Emergence and Flight Activity of Alpine Stream Insects in Two Years with Contrasting Winter Snowpack

Debra S. Finn & N. LeRoy Poff

Emergence and Flight Activity of Alpine Stream Insects in Two Years with Contrasting Winter Snowpack

Debra S. Finn† and
N. LeRoy Poff**

*Department of Biology and Graduate
Degree Program in Ecology, Colorado
State University, Fort Collins, Colorado
80523, U.S.A.
†Corresponding author. Present
address: EAWAG—Aquatic Ecology:
Überlandstrasse 133, 8600 Dübendorf,
Switzerland
Debra.Finn@eawag.ch

Abstract

Flight of alpine stream insects has not been well studied but is an important ecological process that ensures successful mating and allows gene flow among relatively isolated populations. In this study, we collected actively flying insects along a perpendicular transect from an alpine headwater stream in the Colorado Rocky Mountains (U.S.A.) during the summer emergence season in two consecutive years with contrasting hydrology: 2002 had minimal snowfall the previous winter, while 2003 snowfall was above average. Flight activity patterns among four common stream taxa were similar to previously reported results from streams below treeline: Ephemeroptera and Plecoptera declined as an inverse power function, Trichoptera declined as a negative exponential function, and Simuliidae did not decrease with lateral distance. Sex ratios typically were strongly biased, possibly a result of the harsh terrestrial environment negatively influencing the naturally more sedentary sex (which varies among taxa). In 2003, the majority of common species emerged approximately one month later than in 2002, and abundance and diversity were greater in 2003 than 2002, patterns potentially attributable to increased snowpack amount and duration. Late-emerging species, by contrast, were less abundant in 2003, likely because that year emergence was delayed to later in the season, when cooler air temperatures reduce flight activity. Our results suggest that alpine streams are sensitive to interannual variation in snowpack, and therefore more research will be needed to address the potential effects of climate change and associated winter snowfall trends on these unexpectedly diverse aquatic systems.

Introduction

The dominant macrofauna in alpine streams are aquatic insects (Ward, 1994; Hauer et al., 2007), many of which develop from a relatively lengthy stream-dwelling juvenile phase into a short-lived adult form in which some degree of aerial flight is possible. Despite the brevity of the adult stage, across all common taxonomic groups flight plays a major role in among-stream dispersal important to local and regional population dynamics and in successful mating and reproduction (Mackay, 1992; Palmer et al., 1996). Insect flight also provides an important energy subsidy (*sensu* Nakano and Murakami, 2001) to various terrestrial predators such as birds, bats, and spiders.

In the alpine zone (at altitudes above treeline), little is known of the extent of stream insect flight activity, although it has been speculated that the short growing seasons, high winds, low humidity, and cool air temperatures are particularly limiting factors (e.g. Downes, 1965; Ward, 1994; Finn and Poff, 2005). The energetic cost of insect flight can be expected to be increased extensively by these local climatic factors (Nilsson et al., 1993). Indeed, recent genetic studies on alpine stream specialist species have shown strong among-stream genetic structure across a small geographic extent, implicating limited flight dispersal (Finn and Adler, 2006; Finn et al., 2006).

To date, these indirect genetic estimates provide the only insight we have towards understanding alpine stream insect flight. However, there have been several direct observational studies of flight activity in temperate streams below treeline, where climatic conditions are considerably more benign. Where trees occur, for example, the atmospheric boundary layer is thicker (e.g. Jackson and Resh, 1989; Briers et al., 2003) and hence presumably more conducive than alpine conditions to insect flight. Nonetheless, studies below treeline have revealed that flight tends to be concentrated near the natal stream (e.g. Briers et al., 2002; Petersen et al., 1999), although further studies using genetic markers or stable isotopes have demonstrated low but significant levels of long-distance movement (e.g. Wilcock et al., 2001; Briers et al., 2004). These genetic results from non-alpine streams provide an interesting contrast to those cited above for alpine insects, which did not reveal significant long-distance movement. A consequent prediction can therefore be made that direct observational studies in alpine streams should reveal minimal flight activity and flight distance from natal streams.

Due to its patchy distribution and environmental extremes, the alpine ecosystem is considered an important indicator system for global change (Bowman and Seastedt, 2001, and references therein). Alpine streams, at the uppermost extent of often lengthy river systems, share similar characteristics of isolation and confinement of endemic biotic assemblages suited to this extreme (Ward, 1994; Finn and Poff, 2005; Hauer et al., 2007). The current climate change trajectory of warming summer temperatures (IPCC, 2001) has been a growing conservation concern, and particular emphasis has been placed on the shifting hydrologic regime of alpine streams due to loss or reduction of glaciers and

permanent snowfields, which provide continual meltwater supply throughout warmer months (Brown et al., 2007).

Another less widely acknowledged trend is the projected increase in winter snowfall in many alpine areas (cf. IPCC, 2001; Welker et al., 2001; but see Borgstrøm, 2001). Most annual snowfall will melt in the early summer and thus may temporarily increase but not sustain late season streamflow as permanent meltwater sources do. Potentially higher spring/summer flows following winters of increased snowfall are thought to decrease community persistence in alpine streams due to increased flow disturbance (Milner et al., 2006).

In addition to differences in meltwater regime between annual snowfall and permanent sources, these streamflow sources also have distinct spatial differences that may influence aquatic biota. Glaciers and permanent snowfields occur at the head of alpine streams, whereas annual winter snowfall distributes widely throughout the landscape and in many cases completely covers small alpine streams for a large proportion of each year. Depth of annual snowpack positively influences the duration of snow cover into the warm season (Walker et al., 1999; Borgstrøm, 2001). Lengthier snow cover over streams and lakes can maintain colder water temperatures (Borgstrøm and Museth, 2005) that may delay the emergence timing (phenology) of alpine stream insects and indirectly influence flight patterns, which are sensitive to ambient air temperature at emergence.

