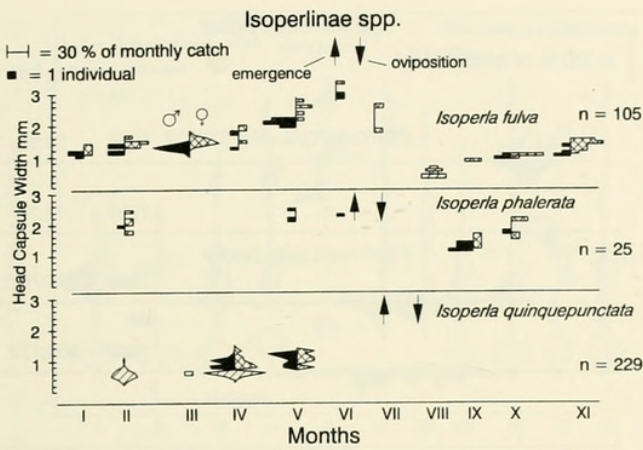


Fig. 12. Growth of *Isoperla* spp. nymphs collected from the Rio Conejos, 1987–1990.

and distribution of this order of aquatic insects in at least some portions of the southern Rocky Mountains.

Responses to Altered Thermal Regime

We became aware of substantial climatic differences (Fig. 2) between the two summers when adults were intensively studied. Though no water temperatures were available for 1989, air temperatures (Fig. 2) and hydrologic data (Fig. 3) suggested that the stream warmed more quickly and attained peak summer highs much earlier than in 1988. Consequently, development of several species was hurried, which narrowed the window of time adults were present streamside. At the assemblage level of organization, this trend is demonstrated by the species richness pattern of Figure 4. The 1989 pattern was more peaked and greatly truncated over that of 1988. Species-level responses can be demonstrated by inspection of the flight diagrams for each species. Nine of the 11 species presented in Table 2 show increased median emergence dates. Additionally, slopes produced by linear regression that were different between years (Table 3) were always higher in 1989. This result was consistent with a hurried nymphal development and shorter emergence period for each species.

Life History Parameters

LEUCTRIDAE

Paraleuctra vershina. Harper (1973b) reports that most *Leuctra ferruginea* in an Ontario stream are semivoltine, but that some univoltine individuals exist. Huryn and Wallace (1987) propose a 2-yr life cycle for a composite of *Leuctra* spp., most of which were probably

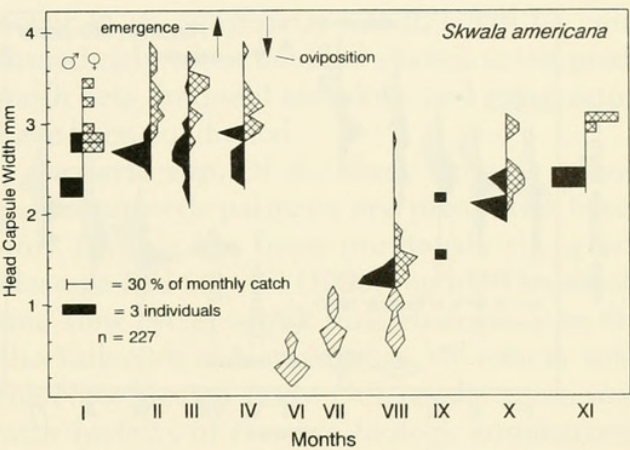


Fig. 13. Growth of *Skwala americana* nymphs collected from the Rio Conejos, 1987–1990.

L. ferruginea (Walker). Snellen and Stewart (1979) record univoltine fast cycles for *Zealeuctra claasseni* and *Z. hitei* in streams of north Texas. Additionally, Ernst and Stewart (1985a) report *Leuctra tenuis* as univoltine-fast in an Ouachita Mountain stream.

