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Channel morphology, water temperature, and assemblage structure of stream insects

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Abstract. Temperature is known to be an important mechanism affecting the growth and distribution of stream insects. However, little information exists that describes how variable temperatures are among streams of similar size, especially in physically heterogeneous landscapes.

We measured summer daytime temperature and the structure of riffle benthic insect assemblages from 45 montane streams in California. Summer stream temperature was nearly randomly distributed across large-scale geographic gradients of latitude (6°) and elevation (2000 m). The lack of geographic trends in summertime stream temperature appeared to be caused by the strong relationship between local channel morphology and summer water temperature. Mean daytime water temperature was most strongly related to the % of the channel present as pools, which did not vary systematically with either latitude or elevation.

We used multiple multivariate regression analysis, non-metric multidimensional scaling (NMDS), and graphical techniques to both quantify differences in insect assemblage structure among streams and to determine the degree to which assemblage structure was related to temperature. NMDS analyses were conducted on 3 similarity matrices based on: 1) presence and absence of all aquatic insect taxa encountered during the study, 2) densities of the 16 most numerically abundant taxa, and 3) population biomasses of the 16 most common taxa. All 3 analyses showed that variation in assemblage structure among streams was significantly related to temperature, although assemblage structure was most strongly related to sampling date—a consequence of sampling over a 98-d period. Temperature probably influenced assemblage structure in 2 ways: 1) by influencing developmental rates of individual taxa and overall assemblage phenology, thus affecting the relative abundances of taxa found on a specific sampling date, and 2) by excluding taxa unable to tolerate certain temperature ranges. Because of the strong dependency of assemblage structure on temperature and the lack of strong geographic trends in temperature among these streams, much of the measured variation in assemblage structure appeared to be unrelated to latitude or elevation. These results have important implications for both our understanding of natural biogeographic patterns of lotic organisms and our ability to detect and model the effects of climate change and other thermal alterations on stream ecosystems.

Key words: aquatic insects, streams, assemblage structure, temperature, channel morphology, distribution, climate change, geographic gradients, landscape ecology, multivariate analysis, non-metric multidimensional scaling, California.

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Differences in temperature regime among streams are thought to be responsible for much of the geographic variation in the presence and abundance of benthic insects (Vannote and Sweeney 1980, Ward and Stanford 1982). Because insects are ectothermic, their physiology and fitness, and hence their abundance and dis-

tribution, should be strongly temperature dependent (Magnuson et al. 1979, Neill 1979, Vannote and Sweeney 1980, Cossins and Bowler 1987). Summer is an especially critical season for many stream insect populations in that 1) much of the biological production occurs when temperatures are highest (Benke 1993), and 2) the maximum temperature reached during summer may limit the occurrence of certain stream species (Vannote and Sweeney 1980, Matthews 1987, Cech et al. 1990).

At the spatial scale of a single stream, water temperature usually increases from source to mouth, and distinct longitudinal zonation of stream biota has been observed to parallel longitudinal shifts in stream temperature (Ide 1935, Hawkes 1975). The existence of such temperature gradients within streams provides 1 line of evidence in support of the idea that stream ecosystems are physical and ecological continua (Vannote et al. 1980, Minshall 1988).

At larger spatial scales, species distributions are known to vary with temperature along both elevational and latitudinal gradients (Vannote and Sweeney 1980, Ward 1985, Quinn and Hickey 1990, Marchant et al. 1994). Vannote and Sweeney (1980) described strong latitudinal patterns in which mean annual temperature (or annual accumulated degree-days) was highly correlated with latitude among streams and rivers in both the eastern ($r^2 = 0.88$) and central ($r^2 = 0.91$) United States (range of latitude $\sim 31^\circ$ to 48°N). These patterns have been used both to model the geographic ranges and emergence synchrony of several mayfly species in eastern North America (Vannote and Sweeney 1980, Newbold et al. 1994) and to predict the biotic consequences of potential changes in climate (Sweeney et al. 1992). However, too few studies have been conducted over large geographic areas to allow useful generalizations either about the magnitude of thermal variation among otherwise similar-sized streams or how this variation affects biota.