In this study, we address two related objectives. First, we present a novel analysis of the flight activity patterns of several alpine stream insect species. Related taxonomic details and taxon-specific expectations are provided in the following Focal Taxa section. This information is fundamental to understanding how effectively alpine stream insects are able both to disperse and colonize neighboring habitats and to sustain local populations via mating. Second, we ask whether the observed patterns, in addition to emergence phenology, vary between years with highly contrasting hydrological properties driven by differences in previous winter snowpack. This two-year comparison provides an initial assessment of how interannual climatic variation may influence insect flight activity and will contribute to developing an understanding of the potential impacts of climate change on alpine stream systems.

Focal Taxa

We collected flying adults from each of four common aquatic insect taxa: Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) (taken together: "EPT"), and Simuliidae (black flies, order Diptera). We anticipated a gradient of flight activity patterns among these major taxa, with Ephemeroptera and Plecoptera expected to be the least active and show the steepest rate of decline in flight activity with distance from the natal stream, Simuliidae the most active and farthest dispersing, and Trichoptera intermediate. Ephemeroptera adults have a brief life span and lack functional mouthparts, thus precluding terrestrial feeding. Below treeline, mayflies have been shown to be relatively weak in flight and typically are not observed at great distances from streams (Jackson and Resh, 1989; Petersen et al., 2004). Similarly, adults in one of the two suborders of Plecoptera lack functional mouthparts, and there are many cases of brachyptery (wing-size reduction) in stoneflies. Similarly to mayflies, stoneflies tend to be relatively weak in flight and concentrate most activity in the vicinity of the stream (e.g. Kuusela and Huusko, 1996; Petersen et al., 1999; Briers et al., 2002).

Of the EPT, Trichoptera are thought to be the strongest and most active fliers, as they are often larger-bodied and with proportionally larger wing size (Kovats et al., 1996). Several temperate-climate studies have shown that while caddisfly flight activity decreases with distance from stream, the decline is less steep and average flight distance for many species is greater than what is observed for mayflies or stoneflies (Svensson, 1974; Jackson and Resh, 1989; Sode and Wiberg-Larsen, 1993). Across all EPT, males are typically more active in flight than females (e.g. Sode and Wiberg-Larsen, 1993; Kuusela and Huusko, 1996), a pattern likely attributable to trade-offs associated with the high energetic cost of egg production (i.e., Rankin and Burchsted, 1992).

Simuliidae include both the common blood-feeding (anautogenous) black flies as well as a number of species that have lost this ability (obligately autogenous) and instead feed either on plant materials or do not feed at all as adults (Adler et al., 2004). Anautogenous black flies are presumed to be very active in flight in order to locate mammalian or avian bloodmeal sources, and individuals have been collected at impressive distances (up to >30 km) from the nearest larval habitat (Baldwin et al., 1975; Choe et al., 1984). Because the bloodmeal is required for egg maturation, the female black fly is typically the stronger and more active flier than the male (Crosskey, 1990). Little is known about flight activity of obligately autogenous black flies, but they are probably considerably less active because a blood meal is not sought (e.g. Rothfels, 1981; Snyder and Linton, 1984). Indeed, two population genetic studies of alpine autogenous blackflies in our study region have demonstrated strong population structure across a small spatial extent, strongly suggesting limited overland dispersal by adults (Finn and Adler, 2006; Finn et al., 2006).

Study Site

The study took place at a first-order alpine reach of the South Fork Cache la Poudre River (SFP) near the northern boundary of Rocky Mountain National Park (RMNP), Colorado, U.S.A. The reach is dominated by riffles interspersed with small pools. Riffles had an average width of 1.6 m and bankfull depth of 34 cm. At an altitude of 3416 m, SFP lies above permanent treeline in a north-facing valley but is unusual among alpine streams in the region in that the valley it occupies is relatively wide and low-gradient with a broad riparian zone dominated by low-lying willow (*Salix* spp.). The annual hydrograph is snowmelt-dominated (*sensu* Poff and Ward, 1989), and stable summer flow is maintained by meltwater from a permanent snowfield. Temperature dataloggers have revealed continuous year-round flow (winter temperature 0–2 °C: Finn, unpublished data), and the stream is covered in snow on average from late October to early June. Winter flow is likely maintained by subsurface sources (e.g. Sueker et al., 2000), in addition to insulation provided by the deep winter snowpack. SFP therefore would best be characterized as nivo-krenal (Brown et al., 2003). The stream insect community is relatively diverse compared to other alpine streams in the region (Finn and Poff, 2005). Summer water temperature averages ca. 5 °C, and mean air temperature is ca. 9 °C with a range from slightly below freezing to 20 °C. Strong winds prevail from the west and are a pervasive feature in our study area (Greenland and Losleben, 2001).

We compared hydrological data collected from nearby subalpine sites within RMNP for the emergence seasons of 2002 and 2003. Total snowfall at Bear Lake (2843 m; ~25 km south of SFP) prior to the 2002 summer season was 3.7 m, and for 2003 it was 7.6 m. The 22-year average (years 1984–2005) total winter snowfall at Bear Lake was 5.8 m (standard deviation 1.3 m, range 3.3–8.5 m). U.S. Geological Survey gage data collected on a stream reach draining an adjacent alpine catchment reflected the
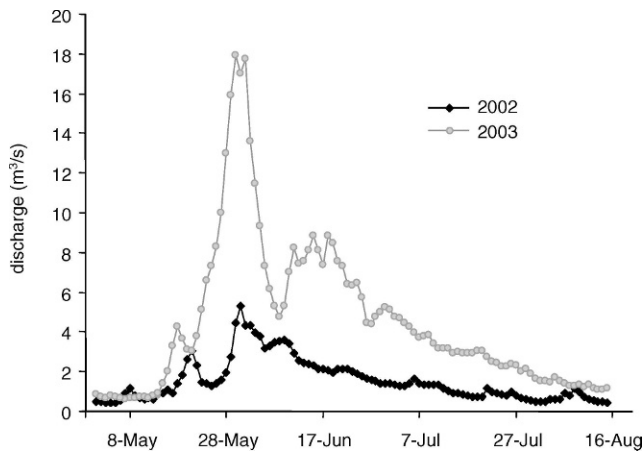
FIGURE 1. Hydrographs for 2002 (black diamonds, lines) and 2003 (gray circles, lines) during the peak runoff season on the Big Thompson River at 2400 m a.s.l. in Rocky Mountain National Park. Data from U.S. Geological Survey gage #402114105350101 (http://water.usgs.gov). Note that the use of black for 2002 and lighter colors for 2003 continues in all figures.

substantial difference in snowpack between 2002 and 2003, revealing significantly greater peak runoff and sustained high flows continuing through a large proportion of the summer season in 2003 vs. 2002 (Fig. 1).

