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PRIMARY RESEARCH PAPER

Effects of thermal regime on mayfly assemblages in mountain streams

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Abstract The variation in thermal regime and elevation among streams in the Sawtooth Mountains of Idaho, USA was used to test hypotheses about forces structuring larval mayfly assemblages. Sites above and below lakes were included to maximize variation in thermal regime. Forty-five sites were sampled for mayfly larvae and their summer thermal regime was measured. Ordination methods were used to analyze variation in the mayfly assemblages. Principal components analysis showed that mayfly assemblages were strongly and consistently affected by lakes within the stream system, apparently through the effects of lakes on stream temperature. Redundancy analysis explained 51% of the variation in assemblages and identified maximum water temperature and elevation as strong predictors of mayfly assemblages. Elevation influenced assemblage structure independently of summer maximum water temperature, suggesting that air temperature or some other elevation-dependent feature is also important. As predicted by the River Continuum Concept, mayfly diversity increased with increasing maximum daily range in temperature.

Keywords Temperature · Ephemeroptera · Mountain streams · Lake outlets · Elevation · Daily temperature range

Introduction

Stream ecologists have been building their understanding of controls on macroinvertebrate assemblage structure for several decades. Much of this work has focused on small-scale distribution patterns, or on longitudinal patterns in individual rivers. Recently, increasing interest in landscape ecology has led to the realization that patterns in distributions and diversity will require regional-scale explanations (Vinson & Hawkins, 1998; Li et al., 2001; Wright & Li, 2002; Parsons et al., 2003). For example, community structure is likely to be the result of both continuous gradients and discontinuous (patchy) processes at multiple scales (Wright & Li, 2002). As the geomorphic properties, ecosystem functions, and spatial scales tend to be confounded among several sites within one portion of a river basin, replication across streams is needed to better understand macroinvertebrate diversity and distributions. However, even with replication, large-scale studies can be difficult to interpret due to correlations among factors such as altitude, stream size, and temperature (Hawkins et al., 1997).

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Mountain streams provide ideal places to test for the effects of physical factors on biotic assemblages (Minshall et al., 1985; Finn & Poff, 2005). Malmqvist (2002) proposed using "natural experiments" on environmentally steep gradients to reduce confounding of some of these factors. In many glacially altered mountain regions, there are streams with different thermal and ecosystem properties due to lakes within the stream networks. The goal of my study was to use lake-stream interactions to study the effects of altitude, thermal properties, stream order, and spatial scale on mayflies. Lakes alter ecosystem factors such as temperature, flow, primary productivity and nutrient concentrations and cycling rates (Kling et al., 2000; Wurtsbaugh et al., 2005; Arp et al., 2006). These effects should vary depending on the size of the lakes and distance downstream from the lake. The longitudinal placement of these factors within the watershed also generates variability. Lakes cause ecosystem factors to vary substantially within small spatial distances (inlet vs. outlet of lake). Lakes thus can be used to separate the spatial distance between sampling points from the ecosystem factors that influence the distribution of the biota.

Natural lake outlet streams have been studied because of their unusual assemblages of insects, with most of the studies focusing on the high densities of filter feeding invertebrates (Perry & Sheldon, 1986; Wotton, 1988; Robinson & Minshall, 1990; Richardson & Mackay, 1991; Malmqvist & Eriksson, 1995). The role of thermal regime at lake outlets has been discussed (Ward & Stanford, 1982; Wotton, 1995), but seldom investigated through comparison of multiple lake outlets. Harding (1992) collected macroinvertebrates and measured mean temperature and annual temperature range in the inlets and outlets of three lakes in New Zealand, but no trend was evident for effects of either of temperature or annual temperature range on mayfly diversity. Harding (1994) compared 20 lake outlets in New Zealand, but temperature was measured only once at each site and was not significantly correlated with the ordination axes for the invertebrate assemblages. Hieber et al. (2005) suggested that the higher mean temperature of lake outlets contributed to dominance of non-insect taxa in alpine lake outlet streams.

Sweeney (1978) and Vannote et al. (1980) proposed that the diversity of stream organisms should be highest in streams with the highest daily fluctuation in temperature, because more species will experience optimal conditions during a day than in streams with more stable temperatures. This portion of the River Continuum Concept has not been adequately tested (Vinson & Hawkins, 1998). These predictions are general enough that they could apply to either the whole community or to taxonomic subsets of the community (including macroinvertebrates or individual insect orders). Kamler (1965) measured temperature variation in a single day at each of eight stream sites and compared this to the diversity of Ephemeroptera and Plecoptera. She found a trend toward more Ephemeroptera species and fewer Plecoptera species in the larger streams that had higher thermal variability (and which were also warmer). Brussock & Brown (1991) estimated diel temperature variation from weekly readings of maximum-minimum thermometers at five sites (stream orders 1–5) in Arkansas, USA, and then compared this to richness of macroinvertebrates. They suggested that macroinvertebrate richness declines as thermal variability decreases, but this conclusion was based on five sites in the same stream. Two studies support an alternative hypothesis that macroinvertebrate diversity increases with maximum temperature (Jacobsen et al., 1997; Miserendino, 2001) and Sponseller et al. (2001) found a decrease in diversity with increasing maximum temperature, but none of these studies measured temperature variation.

