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WINTER MACROINVERTEBRATE COMMUNITIES IN TWO MONTANE WYOMING STREAMS

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ABSTRACT.—Macroinvertebrate communities were examined on 4 winter dates over a 4-yr period in 2 high-altitude Rocky Mountain streams to document overwintering assemblages potentially experiencing spring acid pulses. Taxa richness values were comparable to other published lists for alpine and montane stream systems despite the fact that most literature reflected summer collections. Mean benthic density ranged from 1406 to 19,734 organisms/m^2, and drift rates ranged from 0 to 1740 organisms/100 m^3. Benthic collections showed higher taxa richness than drift collections while the Ephemeroptera and Plecoptera occurred in greater proportions in drift than in benthos. The Nemouridae (Plecoptera), Ephemerellidae and Heptageniidae (Ephemeroptera), Chironomidae (Diptera), and Hydracarina were the numerically dominant taxa in benthic collections. Grazer/scrapers and shredder/detritivores were always the numerically dominant functional feeding groups at all sites, composing 60–90% of the benthos. Predators, constituting approximately 15% of the community, occurred in the same relative proportion at all sites on all dates. Winter macroinvertebrate communities in these low-order, montane streams exhibit high taxonomic richness and benthic densities as great as lower-elevation mountain streams in the West.

Key words: community structure, winter collections, stream insects, functional feeding groups, Wyoming, montane habitat.

Stream ecologists are interested in understanding the forces influencing community structure and composition. However, seasonal changes in habitat features might influence the relative importance of forces structuring stream communities (e.g., Peckarsky 1983, Minshall, Petersen, and Nimz 1985). Wiens (1977, 1981) argued that seasonal, multisite data were needed to make accurate assessments of community structure and resource use because of annual variation in population abundances within and among habitats. Harsh winter conditions (e.g., extreme cold, deep snowpack, ice cover) or the timing of insect life cycles often prevents stream ecologists from sampling some communities on a seasonal basis. Mountain streams, in particular, receive heavy snowfall, making most sites inaccessible during winter months. Yet, winter is the longest season of the year in mountain altitudes, retaining snow cover up to 7 mon.

Few studies have examined macroinvertebrate communities during mid- to late winter in mountain streams. Logan (1963), who sampled aquatic insects biweekly through the winter in Bridger Creek, Montana, found that Trichoptera larvae dominated the benthic taxa. Andrews and Minshall (1979) and Minshall (1981) sampled monthly throughout the year and found all common taxa during all seasons, but at different abundances. Communities sampled were dominated by grazer and collector functional feeding groups. Bruns and Minshall (1986) also sampled through the winter and showed an extreme change in winter niche parameters for the predator guild of an insect community in the Salmon River. They suggested that resource limitation (i.e., low prey numbers) in winter was a factor determining spatial resource partitioning in this system. However, these studies all focused on stream reaches at elevations below 3000 m. Studies at elevations exceeding 3000 m have been restricted primarily to the warmer, open-water season (Dodds and Hisaw 1925, Blake 1945, Elgmork and Saether 1965, Saether 1965, Allan

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1975, Short and Ward 1980, Ward and Berner 1980, Bushnell et al. 1982, 1986, Ward 1986).

Recent documentation of episodic acidification in mountain streams of the western U.S. (e.g., Williams and Melack 1991, Vertucci and Conrad 1994) suggests a need to understand winter stream communities if we are to assess potential impacts from snowmelt-related, spring pH declines. Winter samples collected immediately prior to any potential spring acid pulse could provide a reference picture of stream insect communities while reducing temporal difficulties associated with comparisons to later times of the year. Repeated, short-term acid events may have severe cumulative effects on stream communities in acid-sensitive streams of the West (Kratz et al. 1994). Impacts due to episodic pulses of acidity may reduce streamwater acid neutralizing capacity, influence fish community stability in small streams, and mobilize metals (Baker et al. 1996, Kiffney and Clements 1996, Wigington et al. 1996). Knowledge of winter community structure might enhance our ability to understand these episodic spring events. Our objective was to document the winter macroinvertebrate community structure in high mountain streams in Wyoming for a baseline reference in assessing snowmelt-driven, episodic acidification. We estimated winter benthic macroinvertebrate and drift density, taxonomic richness, and functional feeding group abundance for high-elevation streams having extensive snow cover.

METHODS

Study Area

Two streams were selected for study, West Glacier Lake Creek (WGL) and North Carbon Twin Lakes outlet (NCT). WGL is located within and NCT adjacent to the United States Forest Service Glacier Lakes Ecosystem Experiments Site (GLEES) (106°15′W longitude, 41°22′N latitude). GLEES was established to collect baseline and experimental data for assessing atmospheric deposition effects on sensitive alpine and subalpine ecosystems (Musselman 1994). An upstream and a downstream station were established on each stream such that the upstream station was located within a geologically acid-sensitive zone.

Stations WG and LB are located on WGL, T1 and T2 on NCT (Fig. 1). WG is at an elevation of 3250 m and approximately 150 m downstream from West Glacier Lake. LB, approximately 2 km downstream from WG at an elevation of 3163 m, is located approximately 100 m upstream from Little Brooklyn Lake. T1 is located at 3240 m elevation, approximately 75 m downstream of the easternmost North Carbon Twin Lake and within 100 m of treeline. T2 is approximately 0.25 km downstream from T1 at an elevation of 3230 m and 100 m downstream from the confluence of the eastern and western North Carbon Twin Lakes outflow (Fig. 1).