Methods

We placed four Malaise traps in an offset transect with traps at 1, 10, 30, and 60 m from the east stream bank during the emergence seasons of 2002 and 2003. Malaise traps are non-attracting, and therefore approximate natural spatial occurrences of flying insects. They are particularly effective in capturing our focal taxa. We used large two-sided traps oriented parallel to the stream, similar to those described by Sode and Wiberg-Larsen (1993), with openings on each side of 1.8×2.0 m^2. Although we only were able to place a single transect, the large size of the individual traps yielded a large enough sample size of individual insects to statistically detect between-year differences and lateral patterns of flight activity. Trap roofs sloped up to single collecting heads half-filled with a 50% propylene glycol solution for specimen preservation. We monitored the traps daily during the peak of the emergence season (snowmelt to mid-August), and weekly thereafter. Collections were transferred from each trap just before heads reached capacity. Collections thus were made more frequently when insect emergence and flight activity peaked (e.g. see distribution of dates of concurrent collection from all traps in Fig. 2).

Malaise traps were in continuous operation from 8 July–22 September 2002 and 23 June–21 September 2003. The earlier start date in 2003 occurred immediately following snowmelt from the stream surface. In contrast, 2002 sampling was initiated well after snowmelt: our first arrival at SFP in 2002 was 21 June, at which time the stream and riparian zone were completely snow-free. A nearby stream in RMNP at a higher elevation (3538 m) but similar aspect was snow-free on 5 June (Finn, personal observation), suggesting that full snowmelt was likely to have occurred on the order of a month earlier in 2002 than 2003.

In the laboratory, insects were transferred to 95% ethanol, separated, and species and sex determined for all EPT and Simuliidae. Females of the mayfly genus *Cinygmula* could not be identified to species and were therefore recorded as *Cinygmula*
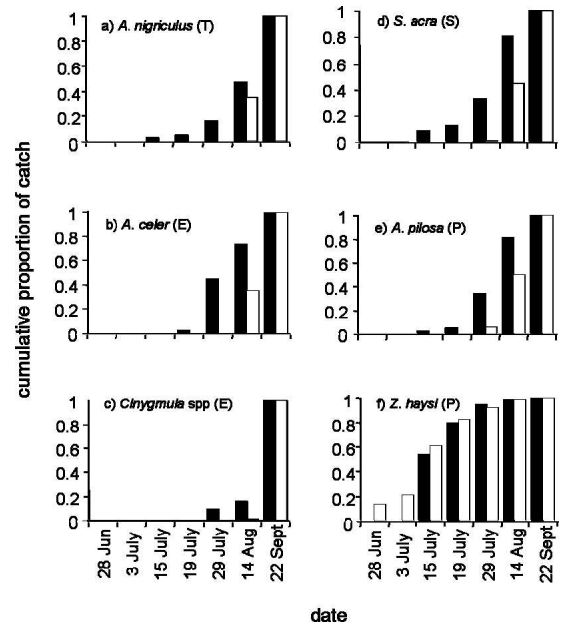

FIGURE 2. Cumulative proportions of the total catch of the six most common lotic species at different dates during the study period: (a) *Asynarchus nigriculus*, (b) *Ameletus celer*, (c) *Cinygmula* spp., (d) *Stegopterna acra*, (e) *Alloperla pilosa*, and (f) *Zapada haysi*. Parenthetic letters following species names indicate higher taxon: E = Ephemeroptera, P = Plecoptera, T = Trichoptera, S = Simuliidae. Black represents 2002 and white represents 2003 collections. Note that dates are not equally distributed and are more densely clustered in July, a peak emergence period for several species. In part f, 2002 collections began 8 July, after the *Z. haysi* emergence period had begun; hence the absence of 2002 data in the first two time categories.

spp. (including two species: *C. par* Eaton and *C. ramaleyi* Dodds). Overall sex ratios were determined and assessed for deviations from 1:1 using *G* log-likelihood statistics (Zar, 1996) for each of the four higher-level taxa, as well as for the six most common species (having >15 individuals collected in both years; see Table 1).

We compared emergence phenology between years for the six common species by pooling the total catch across traps for each year and plotting cumulative proportion of total annual catch by calendar date. These plots provide a visual display of phenological difference between years. We were not able to perform a robust statistical test for a directional phenological shift between years among the six common species because the relatively later start date in 2002 decreased confidence that we had captured the full distribution of emerging insects in that year. Two of the six common species, however, were late-emerging mayflies (*Cinygmula* spp. and *Ameletus celer*) for which we could be sure that the emergence period was fully sampled in both years. These in addition to two relatively common late-emerging caddisflies (*Limnephilus abbreviatus* and *Limnephilus picturatus*, recorded at ≥10 individuals per year) were included in a paired *t*-test of the null hypothesis that there was no mean difference in emergence timing between years. Date of first appearance in any Malaise trap was the response variable.

For each year, we also assessed relationships between distance from the stream and total abundance of individuals for each of the four taxonomic groups as well as the six most common species. For each taxon, we assessed the fit of three decreasing functions: linear, negative exponential, and inverse power. In this order, these functions model faster rates of decrease with linear distance.

TABLE 1

Total numbers of males (m) and females (f) collected for each higher-level taxonomic group and common species, and total species richness within higher-level groups across all traps in 2002 and 2003. Sex ratios marked with stars are significantly different from 1:1 (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$).