CHLOROPERLIDAE

Most Chloroperlidae exhibit a univoltine-slow or -fast growth pattern. *Haploperla brevis* (Banks) is widespread from Oklahoma to Quebec and west to Alberta, Canada. Ontario (Harper and Magnin 1969), Quebec (Harper et al. 1994), and Oklahoma (Ernst and Stewart 1985a) populations exhibited univoltine-fast growth with a 2–5-mo diapause, while Alberta populations were univoltine-slow (Barton 1980). European populations of *Chloroperla tripunctata* (Scopoli) (Elliott 1988), *Siphonoperla torrentium* (Pictet) (Elliott 1967), and *S. burmeisteri* (Pictet) (Benedetto 1973) also exhibited univoltine-slow growth. Species with semivoltine growth include *Sweltsa onkos* (Ricker) and possibly *Utaperla gaspesiana* Harper and Roy (Harper 1973a, Harper et al. 1994), *S. mediana* (Banks) (Cushman et al. 1977), and *S. lateralis* (Banks) (Huryn and Wallace 1987).

Paraperla frontalis. Stanford and Gauvin (1974) presented some evidence for semivoltine growth of this species. Emergence for this species and for *P. wilsoni* Ricker occurs from May through July (Stewart and Stark 1988). Paraperlinae are rather robust chloroperlids that tend to be hyporheic for most of their nymphal development. Their larger size, the more stable stream temperatures in the hyporheic environment (Hendricks 1993), and the possibly low availability of some nutrients in the

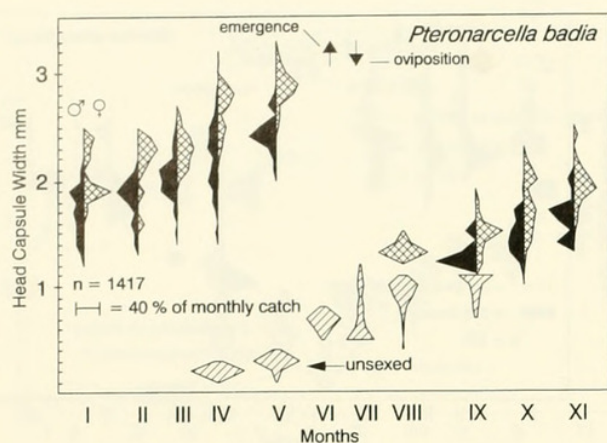


Fig. 14. Growth of *Pteronarcella badia* nymphs collected from the Rio Conejos, 1987–1990.

hyporheic habitat (Stanford and Ward 1993) may have contributed to a preponderance of semivoltinism in this subfamily.

***Plumiperla diversa*.** Stewart et al. (1990) reported a univoltine-slow cycle for this species on the North Slope of Alaska. Emergence occurred from May through September, with recruitment of nymphs from a direct hatch in July. Growth occurred through the summer months with most nymphs attaining maximum size before a winter quiescence. This assessment compared well with our limited data. Failure to collect adults was probably due to our infrequent sampling during their presumed early May emergence.

***Suwallia pallidula* and *Suwallia wardi*.** No aspects of the life histories of either *S. pallidula* or *S. wardi* have been reported. The latter was recently described from a Colorado Front Range springbrook (Kondratieff and Kirchner 1990). It was one of the most abundant chloroperlids in the Rio Conejos. This suggests that its ecological tolerance is wide and that it may soon be found in a variety of streams in the southern Rocky Mountains.

Several explanations are possible for the heavily female-skewed sex ratio (13 ♂:425 ♀) of *S. pallidula* adults. The most probable is a combination of limited use of emergence traps coupled with an inaccessible microhabitat of adult males, probably high in the vegetation. Parthenogenesis may also be possible, but it is exceedingly rare in stoneflies. Harper (1973a) reported that a few eggs of a perlid, *Paragnetina media* (Walker), hatched without fertilization. We did not attempt rearing of eggs from virgin females to check for parthenogenesis in either *Suwallia* spp. These sex ratios are a perplexing problem, compounded by the