The goal of this study was to analyze mayfly (Ephemeroptera) assemblages from mountain streams to compare sites with a wide variety of thermal regimes and thus test these main hypotheses:

(1) Lakes, through their effects on stream temperature, alter the composition of mayfly assemblages. This study focused on mayflies because they are abundant, diverse, are not filter feeders, and in these streams are fairly consistent in their functional role as either scrapers or collector-gatherers (Edmunds & Waltz, 1996).

(2) Biodiversity of mayflies in streams increases with maximum diel temperature range, as predicted by the River Continuum Concept (Vannote et al., 1980).

Materials and methods

A total of 45 sites were selected in the Sawtooth Mountains of Idaho, USA (Fig. 1, Table 1). Sites were selected to represent a range of elevations and

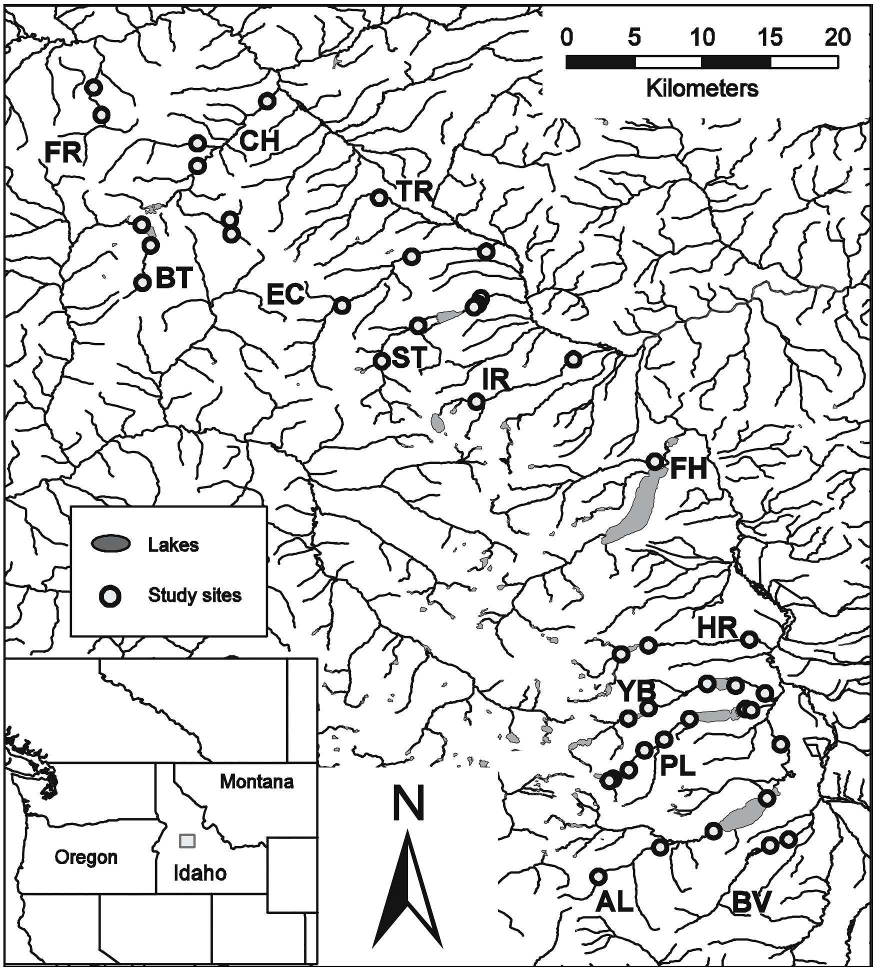

Fig. 1 Location of study sites in the Sawtooth Mountains, Idaho, USA. Inset shows location of study region in the northwestern USA. Two-letter codes indicate stream name as in Table 1

locations relative to lakes (above lakes, below lakes, and in streams without lakes) and to include sites already chosen in a large study of nutrient cycling and hydrology (Wurtsbaugh et al., 2005; Arp et al., 2006). Elevation ranged from 1950 m to 2700 m above sea level. No information on aquatic invertebrate distributions was used prior to selection of the sites. Most of the sites were located on the east side of the Sawtooth range, where many of the streams flow in to the Salmon River, but some sites were within the Middle Fork Salmon and Payette River drainages at the northern end of the Sawtooth range. The maximum distance between two sites was 66 km, between the northernmost site and the southernmost site. The number of sites within a local basin ranged from 1 to 8 (Tables 1, 2). All sites were at least 0.5 km apart, with two exceptions: an invertebrate sample was taken at site ST4 in the stream reach immediately above the site with the temperature logger and PL8 was located 0.5 km downstream from site PL 7. These were used to assess variation due to sampling and due to the smaller differences expected within short stream reaches. The temperature for these sites was assumed to be similar to the adjacent sites. Sites were designated as lake outlets if they were within 1 km of the lake boundary, and these sites were always within stream reaches with steep enough gradients to produce riffle habitats.

