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Winter stoneflies (Plecoptera) in seasonal habitats in New Mexico, USA

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Abstract. Seasonal stream habitats in New Mexico supported 10 species of winter-emerging stoneflies. Winter precipitation in combination with low winter temperatures created a seasonal moisture surplus and seasonal streamflow in this semi-arid region. Study area streams were dry for long periods in spring and autumn. Two different types of seasonal (ahyporheic) habitats were identified. Small high mountain streams fed by seasonal snowmelt runoff (type M) were inhabited by *Capnia decepta, Eucapnopsis brevicauda, Isocapnia vedderensis, Capnia californica, Capnura wanica, Mesocapnia werneri, Taenionema jacobii,* and *Capnura fibula. Mesocapnia arizonensis* and *M. frisoni* seemed to specialize in low-elevation watercourses fed by winter rains and rising water tables (type L). Adaptations for survival during spring and autumn periods of no streamflow, desiccation, or flash flooding include small size, rapid development, and diapause during egg or larval stages.

Key words: Plecoptera (stoneflies), seasonal streams, diapause, ahyporheic zones.

Stoneflies (Plecoptera) typically inhabit perennial streams with high gradients, low water temperature, high dissolved oxygen content, and gravel or cobble substrates. Some North American Plecoptera have been found in intermittent or temporary habitats (Knight and Gaufin 1967, Harper and Hynes 1970, 1972, Lehmkuhl 1971, Oberndorfer and Stewart 1977, Snellen and Stewart 1979, Gray 1981, Gray and Fisher 1981, Pugsley and Hynes 1985, and Nelson and Baumann 1990). Winter emerging taxa in the southwestern USA are found in watercourses that have traditional stonefly habitat characteristics in winter, but may be dry in most other seasons (Baumann and Gaufin 1969, Stewart et al. 1974, Baumann et al. 1977, Jacobi and Cary 1986, and E. C. Masteller, Pennsylvania State University, personal communication). Small size, rapid development, and egg and larval diapause are traits commonly cited (Harper and Hynes 1970, 1972, Hynes and Hynes 1975, Pugsley and Hynes 1985, and Stewart and Stark 1988) to explain how these organisms can occupy temporary habitats. Diapause as egg or larva is widespread in the winter-emerging species in the families Capniidae (Khoo 1968, Harper and Hynes 1972), Taeniopterygidae (Harper and Hynes 1970), Leuctridae (Hynes 1941, Snellen and Stewart 1979), and Nemouridae (Lehm-

Re-examination of previous published data (Jacobi and Baumann 1983, Jacobi and Cary 1986) and unpublished data from more recent collections of winter stoneflies from isolated streams in the southwestern USA (primarily New Mexico) revealed that most of the species collected occurred in temporary habitats. The objectives of this study were to document the occurrence of stoneflies in temporary habitats, document the hydrology and seasonal regularity of these habitats, and discuss adaptive mechanisms for survival in isolated small streams in the southwestern USA. The ability to inhabit seasonal environments appears essential to the existence of many southwestern Plecoptera.

Study Area

Winter stoneflies were collected from several mountain ranges in New Mexico. These include the Magdalena Mountains, Black Range, Pinos Altos Mountains, Brushy Mountains, San Francisco Mountains, Gallo Mountains, Organ Mountains, Animas Mountains, Cooke's Peak, Mogollon Mountains, Johnson Mesa, Sangre de Cristo Mountains, Mount Taylor, and Zuni Mountains (Fig. 1). These are high mountain ranges (Appendix 1) isolated by extensive lowlands where adequate habitat is absent. Over