WG, LB, and T1 are 2nd-order streams, whereas T2 is a 3rd-order stream. Substrates at all sites consist of boulder, cobble and gravel. All sites are within forest habitat dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Scattered stands of quaking aspen (*Populus tremuloides*) also occur near LB. All sites contain populations of brook trout (*Salvelinus fontinalis*). WG, LB, and T2 exhibit perennial flow while T1 experiences some zones of intermittent surface flow. The streams were sampled on 4 winter dates (November 1989, February 1990, 1991, and 1992).

Sampling Design

All sites except LB were snow covered on all sampling dates and required tunneling to reach the streams. We constructed 3 tunnels at each site on each date by digging through the snow to the stream banks and proceeding laterally until we reached the streams. Occasionally, tunnels opened directly over the stream. In such cases, we collected samples only upstream from the tunnel to reduce sampling bias associated with disturbance of the substrate. Snow depth (cm) was measured from the top of each tunnel to the ground.

On each date we took 3 Surber samples (1 sample per tunnel, 929 cm^2, 280-μm mesh) if water was present. All stones within the sampler were brushed to dislodge any organisms and the substrate was agitated to a depth of approximately 10 cm. Organisms were preserved in 80% EtOH in Whirl-Pac bags. In February 1991 and 1992, water was frozen or absent in some tunnels at T1 resulting in 2 and 1 Surber collections on those dates, respectively.

After completing benthic collections, we placed 1 drift net (l × h × w: 100 × 30 × 46 cm; 280-μm mesh) midstream in the upstream-most

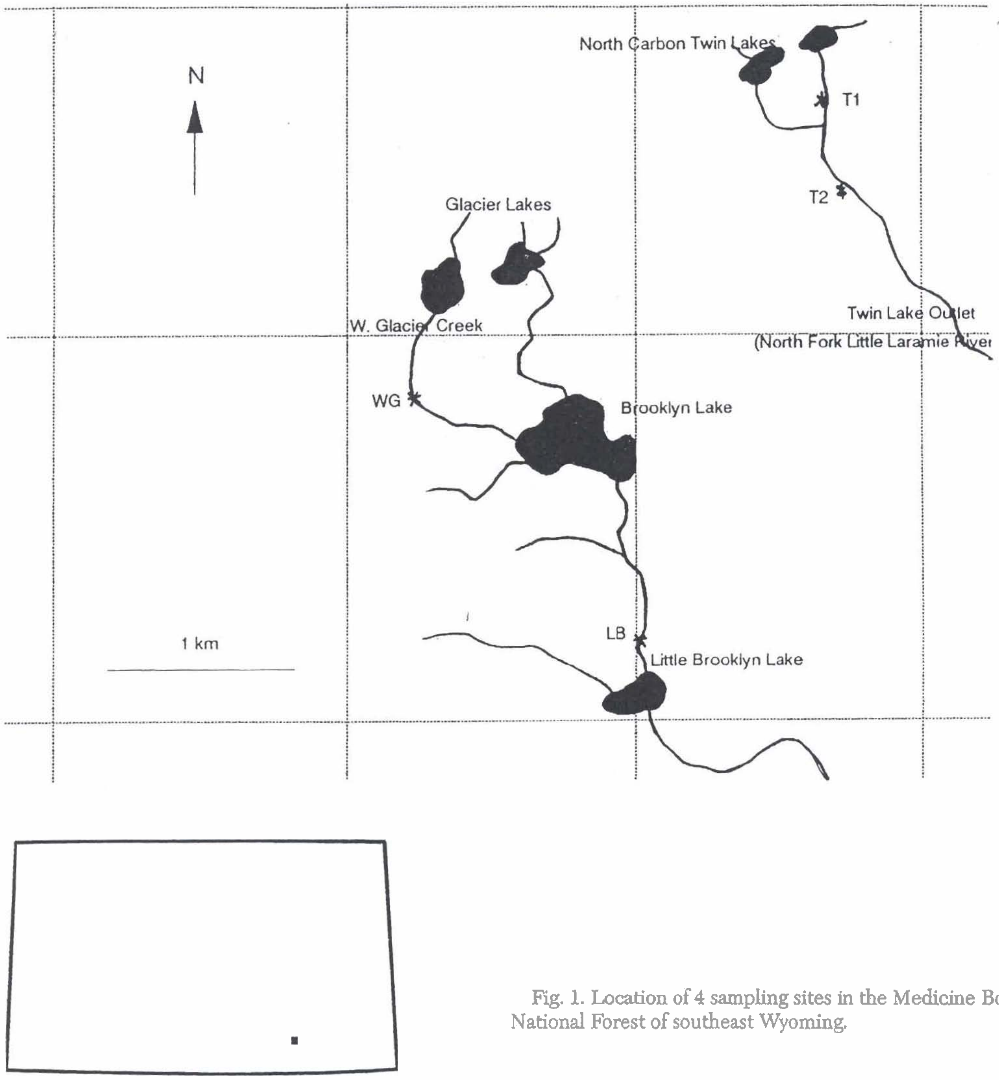

Fig. 1. Location of 4 sampling sites in the Medicine Bow National Forest of southeast Wyoming.

opening for a dusk-to-dawn drift collection (ca 12 h). Tunnels were covered with black plastic and tarps to prevent overnight snowfall accumulating in holes and to eliminate any possibility that starlight or diffuse dusk/dawn lighting might influence drift patterns. Stream volume filtered was estimated from the product of velocity, cross-sectional area, and duration of net set. Average velocity (Swoffer Model 2100 flow meter) and depth were based on 6 measurements, each from the mouth of nets upon placement and retrieval. Total set-time was recorded when nets were retrieved. Sample drift density (no./100m^3) was calculated according to Allan and Russek (1985).