Invertebrate samples were collected between July 12 and August 11, 2004. Since the goal of the study was to compare assemblages among sites, sampling was standardized as follows so that samples would represent riffle habitats for an entire site. At each site, two Surber samples (area of 0.093 m^2 each, mesh size 0.5 mm) were taken at randomly chosen locations from each of four riffles within a stream reach

Table 1 Locations of sampling sites

Major drainage	Local drainage (abbreviation)	Number of lakes	Number of sites
Salmon	Beaver Creek (BV)	0	2
	Alturas Lake (AL)	2	5
	Pettit Lake (PL)	3	8
	Yellow Belly Lake (YB)	3	5
	Hell Roaring Lake (HR)	2	3
	Fishhook Creek (FH)	1	1
	Iron Creek (IR)	1	2
	Stanley Lake (ST)	1	5
	Elk Creek (EC)	0	3
	Trap Creek (TR)	0	1
Payette	Bull Trout Lake (BT)	1	3
Middle Fork Salmon	Cape Horn Creek (CH)	0	5
	Fir Creek (FR)	0	2

Streams are listed from south to north in each major drainage. Number of lakes refers to the number of large lakes upstream of the lowest site. Sites within local drainages were numbered from highest elevation to lowest

of approximately 100 m. All eight samples were pooled to form the sample for the site (total area 0.74 m^2). This sampling method was chosen based on previous work showing how sample size affects comparisons of invertebrate assemblages (Vinson & Hawkins, 1996; Cao et al., 2002). Elevation was estimated from topographic maps and GPS readings. Stream order was estimated from USGS topographic maps at a scale of 1:100,000.

I measured temperature at a minimum of 1.5-hour intervals at all sites using Hobo (Onset Co., Pocasset, Massachusetts, USA) and iButton (Maxim-Dallas Co., Dallas, Texas, USA) thermistors. These devices had temperature resolutions of 0.2 and 0.5°C, respectively. Statistics were based on the period from July 10 to August 19, 2004 because this is the time period for which data were available for all sites. The highest annual temperature for these streams normally occurs within this time period (J. Garrett, unpubl. data). I calculated maximum temperature and maximum daily range for each site because these were a priori predictors of invertebrate assemblages (Vannote et al., 1980; Ward & Stanford, 1982). Mean temperature and minimum temperature for the study period were both highly correlated with maximum temperature ($r = 0.95$, $r = 0.86$, respectively; see Table 3) and were therefore not included in the analyses to avoid problems of multicollinearity.

I used a fixed-count method to standardize the number of invertebrates counted in a sample. A fixed-count of 500 individuals was chosen based on simulation results from Cao et al. (2002) and Doberstein et al. (2000). In the laboratory, samples were thoroughly mixed by floating in water within a 0.25 mm- mesh sieve and then split into halves repeatedly until a subsample that was estimated to have less than 500 insects was achieved. All invertebrates were removed from the subsample by hand under 7× magnification. Annelida and Sphaeridae (Mollusca) were removed but not included in the fixed-count because of their high abundances in some samples. Additional subsamples were counted to achieve total counts that ranged from 487 to 595 individuals. Analyses are based only on the mayflies from these samples. Mayflies were identified to genus using the key by Edmunds & Waltz (1996) and Adams (2004). I did not make species-level determinations in order to reduce processing time and because most early-instar mayflies cannot be identified beyond the genus level. Mayflies that were too small or damaged to identify to genus were not counted (<2% of individuals).

Mayfly assemblage structure

Principal components analysis (PCA) was used to reduce the dimensionality of the assemblage data so that mayfly assemblages could be more easily compared. Genera that contributed <1% of the total mayflies were not included in the ordinations. Mayfly densities were $\ln(x + 1)$-transformed before all analyses. In order to test whether the direction of lake effects was different from stream effects, I compared

Table 2 Environmental conditions for the 45 stream sites in the Sawtooth Mountains, Idaho