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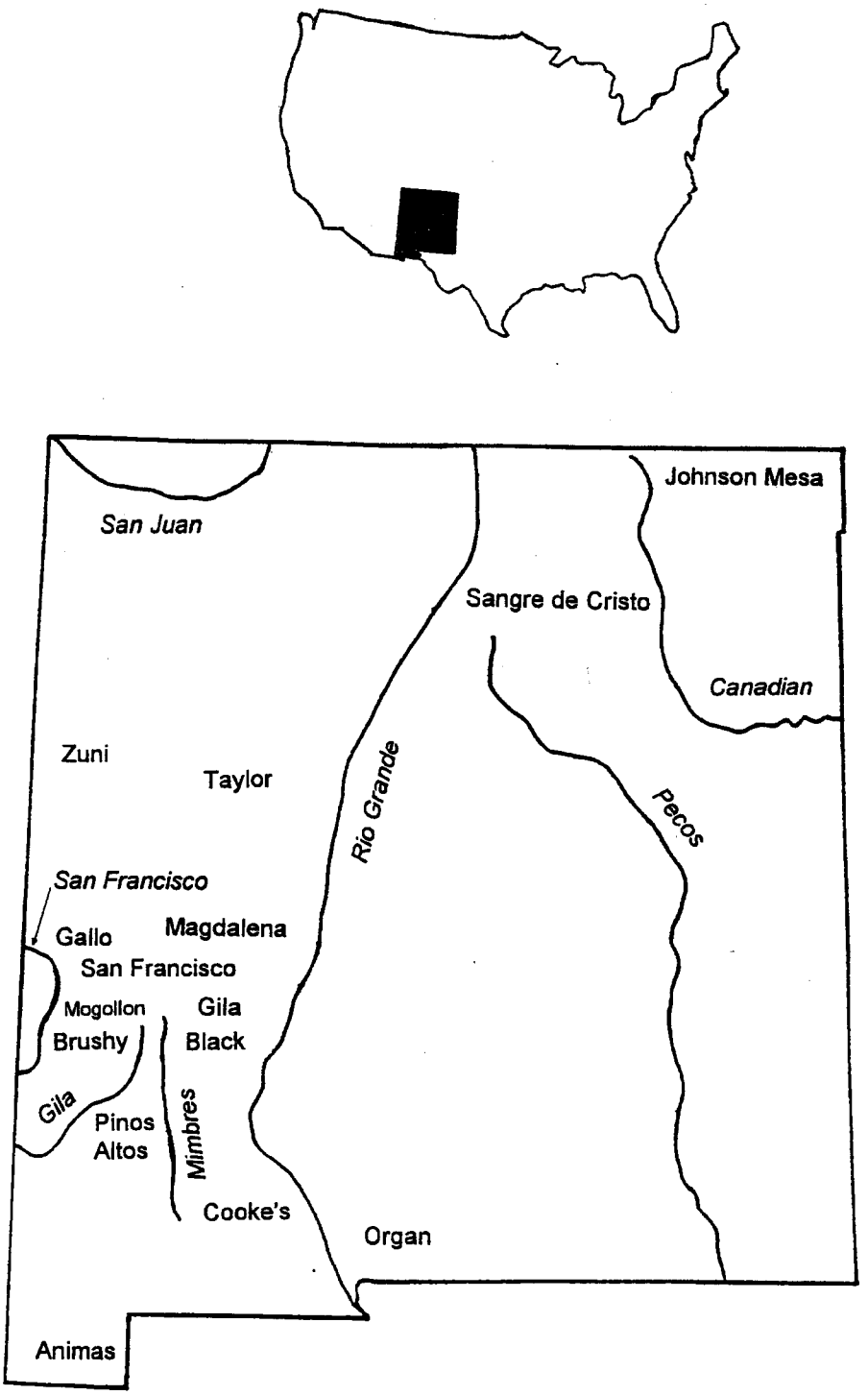

FIG. 1. New Mexico mountains and major rivers. River names are in italic.

quent deposition filled the intervening basins with unconsolidated sediments. These deposits may be 100s of m thick (Trauger 1972) and subsurface water levels may fluctuate greatly within these deposits. Some of these watersheds, e.g., the Mimbres River, are internally drained with no surface outlet. Other parts of the study area are drained by perennial rivers such as the Gila, San Francisco, Canadian, Pecos, and Rio Grande.

Average annual precipitation totals in New Mexico range from <20 cm in the Rio Grande Valley near Las Cruces to >75 cm in the high peaks of the Mogollon Mountains (New Mexico State Engineers Office 1967). Precipitation and moisture availability have a distinct seasonal cy-

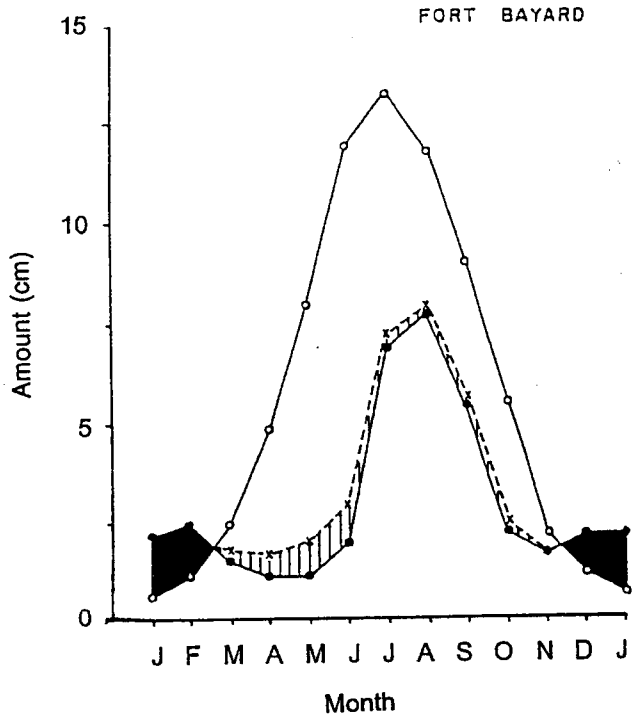

FIG. 2. Seasonal pattern of precipitation (solid circles), potential evapotranspiration (open circle), actual evapotranspiration (crosses), water deficit (white area between 2 upper curves), soil moisture utilization (striped area), and soil moisture recharge (black areas) near Fort Bayard in southwestern New Mexico. From Tuan et al. (1973).

cle (Tuan et al. 1973). A 3-mo summer rainy season (monsoon or "chubasco") contributes >50% of the annual precipitation whereas spring through early summer is the driest season (Fig. 2). Winter precipitation is much less than the summer rains, but winter is the only season with moisture surplus because of low evapotranspiration rates (Tuan et al. 1973 and Dunne and Leopold 1978).