In this paper we examine how summertime water temperatures and the structure of benthic insect assemblages varied among 45 montane streams in California. Our specific objectives were to: 1) quantify variation in summer water temperature among streams, 2) determine which environmental factors were most strongly related to water temperature, 3) determine if differences in water temperature were significantly

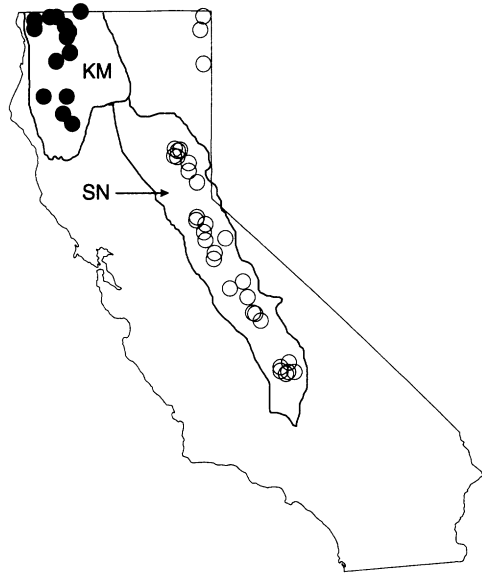


FIG. 1. Locations of the 45 study streams. All streams were 3rd or 4th order and drained mountainous landscapes within California. The streams in the northwestern part of the state (black symbols) are in the Klamath Mountain (KM) Ecoregion (Klamath and Shasta-Trinity Mountains). The 3 streams in the northeastern corner of the state are in the Eastern Cascades Slopes and Foothills Ecoregion (Warner Mountains) and were included with streams in the Sierra Nevada (SN) Ecoregion (white symbols) for this analysis. Approximate boundaries of the KM and SN ecoregions are shown and were redrawn based on original maps in Omernik (1987) and Barbour et al. (1997).

related to insect assemblage structure, and 4) determine if the type of data (presence or absence, densities, population biomasses) used in analyses affected interpretations of how assemblage structure was related to temperature.

Methods

Study streams

During the summers of 1988 and 1989 we sampled 3rd- and 4th-order (Strahler 1964) streams from 45 catchments in 3 mountainous ecoregions (sensu Omernik 1987 and Barbour et al. 1997) of California (Fig. 1): 28 streams in the Sierra Nevada Ecoregion (hereafter SN), 14 streams in the more densely forested Klamath Mountain Ecoregion (Klamath and Shasta-Trinity Mountains) in northwestern and northcentral

California; hereafter KM), and 3 streams in the Eastern Cascades Slopes and Foothills Ecoregion (Warner Mountains of eastern California), which were combined with the SN streams. Two streams in each ecoregion (KM and SN) were sampled in both 1988 and 1989, thereby providing 49 total observations. Study basins ranged from $\sim 36^\circ$ to 42°N latitude and from 250 to 2250 m in elevation. The predominant bedrock geology underlying these basins can vary considerably and includes granitic, volcanic, or sedimentary rock (Mount 1995). Like small catchments in most western mountain ranges, these basins have shallow soils and appear to have low potential for groundwater storage and delivery (van der Leeden et al. 1990). Most stream segments are constrained by nearby hillsides, floodplains are generally narrow (< 50 m), and stream bed material consists largely of cobbles and boulders.

Runoff in all of these streams is strongly unimodal, but streams differ in time of peak runoff (Cayan and Riddle 1993). In streams of the Sierra Nevada, Warner Mountains, Shasta-Trinity Mountains, and Klamath Mountains $> 50\%$ of total runoff is derived from snow that melts from early April to early June (Mount 1995). In lower-elevation streams of the north Coast Range, runoff is caused mainly by rainfall, and peak runoff typically occurs in February. Although these 2 types of streams differ in timing of peak runoff, all streams have relatively stable, low base flows from July through September.

The dominant land use in these basins is silviculture, and the proportion of the basin harvested for timber at the time of our study ranged from 0 to nearly 100%. Biotic structure appears to be only weakly related to the amount of land use in these basins and stream temperature was unrelated to land use (unpublished data, Hawkins et al. 1994). We have therefore assumed that the patterns reported here are largely natural in origin.

Sampling design

Streams were sampled each year from south to north in an attempt to collect biota at an approximately similar stage of phenology in all streams. Sampling began in mid-June in the southern Sierra Nevada and ended in mid-September near the Oregon border. We designed our sampling schedule based on the assump-

tions that 1) the relative abundances of species within a stream change in response to species-specific and temperature-sensitive seasonal schedules of hatching, growth, mortality, and emergence, and 2) streams exhibit a south-to-north gradient in the date they reach a given temperature. Both of these assumptions appear valid. Newbold et al. (1994) showed both patterns for eastern streams as measured by emergence dates of 8 mayfly species. In their study, it took ~ 6.5 d for a stream 1° north of another to reach the same temperature. Our sites spanned 6° of latitude, so we needed to sample all sites within ~ 39 d to theoretically control for seasonal shifts in assemblage structure related to phenology. However, our sampling took 98 d, so we were unable to completely compensate for these anticipated seasonal shifts. As a consequence, we expected some of the measured differences in assemblage structure among streams to be correlated with date of sampling. Furthermore, our sampling design confounded date and latitude as well as elevation and ecoregion.