Site	Elevation (m)	Mean temp. (°C)	Max. temp. (°C)	Max. daily temp. range (°C)	Stream order
AL1	2290	8.6	12.6	6.4	1
AL2	2190	10.3	15.6	8.3	2
AL3	2140	10.5	15.0	7.0	3
AL4	2130	18.2	22.0	4.5	3
AL5	2120	17.8	25.6	13.0	4
BT1	2180	6.3	11.0	7.0	1
BT2	2130	6.0	11.0	7.5	2
BT3	2120	17.9	23.0	7.5	2
BV1	2240	11.9	17.1	7.8	2
BV2	2200	12.3	17.5	8.2	2
CH1	2200	7.9	11.5	6.5	1
CH2	2190	8.0	11.0	5.0	1
CH3	2090	9.3	12.5	5.5	2
CH4	2090	8.2	13.0	7.0	2
CH5	2050	10.5	17.0	10.5	3
EC1	2070	9.4	14.9	8.8	2
EC2	2050	13.6	19.0	10.1	2
EC3	2000	14.2	18.7	8.5	2
FH1	2010	10.5	14.0	6.5	2
FR1	2070	9.4	15.0	9.5	2
FR2	2050	9.7	15.5	10.0	2
HR1	2260	13.8	17.5	5.4	2
HR2	2250	17.0	21.0	5.3	2
HR3	2180	16.3	22.4	11.1	2
IR1	2130	10.9	14.0	4.0	2
IR2	1950	11.4	15.5	7.5	2
PL1	2700	15.4	21.0	7.0	1
PL2	2630	14.1	20.5	9.5	1
PL3	2620	16.2	20.5	6.0	2
PL4	2450	13.9	18.0	6.0	2
PL5	2280	11.5	15.5	6.5	2
PL6	2150	11.3	14.0	4.0	2
PL7	2130	18.8	23.5	7.0	2
PL8	2120	18.8	23.5	7.0	2
ST1	2100	10.4	14.5	6.5	2
ST2	2000	10.2	15.5	7.5	2
ST3	1990	18.2	22.5	7.5	2
ST4	1980	18.0	23.5	10.0	2
ST5	1980	18.0	23.5	10.0	2
TR1	2060	11.0	15.0	7.0	2
YB1	2370	12.9	17.0	7.0	2
YB2	2360	16.1	18.5	3.0	2
YB3	2170	15.3	19.0	6.0	2

Table 2 continued

Site	Elevation (m)	Mean temp. (°C)	Max. temp. (°C)	Max. daily temp. range (°C)	Stream order
YB4	2160	18.3	20.0	2.5	2
YB5	2090	17.9	22.5	8.4	2

See Table 1 for explanation of site names

Table 3 Pearson correlation coefficients for environmental variables of stream sites

	Mean temp. (°C)	Max. temp. (°C)	Max. daily temp. range (°C)	Stream order
Elevation	0.15	0.14	−0.22	−0.37*
Mean Temp. (°C)		0.95*	0.02	0.32*
Max. Temp. (°C)			0.29	0.38*
Max. Daily Temp. Range (°C)				0.28

Temperature measurements are for the period July 10–August 19 2004. Correlations that were significant at the $P < 0.05$ level are noted with an asterisk

the direction of the vectors on the plot of the first two principal components between pairs of upstream and downstream sites. Eight site pairs with a lake were compared to eight site pairs without a lake. Sites were chosen such that no site was used twice within the analysis. The distribution of the directions of the vectors for the two groups were compared with Watson's test (Zar, 1996), implemented in the CircStats package for R (Version 0.2–1).

I used redundancy analysis (RDA), a method of direct gradient analysis, to explore the influence of environmental variables on the mayfly assemblages. RDA is based on the assumption that species respond linearly to environmental gradients (Jongman et al., 1995), which was expected based on the small geographic area of the study and supported by inspection of plots of species density vs. the environmental factors. Maximum temperature, maximum diel range in temperature, elevation, and stream order were the physical factors included in the analysis. I repeated the RDA analysis for 24 sites below lakes, and included distance below a lake as an additional physical factor. RDA and PCA were computed using the Vegan package for R (Version 1.8–2).

Effects on mayfly diversity

Before testing for effects on mayfly diversity, I tested for effects of the number of mayflies counted from the samples on diversity. Regression of number of genera on the number counted showed that sites with low-counts also had low-diversity. Therefore, six sites with less than 60 mayflies counted were removed from the analysis, eliminating the relationship between number counted and number of genera ($R^2 = 0.004$). Linear regression on the remaining sites was used to test the hypotheses that maximum daily temperature range or maximum temperature affect diversity. These results were also compared to regressions without the six sites removed.

As an additional test of the same hypotheses, I used data collected during another study of streams of central Idaho (Ott & Maret, 2003). This study had a broader geographic range and did not include lake outlets. The authors sampled 34 sites in second- through fifth-order streams. Temperature was measured at most sites from July 1 to September 30, 2001. At each site, the authors used a 0.425-mm mesh net to collect a kick sample of 0.25 m^2 from each of three riffle areas. Mayfly diversity in their study was based on both genus- and species-level identifications. The authors did not analyze their data with respect to factors influencing biodiversity.