Taxon	2002 N (m/f)	2003 N (m/f)	2002 richness	2003 richness
Ephemeroptera	94/31***	45/19***	4	4
Ameletus celer	47/1***	16/1***		
Cinygmula spp. *(C. ramaleyi + C. par)*	44/26*	27/17		
Plecoptera	111/102	299/173***	9	15
Zapada haysi	55/64	244/129***		
Alloperla pilosa	29/10**	19/9		
Trichoptera	127/28***	101/42***	12	16
Asynarchus nigriculus	82/2***	56/7***		
Diptera				
Simuliidae	23/46**	114/387***	9	18
Stegopterna acra	20/33	31/64***		

Each of the three models was fitted to linearly transformed data (i.e., no transformation for the linear model, log-linear for exponential, and log-log for power function) and analyzed using linear regression. The single model producing the greatest R^2 values within each taxon was selected to compare lateral flight patterns between years using analysis of covariance (ANCOVA, SAS Institute, Inc., 2003). ANCOVA used distance from stream as the covariate, year as the main factor, and total number of individuals captured as the response variable. Data were appropriately transformed according to the best-fit model to meet the ANCOVA requirement of linearity. A resulting difference in intercept would indicate a difference in total abundance between years, while an interaction with distance would indicate different slopes and therefore different rates of lateral decline in flight activity between years. In some taxa (all simuliids and the mayfly species *Ameletus celer*), there was no statistical evidence for decreasing flight activity with distance in either year; therefore, these taxa were not analyzed further.

We also looked for evidence of lateral variation in sex ratio for five of the six most common species and the family Simuliidae (*Cinygmula* was not included here because this group actually contained 2 species *sensu stricto*). With a similar approach as above, we used linear regression with arcsin-squareroot percent females in each year as the response variable and distance from stream as the independent variable. Regressions revealed a significant trend at $\alpha = 0.05$ for only a single taxon in a single year; therefore, we did not run ANCOVA to assess differences in lateral patterns of sex ratio between years.

Results

Over the course of two alpine emergence seasons, we collected a total of 1742 individuals representing 60 species (Ephemeroptera—4, Plecoptera—17, Trichoptera—18, Simuliidae—21). All Simuliidae collected were anautogenous. Between years, we collected considerably more individuals and species in 2003 than 2002, and most of the increase in both abundance and diversity was accounted for in the stoneflies and the black flies (Table 1). In the mayflies, there was a reverse trend in abundance, which was higher in 2002 than 2003 (Table 1). Across all orders, there were six species that we considered common (range 17–373 individuals/year): *Ameletus celer* McDunnough and *Cinygmula* spp. (Ephemeroptera), *Zapada haysi* Ricker and *Alloperla pilosa* Needham and Claassen (Plecoptera), *Asynarchus nigriculus* Banks (Trichoptera), and *Stegopterna acra* Currie, Adler, and Wood (Simuliidae).

Among the rarer taxa, a female and several males of an undescribed species of *Prosimulium* (Simuliidae) were identified in 2003. Also, several *Greniera denaria* Davies, Peterson, and Wood (Simuliidae) females were discovered and are a state record for Colorado and only the third record for the U.S.A. (Adler et al. 2004).

For five of the six common species, we observed the progress of emergence over the full season at an approximately one-month delay in 2003 compared to 2002 (Fig. 2). The lone exception was the stonefly *Zapada haysi*, which is one of the earliest emergers from this stream and exits the water as soon as snowcover recedes. Because traps were set immediately following snowmelt in 2003 but not in 2002, data are considerably lacking for *Z. haysi* in early 2002; therefore, Figure 2f should be interpreted with caution. A paired *t*-test using the four most common later-emerging species revealed that timing of earliest emergence was significantly different between years (one-tailed test: $p = 0.003$).

Sex ratios were consistently male dominated in both collection years for all EPT and female dominated for Simuliidae (Table 1). In many cases, the unbalanced sex ratios were extreme; for example, only two females of the mayfly *Ameletus celer* were collected across both years, compared to 63 males (Table 1). There were no consistent trends in sex ratio with distance from stream for any of the taxa evaluated. The single instance of a significant lateral trend was for Simuliidae in 2002, in which there was an increase in percent females with distance ($R^2 = 0.92$; $p = 0.03$). In 2003, when simuliid sample size increased nearly tenfold as compared to 2002, the trend was not evident.

Each of the EPT taxa demonstrated a significant lateral decline in total number of individuals collected in 2003. In 2002 each of the three decreasing functions for Trichoptera were insignificant at $\alpha = 0.05$, while for Ephemeroptera and Plecoptera the 2002 decreasing function was significant and similar in shape to 2003 (Table 2, Fig. 3). The best-fit model for Ephemeroptera and Plecoptera in both years was an inverse power function (Table 2). ANCOVA results confirmed a significantly greater abundance of stoneflies collected in 2003 than 2002, compared to a significantly smaller abundance of mayflies in 2003 than 2002 (Table 3, Fig. 3). Power function slopes did not differ between years in either case, indicating similar lateral dispersal between years. For Trichoptera, the decreasing trend was significant only in 2003, but the negative exponential model had the best fit in both years ($p = 0.10$ in 2002; see Table 2, Fig. 3). Simuliidae showed no evidence of decreasing abundance with distance from stream in either year. Indeed, there were far more black flies collected in the

TABLE 2

Lateral dispersal statistics for each major taxon and common species within each, along perpendicular transects in each of two years. R^2, slope, and p-value are for the best-fit models for each order. ND = not decreasing (p-values > 0.2 for decreasing slope). P-values in bold are those significant at $\alpha = 0.05$.