Data collection

We quantified several environmental features potentially important to either stream temperature or stream insects. Latitude, base elevation, and azimuth for each stream channel were obtained from 7.5' topographic maps (US Geological Survey). Azimuth was measured as the angle (degrees) that the overall stream channel differed from due south, where due south = 0° , due west = $+90^\circ$, and due east = -90° (Bartholow 1989). For subsequent analyses, the absolute value of azimuth was used because streams with orientations of equal magnitude but different sign would generally receive the same amount of solar radiation. The % of stream shaded by riparian vegetation, riffle current velocity, channel slope, and riffle widths and depths were measured at ~ 30 locations within each stream channel. The proportion of each channel present as different habitat types (sensu Hawkins et al. 1993) was calculated from inventories of habitat lengths conducted between the 1st and last sampling point (6–10 km) of each channel. Habitat type was based on hydraulic and geomorphic criteria that distinguished different types of fast-water (riffle) and slow-water (pool) habitats. Summer base discharge was measured using the velocity-area method (Platts

et al. 1983) once near the most downstream sampling location.

Temperature was recorded hourly from ~0900 to 1800 h during each of the 8 d we sampled a stream, providing ~80 observations per stream. Mean, maximum, and minimum temperature values and temperature range were calculated from these data for the period of sampling. Because temperature measurements were taken during daylight hours, we refer to these estimates as daytime temperature (DT) values. We also estimated the mean DT, maximum DT, and DT range that each stream experienced on a common, midsummer date (15 July) by fitting the raw temperature estimates and median sampling date (day past 1 January) for each stream to a quadratic model, and then adding the residual variation for each stream (unaccounted for by the models) to model estimates for 15 July. Standardizing temperature estimates to a common date removed the potentially confounding effect of date on temperature values.

We collected 9 0.1-m² benthic samples (modified Surber sampler with 250- μ m-mesh net) from 6 to 17 riffles per stream to quantify species abundances and assemblage structure. Samples from each riffle were combined (0.9 m² sample/riffle) prior to preservation in 80% ethanol. Within each stream, riffles were sampled sequentially at ~600-m intervals along the main stream channel. Insect taxa were later identified to the lowest possible taxonomic level (species or genus), counted, and measured (length) to the nearest mm. Population biomass for each taxon was estimated by converting lengths to mass based on either published (Smock 1980, Meyer 1989) or our own empirically derived length-mass relationships, and then summing individual masses. Of the >200 invertebrate taxa (exclusive of chironomid midges) collected, we used 182 taxa of aquatic insects, identified to species or genus, in our analyses. Densities and biomasses of each taxon were expressed as catchment means calculated over the number of riffles sampled.

Analyses

Water temperature.—We determined which geographic and environmental factors were most strongly associated with variation in water temperature among streams by conducting sev-

eral stepwise multiple regression analyses. We regressed 15 July-adjusted estimates of mean DT (MDT15J), maximum DT (MxDT15J), minimum DT (MnDT15J), and DT range (RDT15J = maximum – minimum) against variables that were likely to be correlated with stream temperature—i.e., latitude, elevation, azimuth, catchment area, discharge, current velocity, channel slope, channel width, % of the channel shaded by riparian vegetation, and % of the channel present as pools.

To evaluate how well our short-term field measurements of temperature characterized overall thermal heterogeneity among sample streams, we compiled daily temperature records from 40 US Geological Survey gaging stations from California that met the following criteria: at least 1 y of continuous mean daily temperature records, the station was not near a dam or major diversion, and the elevation and latitude of the gage were known. We used these data to determine how strongly mean monthly summer temperature was related to latitude and elevation.

Insect assemblage structure.—We used 3 sets of analyses to test the hypothesis that assemblage structure would vary among streams as a function of temperature. First, we used multivariate multiple regressions, the regression equivalent of multivariate analysis of variance (Scheiner 1993) to describe how assemblage structure as a whole varied with independent variables of interest. These analyses also allow identification of those taxa that contribute most strongly to the overall relationships (Scheiner 1993).