Results

Variation in thermal regime among sites

The sites chosen had a wide variety of temperature regimes, based on the results for maximum temperate

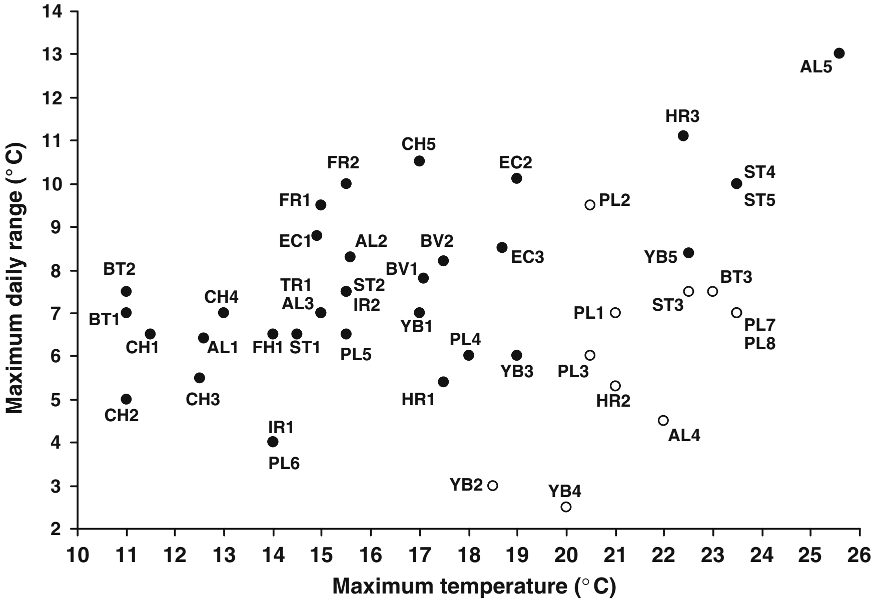

Fig. 2 Thermal regime of the sites based on maximum temperature and maximum daily range during the study period of July 10–August 19 2004. Sites within 1 km below a lake are shown as empty circles, all other sites are filled circles. Two-letter codes represent local drainages as in Table 1, with numbers increasing downstream within a drainage

and maximum daily range (Fig. 2). The correlation between these two variables was $r = 0.29$ ($r^2 = 0.09$, $P = 0.06$, df $= 41$) using all thermistor sites. These data suggest that the selection of sample sites was effective in producing sites with a low level of dependence in maximum temperature and maximum daily range. Elevation was also only weakly correlated with maximum temperature ($r = 0.14$, $r^2 = 0.02$, $P = 0.36$, df $= 41$) and with maximum daily temperature range ($r = -0.22$, $r^2 = 0.05$, $P = 0.16$, df $= 41$). Correlations among the environmental variables are shown in Table 3.

Mayfly assemblage structure

A total of 6929 individuals in 15 genera of mayflies were identified. Four of these genera comprised together less than 1% of the total, and were excluded from the multivariate analyses. The Supplementary material provides densities of the 11 common genera. Densities of five genera (*Cinygmula, Epeorus, Rhithrogena, Drunella*, and *Ameletus)* were significantly negatively correlated with maximum temperature ($P < 0.05$), while three genera (*Diphetor, Paraleptophlebia*, and *Attenella)* were significantly positively correlated with maximum temperature (Fig. 3). Three genera (*Baetis, Acentrella*, and *Serratella*) showed no dependence on maximum temperature.

The first two axes of the PCA of the 11 common genera explained 58% of the variance in abundance. PC1 explained 44% of the variance, and PC2 explained 14%. The third PC axis explained an additional 11% of the variance but was not analyzed further. The first axis was positively correlated with abundance of *Diphetor*, *Paraleptophlebia*, and *Attenella*, and most strongly negatively correlated with the abundance of *Cinygmula*, *Epeorus*, and *Rhithrogena*. *Acentrella* and *Serratella* abundances were negatively correlated with the second PC axis (see RDA results below). Other taxa were closer to the center of the PCA axes. Sites within a stream were often widely distributed across the PC axes, with lake outlets all occurring to the right on axis 1 and sites higher in the landscape located higher on axis 2 (Fig. 4A). Lake outlets did not form a small cluster of sites but instead were widely distributed on axis 2.

The eight pairs of lake-influenced stream reaches and reaches without lakes were plotted based on their first two principal components (Fig. 4B). This plot shows that lakes have a fairly consistent direction in their effect on the mayfly assemblages, despite the variation in assemblages upstream of the lakes. The vectors for the pairs of sites with lakes were significantly different in direction than the vectors for the pairs of sites without lakes (Watson's $U^2 = 0.19$, $P < 0.05$).

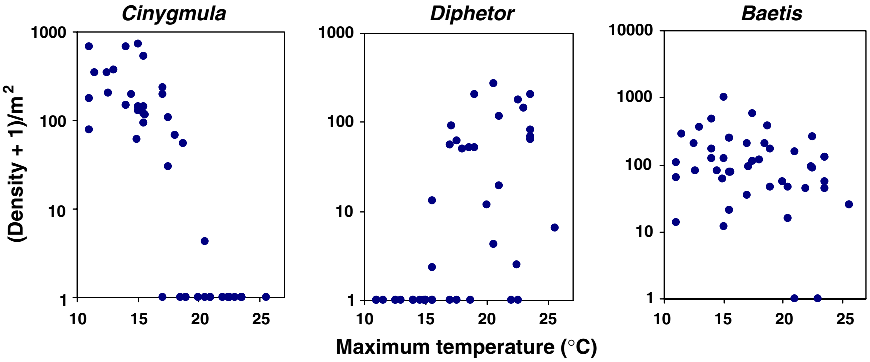

Fig. 3 Density of three of the abundant mayfly taxa relative to maximum temperature