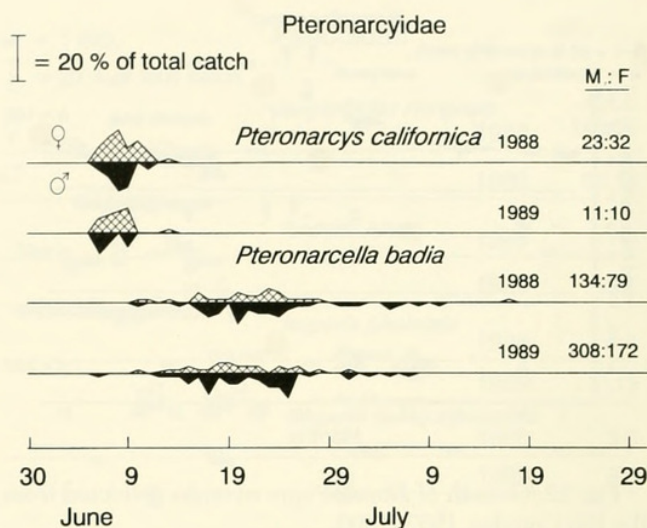


Fig. 15. Emergence of *Pteronarcella badia* and *Pteronarcys californica* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

fact that 0 ♂: 657 ♀ of the closely related *S. lineosa* were caught during concurrent sampling on Massey Creek, a tributary of the Rio Conejos.

***Triznaka signata*.** Hassage and Stewart (1990) studied the widely distributed *T. signata* in the Rio Vallecitos of northern New Mexico. They reported a univoltine-slow growth pattern, with which we concur. No study of the emergence of this species has previously been published.

PERLIDAE

***Claassenia sabulosa*.** Hassage and Stewart (1990) and Barton (1980) report a merovoltine (>2 yr) growth pattern for New Mexico and Alberta populations of this species. No egg batches from the Rio Conejos hatched in our laboratory, but this Colorado population showed some evidence of an extended hatch leading to cohort splitting (Stewart and Stark 1988). Eggs may undergo a temperature-dependent quiescence as occurs in *Dinocras cephalotes* (Curtis) when fall temperatures decline to 8°C (Lillehammer et al. 1989). Presence of first-instar nymphs in the fall, eyed eggs in October and November, and more first-instar nymphs in March supported this contention.

Life histories have been reported for at least one species in every genus in the tribe Perlina, to which *C. sabulosa* belongs. All growth patterns involve 2–3 yr of development. *Agnetina flavescens* (Walsh), from an Ozark stream, exhibits a 2-yr life cycle, a short egg incubation period, and an extended emergence period

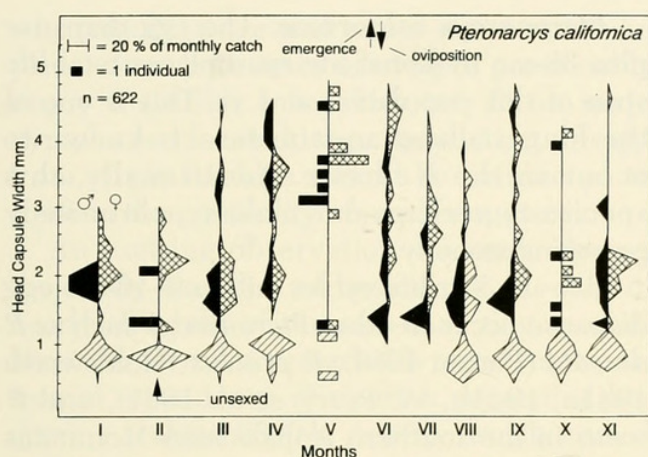


Fig. 16. Growth of *Pteronarcys californica* nymphs collected from the Rio Conejos, 1987–1990.

(Ernst and Stewart 1985b). *Agnetina capitata* (Pictet) was shown to have a 3-yr cycle, extended emergence, and a 40–80-d egg incubation period in Ontario (Harper 1973a). This range of incubation coupled with a long emergence promotes great differences in size of nymphs that ultimately prevents the separation of cohorts and determination of voltinism. This was also a problem for *C. sabulosa* in the Rio Conejos.

PERLODIDAE

This family contains over 115 species (Stark et al. 1986, Stewart and Stark 1988) in the Nearctic. Although life histories of only 26 species are known, a clear trend toward univoltine-slow cycles occurs among the subfamilies Isoperlinae and Perlodinae (Stewart and Stark 1988). Growth and emergence had not previously been studied for three of the seven perlodids in the Rio Conejos. These include *I. zionensis*, *I. quinquepunctata*, and *I. phalerata*.