Second, we used ordination scores derived from separate non-metric multidimensional scalings (NMDS) of abundance (density and biomass) and presence or absence data as response variables in a series of multivariate regressions identical to those used in the multiple multivariate regression analyses. NMDS is an indirect gradient analysis procedure (Jongman et al. 1987) that reduces the dimensionality of multivariate data and hence can facilitate its interpretation. Although no ordination procedure has been universally adopted by ecologists (Jongman et al. 1987), Minchin (1987) has shown that NMDS is a more robust method of indirect gradient analysis than principal components analysis or detrended correspondence analysis. NMDS reduces the dimensionality of multivariate data by describing major trends among sites

in the joint occurrence or abundance of taxa. Much of the variation in multivariate data is often captured in 2 or 3 derived axes (dimensions). Variation in axis scores among sites can then be related (statistically or graphically) to environmental variables to reveal patterns.

Third, we graphed how temperature, date of sampling, site latitude, and site elevation varied across a 2-dimensional NMDS ordination space. In conjunction with the graphical analyses, we calculated the extent to which variation across the 2-dimensional ordination surface was correlated with each of the above factors, using canonical correlations to describe the degree to which variation across a multidimensional space was related to 1 or more variables (Manly 1994). This procedure was used for 2 reasons. First, it allowed us to examine how the factors varied jointly with the 2 NMDS dimensions, potentially revealing patterns only incompletely detected by examining each NMDS dimension separately. Second, separate graphs of how the ordination varied with respect to temperature, date of sampling, latitude, and elevation would reveal the extent to which these variables were confounded.

We used MDT15J and median date of sampling (d since 1 January) as independent variables in all analyses. We considered MDT15J as the best single descriptor of differences between streams in overall thermal conditions, and we included sampling date in analyses because we expected some variation among streams in assemblage structure to be associated with phenological processes alone.

We restricted our analysis on abundance values to the 16 insect taxa with the highest densities and population biomasses, for 2 reasons. First, restricting these regressions to the 16 most abundant taxa rather than the full array of taxa encountered emphasized the influence of dominant taxa. These taxa represented ~80% of the total density and assemblage biomass in these streams (unpublished data). Moreover, use of both density and biomass to describe abundance of common taxa allowed us to explore if analyses based on both smaller, shorter-lived taxa (density) and larger, longer-lived taxa (biomass) produced similar results. Second, restricting the analysis to 16 taxa reduced the possibility that ordinations would lead to spurious results. For example, Grossman et al. (1991) showed that for principle components analysis

the ratio of objects being compared (sites) to variables used in the ordination (taxa) should be at least 3:1 to minimize the risk of producing spurious relationships. We followed these guidelines even though similar risks apparently have not been explored for MANOVA or NMDS. For all analyses, abundances were \log_{10} -transformed both to help meet the assumptions of normality and homoscedasticity required by multivariate regression analysis and to down-weight the effects of extremely abundant taxa on ordination results.

We used NMDS to describe overall trends among sites in terms of both the presence or absence and abundance of taxa. NMDS uses pairwise similarity or dissimilarity matrices to calculate the positions of each site in 'taxa space'. The nearness of sites to 1 another in taxa space is a measure of their overall similarity, and this similarity can be expressed as 1 or more scores that measure where a site falls along 1 or more derived axes representing major gradients in taxonomic composition. An inherent limitation of such analyses, however, is that sites can have similar values for different reasons, a problem that can potentially confuse interpretation of differences among sites. Our primary use of NMDS was to calculate ordination scores for each stream that could be used in simple multiple regression analyses. NMDS also simplified visual examination and graphical presentation of trends in the biotic data.

For NMDS analyses, we used 3 sets of response variables. The 1st analysis was conducted on a site similarity matrix calculated from patterns of presence and absence for the 182 taxa collected over all sites. This analysis weighted all taxa equally (i.e., it was insensitive to abundance). Assemblage similarity between all possible pairs of streams was calculated using the simple matching coefficient ($S = (a+d)/(a+b+c+d)$), where similarity (S) can range from 0 to 1, a = the number of taxa shared between 2 streams, b = the number of taxa present in stream 1 but absent in stream 2, c = the number of taxa present in stream 2 but absent in stream 1, and d = the number of taxa absent from both streams. This similarity index is appropriate if all taxa can potentially occupy any site (Romesburg 1984), a reasonable assumption given that the geographic ranges of most of the taxa collected appear to encompass the study area (unpublished data). Because no site con-

tained >42% of the total taxa encountered (range = 18 to 42%), the large number of joint absences produced relatively high similarity values among pairs of streams (range = 0.59 to 0.90).