On each date we collected a single water sample for chemical analyses. Water temperatures were taken with a hand-held thermometer just prior to sample collection. Samples were collected in dark, acid-washed plastic bottles, laboratory-filtered (Gelman 0.45-μm glass microfiber filters), and split into an acid-preserved (0.1 μl of 6.0 N nitric acid) and a nonpreserved subsample. Samples were refrigerated and usually analyzed within 48 h of collection. All samples were analyzed by the United States Forest Service Water Chemistry Laboratory in Fort Collins, CO. Major anions and cations were estimated on a Dionex 2010i ion chromatograph. Cations were also verified with a Smith-Hieftja 22 atomic absorption spectrophotometer. Conductivity was measured with a YSI conductance meter (Model 32). Acid neutralizing capacity (ANC) and pH were determined using an ARAS (Acid Rain Analysis System) radiometer.

Community Analysis

Macroinvertebrates were identified to the lowest possible taxonomic unit (usually species for insects except Diptera) using the following taxonomic keys: Allen and Edmunds 1962, Jensen 1966, Smith 1968, Edmunds et al. 1976, Baumann et al. 1977, Pennak 1978, Szczytko and Stewart 1979, Merritt and Cummins 1984, Klemm 1985, Peckarsky et al. 1985, Stewart and Stark 1988, and Ward and Kondratieff 1992; also G.T. Baxter, University of Wyoming, unpublished manuscript. Some taxa were verified by comparison to the Kansas Biological Survey (KBS) Reference Collection, to which new records were added. Functional feeding group designations followed tables in Merritt and Cummins (1984).

RESULTS

Data from November 1989 samples are omitted from any comparisons across years due to potentially confounding time effects. However, the November 1989 data are illustrated for completeness.

Physicochemical Analysis

Snow depths ranged from no cover (at LB in all years) to a maximum of 290 cm at WG in 1990 (Table 1). Generally, the 2 higher-elevation sites (WG and T1) had deeper snow cover than the 2 lower-elevation sites (LB and T2). Morning and evening water velocities were typically within 5 cm/sec of each other (Table 1). The minimum difference recorded was 0.3 cm/sec at T2 in 1992, the maximum 5.3 cm/sec at WG in 1990. Water depth rarely exceeded 10 cm. Surface ice was encountered only at T1 in 1991 and 1992, although all sites contained both anchor and frazil ice in varying amounts. Water temperature ranged from 0.3° to 1.8°C (Table 1).

All sites were characterized by circumneutral pH values (Table 2). WG had the lowest pH readings while LB always had the highest pH, ANC, and conductivity values. Mean conductivities ranged from 30.2 µS/cm at T1 to 138.0 µS/cm at LB. Major cation and anion concentrations varied across years and sites. Calcium and magnesium levels were 3–5 times greater at LB than at the remaining sites while anion levels were similar across sites and lowest at WG (Table 2).

Community Analyses

Of the 56 taxa we identified, no taxa occurred at all sites on all dates. Richness was greatest at LB in all years and lowest at T1 in all years (Appendix). Three sites (WG, LB, and T2) showed low year-to-year variation in richness values (CV = 10.4%, 9.8%, and 13.6%, respectively), whereas yearly variation in richness at T1 was higher (CV = 41.1%). Richness ranged from 9 (T1 in 1992) to 41 (LB in 1991).

All sites contained representatives of the 4 major functional groups. The grazer/scraper guild varied most annually (CV = 63.7%), whereas the predator guild varied least (CV = 25.1%). Grazer/scraper and shredder/detritivore groups dominated all sites; collectors were always least abundant (Fig. 2). Collectors represent the combined numbers of collector/gatherers and collector/filterers. Predators comprised approximately 15% of the communities at all sites on all dates.

Diptera composed the greatest proportion of the benthos (i.e., no. of Diptera in benthic samples/total no. in benthic samples) in all years at all sites except that in 1990 at T2 Ephemeroptera were highest (Fig. 3). On average, Nemouridae (Plecoptera), Baetidae (Ephemeroptera), and Hydracarina were the other numerical dominants in the benthos (Appendix). Few taxa were found at all sites on all dates. The most ubiquitous taxa included Plecoptera (*Sweltza lamba, Zapada haysi,* and *Z. cinctipes*), Ephemeroptera (*Ephemerella infrequens, Cinygmula* sp., and *Baetis bicaudatus*), and Trichoptera (*Rhyacophila brunnea* and *R. verrula;* Appendix). Seven taxa (*Plumiperla diversa, Paraleuctra vershina, Arctopsyche grandis, Rhyacophila pellisa, Anagapetus* sp., *Lepidostoma* sp., and *Oligophlebodes minutus*) were collected only from LB. Trichoptera always accounted for <10% of the benthic community.