Redundancy analysis explained 51% of the variation in mayfly assemblages, with the first two axes explaining 38% and 9% of the variance (Fig. 5). The arrangement of sites and species on the first two RDA axes was very similar to the arrangement on the PCA axes (Fig. 4A). Maximum temperature was correlated with the first RDA axis. The second axis was most strongly correlated with elevation and stream order. As in the PCA analysis, sites below lakes had higher scores on the first axis than sites above lakes or in streams without lakes. When RDA was used on 24 sites below lakes and distance below lakes was included as a physical factor, the results were very similar to those of Fig. 5, with the distance arrow pointing in the opposite direction of the maximum temperature arrow and lake outlet assemblages not forming a cluster.

Effects on mayfly diversity

The hypothesis that mayfly diversity (number of genera) would increase with increasing maximum daily range in temperature was supported by the regression analysis ($y = 0.35x + 4.8$, $P = 0.009$), however, this variable only explained 18% of the variance in mayfly diversity (Fig. 6A). A similar effect was evident when the Shannon diversity index for each site was used ($y = 0.07x + 1.0$, $P = 0.005$, $R^2 = 0.21$). There was no effect of maximum temperature on number of mayfly genera ($P = 0.98$). The results were similar when the six low-count sites were not removed ($P = 0.03$ for maximum daily range and $P = 0.45$ for maximum temperature). The data from Ott & Maret (2003) showed similar patterns in mayfly diversity (Fig. 6B). The number of mayfly taxa was significantly related to maximum daily temperature range ($y = 0.50x + 7.7$, $P = 0.02$, $R^2 = 0.17$), but was not predicted by maximum temperature ($P = 0.09$). Replacing the number of mayfly taxa with the number of mayfly genera gave similar results for maximum daily temperature range ($y = 0.28x + 6.0$, $P = 0.01$, $R^2 = 0.19$), despite the reduced taxonomic resolution. The total number of all invertebrate taxa was not significantly related to maximum daily temperature range ($P = 0.30$) or maximum temperature ($P = 0.11$).

Discussion

The PCA and RDA ordinations supported the first hypothesis that lakes have strong effects on the mayfly assemblages downstream. The lake outlet assemblages were not uniform, however. Mayfly assemblages of lake outlets higher in the stream network were as different from those of low-elevation lakes as assemblages of high-elevation streams were from those of low-elevation streams. This suggests that for mayflies there is not one particular lake outlet assemblage that dominates these habitats. The effects of lakes were associated with increased temperature in these streams (Figs. 4, 5). Lakes are also known to alter the variability in flow at downstream sites by buffering the effects of heavy precipitation upstream (Richardson & Mackay, 1991; Arp et al., 2006), but the effects of this on insects are unknown.

The mountain streams in this study exhibited a wide range in thermal regimes, from those with consistent low temperatures to those with temperatures that were high and either variable or constant (Fig. 2). Sites directly below lakes had higher maximum temperature and lower daily fluctuations

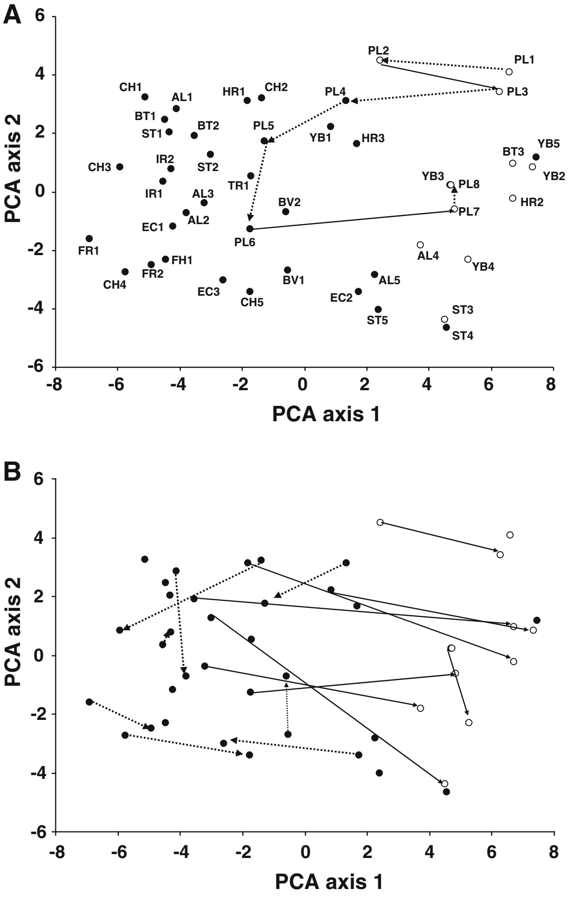

Fig. 4 Effects of landscape structure on principal components of mayfly assemblages. Sites within 1 km below a lake are shown as empty circles, all other sites are filled circles. Solid arrows show the effect of a lake between the stream sites, while dashed arrows indicate no lake between sites. (**A**) First two principal components for the mayfly assemblage of each site. Two-letter codes represent local drainages as in Table 1, with numbers increasing downstream within a drainage. The connections within the Pettit Lake drainage are shown. (**B**) PCA plot showing effects of eight lakes and eight non-lake-stream segments. Direction of arrows was significantly different between the two groups (see Results)