Taxon	Year	Best model	R^2	Slope	P
Ephemeroptera	2002	*power*	0.99	−0.43	**0.006**
	2003	*power*	0.91	−0.49	**0.05**
Cinygmula spp.	2002	*power*	0.96	−0.92	**0.02**
	2003	*power*	0.97	−0.95	**0.02**
Ameletus celer	2002	*ND*			
	2003	*ND*			
Plecoptera	2002	*power*	0.93	−0.71	**0.02**
	2003	*power*	0.86	−0.31	**0.05**
Zapada haysi	2002	*power*	0.89	−0.64	**0.04**
	2003	*power*	0.79	−0.25	0.11
Alloperla pilosa	2002	*power*	0.80	−0.75	0.07
	2003	*power*	0.97	−0.51	**0.02**
Trichoptera	2002	*exponential*	0.80	−0.03	0.10
	2003	*exponential*	0.99	−0.05	**0.003**
Asynarchus nigriculus	2002	*exponential*	0.66	−0.03	0.19
	2003	*exponential*	0.96	−0.06	**0.02**
Simuliidae	2002	*ND*			
	2003	*ND*			
Stegopterna acra	2002	*ND*			
	2003	*ND*			

most distant trap than any other in 2003 (Fig. 3). Therefore, none of the three models were applicable (Table 2).

Most common species showed patterns of abundance with distance inland similar to the overall pattern for each of their respective higher-level taxa (Table 2). A notable exception was the mayfly *Ameletus celer*, which, similarly to the black flies, showed no evidence of decreasing abundance with distance in either year (Table 2).

Discussion

Although alpine streams generally are considered depauperate relative to temperate streams (e.g. Ward, 1986), our detailed study of the insects emerging from the South Fork Poudre River headwaters has revealed surprisingly high species diversity. The total species count of 60 among EPT and Simuliidae captured across 2002–2003 is nearly three times the total number of taxa reported from benthic samples in the same stream (Finn and Poff, 2005). This higher diversity resulted from our ability here to reveal "hidden" diversity that occurs in the aquatic larvae, many of which are more difficult to identify than the adults. Also, traps in this study integrated over all local microhabitats (likely including tiny ephemeral snowmelt tributaries, see below), while Finn and Poff (2005) sampled only from shallow riffles in the main stream. Further, our discovery of a previously undescribed *Prosimulium* species, in addition to the state record for *Greniera denaria*, reflects that alpine streams in the southern Rockies have been understudied and are likely to house a higher biological diversity than previously considered.

Overall, lateral flight activity varied among major taxa as predicted from studies conducted below treeline. The tight fit of inverse power functions for Ephemeroptera and Plecoptera demonstrated a rapid decrease in flight activity with distance from stream for these taxa, as has been shown previously (e.g. Briers et al., 2002; Petersen et al., 2004). Trichoptera also showed decreased flight activity with distance away from the stream, but the less steep negative exponential function was the best fit for this taxon. As in some sub-treeline streams (e.g. Svensson, 1974;

Jackson and Resh, 1989), caddisflies, which at our alpine site are predominantly members of the large-bodied family Limnephilidae, appear to be stronger in flight than the other EPT. Simuliidae, conversely, showed no evidence of decreasing flight activity away from the stream. Black flies are known to be strong fliers (Crosskey, 1990), and the female need for a bloodmeal in many species (including all trapped in the current study) often requires relatively distant flight.

Sex ratios of flying insects also followed expected trends, with more males in flight for most EPT and fewer males for Simuliidae. In most cases, the unbalanced sex ratios were highly significant. This result is potentially explained by the particularly harsh terrestrial flight conditions in the alpine zone, which could skew sex ratios strongly against the weaker-flying sex if there is selection for increased sedentary behavior. The unbalanced sex ratios have important implications for choosing molecular markers for population genetics of alpine stream insects. For example, Hughes et al. (2003) have shown that mitochondrial DNA (a maternally transmitted lineage) reveals stronger geographic structure among populations of a Rocky Mountain mayfly than does a set of nuclear markers (transmitted by both males and females), as expected if females are more sedentary than males.

Flight patterns for common species were representative of the overall patterns shown in their respective taxonomic groups, with the exception of the mayfly *Ameletus celer*, which did not decrease in abundance with lateral distance. The other common mayfly, *Cinygmula* spp., had the steepest decreasing slope of any species (Table 2) and drove the overall decreasing pattern for Ephemeroptera, despite the incongruous pattern for *A. celer*. This interesting contrast between species within the same order supports the contention that broad generalizations about dispersal behavior in aquatic invertebrates can be unwarranted and that information about species differences is likely to be more meaningful ecologically (Bohonak and Jenkins, 2003). *A. celer* is an unusually large-bodied mayfly in which the male also has exceptionally large eyes (Pritchard and Zloty, 1994). Both traits may be associated with stronger flight ability (e.g. Corkum, 1987),
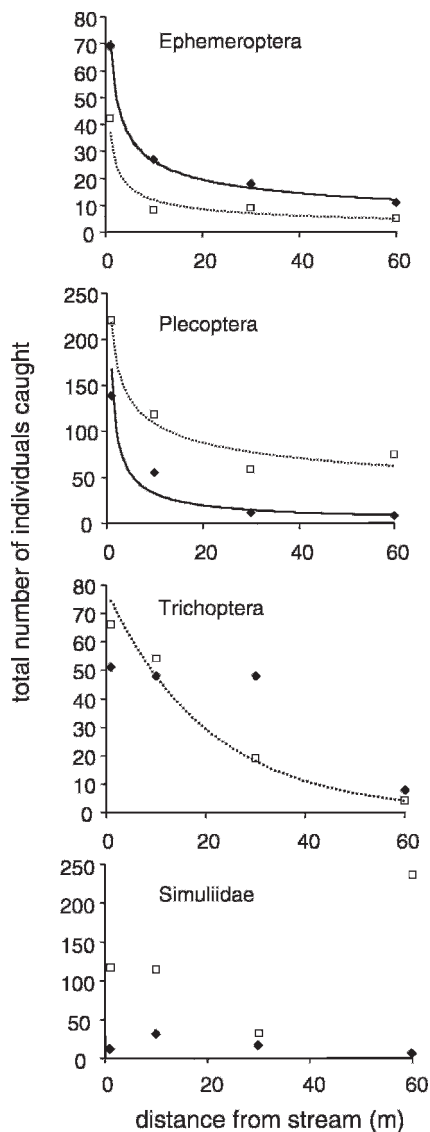
FIGURE 3. Total numbers collected per year of each of the four major taxa as a function of trap distance from the stream. Filled diamonds are 2002 and open squares are 2003 values. Lines (solid—2002; broken—2003) are fitted functions as per Table 2 and are included only in cases of significant decrease.