Diptera and Ephemeroptera comprised the greatest proportion of drifting taxa (e.g., no. of Diptera drifting/total no. drifting), whereas Trichoptera and Hydracarina constituted the least (Fig. 4). Proportions of Ephemeroptera

TABLE 1. Mean winter stream conditions (± $s_{\bar{x}}$; $n = 3$) at 4 sampling sites on 4 sampling dates. For ice cover, N = none present; Y = present. For water depth, $n = 6$. Temperature is a single a.m. reading.

	Year/Site															
	November 1989				February 1990				February 1991				February 1992			
Parameter	WG	LB	T1	T2	WG	LB	T1	T2	WG	LB	T1	T2	WG	LB	T1	T2
Snow depth (cm)	122.0	0	125.0	61.0	290.0	0	180.0	110.0	225.0	0	150.0	94.0	250.0	0	170.0	100.0
	(7.0)		(8.7)	(13.1)	(20.8)		(17.3)	(5.0)	(11.2)		(13.9)	(9.8)	(12.1)		(14.8)	(14.4)
Velocity (cm/s)																
p.m.	20.0	9.3	9.8	9.3	13.6	4.6	7.3	7.0	4.0	20.0	<1.0	7.0	6.1	<1.0	n/a	1.3
	(3.2)	(1.1)	(2.0)	(1.5)	(1.4)	(0.2)	(0.6)	(0.8)	(0.6)	(1.7)		(0.4)	(0.2)			(0.1)
a.m.	20.0	9.0	8.9	8.3	8.3	2.0	n/a	n/a	8.0	18.1	<1.0	12.0	7.3	<1.0	n/a	1.0
	(1.1)	(1.1)	(1.5)	(1.7)	(1.1)	(0.1)			(0.3)	(0.9)		(1.2)	(0.2)			(0.1)
Water depth (cm)	9.9	5.5	8.4	7.6	7.4	11.4	6.0	5.4	12.7	3.7	11.0	9.4	4.7	3.3	n/a	5.3
	(0.3)	(0.6)	(0.7)	(0.1)	(0.6)	(1.4)	(0.5)	(1.5)	(0.1)	(0.6)	(0.2)	(1.1)	(0.1)	(0.4)		(1.1)
Temperature (°C)	0.5	2.0	1.0	0.8	0.5	1.8	0.3	n/a	0.3	1.0	1.0	1.0	0.4	1.0	n/a	1.0
Ice cover	N	N	N	N	N	N	N	N	N	N	Y	N	N	N	Y	N

TABLE 2. Mean stream water chemistry for 3 February sampling dates (±$s_{\bar{x}}$). All measurements are μEq/l except conductivity and pH. Conductivity is μS/cm. ANC = acid neutralizing capacity.

	Site			
	WG	LB	T1	T2
pH	6.9 (0.12)	8.0 (0.06)	7.0 (0.06)	6.9 (0.14)
Conductivity	30.0 (14.32)	138.0 (12.99)	30.2 (1.20)	31.4 (1.49)
ANC	255.1 (85.35)	1473.6 (83.66)	199.7 (11.35)	238.4 (9.06)
Calcium	177.6 (51.07)	938.5 (126.66)	139.2 (6.71)	156.2 (6.58)
Magnesium	100.8 (24.99)	523.5 (25.34)	65.6 (0.28)	79.9 (2.49)
Sodium	13.6 (0.99)	22.6 (1.41)	42.2 (1.68)	29.9 (1.54)
Potassium	6.2 (0.75)	16.4 (0.47)	8.8 (1.06)	7.5 (0.35)
Ammonium	1.3 (0.95)	2.2 (1.69)	1.8 (0.48)	0.9 (0.78)
Chloride	3.9 (0.97)	3.6 (1.83)	7.6 (1.03)	4.8 (0.56)
Sulfate	22.3 (1.35)	27.6 (0.90)	22.9 (2.68)	22.2 (0.92)
Nitrate	7.8 (1.55)	12.9 (2.46)	25.7 (10.35)	10.6 (1.24)

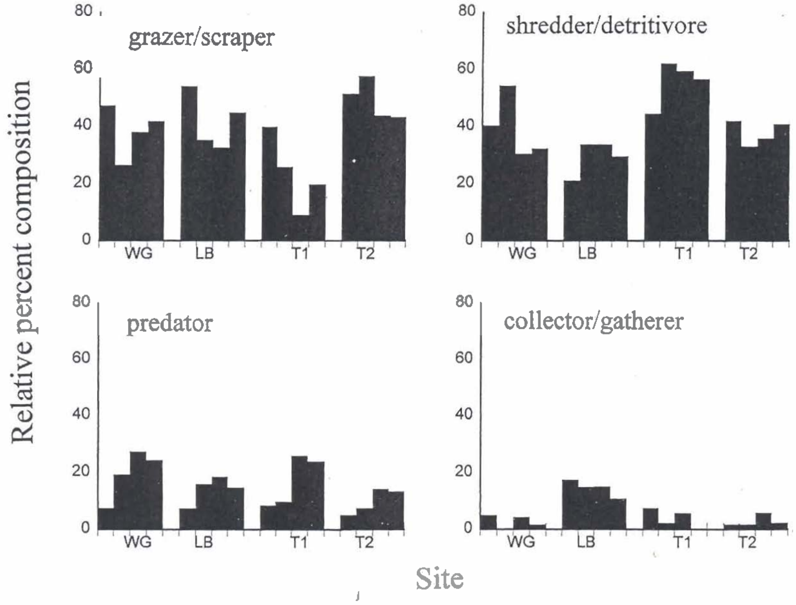

Fig. 2. Relative percent composition of functional feeding groups in the benthos during winter months in 2 mountain streams. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