than sites above lakes, and sites further below the large lower-elevation lakes had even higher maximum temperature and daily range. Thus these sites provide a useful test for the ability of temperature to alter mayfly assemblages. The results indicate that taxa such as *Epeorus* and *Cinygmula* are more abundant in cold water and taxa such as *Diphetor* and *Paraleptophlebia* are more abundant in warm water. Despite the possible influences of other factors associated with the lake outflow, this study and others (Hawkins et al., 1997; Brittain et al., 2003; Haidekker & Hering, 2007) show that temperature is an important predictor for mayfly assemblages, due to variation in thermal preferences among the genera within this order.

The RDA results show that in addition to maximum temperature, elevation is also correlated with mayfly assemblages in mountain areas, as has been found in other studies (Finn & Poff, 2005). In my study, stream temperatures were not strongly correlated with elevation, largely because lakes resulted in higher temperatures whether they were high or low in the watershed. However, I did not measure air temperature, which would be expected to be highly correlated with elevation and not affected much by lakes. While the terrestrial stage of mayflies is short, the influence of air temperature on the dispersal and mating success of mayflies may be substantial. Briers et al. (2003) showed that air temperature affected flight activity of stoneflies. Based on four sites in the central Idaho region from a network of mountain weather stations (USDA SNOTEL, unpubl. data), the environmental lapse rate for July 2004 maximum air temperature was −8.6°C/km. Thus maximum air temperature should vary by approximately 6.5°C between the highest and lowest sites in this study, compared to the range of 15°C in maximum stream temperature. Studies in which both air temperature and water temperature are measured, and which utilize sites of similar elevation but different aquatic thermal regime are needed to understand the relative roles of air temperature and water temperature. Another possible explanation for the patterns due to elevation could be effects of the riparian vegetation, as this would also be strongly correlated with elevation.

One of the problems in interpreting the literature on the factors that influence macroinvertebrate assemblages is that each study includes a different set of environmental factors and a different geographic combination of sites. Both of these factors will affect the results of the study. In this study, the first two PCA axes explained 58% of the variance in assemblage structure, leaving 42% of the variance that was due to sampling error, nonlinear relationships, or to factors that are unique to each site. By comparison, the first two RDA axes explained 47% of the variance. As the RDA axes are constrained to be linear combinations of the environmental variables, the reduction in explained variance can be interpreted as variance in assemblages

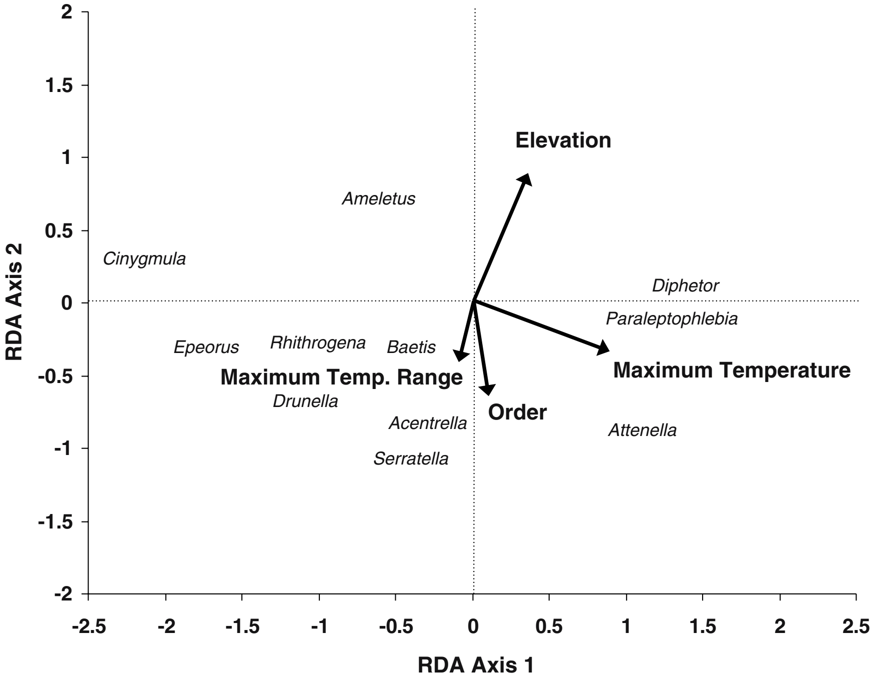

Fig. 5 Plot of RDA scores for species and constraining variables. The first axis explained 38% of the variance in mayfly abundance and the second axis explained 9%. Maximum temperature range indicates the maximum range in daily temperature during the study. Order denotes stream order