alpine streams, an effect that potentially has a strong influence on emergence phenology, and may also influence richness and diversity, although less directly (more below). Snowpack over the stream acts not only as a physical barrier to insect emergence and flight, but it also can directly affect water temperature via its insulating properties. Indeed, most of the small alpine streams in our study area remain covered by thick snowpack throughout the winter with no open "leads" above treeline, no matter the relative snowfall amount (Finn, personal observation). Such continuous snowcover effectively insulates streams to maintain temperatures ≥ 0 °C and to support permanent flow through the winter months in spite of average air temperatures well below freezing (Greenland and Losleben, 2001). In contrast, extended snow cover into the warmer months likely has the opposite insulating effect, serving to maintain lower temperatures in the water column despite warming air temperatures (Borgstrøm and Museth, 2005). Snow depth covering our study site on 21 May 2003, during the first month that average maximum air temperature exceeds 0 °C, was approximately 2 m (Finn, unpublished data). Maintenance of colder water temperatures effectively delays the accumulation of degree days that provide essential developmental cues for many aquatic insects (Vannote and Sweeney, 1980). Our observations of both snowmelt and emergence of several species at an approximately one month delay in 2003 compared to 2002 is thus unlikely to be merely coincidence, although the short duration of our study and the lack of literature on the relationship between snowpack duration and emergence phenology in alpine streams precludes our drawing a firm conclusion (but see Borgstrøm, 2001, regarding the negative effect of lengthier snowcover on growth in trout).

A second effect of increased snowpack was higher peak runoff flow (Fig. 1), which is expected to act as a disturbance to stream communities (Gibbins et al., 2001; Milner et al., 2006). In Alaskan streams, Milner et al. (2006) reported a negative correlation between community persistence (constancy of species presence/absence) and total snowfall in the winter previous to sampling. The authors speculated that greater flow disturbance in years with increased snowmelt runoff led to greater shifts in community composition. In the current study, we observed a 1.5× increase in total species richness following the winter with above-average snowfall. Although disturbance in some cases can be expected to increase diversity (e.g. Connell, 1978), the trend we observed of a significant addition of species following the 2002–2003 winter was opposite what was expected given the results of the Milner et al. (2006) study.

In addition to phenological and diversity disparities, there were notable differences in overall abundance of flying insects between 2002 and 2003. Both abundance and species richness were greater in 2003, primarily driven by increases in Plecoptera and Simuliidae. At first glance, the combination of earlier emergence timing with later study initiation in 2002 seems a likely explanation for these patterns, i.e., perhaps we simply missed several early-emerging individuals and species in 2002 due to the later starting date of trapping. This argument can at least partially explain the large differences in abundance as well as sex ratio of the stonefly *Zapada haysi* that we recorded between years. We did not capture the earliest-emerging *Z. haysi* in 2002; therefore, total individuals reported in Table 1 are less than what actual annual totals would have been had we set traps that year immediately following snowmelt, as in 2003. Furthermore, *Z. haysi* is protandrous, with males emerging earlier than females (Cather and Gaufin, 1976); hence the expected male bias in sex ratio was observed in 2003 after thorough temporal sampling but not in 2002 when early emergence was unsampled (Table 1).

although not necessarily related to lateral dispersal as, for example, black fly males have larger eyes useful in swarming and mating but do not tend to disperse long distances relative to females (Crosskey, 1990).

Among our most striking results were differences in emergence phenology, abundance, and richness between years. The major environmental difference among years at the study site was a greater than twofold increase in winter snowpack between 2002 and 2003. Increased snowpack leads to longer duration of insulating snow physically covering the stream, causes higher peak snowmelt flows (Fig. 1), and increases heterogeneity of local aquatic habitat by supporting ephemeral shallow water habitats after flows have peaked. These important hydrologic responses are likely to influence benthic insects directly; therefore, we interpret many of the biological differences we observed between years to the associated difference in winter snowpack, recognizing that thus far there are just two years of observation.

A generally little-appreciated influence of increased winter snowfall is the lengthier duration of snowpack covering small

TABLE 3

ANCOVA results summary. Note that ANCOVA was only assessed for taxa that showed significant decrease with distance according to regression of number collected on distance from stream for *either or both* 2002 and 2003. See Table 2 ("best model") for transformations made to achieve linearity for the ANCOVA for each taxon. *P*-values in bold are those significant at α = 0.05.

Taxon	Factor	df	MS	F	P
Ephemeroptera	distance	1	0.77	62.03	**0.001**
	year	1	0.24	19.58	**0.01**
	distance*year	1	0.003	0.23	0.65
Cinygmula spp.	distance	1	3.16	100.6	**0.0006**
	year	1	0.20	6.47	0.06
	distance*year	1	0.0009	0.03	0.88
Plecoptera	distance	1	0.94	40.78	**0.003**
	year	1	0.60	26.1	**0.007**
	distance*year	1	0.15	6.65	0.06
Alloperla pilosa	distance	1	1.42	21.42	**0.01**
	year	1	0.00008	0	0.97
	distance*year	1	0.052	0.79	0.42
Zapada haysi	distance	1	0.72	24.64	**0.008**
	year	1	0.93	31.79	**0.005**
	distance*year	1	0.14	4.85	0.09
Trichoptera	distance	1	1.24	51.29	**0.002**
	year	1	0.04	1.50	0.29
	distance*year	1	0.06	2.50	0.19
Asynarchus nigriculus	distance	1	1.61	21.97	**0.009**
	year	1	0.10	1.41	0.30
	distance*year	1	0.11	1.44	0.30

Although trapping start time differences between years probably affected abundance estimates of early-emerging species in 2002, there is little evidence that they influenced the strong between-year differences in species richness or the differences in abundance of the later-emerging species. Indeed, the vast majority of species had mid–late season emergence that would have either spanned or followed the 2002 study initiation date (and thus allowed inclusion in the total 2002 species count). Lower species richness revealed in 2002 vs. 2003 therefore was not due to failure on our part to trap for the full extent of the season but more likely was influenced by between-year habitat differences, again likely driven by differences in snowpack.