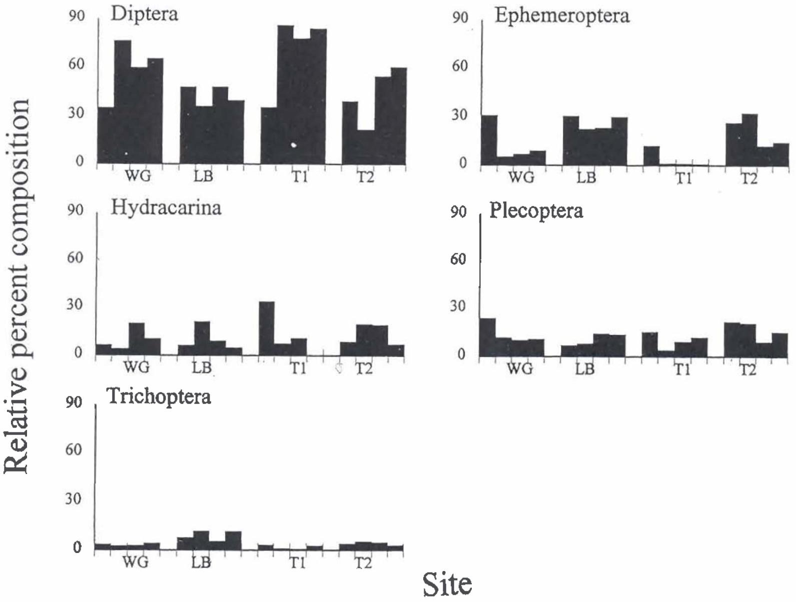

Fig. 3. Relative percent composition of major orders in the benthos. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

and Plecoptera in drift samples exceeded benthic proportions while Diptera occurred in lower proportions in the drift relative to benthos. Hydracarina and Trichoptera were approximately equally represented in benthos and drift (Figs. 3, 4).

The mean number of organisms in the benthos (no./m^2) ranged from <1500 to >15,000 organisms (Fig. 5). Chironomidae were always the most numerous. Sample drift densities generally ranged from 100 to 600 organisms per 100 m^3 and showed no consistent pattern across sites or times (Fig. 6).

DISCUSSION

Unlike other faunistic studies in mountain stream habitats, this study examined macroinvertebrate communities in 2 high-elevation streams under winter conditions. Taxonomic richness observed in this study was slightly higher than summer faunal surveys from other western mountain streams (Ward 1975, 1986). As expected, the highest richness values were found at the lower-elevation sites LB and T2. Also, the 3 sites with permanent water flow exhibited lower annual variation in richness values (CVs < 15%) than T1, which had no flow on 1 of 4 dates. Community composition was similar to that recorded by Kondratieff (1994) during a qualitative summer collection of aquatic macroinvertebrates from lakes and streams in the GLEES area. He collected 72 taxa during that study. While this represents 16 taxa more than we collected during this study, his collections focused on littoral zones of lakes and streams and were made during summer months. Our samples were all collected during winter from streams only and within midstream microhabitats.

Functional feeding groups in these streams during winter were compositionally similar to, yet proportionally different from, summer collections in other mountain streams and fit well with expectations of an expanded river continuum concept (RCC; Vannote et al. 1980, Minshall et al. 1985). We found the grazer/scraper guild present in higher proportions and collector/gatherers in lower proportions than might be expected for low-order, eastern woodland streams, which are expected to be heavily shaded by riparian canopies that limit autochthonous food resources (Vannote et al. 1980). However, new syntheses of the RCC incorporate the effects of local lithology/geomorphology on insect community development. These high-elevation streams are near the treeline in relatively open woodlands where potential autochthonous production is expected to be high, offering ample food resources for the grazer/scraper guild. These patterns suggest that the RCC predicts well for the grazer/scraper guild in high-elevation western streams. Further study is warranted on these streams to correlate grazer/scraper abundance with algal productivity under winter conditions.

Shredders were the other dominant functional guild, composed primarily of nemourid stoneflies. This contrasts with results of Short and Ward (1980) for a stream of similar altitude (though a summer study) in which shredders constituted a much smaller percentage of the benthos, but were still primarily nemourid stoneflies. Their study site flowed through a meadow while our sites were principally within forested reaches, potentially offering higher quantities of allochthonous material for shredders. Also, our functional guild is a mix of shredders and detritivores. Possibly, the detritus feeders dominate these sites and the shredders are of less importance.

Proportions of the major insect orders were similar to many other mountain stream studies (e.g., Saether 1965, Allan 1975, Ward 1975, 1986, Short and Ward 1980, Minshall 1981), even though most studies reflect summer collections. Diptera (primarily Chironomidae) and Ephemeroptera were always the most numerous taxa in our study. In general, Ephemeroptera and Plecoptera occurred in greater proportions in the drift than in the benthos while the reverse was observed for the remaining orders, indicating that mayflies and stoneflies are more prone to drift than the remaining taxa. However, drifting mayflies and stoneflies were predominantly early instar Baetidae and Nemouridae, suggesting that these 2 groups are winter active or more susceptible to passive drift than the remaining taxa.