***Isogenoides zionensis*.** Few detailed life history studies of the genus have been reported (Stewart and Stark 1988). Barton (1980) suspected semivoltinism for an Alberta population of *I. colubrinus*, since two size classes of nymphs were collected in early May. Flannagan (1977) reported great body length variation in May for this species in another Alberta watershed but concluded a univoltine-slow cycle. Hilsenhoff and Billmeyer (1973) and Dosdall and Lehmkuhl (1979) proposed univoltine growth patterns for the May–June-emerging *I. frontalis* in Wisconsin and Saskatchewan streams, respectively, based on samples taken a few months of the year. Semivoltinism, as reported for *I. zionensis* in the Rio Conejos, may also

occur in its congeners, but this will be confirmed only when detailed studies using small mesh nets, frequent sampling, and egg rearing have been conducted.

***Isoperla* spp.** Of the three *Isoperla* whose partial growth patterns are presented here, only *I. fulva* has been previously reported. Hassage and Stewart (1990) reported a univoltine-slow cycle, with a June emergence in the Rio Vallecitos of New Mexico. We concur with the New Mexico study. Our results agree well with reviews of *Isoperla* biology, summarized for 12 Nearctic species through 1987 (Stewart and Stark 1988). Ten species were univoltine-slow, while only two were univoltine-fast.

In more recent literature Stewart et al. (1990) reported univoltine-slow growth for *I. petersoni* Needham & Christenson of Alaska. Additionally, Harper et al. (1994) added as univoltine-slow *I. francesca* Harper and *I. montana* (Banks) from Quebec populations. These and our Rio Conejos work bring to 17 the Nearctic *Isoperla* species known to exhibit univoltine-slow cycles, while only three species appear to be univoltine-fast. *Isoperla grammatica* (Poda) and *I. difformis* (Klapálek) (Malmqvist and Sjöström 1989) and *I. obscura* (Zetterstedt) studied by Ulfstrand (1968) are univoltine-slow in the Palearctic.

Up to seven species of *Isoperla* commonly occur in streams in North America (Stewart and Stark 1988); conversely, in Scandinavia rarely more than two species occur simultaneously (Malmqvist and Sjöström 1989). Congenerics of aquatic insects often partition resources along one or more resource gradients (Grant and Mackay 1969). Though only small numbers of adults were collected, a pattern of successive emergence of *I. fulva*, *I. quinquepunctata*, and *I. phalerata* was clear in the Rio Conejos. Fifty percent cumulative catch dates for *I. fulva*, *I. phalerata*, and *I. quinquepunctata* were 22 June, 28 June, and 14 July, respectively, for 1988. These dates for 1989 were 18 June, 25 June, and 5 July. Temporal segregation brought about by a gradual change in dominance (Illies 1952) of these species may have accounted for the present coexistence of these stoneflies.

***Skwala americana*.** Two other studies reported univoltine-slow cycles with emergence from February through April for this species in northern New Mexico and central Colorado (Short and Ward 1980, Hassage and Stewart

1990). *Skwala curvata* (Hanson) of California also exhibited a univoltine-slow cycle, with emergence in April and May (Sheldon 1972). Other Arcynopterygini with univoltine-slow growth include *Frisonia picticeps* (Hanson) in California (Sheldon 1972), *Megarcys signata* (Hagen) in Utah (Cather and Gaufin 1975), and *Perlinodes aurea* (Smith) in California and Alberta (Radford and Hartland-Rowe 1971, Sheldon 1972).

Sheldon (1972) estimated average total fecundity of *S. curvata* to be near 1780 eggs for preemergent nymphs. This is much greater than that proposed for *S. americana* from the Rio Conejos. He used interocular width as an index to predict fecundity. Conversion of interocular width to HCW likely involves a factor of 2X, which would make *S. curvata* the larger of the two stoneflies. This largely accounts for differences in fecundity. Mutch and Pritchard (1986) reported that *S. americana* (as *S. parallela*) had a warm, stenothermal egg development.