The greater quantity and duration (see Fig. 1) of snowmelt in 2003 likely provided more extensive and diverse aquatic habitat, including the formation of smaller rills and seeps in the floodplain adjacent to the sample stream. Increased habitat area could have two primary effects on our results. First, it likely would yield an increase in total numbers of insects (directly affecting total abundance collected by the traps) and, as a simple sampling effect, would increase detection ability of rare species, thereby boosting species richness. Second, the increased diversity of habitat types in 2003, particularly the addition of tiny ephemeral tributaries fed by sustained snowmelt, likely spurred development of species with life histories specialized to these conditions. For example, several black flies that we trapped in 2003, including the state record *Greniera denaria*, are known to develop in tiny, ephemeral flowing-water habitats (P. H. Adler, personal communication).

Increased habitat area and diversity of habitat types may help explain the significantly greater abundance and richness of stoneflies and black flies in 2003, but Ephemeroptera showed an opposite pattern, with significantly greater abundance in 2002, although they showed no difference in richness between years. Each of the four mayfly species emerges very late in the season, and in 2003 as compared to 2002, emergence was delayed by a month, such that

the flight period for mayflies did not begin until well into August. Average air temperature in late August and September in the southern Rockies alpine zone is <5 °C (Greenland and Losleben, 2001), which is below the low temperature threshold for most stream insect flight (Waringer, 1991; Briers et al., 2003). July has the highest annual average air temperature, however, and July had a corresponding peak in flying insect density in both years of our study. Therefore, insects that begin emerging during or prior to July probably have strong potential for increased flight activity. Earlier mayfly emergence in 2002 likely allowed us to trap significantly greater numbers of individuals in flight. The caddisfly *Asynarchus nigriculus*, itself a particularly late emerger, was also significantly more abundant in 2002 vs. 2003.

In summary, then, these conclusions suggest that increased snowpack has a strong potential for explaining three notable observations in 2003 vs. 2002: (1) emergence timing approximately one month later; (2) increase in diversity of earlier-emerging species; and (3) decrease in abundance of later-emerging species.

In light of the predicted climate change trajectory towards increased winter snowfall (IPCC, 2001; Welker et al., 2001), it will be important to bolster these results with further study in alpine regions of the Rocky Mountains and elsewhere. The unexpectedly high diversity of aquatic insects collected from this single study site in an alpine stream in the southern Rockies accentuates the need to monitor these systems more closely as climate change progresses. As in the terrestrial alpine system, these high elevation streams are effectively isolated at the top of the stream's longitudinal gradient and are therefore likely to be sensitive indicators of change.

References Cited

Adler, P. H., Currie, D. C., and Wood, D. M., 2004: *The Black Flies (Simuliidae) of North America*. Ithaca, NY: Comstock Publishing Associates (a division of Cornell University Press), 941 pp.

Baldwin, W. F., West, A. S., and Gomery, J., 1975: Dispersal patterns of black flies (Diptera: Simuliidae) tagged with ^{32}P. *The Canadian Entomologist*, 107: 113–118.

Bohonak, A. J., and Jenkins, D. G., 2003: Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters*, 6: 783–796.

Borgstrøm, R., 2001: Relationship between spring snow depth and growth of brown trout, *Salmo trutta*, in an alpine lake: predicting consequences of climate change. *Arctic, Antarctic, and Alpine Research*, 33: 476–480.

Borgstrøm, R., and Museth, J., 2005: Accumulated snow and summer temperature—Critical factors for recruitment to high mountain populations of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish*, 14: 375–384.

Bowman, W. D., and Seastedt, T. R., 2001: *Structure and function of an alpine ecosystem: Niwot Ridge, Colorado*. New York: Oxford University Press, 337 pp.

Briers, R. A., Cariss, H. M., and Gee, J. H. R., 2002: Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie*, 155: 627–644.

Briers, R. A., Cariss, H. M., and Gee, J. H. R., 2003: Flight activity of adult stoneflies in relation to weather. *Ecological Entomology*, 28: 31–40.

Briers, R. A., Gee, J. H. R., Cariss, H. M., and Geoghegan, R., 2004: Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. *Freshwater Biology*, 49: 425–431.

Brown, L. E., Hannah, D. M., and Milner, A. M., 2003: Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water source contributions. *Arctic, Antarctic, and Alpine Research*, 35: 313–322.

Brown, L. E., Hannah, D. M., and Milner, A. M., 2007: Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology*, 13: 958–966.

Cather, M. R., and Gaufin, A. R., 1976: Comparative ecology of three *Zapada* species of Mill Creek, Wasatch Mountains, Utah (Plecoptera: Nemouridae). *American Midland Naturalist*, 95: 464–471.

Choe, J. C., Adler, P. H., Kim, K. C., and Taylor, R. A. J., 1984: Flight patterns of *Simulium jenningsi* (Diptera: Simuliidae) in central Pennsylvania, USA. *Journal of Medical Entomology*, 21: 474–476.

Connell, J. H., 1978: Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302–1310.

Corkum, L. D., 1987: Patterns in mayfly (Ephemeroptera) wing length: adaptation to dispersal? *The Canadian Entomologist*, 119: 783–790.

Crosskey, R. W., 1990: *The Natural History of Blackflies*. Chichester, England: John Wiley & Sons, 711 pp.

Downes, J. A., 1965: Adaptations of insects in the Arctic. *Review of Entomology*, 10: 257–274.

Finn, D. S., and Adler, P. H., 2006: Population genetic structure of a rare high-elevation black fly, *Metacnephia coloradensis*, occupying Colorado lake outlet streams. *Freshwater Biology*, 51: 2240–2251.