Hydracarina often exceeded Plecoptera and Trichoptera in benthic abundance, an occurrence not generally reported. Because other faunal surveys, based primarily on summer collections and focusing on insects, have not included the Hydracarina, comparisons are difficult to make. However, failure to include the Hydracarina in community analyses will overemphasize proportions of remaining

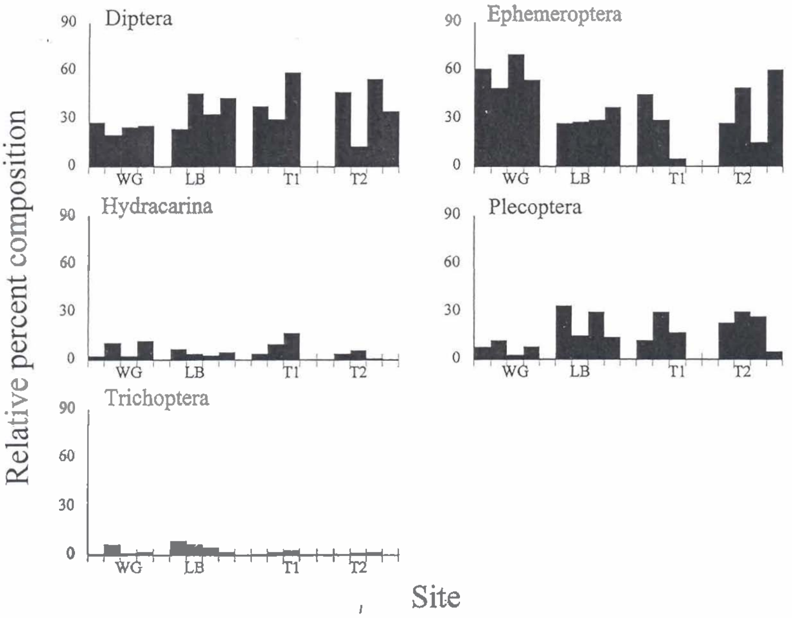

Fig. 4. Relative percent composition of major orders in the drift. From left to right, bars reflect samples collected in November 1989, February 1990, 1991, and 1992, respectively.

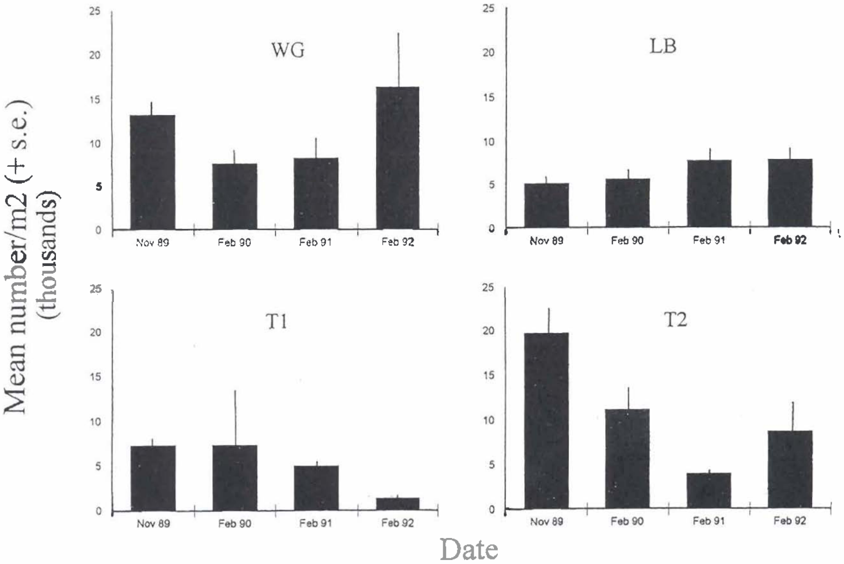

Fig. 5. Mean ($n = 3$) density of benthic organisms (no./m^2). Only 2 and 1 samples were collected for T1 in 1991 and 1992, respectively. Error bars are $+s_{\bar{x}}$.

community members. Most Hydracarina are predatory as adults or parasitic as larvae (Pennak 1978) and may have significant impacts on macroinvertebrate numbers. Drift estimates changed little with or without inclusion of the Hydracarina.

Total density of benthic organisms in these streams was very high compared to other mountain streams of similar altitude (Short and Ward 1980) but comparable to estimates made by Minshall (1981) in a lower-altitude stream reach. However, mesh sizes in all our nets

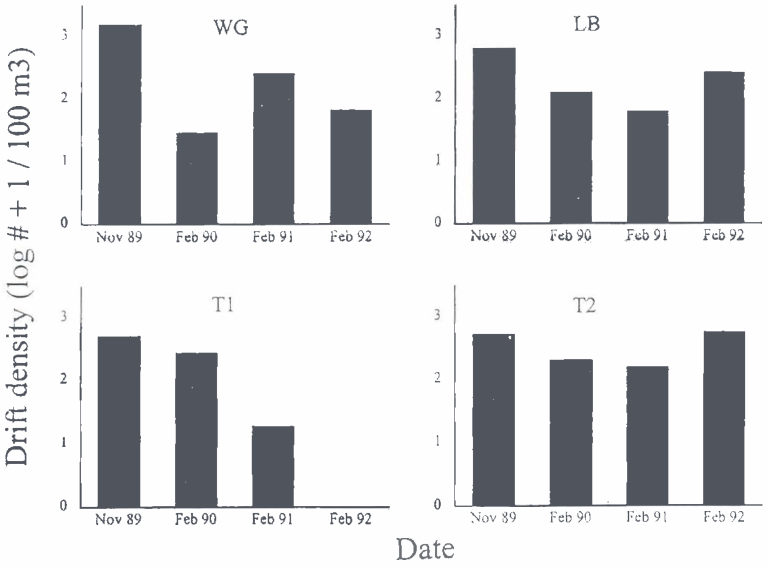

Fig. 6. Sample drift density (no./100m^3) for all organisms.