Most species in this family have conserved the life history traits that Lillehammer et al. (1989) proposed as ancestral. These traits include univoltine-slow cycles, temperature-dependent growth, and direct egg development. *Isoperla quinquepunctata* and *I. zionensis* have likely abandoned all of these except temperature-dependent growth.

PTERONARCYIDAE

***Pteronarcella badia*.** Gaufin et al. (1972) reported that a 2-yr life cycle was possible for this species in Utah; however, S. Perry et al. (1987) and Stanford (1975) reported a univoltine life history in Montana. No eggs were reared in either Montana study, and it is apparent from their growth histograms that early instars were missed entirely. Therefore, semivoltine life history is most probable throughout its range.

Nymphs of this species are more likely to be found aggregated on filter paper leaf models than alone (Hassage et al. 1988). We have also observed nymphs aggregating under margin cobble immediately before emergence. Adults aggregate in leaf debris at the base of willow and cottonwood coppices at the Rio Conejos. This behavior may be attributable to the transformation and nighttime refuge sites being contagiously distributed. Hassage et al. (1988) also postulated that aggregation in *P. badia* lowers individual risk to predation.

***Pteronarcys californica*.** The egg diapause plus 38-mo nymphal life span places total life span of this population at 4 yr. This is one of the longest-lived aquatic insects known to occur in the Nearctic. Additionally, this species is perhaps our most synchronously emerging stonefly.

Two- to 3-yr life cycles with a 9–10-mo egg diapause occur in other *Pteronarcys* such as *P. dorsata* (Barton 1980), *P. proteus* (Holdsworth 1941a, 1941b, W. Perry et al. 1987), and *P. scotti* in the southern Appalachian Mountains (Folsom and Manuel 1983). However, Lechleitner and Kondratieff (1983) detailed a 1-yr life history for *P. dorsata* in Virginia.

Multiple-year life histories are common among larger species of the Pteronarcyidae (Stewart and Stark 1988). Accompanying this long nymphal growth, and perhaps contributing to it, is another life history trait, long egg diapause. Univoltine growth patterns and direct egg development are ancestral patterns, while the semivoltine growth and diapause of *P. badia* and *P. californica* are derived traits (Lillehammer et al. 1989). Future studies of egg incubation in lower latitudes of North America will enable us to outline the range of responses of which *Pteronarcys* and *Pteronarcella* are capable.

Unanswered Questions

Several largely unanswered questions persist about the life histories of stoneflies in and along the Rio Conejos. We have found that nymphs of many chloroperlids are not available in surface sediments until just prior to emergence. They must be hyporheic in their habitat choice. Second, chloroperlids of the present study did not readily produce eggs in captivity, and those incubated never hatched. We can still ask many questions about their life histories. The answers would require a detailed study of the hyporheic habitat of an open-sediment stream like the Rio Conejos. This study should concentrate only on the chloroperlids, since they are generally abundant and diverse. Such a study would still fit within the comparative study approach of Sheldon (1972), but the guild would involve hyporheic chloroperlids.

To settle the dilemma of aberrant sex ratios in this family, studies must concentrate on the presence of male nymphs in the stream. In this way the search for adult males whose

whereabouts are unknown need not take place, since both sexes of nymphs presumably enjoy a similar microhabitat. If no male nymphs are located, then incubation of eggs from virgin females should be conducted to confirm the possibility of parthenogenesis.

An exciting observation we made during the study was that of basking in the sun of nearly all adults of summer-emerging species. Most displayed a remarkably consistent pattern of ascendance of riparian vegetation beginning at about 0800 h. Activity usually ceased by 1300 h when air temperatures were hottest. This ascendance culminated for females in egg batching and oviposition flights, while males used these riparian staging grounds for mate searching, drumming, and mating. Stoneflies should be investigated for potential to benefit from basking, an unreported phenomenon for Plecoptera.