Orographic effects on moisture availability are important in creating temporary habitats for stoneflies. In areas sharing similar climatic influences, high altitude terrains get far more precipitation than lowlands (Tuan et al. 1973). Another important orographic effect on moisture is related to temperature, which declines with increasing elevation at a rate of 2.78°C for every 305 m (Tuan et al. 1973). Much winter precipitation falls as snow at higher elevations but as rain at lower elevations.

Limited precipitation in May through June, and October through December, (Fig. 2) means that most small streams in the study area are dry at those times (Fig. 3). Although stream gauging data are not available for most small streams, we have traversed the state on numerous occasions and have seen our study streams dry during non-winter seasons and sometimes for consecutive years. Moreover, Reiland and Haynes (1963) documented that many New Mexico watercourses have zero flow for many months of typical years.

Independent of climate, "southwestern rivers flowing from mountains across deserts often have diminution of discharge both up- and down-stream from intermediate elevations" (Minckley and Brown 1982). From this generalization, we defined 3 types of stream habitats in the study area based on location in the landscape (Fig. 3). Intermediate elevation streams (Type P) are perennial or nearly perennial (interrupted). They combine water flows and sediments delivered from upland tributaries. They have moderate gradients with enough rubble and gravel alluvium to provide a useful hyporheic zone where larvae can survive during times of no surface flow in the channel. We use the term "ahyporheic" to describe seasonal habitats in which either there is no water flow beneath the channel or the wetted zone is deep, inaccessible, and unusable. The uppermost habitats (Type M) in watersheds are small montane streams with steep gradients, high flow velocities, and boulder and rubble substrates. These ephemeral streams flow in response to melting snow. They are ahyporheic because they have no flow in dry seasons and there is inadequate alluvium for water storage. Lowland streams (Type L) have gentle gradients and flow in response to rising water tables. Because underlying gravel and sand alluvium may be many m thick, the water table may fall far below the channel bottom in the dry season, causing an ahyporheic condition. Some stream sample locations are transitional (M/P or P/L).

Methods

We made collections throughout New Mexico during January, February, March, and April from 1979 through 1995. Initial reconnaissance of mountain ranges or lowlands was followed by exhaustive collections from watercourses using a variety of sampling methods. US Geological Survey, US Bureau of Land Management, and US Forest Service maps were used to locate potential sample locations. Every watercourse