were considerably smaller than those used by Short and Ward (280 µm in our study vs. 700 µm in theirs); thus, the range of sizes captured was greater. Maximum densities exceeded 15,000 organisms/m^2 on some dates, but were usually nearer 5000/m^2. We expected low organism abundance during our winter sampling because egg diapause was a suspected life history attribute of some community members, especially within the Trichoptera and Ephemeroptera (e.g., see tables in Merritt and Cummins 1984). The great abundance of small (≤ 2 mm) Baetidae (Ephemeroptera) during November sampling suggests they have a short incubation period prior to hatching. Minshall (1981) also reported the Baetidae occurred in high abundance during winter months in an Idaho stream.

Density of drifting organisms was not particularly high relative to summer drift collections in other high-elevation streams (Allan 1987). Because we did not record diel periodicity in drift, it is hard to ascertain whether this proximal cue is important during winter. In fact, under prolonged darkness it is possible that drift is equally abundant at all hours of day and night. Extended periods of darkness may reduce insect susceptibility to predation by visual-feeding fishes, resulting in high drift densities. Likewise, drift rates might be high if encounters with predatory invertebrates increase (Peckarsky 1980, Soluk and Collins 1988) because the predators are also released from fish predation constraints.

This study provides a preliminary assessment of winter macroinvertebrate community structure in high-elevation streams and suggests that winter communities are diverse and numerically abundant. Though Vertucci and Conrad (1994) documented spring acid pulses in some glacial-melt headwater streams of GLEES, winter pH in our sites was circumneutral, indicating that pH depressions do not begin until early snowmelt. Similarly, the macroinvertebrate community composition was not indicative of one stressed by acidity. Further studies comparing these communities in different seasons may provide insights to the role of seasonal heterogeneity in community ecology.

Although winter stream conditions are harsh (i.e., extreme cold, reduced flow, lack of sunlight), there may be less variability in key abiotic parameters during this season than at other times of the year. For example, stream flow and temperature are 2 critical features for aquatic insect ecology and biology (Hynes 1970, Ward 1989). Variation in stream discharge and velocity during winter is minimal because cloudbursts and thaws, which may lead to rapid discharge increases, do not occur. Temperature fluctuations are also minimized because there are no direct effects from solar radiation as streams are snow covered. These observations suggest that winter may be a time when physical habitat features exhibit low temporal heterogeneity (sensu Kolasa and Rollo 1991) and may influence winter community structure. Likewise, the recent documentation of episodic acidification associated with spring snowmelt in the West (Vertucci and Conrad 1994) suggests a need for greater understanding of winter community structure. A knowledge of overwintering communities will help us accurately assess the effects of these episodic events. Also, seasonal comparisons of community structure and function and a detailed focus on winter stream dynamics may further our understanding of the forces important in structuring stream communities.

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The appendix follows on the next 3 pages.

APPENDIX. Benthic abundance at 4 sampling locations on 4 sampling dates. The 4 numbers under each site are the total number of each taxa collected in 3 pooled Surber samples in November 1989, and February 1990, 1991, and 1992, respectively. Only 2 and 1 samples were taken from T1 in 1991 and 1992, respectively. Functional group categories are based on Merritt and Cummins (1984): P = predator, C/G = collector/gatherer, S/D = shredder/detritivore, G/S = grazer/scraper.

Taxa	Site																Functional group
	WG				LB				T1				T2				
Plecoptera																	
PERLODIDAE																	
Isoperla quinquepunctata	1	2	11	8	4	2	5	5	4	0	3	0	0	9	1	4	P
I. fulva	4	0	4	8	6	3	0	5	9	8	1	3	2	12	0	6	P
I. petersoni	1	1	0	0	0	0	0	3	0	1	0	0	0	0	0	1	P
Cultus sp.	0	0	0	0	0	16	5	0	0	0	0	0	0	0	0	11	P
Kogotus modestus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	P
Megarcys signata	2	0	2	4	1	0	1	0	0	0	0	0	0	0	0	0	P
Unidentified perlodid	14	4	0	0	7	0	2	0	2	0	0	1	19	0	0	3	
CHLOROPERLIDAE																	
Sweltza lamba	32	23	72	98	22	12	107	112	23	0	24	9	1	43	0	31	P
Suwallia spp.	5	0	9	25	0	0	13	20	0	0	1	0	1	2	1	0	P
Plumiperla divera	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	S/D
Triznaka signata	0	0	2	0	0	0	0	0	0	0	8	0	19	0	0	0	S/D
Unidentified chloroperlid	174	18	0	0	219	41	0	0	8	2	0	0	10	3	0	0	
LEUTRIDAE																	
Paraleutra vershina	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	S/D
NEMOURIDAE																	
Zapada haysi	758	210	90	270	16	46	48	73	181	80	50	26	764	240	35	116	S/D
Z. cinctipes	79	10	49	77	43	32	89	59	86	0	41	0	349	338	63	194	S/D
Malenka coloradensis	0	0	0	0	5	6	5	0	0	0	1	0	57	6	0	0	S/D
Prostia besametsa	0	0	0	0	0	2	0	0	10	0	0	0	0	0	0	0	S/D
CAPNIIDAE																	
Capnia spp.	0	0	0	0	0	4	30	23	0	1	0	0	0	0	0	2	S/D
Ephemeroptera																	
EPHEMERELLIDAE																	
Drunella coloradensis	0	0	0	0	20	58	101	164	0	0	0	0	5	11	0	0	S/D
D. doddsi	30	5	1	6	10	6	7	3	2	0	0	0	20	7	4	6	S/D
Ephemerella infrequens	100	0	13	5	58	53	52	32	30	0	7	0	40	9	12	5	S/D
Serratella sp.	0	0	0	0	17	0	3	0	5	0	0	0	0	0	0	0	S/D
LEPTOPHLEBIIDAE																	
Paraleptophlebia debilis	0	0	0	0	37	22	65	86	1	0	0	0	0	0	0	2	C/G
SIPHLONURIDAE																	
Ameletus velox	8	0	5	10	0	0	6	0	11	3	2	0	8	5	5	7	C/G