The resultant matrix describing similarities of all pairwise comparisons of streams was used in the NMDS analysis to produce an ordination of sites. Kruskal scaling and a monotonic regression function was used when scaling these data (Wilkinson et al. 1996). NMDS requires a priori selection of the number of derived dimensions onto which the original data are collapsed to create an ordination. Preliminary analyses showed 2 major trends of variation in the data. Separate analyses based on 1–4 dimensions showed that the 2-dimensional solution had a reasonably low stress value of 0.2375 (low stress values imply better fits between the data and ordination, see Wilkinson et al. 1996) and accounted for about 71% of the variation (R^2) in the multi-taxon data. Increasing the dimensionality of the analysis resulted in only a negligible increase in R^2 . Ordination scores along each of these 2 dimensions were then extracted for each stream. The location of sites relative to these 2 ordination axes (hereafter NMDS 1 and NMDS 2) measured the overall similarity of streams to one another: those with similar assemblage structure had similar ordination scores and vice versa. NMDS scores range from negative to positive values (0 = center of data), but the direction of scaling is arbitrary. To facilitate comparisons among the different ordinations and subsequent regressions, we therefore reversed the scaling on some axes so that all 3 ordinations had similar orientations.

Pearson product-moment correlations were used to measure similarity between sites for the NMDS analyses conducted on the density and biomass data. Product-moment correlations standardize each variable so the resultant ordination is not influenced by differences among sites in absolute abundance (Jackson 1993), a desirable attribute in this analysis because we wanted to minimize potential effects of differences among sites in productive capacity on the ordination. As in the 1st NMDS analysis, we found that 2 derived dimensions accounted for most of the variation in similarities among sites ($R^2 = 0.80$ and 0.83 for density and biomass data). These high R^2 values together with low final stress values (0.1934 for density and 0.1758

for biomass) implied that there were 2 major trends in these data as well.

Results

Variation in temperature among streams

Mean DT ranged from 8 to 20°C across the study sites, maximum DT ranged from 14 to 29°C, and minimum DT ranged from 3.5 to 16°C (Table 1). Variation in mean and maximum DT was related to sampling date; streams sampled at approximately the same date consistently differed by ~6° (Fig. 2). Date of sampling accounted for 10% of the variation in mean DT, 26% of maximum DT, < 1% of minimum DT, and 35% of DT range. However, even after standardizing all temperatures to 15 July, variation among streams remained high: mean adjusted DT ranged from 9 to 21°C, maximum adjusted DT ranged from ~14 to 29°C, and adjusted DT range varied between 6 and 17°C.

Stepwise regression analyses showed that stream temperatures were most strongly related to differences among streams in channel morphology and hydrology, and were seldom related to geographic gradients (Table 2). The following relationships are listed in descending magnitude of the standardized regression coefficient, a measure of relative influence on the dependent variable. MDT15J was positively related to % of the channel as pool, negatively related to mean pool depth, and positively related to mean riffle width. There was no evidence that mean daytime temperature was related to either latitude or elevation (Fig. 3). MxDT15J was negatively related to mean pool depth, positively related to % of the channel as pool, and negatively related to riparian shading. MnDT15J was negatively related to basin elevation, positively related to % of the channel as pool, negatively related to latitude, and negatively related to stream gradient. RDT15J was negatively related to both mean pool depth and riparian shading.

Differences among streams in groundwater inputs did not appear to be related to stream temperature. Although we had no direct measure of groundwater inflow into each stream, conductivity is related to the length of time water has been in contact with mineral substrates; hence, deep groundwater sources should have higher conductivities than shallow sources (Feth et al. 1964). Conductivity varied over 15-fold

TABLE 1. Variation in environmental attributes among the 45 study basins. Coefficients of variation (CV) are expressed as percents. $n = 49$ because 4 streams were sampled in both 1988 and 1989. DT = daytime temperature ($^{\circ}\text{C}$). The estimated 15 July minimum DT was not significantly different from measured DT range. Azimuth values are given as degrees (0–90) west or east of due south. na = not applicable.