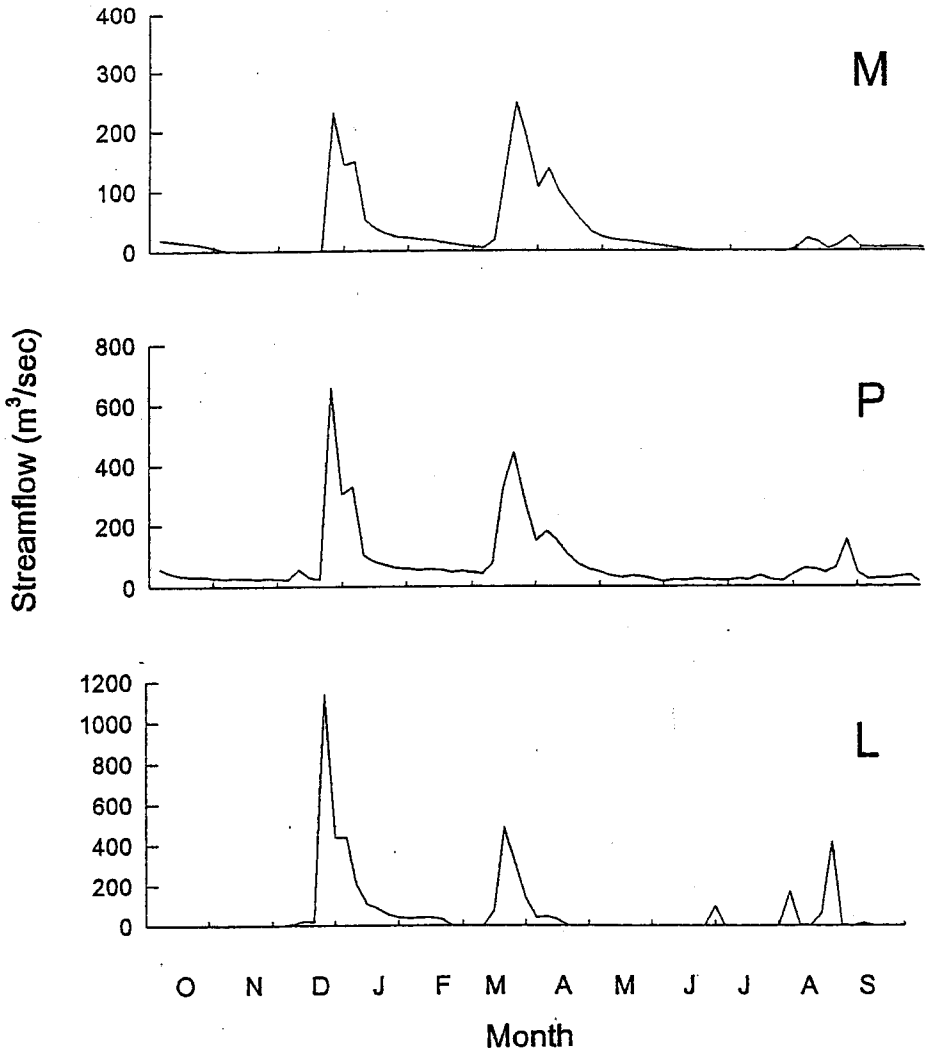

FIG. 3. Stream discharge in the Mimbres River, Grant Co., New Mexico, for water year 1965 (data from US Geological Survey). Habitat type M is 0.5 km N of the US Forest Service ranger station near the continental divide: elev. = 1901 m, drainage area = 252 km². Habitat type P is 2.4 km NW of Mimbres: elev. = 1888 m; drainage area = 392 km². Habitat type L is 2.4 km NE of Spaulding: elev. = 1448 m; drainage area = 1218 km².

encountered during our travels by road or footpath was sampled for at least 30 min and some locations were sampled on several occasions. Emerged adults and exuviae were hand picked from natural riparian materials such as rocks, logs, grasses, leaf packs, and woody vegetation. We also examined culverts, bridge abutments, bridge surfaces including the undersides, and rip-rap. A sweep net and beating sheet were used to collect adults from grasses, shrubs, and trees. If no adults were found, we searched for larvae and collected them with fingers or forceps from stream substrates. The presence of exuviae and the lack of larvae were noted and the location was revisited earlier in the season during a following year for collection of adults. If larvae were observed, the location was revisited later in the year or later in the season during a following year. On a few occasions, larvae were captured live, placed into jars with vented lids, and taken to a laboratory refrigerator to await emergence. Specimens were placed in 15-mL vials containing 70% ethyl alcohol for preservation. In the laboratory, specimens were identified, sexed, occasionally measured, and counted.

Results

Appendix 1 summarizes winter stonefly collections and provides stream types (M, L, and P) for the 10 species collected from 70 locations on 51 streams. Elevation of collection sites varied from 1293 m to 2350 m. The following Ple-