Appendix. Continued.

Taxa	Site																Functional group
	WG				LB				T1				T2				
Heptageniidae																	
Rhithrogena spp.	0	0	0	2	0	17	4	12	0	0	0	0	0	15	1	3	C/G
Cinygmula spp.	199	67	88	253	110	76	88	293	83	4	5	3	108	457	37	130	G/S
Baetidae																	
Baetis bicaudatus	810	43	58	139	83	80	69	37	119	20	2	0	1276	495	71	177	G/S
B. tricaudatus	0	0	0	0	100	44	102	31	0	0	0	0	0	11	5	18	G/S
Trichoptera																	
Hydropsychidae																	
Arctopsyche grandis	0	0	0	0	1	2	0	2	0	0	0	0	0	0	0	0	C/G
Rhyacophilidae																	
Rhyacophila pellisa	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	P
R. brunnea	51	45	21	67	11	42	10	22	13	6	3	1	76	54	26	44	P
R. verrula	40	10	6	56	2	28	27	14	4	4	0	1	37	15	10	8	P
R. coloradensis	25	0	0	0	3	0	0	0	0	0	0	0	10	1	3	1	P
Glossosomatidae																	
Glossosoma spp.	5	0	0	6	6	11	9	14	0	0	0	0	10	1	3	1	G/S
Anagapetus spp.	0	0	0	0	6	6	1	0	0	0	0	0	0	0	0	0	G/S
Uenoidae																	
Neothremma sp.	0	0	0	6	0	2	3	9	0	0	0	0	0	0	0	0	G/S
Brachycentridae																	
Micrasema sp.	0	1	2	0	40	56	26	33	0	0	0	0	0	0	0	0	S/D
Lepidostomatidae																	
Lepidostoma sp.	0	0	0	0	6	17	4	4	0	0	0	0	0	0	0	0	S/D
Hydroptilidae																	
Agraylea sp.	5	0	31	52	0	2	0	0	47	10	7	6	85	94	12	13	G/S
Limnephilidae																	
Ecclisomyia maculosa	0	0	2	0	1	7	9	1	0	0	0	0	0	1	0	2	C/G
Dicosmoecus atripes	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	S/D
Oligophlebodes minutus	0	0	0	0	35	21	28	160	0	0	0	0	0	0	0	0	G/S
Diptera																	
Chironomidae	1300	1617	1380	3960	680	70	1020	870	720	764	1086	146	2154	681	600	1460	
Tipulidae	11	37	22	2	23	0	1	17	4	10	21	0	18	9	12	8	
Ceratopogonidae	6	4	0	24	22	5	5	0	0	0	0	0	31	0	0	0	
Dixidae	2	4	0	0	4	3	5	0	2	0	0	0	2	0	2	0	

APPENDIX. Continued.

Taxa	Site																Functional group
	WG				LB				T1				T2				
Coleoptera																	
DYTICIDAE																	
Hygrotus spp.	0	0	1	2	1	0	0	0	1	0	0	0	1	3	9	2	P
ELMIDAE																	
Cleptelmis sp.	0	0	0	0	0	0	2	1	0	0	0	0	2	0	0	2	C/G
Heterlimnius corpulentis	0	0	0	0	9	14	15	17	1	0	0	0	9	13	12	47	C/G
Narpus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	C/G
Miscellaneous																	
Oligochaeta																	
Limnodrilus sp.	0	1	0		8	6	5	5	16	2	4		11	29	0	22	
Mollusca																	
Pelecypoda																	
Sphaerium sp.	17	14	4	26	0	5	2	0	7	0	10	0	11	3	23	15	
Collembola	0	0	2	0	0	0	0	0	0	1	0	0	6	1	4	0	
Ostracoda	27	15	38	580	0	16	161	65	0	0	0	0	3	0	0	6	
Hydracarina	240	89	466	485	91	333	196	109	685	152	170	21	488	618	695	172	
Turbellaria	8	3	40	106	1	7	2	48	0	0	0	0	0	0	0	0	
TAXA RICHNESS	28	22	26	26	41	37	41	33	26	17	19	9	31	32	24	32	