ACKNOWLEDGMENTS

We thank the Conejos Peak District of the U.S. Forest Service for providing lodging and laboratory space during the study. Special thanks go to J. B. Moring for his help with sample collection and D. Ziegler for providing some fecundity data for *P. badia*. This project was partially funded by faculty research funds of UNT and a National Science Foundation grant, BSR 8308422, to KWS.

LITERATURE CITED

- BARTON, D. R. 1980. Observations on the life histories and biology of Ephemeroptera and Plecoptera in north-eastern Alberta. *Aquatic Insects* 2: 97–111.
- BAUMANN, R. W., A. R. GAUFIN, AND R. F. SURDICK. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. *Memoirs of the American Entomological Society* 31.
- BENEDETTO, L. A. 1973. Growth of stonefly nymphs in Swedish Lapland. *Entomologisk Tidskrift* 94: 15–19.
- CATHER, M. R., AND A. R. GAUFIN. 1975. Life history and ecology of *Megarcys signata* (Plecoptera: Perlodidae), Mill Creek, Wasatch Mountains, Utah. *Great Basin Naturalist* 35: 39–48.
- CUSHMAN, R. M., J. W. ELWOOD, AND S. G. HILDEBRAND. 1977. Life history and production dynamics of *Alloperla mediana* and *Diplectrona modesta* in Walker Branch, Tennessee. *American Midland Naturalist* 98: 354–364.
- DOSDALL, L., AND D. M. LEHMKUHL. 1979. Stoneflies (Plecoptera) of Saskatchewan. *Quaestiones Entomologicae* 15: 3–116.
- ELLIOTT, J. M. 1967. The life histories and drifting of Plecoptera and Ephemeroptera in a Dartmoor stream. *Journal of Animal Ecology* 36: 343–362.
- . 1988. Interspecific and intraspecific variation in egg hatching for British populations of the stoneflies *Siphonoperla torrentium* and *Chloroperla tripunctata* (Plecoptera: Chloroperlidae). *Freshwater Biology* 20: 11–18.
- ERNST, M. R., AND K. W. STEWART. 1985a. Growth and drift of nine stonefly species (Plecoptera) in an Oklahoma Ozark foothills stream, and conformation to regression models. *Annals of the Entomological Society of America* 78: 635–646.
- . 1985b. Emergence patterns and an assessment of collecting methods for adult stoneflies (Plecoptera) in an Ozark foothills stream. *Canadian Journal of Zoology* 63: 2962–2968.
- FLANNAGAN, J. F. 1977. Life cycles of some common aquatic insects of the Athabasca River, Alberta. Alberta Oil Sands Environmental Research Program, Report 11. 20 pp.
- FOLSOM, T. C., AND K. L. MANUEL. 1983. The life cycle of *Pteronarcys scotti* (Plecoptera: Pteronarcyidae) from the southern Appalachians, U.S.A. *Aquatic Insects* 5: 227–232.
- GAUFIN, A. R., W. E. RICKER, M. MINER, P. MILAM, AND R. A. HAYS. 1972. The stoneflies (Plecoptera) of Montana. *Transactions of the American Entomological Society* 98: 1–161.
- GRANT, P. R., AND R. J. MACKAY. 1969. Ecological separation of systematically related stream insects. *Canadian Journal of Zoology* 47: 691–694.
- HARPER, P. P. 1973a. Emergence, reproduction, and growth of setipalpiian Plecoptera in southern Ontario. *Oikos* 24: 94–107.
- . 1973b. Life histories of Nemouridae and Leuctridae in southern Ontario (Plecoptera). *Hydrobiologia* 41: 309–356.
- HARPER, P. P., AND H. B. N. HYNES. 1972. Life histories of Capniidae and Taeniopterygidae in southern Ontario (Plecoptera). *Archiv für Hydrobiologie, Supplement* 40: 274–314.
- HARPER, P. P., AND E. MAGNIN. 1969. Cycles vitaux de quelques Plecopteres des Laurentides (Insecta). *Canadian Journal of Zoology* 47: 483–494.
- HARPER, P. P., M. LAUZON, AND F. HARPER. 1994. Life cycles of sundry stoneflies (Plecoptera) from Quebec. *Review d'Entomologie Quebec* 36: 28–41.
- HASSAGE, R. L., AND K. W. STEWART. 1990. Growth and voltinism of five stonefly species in a New Mexico mountain stream. *Southwestern Naturalist* 35: 130–134.
- HASSAGE, R. L., R. E. DEWALT, AND K. W. STEWART. 1988. Aggregation of *Pteronarcella badia* nymphs and effects of interaction with *Claassenia sabulosa* (Plecoptera). *Oikos* 53: 37–40.
- HENDRICKS, S. P. 1993. Microbial ecology of the hyporheic zone: a perspective integrating hydrology and biology. *Journal of the North American Benthological Society* 12: 70–78.
- HILSENHOFF, W. L., AND S. J. BILLMEYER. 1973. Perlodidae (Plecoptera) of Wisconsin. *Great Lakes Entomologist* 6: 1–14.
- HOLDSWORTH, R. P. 1941a. The life history and growth of *Pteronarcys proteus* Newman (Pteronarcyidae: Plecoptera). *Annals of the Entomological Society of America* 34: 495–502.
- . 1941b. Additional information and a correction concerning the growth of *Pteronarcys proteus* Newman (Pteronarcyidae: Plecoptera). *Annals of the Entomological Society of America* 34: 714–715.