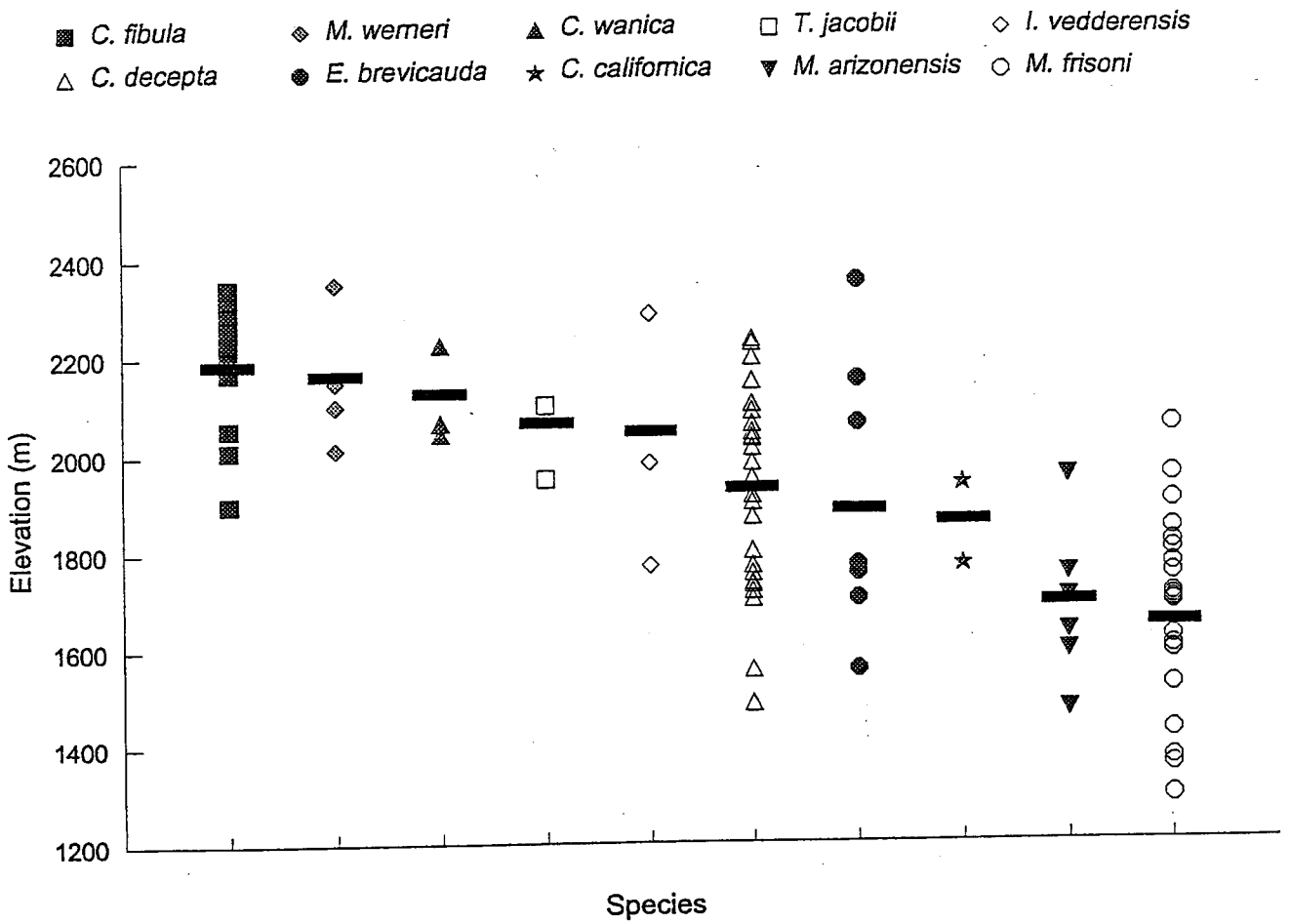

FIG. 4. Altitude of collection locations for winter-emerging stoneflies in the study area. Each point represents a collection elevation. A species may have been collected at one location several times. The horizontal bar represents the mean elevation of collection locations.

coptera were found to inhabit ahyporheic habitats (M and L) in New Mexico: *Eucapnopsis brevicauda* Claassen, *Isocapnia vedderensis* (Ricker), *Capnia decepta* (Banks), *Capnia californica* Claassen, *Capnura fibula* Claassen, *Capnura wanica* Frison, *Mesocapnia arizonensis* (Baumann and Gaufin), *M. frisoni* (Baumann and Gaufin), *M. werneri* (Baumann and Gaufin), and *Taenionema jacobii* Stanger and Baumann. Half of these winter-emerging species (*M. frisoni, C. decepta, M. arizonensis, C. fibula* and *E. brevicauda*) were also present in perennial stream reaches (P).

Plotting species occurrence along an elevational gradient showed some habitat differences among winter stonefly species (Fig. 4). *Capnura fibula* occured at a higher mean elevation (2174 m) than any other species in this study and observations were clustered within a narrow range of elevations (1900–2345 m). Three winter stoneflies (*C. wanica, M. werneri* and *T. jacobii*) were observed only at high elevation seasonal habitats, whereas 3 other species (*C. decepta, E. brevicauda* and *M. frisoni*) showed broad elevational ranges. Altitudinal ranges for *E. brevicauda* and *C. decepta* overlapped almost exactly. The lowest mean elevation of occurrence (1668 m) was for *M. frisoni* although we collected this species over a wide range of elevations (1293–2055 m). The mean elevation of occurrence for *M. arizonensis* was slightly higher (1684 m) but its range was narrower (1470–1950 m).

Capnia decepta (28 sites) and *M. frisoni* (21 sites) were the 2 winter-emerging species collected most frequently in the study area (Appendix 1). Despite their frequent occurrence, they were found at the same location only 3 times. Failure of these 2 widespread species to occur together suggested diversity among ahyporheic habitats.

The less frequently collected *Eucapnopsis brevicauda* (8 sites) was collected 6 times with *C. decepta*. Other species that were found preferentially with *C. decepta* or *E. brevicauda* included *M. werneri, C. fibula, T. jacobii, C. wanica, I. vedder-*