Variable (units)	Mean	Minimum	Maximum	Range	CV
Date (d \geq Jan 1)	204	157	255	98	na
Latitude ($^{\circ}\text{N}$)	39.4	36	42	6	na
Base elevation (m)	1034	500	1568	1068	na
Azimuth ($^{\circ}$)	-1	-82	86	168	na
Basin area (ha)	4806	2727	10,660	7934	28
Baseflow discharge (L/s)	202	0.8	1371	1370	137
Channel slope (%)	5.4	2.0	11.4	9.4	39
Riffle depth (cm)	16	6	44	38	39
Riffle width (m)	3.8	2.0	6.5	4.5	28
Pool depth (cm)	33	18	63	45	30
Pool width (m)	4.3	2.7	6.4	3.6	23
Riffle current velocity (cm/s)	63	17	104	87	33
Specific conductance ($\mu\text{S}/\text{cm}^2$ at 25°C)	106	29	447	418	72
% of the channel as pool	36	9	69	60	39
Riffle riparian shade (%)	50	17	90	72	42
Pool riparian shade (%)	51	17	91	75	43
Mean DT	15.6	8.4	20.3	12.0	na
Maximum DT	20.1	14.0	29.0	15.0	na
Minimum DT	11.6	3.5	16.0	12.5	na
DT range	8.5	2.0	15.0	13.0	na
15 July mean DT	16.5	8.6	20.6	12.0	na
15 July maximum DT	21.6	13.8	28.8	15.0	na
15 July DT range	10.1	5.6	16.8	11.2	na

across our study streams, but stream temperature was unrelated to conductivity ($r^2 = 0.01$, $p > 0.23$).

US Geological Survey data

US Geological Survey data from other streams in the region that spanned the same latitudinal gradient as we sampled (36° – 42°N) also revealed that summertime water temperatures were not as strongly related to geographic gradients as might be expected. Mean monthly temperatures (MMT) for July, August, and September were unrelated to latitude ($r^2 = 0.02$ – 0.05 , $n = 40$). June was the exception to this lack of trend. During June MMT was negatively related ($r^2 = 0.34$) to latitude. MMT was moderately and negatively related to elevation for July, August, and September ($r^2 = 0.34$ – 0.42) but was weakly related to elevation in June ($r^2 = 0.14$). In combination, latitude and elevation accounted for <50% of the variation in temperature among sites (R^2 for June = 0.48, July = 0.39, August = 0.39, and September = 0.44). Al-

though we were unable to collect data describing the annual temperature regimes of our study streams, the US Geological Survey data suggest that our measurements may provide a generally accurate index of differences in annual degree-day (DD) accumulations among streams. For these data, total DD was highly related to measures of summertime temperature. For example, $\text{DD} = 743 + 206 \cdot \text{MJT}$, $n = 40$, $r^2 = 0.70$, where MJT = mean July temperature.

Variation in insect assemblage structure

Abundance patterns of dominant taxa.—Of the 182 taxa we collected, no more than 76 came from a single stream. Similarity among sites (S), as measured by the simple matching coefficient, varied from 0.59 to 0.90, with a median value of 0.74. Taxonomic composition, rank order of taxa, and % composition of the assemblage differed depending on whether density or biomass was used to quantify abundance of the 16 most common taxa (Tables 3, 4). Ephemeroptera (mayflies), Trichoptera (caddisflies), and Cole-

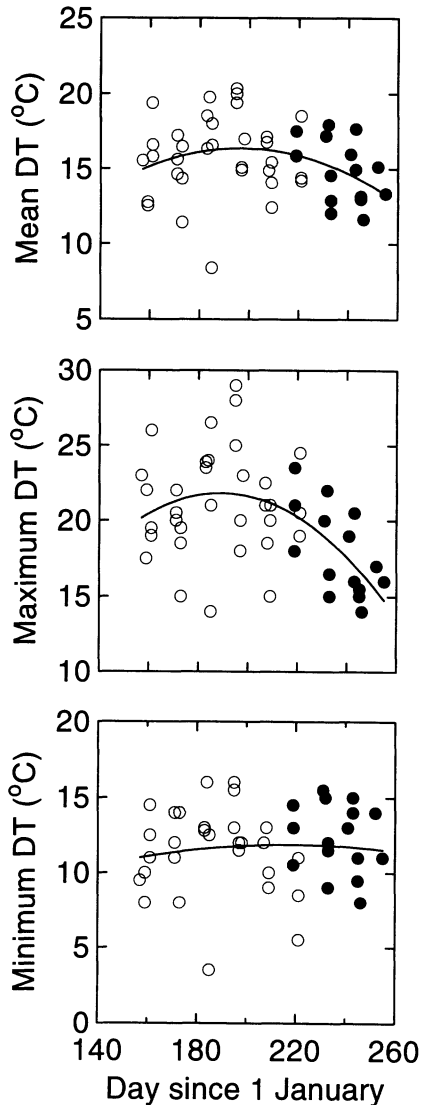


FIG. 2. Relationships between mean, maximum, and minimum daytime temperature (DT) and sampling date. The lines were fitted by quadratic nonlinear regression. Sites in the Klamath Mountain Ecoregion are black; Sierra Nevada sites are white.