- HURYN, A. D., AND J. B. WALLACE. 1987. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. *Aquatic Insects* 9: 229–251.
- HYNES, H. B. N. 1992. Some thoughts on unanswered questions about stoneflies. XI International Symposium on Plecoptera, Tomahawk, WI.
- ILLIES, J. 1952. Die Plecopteren und das Monardsche Prinzip. *Berlin Limnologische Flubstation Freudenthal* 3: 53–69.
- KNIGHT, A. W., AND A. R. GAUFIN. 1966. Altitudinal distribution of stoneflies (Plecoptera) in a Rocky Mountain drainage system. *Journal of the Kansas Entomological Society* 39: 668–675.
- KONDRATIEFF, B. C., AND R. F. KIRCHNER. 1991. New Nearctic Chloroperlidae (Plecoptera). *Journal of the New York Entomological Society* 99: 199–203.
- LECHLEITNER, R. A., AND B. C. KONDRATIEFF. 1983. The life history of *Pteronarcys dorsata* (Say) (Plecoptera: Pteronarcyidae) in southwestern Virginia. *Canadian Journal Zoology* 61: 1981–1985.
- LILLEHAMMER, A., J. E. BRITAIN, S. J. SALTVEIT, AND P. S. NIELSEN. 1989. Egg development, nymphal growth and life cycle strategies in Plecoptera. *Holarctic Ecology* 12: 173–186.
- MALMQVIST, B., AND P. SJÖSTRÖM. 1989. The life cycle and growth of *Isoperla grammatica* and *I. difformis* (Plecoptera) in southernmost Sweden: intra- and interspecific considerations. *Hydrobiologia* 175: 97–108.
- MUTCH, R. A., AND G. PRITCHARD. 1986. Developmental rates of eggs of some Canadian stoneflies (Plecoptera) in relation to temperature. *Journal of the North American Benthological Society* 5: 272–277.
- NELSON, C. R., AND R. W. BAUMANN. 1989. Systematics and distribution of the winter stonefly genus *Capnia* (Plecoptera: Capniidae) in North America. *Great Basin Naturalist* 49: 289–366.
- PERRY, S. A., W. B. PERRY, AND J. A. STANFORD. 1987. Effects of thermal regime on size, growth rates and emergence of two species of stoneflies (Plecoptera: Taeniopterygidae, Pteronarcyidae) in the Flathead River, Montana. *American Midland Naturalist* 117: 83–93.
- PERRY, W. B., E. F. BENFIELD, S. A. PERRY, AND J. R. WEBSTER. 1987. Energetics, growth, and production of a leaf-shredding stonefly in an Appalachian Mountain stream. *Journal of the North American Benthological Society* 6: 12–25.
- PETSCH, H. E., JR. 1987. Water resources data—Colorado water year 1986. Vol. 1. Missouri River Basin, Arkansas River Basin, and Rio Grande River Basin water data report CO-86-1. United States Geological Survey, Department of the Interior.
- . 1988. Water resources data—Colorado water year 1987. Vol. 1. Missouri River Basin, Arkansas River Basin, and Rio Grande River Basin water data report CO-87-1. United States Geological Survey, Department of the Interior.
- . 1989. Water resources data—Colorado water year 1988. Vol. 1. Missouri River Basin, Arkansas River Basin, and Rio Grande River Basin water data report CO-88-1. United States Geological Survey, Department of the Interior.
- . 1990. Water resources data—Colorado water year 1989. Vol. 1. Missouri River Basin, Arkansas River Basin, and Rio Grande River Basin water data report CO-89-1. United States Geological Survey, Department of the Interior.