that is detectable but not related to the environmental variables that were measured. Therefore, a small difference suggests that most of the explanatory variables (or ones highly correlated with them) have been included (Jongman et al., 1995). For this study, it appears that most of the explanatory variables are included or are highly correlated with those that are included. Haidekker & Hering (2007) is the only similar study in which this comparison can be made. In their study of Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera (EPTC) in 20 mountain streams in Germany, they measured temperature continuously for one year and found that "cumulative degree days for summer" was the best correlate of the insect assemblages, although maximum temperature was also highly correlated with assemblage structure. Their first two PCA axes explained 45% of the variation in assemblages, and the first two axes of an RDA (in which the first axis was constrained to be the temperature variable) explained 41% of the variation. Thus, Haidekker & Hering (2007) and this study both suggest that a large portion of the variance in assemblages can be explained by measuring thermal regime. By comparison, the first two axes of RDA explained 27% in Finn & Poff (2005) despite a larger number of environmental variables, and the first two axes of canonical correspondence analysis explained 23% of the variation in Miserendino (2001). Due to the natural variability in stream temperature, continuous measurements using data loggers will decrease

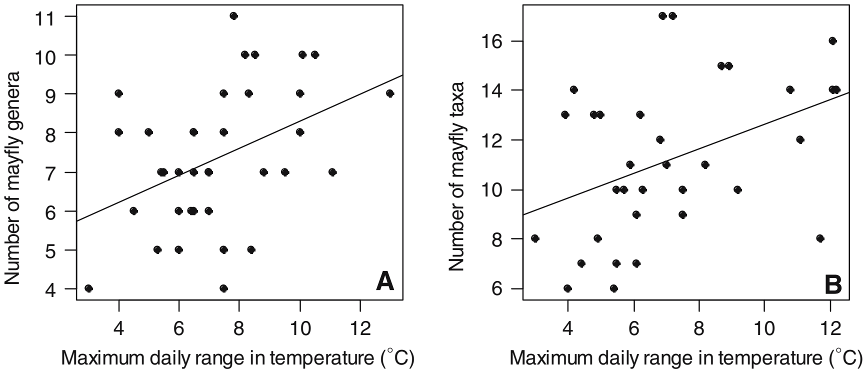

Fig. 6 Relationships between maximum daily range in temperature and mayfly diversity (**A**) for this study and (**B**) for data from Ott & Maret (2003). Lines of best fit by linear regression are shown

measurement error compared to single-sample temperature measurements (see Yuan, 2007), and should increase our understanding of how temperature affects stream invertebrates. The extra visits required to each site to deploy and retrieve the loggers are probably the main impediments in most studies to collecting this data.

As thermal regime, elevation, and stream order explained a large portion of the variation in the mayfly assemblages in this study, and because the sites included a wide variety of stream types, it seems unlikely that the correlation of assemblage structure and thermal regime is due to correlation with other factors such as flow variability or nutrient concentrations that were not measured in this experiment. However, there may be additional effects of thermal regime beyond the period of summer temperatures measured in this study that could affect mayfly assemblages or diversity. Haidekker & Herring (2007) calculated nine different temperature parameters, including winter, summer, spring, and annual degree days, but found that the parameters associated with summer (including degree days, mean temperature, and maximum temperature) had the highest correlation with species composition. They did not find any correlations with the magnitude of daily temperature range. A possible explanation is that their streams had a lower range of diel thermal variation (range 2.6–7.9°C) than the Idaho streams in this study (range 2.5–13.0°C) and that of Ott & Maret (2003) (range 3.0–12.0°C).

This study provides the first direct test of Vannote et al.'s (1980) prediction that diversity should be highest in streams with high daily fluctuations in temperature. Despite different methods, stream types, and locations, there was a striking correspondence in the effects of maximum daily temperature range on mayfly diversity between this study and my analysis of the data from Ott & Maret (2003). Analysis of the Ott & Maret (2003) data also show that generic-level taxonomic resolution is sufficient for detecting this pattern in mayflies. However, in both studies only about 20% of the variability in mayfly diversity was explained, demonstrating that other factors are also important in determining diversity. The lack of tests of this important component of the River Continuum Concept has probably been due to the difficulty of obtaining accurate data on thermal regime. Further tests are necessary to confirm that the lower thermal variability expected in large streams is also associated with decreases in mayfly diversity.

Conclusion

While this study is similar to most other studies of aquatic insect assemblages in using correlation between environmental variables and assemblage data to try to explain patterns in assemblages, it shows the advantages that can be gained by using landscape features such as lakes to study large changes in abiotic factors over short distances. Further work on lake outlet streams should include more detailed measurements of environmental factors to better understand the forces structuring the assemblages in these unique habitats, which should increase our understanding of other stream habitats as well. Maximum daily temperature range has been largely ignored as an important variable, but it appears to be correlated with mayfly diversity in mountain streams and should be studied further, especially as climate changes in the future.

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