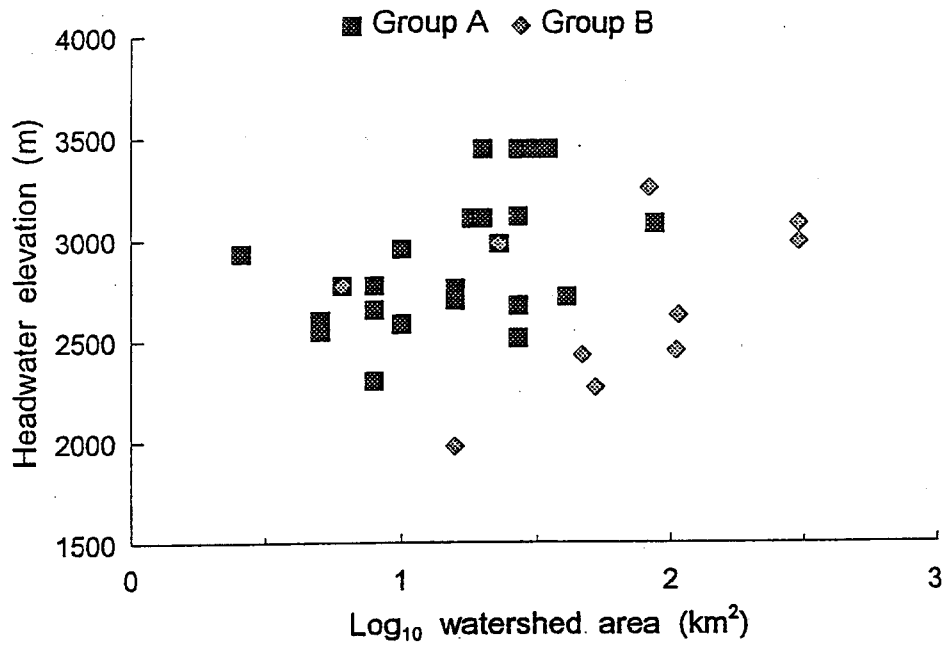

FIG. 5. Winter-emerging stoneflies in seasonal streams (types M and L) in New Mexico segregated by watershed area and headwater elevation. Group A consists of high elevation species: *M. werneri, C. fibula, C. wanica, I. vedderensis, T. jacobii, E. brevicauda, C. decepta,* and *C. californica.* Group B consists of lower elevation species: *M. arizonensis* and *M. frisoni.*

ensis, and *C. californica.* These associations suggest that these 8 species (Group A) share similar habitat requirements in New Mexico.

Mesocapnia arizonensis was observed at 7 localities. The only other species with which it shared a site was *M. frisoni.* Collectively these 2 species were found only 4 times with species in Group A and they had the lowest mean collection elevations (Fig. 4). They form Group B.

The maximum elevation of land in the contributing watershed in which a species was found was plotted against the watershed area upstream from the point of collection for seasonal streams, hydrologic types M and L (Fig. 5). Group A species occurred mainly in higher elevation streams with smaller watersheds (type M). Group B species occurred in low elevation streams with larger watersheds (type L). Group B species also occurred in some of the higher altitude streams.

Discussion

In this paper we have documented the presence of 10 species of winter stoneflies in ahyporheic environments. Thirteen other winter-emerging Plecoptera are found in New Mexico, but are not known to occur in temporary habitats (Jacobi and Baumann 1983). We first believed that observed occurrences in temporary habitats represented occasional introductions. For example, aquatic macroinvertebrates are known to colonize new habitats through flight by adults, drift by immatures, and upstream movement by larvae (Williams and Hynes 1976). After all, many study area streams have a perennial section (Type P) between the upstream (type M) and downstream (type L) ephemeral reaches that could serve as a continual source of new introductions.

Now we believe winter-emerging Plecoptera have lived and completed their life cycles in these ahyporheic environments since the wetter Pleistocene (Stewart et al. 1974, Jacobi and Cary 1986). Drift cannot explain the presence of up to 150 *M. frisoni* larvae/m^2, at a site 20 km downstream from perennial water, as occurred in Las Animas Creek 3 wk after a rising water table created surface flow at the collection site. Similarly, flight by adults cannot explain the presence of *C. californica* in Indian Creek, 50 km from the nearest known population in the Chiricahua Mountains in Arizona (E. C. Masteller, personal communication).

Survival in seasonal habitats is credible considering the presence of several adaptive mechanisms exhibited by study area organisms. For example, small adult size helps to minimize du-

ration of the developmental period (Hynes 1976, Stewart and Stark 1988), whereas a long development period (larger size) would be non-adaptive in short-lived habitats. The smallest adults (5.0–7.1 mm) were seen in *M. arizonensis* and *C. californica*—some of the smallest of North American Plecoptera. Brief development time has been reported for Lepidoptera that are sensitive to seasonal moisture (Ross 1995) and for some Ephemeroptera and Plecoptera in temporary habitats and those that periodically flood (Hynes 1941, 1976, Gray 1981, Nolte et al. 1996).

In some temporary or seasonal habitats, larvae migrate vertically within the hyporheic zone (Williams 1977). Smaller Plecoptera larvae might be able to penetrate farther down into the substrate of a desiccating streambed because they would be less hindered by the small size of interstices. Snellen and Stewart (1979) extracted substrate of an ephemeral stream to a depth of 1 m and found 1 half-grown larva of a small species, *Zealeuctra claasseni*, in Texas. Small size of larvae may be important for survival in hyporheic zones, but the ability to penetrate substrates is irrelevant in ahyporheic environments.