Finn, D. S., and Poff, N. L., 2005: Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology*, 50: 243–261.

Finn, D. S., Theobald, D. M., Black, W. C., and Poff, N. L., 2006: Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology*, 15: 3553–3566.

Gibbins, C. N., Dilks, C. F., Malcolm, R., Soulsby, C., and Juggins, S., 2001: Invertebrate communities and hydrological variation in Cairngorm mountain streams. *Hydrobiologia*, 462: 205–219.

Greenland, D., and Losleben, M., 2001: Climate. *In* Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and function of an alpine ecosystem: Niwot Ridge, Colorado*. New York: Oxford University Press, 15–31.

Hauer, F. R., Stanford, J. A., and Lorang, M. S., 2007: Pattern and process in Northern Rocky Mountain headwaters: ecological linkages in the headwaters of the Crown of the Continent. *Journal of the American Water Resources Association*, 43: 104–117.

Hughes, J. M., Mather, P. B., Hillyer, M. J., Cleary, C., and Peckarsky, B., 2003: Genetic structure in a montane mayfly *Baetis bicaudatus* (Ephemeroptera: Baetidae), from the Rocky Mountains, Colorado. *Freshwater Biology*, 48: 2149–2162.

IPCC, 2001, *Climate change 2001: impacts, adaptation, and vulnerability*, Houghton, J. T., et al. (2001). New York: Cambridge University Press, 881 pp.

Jackson, J. K., and Resh, V. H., 1989: Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. *Environmental Entomology*, 18: 278–283.

Kovats, Z. E., Ciborowski, J. J. H., and Corkum, L. D., 1996: Inland dispersal of adult aquatic insects. *Freshwater Biology*, 36: 265–276.

Kuusela, K., and Huusko, A., 1996: Post-emergence migration of stoneflies (Plecoptera) into the nearby forest. *Ecological Entomology*, 21: 171–177.

Mackay, R. J., 1992: Colonization by lotic macroinvertebrates—A review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 617–628.

Milner, A. M., Conn, S. C., and Brown, L. E., 2006: Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: implications for biological monitoring. *Freshwater Biology*, 51: 373–387.

Nakano, S., and Murakami, M., 2001: Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences*, 98: 166–170.

Nilsson, A. N., Pettersson, R. B., and Lemdahl, G., 1993: Macroptery in altitudinal specialists versus brachyptery in generalists: a paradox of alpine Scandinavian carabid beetles (Coleoptera, Carabidae). *Journal of Biogeography*, 20: 227–234.

Palmer, M. A., Allan, J. D., and Butman, C. A., 1996: Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution*, 11: 322–326.

Petersen, I., Winterbottom, J. H., Orton, S., Friberg, N., Hildrew, A. G., Spiers, D. C., and Gurney, W. S. C., 1999: Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. *Freshwater Biology*, 42: 401–416.

Petersen, I., Masters, Z., Hildrew, A. G., and Ormerod, S. J., 2004: Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, 41: 934–950.

Poff, N. L., and Ward, J. V., 1989: Implications of streamflow variability and predictability for lotic community structure—A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 1805–1818.

Pritchard, G., and Zloty, J., 1994: Life histories of two *Ameletus* mayflies (Ephemeroptera) in two mountain streams: the influence of temperature, body size, and parasitism. *Journal of the North American Benthological Society*, 13: 557–568.

Rankin, M. A., and Burchsted, J. C. A., 1992: The cost of migration in insects. *Annual Review of Entomology*, 37: 533–559.

Rothfels, K., 1981: Cytological approaches to the study of blackfly systematics and evolution. *In* Stock, M. W. (ed.), *Application of Genetics and Cytology in Insect Systematics and Evolution*. Moscow, ID: Forest, Wildlife and Range Experiment Station, University of Idaho, 67–83.

Snyder, T. P., and Linton, M. C., 1984: Population structure in black flies: allozymic and morphological estimates for *Prosimulium mixtum* and *P. fuscum* (Diptera: Simuliidae). *Evolution*, 38: 942–956.

Sode, A., and Wiberg-Larsen, P., 1993: Dispersal of adult Trichoptera at a Danish forest brook. *Freshwater Biology*, 30: 439–446.

Sueker, J. K., Ryan, J. N., Kendall, C., and Jarrett, R. D., 2000: Determination of hydrologic pathways during snowmelt for alpine/subalpine basins, Rocky Mountain National Park, Colorado. *Water Resources Research*, 36: 63–75.

Svensson, B. W., 1974: Population movements of adult Trichoptera at a south Swedish stream. *Oikos*, 25: 157–175.

Vannote, R. L., and Sweeney, B. W., 1980: Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, 115: 667–695.

Walker, M. D., Walker, D. A., Welker, J. M., Arft, A. M., Bardsley, T., Brooks, P. D., Fahnestock, J. T., Jones, M. H., Losleben, M., Parsons, A. N., Seastedt, T. R., and Turner, P. L., 1999: Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, 13: 2315–2330.

Ward, J. V., 1986: Altitudinal zonation in a Rocky Mountain stream. *Archiv für Hyrdrobiologie, Supplement*, 74: 133–199.

Ward, J. V., 1994: Ecology of alpine streams. *Freshwater Biology*, 32: 277–294.

Waringer, J. A., 1991: Phenology and the influence of meteorological parameters on the catching success of light-trapping for Trichoptera. *Freshwater Biology*, 25: 307–319.

Welker, J. M., Bowman, W. D., and Seastedt, T. R., 2001: Environmental change and future directions in alpine research. *In* Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and function of an alpine ecosystem: Niwot Ridge, Colorado*. New York: Oxford University Press, 304–322.

Wilcock, H. R., Hildrew, A. G., and Nichols, R. A., 2001: Genetic differentiation of a European caddisfly: past and present gene flow among fragmented larval habitats. *Molecular Ecology*, 10: 1821–1834.

Zar, J. H., 1996: *Biostatistical Analysis. 3rd edition*. Upper Saddle River, NJ: Prentice Hall, 662 pp.