- RADFORD, D. S., AND R. HARTLAND-ROWE. 1971. The life cycles of some stream insects (Ephemeroptera, Plecoptera) in Alberta. *Canadian Entomologist* 103: 609–617.
- SHELDON, A. L. 1972. Comparative ecology of *Arcynopteryx* and *Diura* (Plecoptera) in a California stream. *Archiv für Hydrobiologie* 69: 521–546.
- SHELDON, A. L., AND S. JEWETT. 1967. Stonefly emergence in a Sierra Nevada stream. *Pan-Pacific Entomologist* 43: 1–8.
- SHORT, R. A., AND J. V. WARD. 1980. Life cycle and production of *Skwala parallela* (Frisson) (Plecoptera: Perlodidae) in a Colorado montane stream. *Hydrobiologia* 69: 273–275.
- SNELLEN, R. K., AND K. W. STEWART. 1979. The life cycle and drumming behavior of *Zealeuctra claasseni* (Frisson) and *Zealeuctra hitei* Ricker and Ross (Plecoptera: Leuctridae) in Texas, U.S.A. *Aquatic Insects* 1: 65–89.
- STANFORD, J. A. 1975. Ecological studies of Plecoptera in upper Flathead and Tobacco rivers, Montana. Unpublished doctoral dissertation, University of Utah, Salt Lake City.
- STANFORD, J. A., AND A. R. GAUFIN. 1974. Hyporheic communities of two Montana rivers. *Science* 185: 700–702.
- STANFORD, J. A., AND J. V. WARD. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. *Journal of the North American Benthological Society* 12: 49–60.
- STARK, B. P., S. W. SZCZYTKO, AND R. W. BAUMANN. 1986. North American stoneflies (Plecoptera): systematics, distribution, and taxonomic references. *Great Basin Naturalist* 46: 383–397.
- STEWART, K. W., AND B. P. STARK. 1988. Nymphs of North American stonefly genera (Plecoptera). *Entomological Society of America, Thomas Say Foundation* 12: 1–460.
- STEWART, K. W., R. L. HASSAGE, S. J. HOLDER, AND M. W. OSWOOD. 1990. Life cycles of six stonefly species (Plecoptera) in subarctic and arctic Alaska streams. *Annals of the Entomological Society of America* 83: 207–214.
- SZCZYTKO, S. W., AND K. W. STEWART. 1979. The genus *Isoperla* (Plecoptera) of western North America: holomorphology and systematics, and a new stonefly genus *Cascadoperla*. *Memoirs of the American Entomological Society* 31.
- ULFSTRAND, S. 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera: Plecoptera: Trichoptera: Diptera-Simuliidae). *Oikos* 19: 167–190.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd edition. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.

Received 1 October 1993

Accepted 11 April 1994



DeWalt, R. Edward and Stewart, Kenneth W. 1995. "Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado." *The Great Basin naturalist* 55, 1–18. <https://doi.org/10.5962/bhl.part.22804>.

View This Item Online: <https://www.biodiversitylibrary.org/item/33678>

DOI: <https://doi.org/10.5962/bhl.part.22804>

Permalink: <https://www.biodiversitylibrary.org/partpdf/22804>

Holding Institution

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Sponsored by

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Brigham Young University

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.