Diapause is widespread in winter-emerging Plecoptera and provides the group with a valuable survival mechanism. Diapause is known to occur in *M. arizonensis* in the region (Gray 1981) and for capniids in general in the egg stage (Harper and Hynes 1972, Snellen and Stewart 1979, Stewart and Stark 1988). Winter streamflow is essential for winter-emerging stoneflies, but dry conditions during the rest of the year may have minimal influence. Eggs are deposited when the stream is flowing, fall to the substrate, remain there while the streambed is dry for several months, then resume development when winter flows return (K. W. Stewart, University of North Texas, personal communication). Because the tolerant egg stage can withstand drying or other unsuitable external conditions, the organism is able to occupy an otherwise inhospitable habitat. Neither several months of desiccation nor summer flash floods appear to be serious obstacles to these taxa. The geographic extent of this phenomenon is likely to be much greater than previously thought, probably occurring throughout western North America.

Multi-year diapause is well documented among Lepidoptera (Scott 1986). Some desert Lepidoptera can stay in diapause for more than 15 y then conclude development when environmental conditions are right (Powell 1989). It is unknown how long winter-emerging Plecoptera can stay in diapause, but Snellen and Stewart (1979) suggest that it could be for several years. Species with multi-year diapause would have an additional advantage in southwestern streams with unpredictable winter flow from year to year.

Most winter stoneflies are weak fliers (Hynes 1976, Stewart and Stark 1988), in contrast to other aquatic insects that specialize in temporary environments and are strong fliers. Representatives of Coleoptera, Hemiptera, and Odonata in temporary habitats depend on flight to find, colonize, and use temporary habitats (Williams 1996). These strong-flying insects can fly many km to new habitats to complete their life cycles. Weak flight of southwestern winter-emerging Plecoptera (e.g., *C. fibula* males are brachypterous) is not maladaptive, despite the seasonality and disjunct nature of some local stream habitats. Our study Plecopera have no need to fly great distances to new habitats because other adaptations, such as egg diapause and small size, allow them to wait in the existing habitat until conditions are favorable for completion of the life cycle.

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APPENDIX 1. Winter stonefly records and supporting data from selected (70) collection sites. Hydrologic types are: M = small montane snowmelt-driven ahyporheic stream; P = perennial or near-perennial stream with hyporheic zone; L = lowland groundwater-driven ahyporheic stream.

Stream	Mountain range	County	Water-shed area (km²)	Ele-vation (m)	Source (m)	Hydro-logic type	Species
Water Canyon	Magdalena	Socorro	18	2146	3100	M	*Capnia decepta*
			20	1981	3100	M	*C. decepta*
Las Animas Creek	Black	Sierra	311	1293	3075	L	*Mesocapnia frisoni*
Oak Springs Canyon	Black	Sierra	16	1590	1975	L	*M. frisoni*
Percha Creek	Black	Sierra	194	1600	2975	P/L	*M. frisoni*
Percha Creek	Black	Sierra	75	1605	2975	P/L	*M. frisoni*
Percha Creek	Black	Sierra	130	1750	2975	P	*Mesocapnia arizonensis*
Percha Creek	Black	Sierra	26	1870	2975	M/P	*C. decepta*
Percha Creek	Black	Sierra	23	1900	2975	M	*Capnura fibula*
							M. frisoni
							C. decepta
Sawpit Creek	Black	Sierra	8	1950	2650	M/P	*M. arizonensis*
Berrenda Creek	Black	Sierra	47	1700	2425	L	*M. arizonensis*
Chloride Creek	Black	Sierra	41	1913	2710	M	*C. decepta*
Macho Canyon	Black	Sierra	52	1630	2265	L	*M. arizonensis*
Iron Creek	Black	Grant	3	2350	2930	M	*Mesopcapnia werneri*
							Eucapnopsis brevicauda
Iron Creek	Black	Grant	8	2149	2930	M	*E. brevicauda*
							M. werneri
Gallinas Canyon	Black	Grant	49	2060	2930	M/P	*E. brevicauda*
							C. decepta
Dry Gallinas	Black	Grant	8	2033	2650	M	*C. decepta*
Mimbres River	Black	Grant	313	1730	3051	P	*C. decepta*
Hadley Draw	Cooke's	Luna	8	1700	2565	P/L	*M. arizonensis*
Indian Creek	Animas	Hidalgo	5	1935	2600	M	*Capnia californica*
Sotol Creek	Organ	Dona Ana	3	1800	2560	M/P	*C. decepta*
Sapello Creek	Pinos Altos	Grant	132	1844	2194	P	*M. frisoni*
Sapello Creek	Pinos Altos	Grant	212	1770	2194	P	*M. frisoni*
							C. decepta
							E. brevicauda
Gila River	Mogollon	Grant	4827	1356	3283	P	*M. frisoni*
E. Fork Gila River	Black	Catron	414	1620	2705	P	*M. frisoni*
E. Fork Gila River	Black	Grant	388	1690	2705	P	*M. frisoni*
W. Fork Gila River	Mogollon	Catron	1318	1716	3283	P	*C. decepta*
W. Fork Gila River	Mogollon	Catron	1297	1735	3283	P	*C. decepta*
W. Fork Gila River	Mogollon	Catron	1300	1730	3283	P	*C. decepta*
Cliff Dweller Canyon	Mogollon	Catron	5	1753	1829	M/P	*C. decepta*
							E. brevicauda
Little Creek	Mogollon	Catron	144	1700	2660	P	*C. decepta*
							E. brevicauda
							M. frisoni
Little Cherry Creek	Pinos Altos	Grant	16	2100	2755	M	*C. decepta*
							M. werneri
							Taenionema jacobii
Cherry Creek	Pinos Altos	Grant	18	2012	2740	M/P	*M. werneri*
							C. decepta
Bear Creek	Pinos Altos	Grant	34	1950	2780	M/P	*C. decepta*
							T. jacobii
Bear Creek	Pinos Altos	Grant	28	2100	2780	M/P	*T. jacobii*
Big Dry Creek	Mogollon	Grant	83	1470	3250	L	*M. arizonensis*