optera (beetles) dominated densities, whereas Trichoptera, Ephemeroptera, and Plecoptera (stoneflies) dominated biomass. *Baetis tricaudatus/bicaudatus* (density and biomass), *Paraleptophlebia* (density), and *Rhyacophila* (biomass) were the only taxa found at every site, and their abundances were generally the least variable among sites. All other taxa were absent from 1 to 26 of the 49 collections, and the abundances of most

taxa were extremely variable among streams. For example, the elmid beetles *Optioservus*, *Ampumixis*, *Cleptelmis*, and *Heterlimnius* and the caddisfly *Apatania* had coefficients of variation (CVs) of density >200% (Table 3). Population biomasses of the elmids *Optioservus* and *Rhizelmis*; the caddisflies *Hydropsyche*, *Dicosmoecus*, *Psychoglypha*, and *Wormaldia*; the stonefly *Pteronarcys*; and the mayfly *Cinygmula* also had CVs >200% (Table 4). The variation in abundance among sites for some taxa appeared to be associated with date of sampling; however, abundances of many taxa often differed by >1 order of magnitude across streams sampled on approximately the same date.

Multiple multivariate regressions.—The multiple multivariate regression analyses showed that assemblage structure was related both to date and mean temperature (Table 5). For both densities and biomasses of common taxa, overall *F*-values associated with the multivariate test statistic (Wilks' λ) were higher for date than for mean temperature, implying that date of sampling (or a correlate) influenced assemblage structure more strongly than stream temperature.

As implied by the multivariate regression analyses, densities or biomasses of several individual taxa were also related to either date of sampling or stream temperature (Table 6). Densities of 8 taxa and biomasses of 4 taxa increased with increasing date; densities of 2 taxa decreased and biomasses of 5 taxa decreased with increasing date. Densities of 2 taxa and biomasses of 5 taxa increased with increasing temperature, whereas densities and biomasses of 3 taxa decreased with increasing temperature. There was no obvious functional or taxonomic similarity among the groups of taxa that were related to either date of sampling or temperature.

NMDS ordinations.—All of the ordinations (presence or absence, density, and biomass) were consistent in showing continuous variation in assemblage structure among streams (Fig. 4). Sites from the more heavily forested KM basins were generally different in assemblage structure from most SN sites; however, there was some overlap between the 2 regions. In all ordinations, SN and KM sites were most strongly separated along NMDS 1, although there was a strong tendency for KM sites to have high scores on both NMDS 1 and 2 axes and for SN sites to have low scores on these axes. This trend

TABLE 2. Results of forward stepwise multiple regressions of mean daytime temperature on 15 July (MDT15J), maximum daytime temperature on 15 July (MxDT15J), minimum daytime temperature (MnDT15J), and temperature range on 15 July (RDT15J) on latitude, \log_{10} basin area, basin elevation, azimuth, \log_{10} discharge, % of riffle and pool shaded by riparian vegetation, riffle and pool channel slopes, mean riffle width and depth, mean pool width and depth, mean riffle current velocity, and % of the channel present as pools (PCP). Raw and standardized regression coefficients are given for the statistically significant environmental variables.

Source	SS	df	MS	F	p	Regression coefficients		R ²
						Raw	Standardized	
MDT15J:								
Regression model	167.002	3	55.667	24.455	<0.001			0.62
Constant					<0.001	13.374	0.000	
PCP					<0.001	0.129	0.764	
Mean pool depth					<0.001	-10.745	-0.448	
Mean riffle width					0.042	0.536	0.236	
Residual	102.433	45	2.276					
MxDT15J:								
Regression model	260.219	3	86.740	18.283	<0.001			0.55
Constant					<0.001	27.007	0.000	
Mean pool depth					<0.001	-19.823	-0.623	
PCP					<0.001	0.099	0.446	
Riffle riparian shade					0.011	-0.048	-0.322	
Residual	102.433	45	2.276					
MnDT15J:								
Regression model	219.351	4	54.838	19.348	<0.001			0.64
Constant					<0.001	8.856	0.000	
Basin elevation					<0.001	-0.003	-0.604	
PCP					<0.001	0.100	0.524	
Latitude					0.005	-0.415	-0.309	
Stream slope					0.038	-0.391	-0.308	
Residual	124.707	44	2.834					
RDT15J:								
Regression model	148.059	2	74.030	18.846	<0.001			0.45
Constant					<0.001	20.433	0.000	
Mean pool depth					<0.001	-18.460	-0.696	
Riffle riparian shade					<0.001	-0.084	-0.679	
Residual	180.693	46	3.928					

implied that NMDS 1 and 2 were each measuring parts of a gradient in assemblage structure that ran diagonally across the ordination space.