APPENDIX 1. Continued.

Stream	Mountain range	County	Watershed area (km²)	Elevation (m)	Source (m)	Hydrologic type	Species
Duck Creek	Mogollon	Grant	104	1370	2450	L	*M. frisoni*
Mule Creek	Brushy	Grant	44	1591	2119	P/L	*M. frisoni*
							M. arizonensis
Whitewater Creek	Mogollon	Catron	117	1427	3320	P	*M. frisoni*
		Catron	104	1555	3320	P	*C. decepta*
							E. brevicauda
Silver Creek	Mogollon	Catron	10	2030	2950	M	*C. decepta*
Mineral Creek	Mogollon	Catron	88	1486	3075	M	*C. decepta*
San Francisco River	San Francisco	Catron	4281	1521	2639	P	*M. frisoni*
		Catron	181	2250	2639	P	*C. fibula*
		Catron	3416	1707	2639	P	*M. frisoni*
		Catron	3108	1750	2639	P	*M. frisoni*
Cottonwood Canyon	San Francisco	Catron	31	1770	2675	M/P	*E. brevicauda*
							C. decepta
							Isocapnia vedderensis
							C. californica
Dry Leggett Creek	San Francisco	Catron	16	2238	2695	M	*C. fibula*
Starkweather Canyon	San Francisco	Catron	106	1800	2620	L	*M. frisoni*
Tularosa River	San Francisco	Catron	311	1814	2985	L	*M. frisoni*
Apache Creek	Gallo	Catron	311	1953	2860	L/P	*M. frisoni*
Yankee Gulch	Gallo	Catron	6	2055	2770	M	*M. frisoni*
							C. fibula
Bluewater tributary	Zuni	Cibola	6	2345	2550	M	*C. fibula*
Bluewater Creek	Zuni	Cibola	90	2309	2770	P	*C. fibula*
Bluewater tributary	Zuni	Cibola	8	2290	2770	M	*C. fibula*
Bluewater Creek	Zuni	Cibola	18	2287	2821	P	*C. fibula*
Rio Nutria	Zuni	McKinley	145	2171	2630	P	*C. fibula*
Water Canyon	Taylor	Cibola	27	2233	3445	M	*C. decepta*
			30	2195	3445	M	*C. decepta*
			35	2085	3445	M	*C. decepta*
Rinconada Creek	Taylor	Cibola	20	2043	3445	M	*C. decepta*
							Capnura wanica
Oak Creek	Johnson Mesa	Union	25	1900	2250	M/P	*C. fibula*
Trinchera Creek	Johnson Mesa	Colfax	8	2011	2300	M	*C. decepta*
							C. fibula
Rathbun Creek	Johnson Mesa	Colfax	10	2261	2580	M	*C. fibula*
San Isidro Creek	Johnson Mesa	Colfax	27	2231	2510	M	*C. fibula*
Chicorica Creek	Johnson Mesa	Colfax	27	2225	2668	M	*C. wanica*
							C. decepta
Water Canyon	Johnson Mesa	Colfax	38	2194	2688	M/P	*C. fibula*
			55	2066	2688	M/P	*C. wanica*
Le Cueva Creek	Sangre de Cristo	Santa Fe	27	1981	3109	M	*I. vedderensis*
El Porvenir Creek	Sangre de Cristo	San Miguel	60	2286	3500	P	*I. vedderensis*