The abundances of several taxa were correlated with axis scores of either NMDS 1 or 2 (Table 7). Sites with large negative values of NMDS 1 had high densities or biomasses of the mayflies *Paraleptophlebia* and *D. coloradensis/flavilinea*; the caddis *Wormaldia*, *Hydropsyche*, *Dicosmoecus*, and *Psychoglypha*; and the elmids *Cleptelmis* and *Optioservus*. Abundances of these taxa de-

creased with increasing values of NMDS 1, whereas abundances of the mayflies *Epeorus*, *Cinygmula*, and *D. doddsi*; the stonefly *D. baumanni*; the caddis *Rhyacophila* and *Arctopsyche*; and the elmids *Ampumixis*, *Heterlimnius*, and *Rhizelmis* increased. Fewer taxa were strongly associated with variation along NMDS 2. Abundances of the mayflies *Epeorus* and *D. coloradensis/flavilinea* and the caddis *Apatania* and *Psychoglypha* were highest at sites with high negative values of NMDS 2, whereas the may-

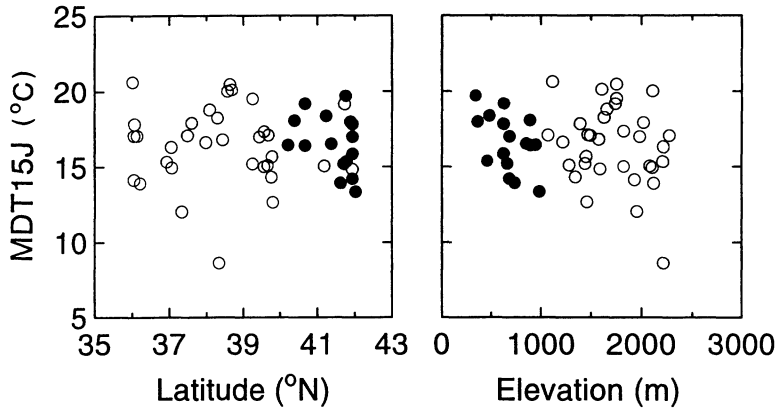


FIG. 3. Lack of relationships between latitude and elevation and mean daytime temperature on 15 July (MDT15J). Klamath Mountain Ecoregion sites are black; Sierra Nevada sites are white.

flies *Ameletus* and *D. hageni*, the stonefly *C. californica*, the caddis *Hydropsyche*, *Wormaldia*, and *Micrasema*, and the elmid beetle *Ampumixis* tended to have higher abundances at sites with high positive values of NMDS 2. No clear pattern existed for densities of the caddis *Agapetus*; densities of this taxon were negatively related to NMDS 2 based on density data but were positively related to NMDS 2 based on presence or absence data.

NMDS regressions.—Variation along both or-

dination axes was related to date of sampling and temperature, although the nature of these relationships differed somewhat with the response variable used in ordinations (Table 8). In general, values of NMDS 1 for all ordinations were strongly and positively related to date of sampling and negatively and less strongly related to temperature. Values of NMDS 2 also were positively and strongly related to temperature for the presence or absence and biomass data, but not for density data. Values of NMDS

TABLE 3. Variation among the 45 sites (49 observations) in densities (no./m²) of the 16 most common taxa. Densities are rounded off to the nearest integer. E = Ephemeroptera, T = Trichoptera, C = Coleoptera, and D = Diptera. CV = coefficient of variation (%). No. of streams = the number of streams from which a taxon was collected. Values in the % column represent a taxon's abundance relative to the combined abundances of the 16 taxa across all sites.

Taxon	Min.	Max.	Mean	CV	No. of streams	%
<i>Baetis tricadatus/bicaudatus</i> (E)	154	3527	1443	58	49	59.1
<i>Epeorus</i> (E)	0	678	166	92	48	6.8
<i>Optioservus</i> (C)	0	2894	119	352	41	4.9
<i>Micrasema</i> (T)	0	749	109	159	43	4.5
<i>Dephetor hageni</i> (E)	0	770	86	163	47	3.5
<i>Paraleptophlebia</i> (E)	4	475	75	117	49	3.1
<i>Rhyacophila</i> (T)	>0	233	68	75	49	2.8
<i>Apatania</i> (T)	0	882	58	248	33	2.4
<i>Agapetus</i> (T)	0	443	56	167	38	2.3
<i>Drunella doddsi</i> (E)	0	184	51	113	43	2.1
<i>Cleptelmis</i> (C)	0	612	45	276	25	1.8
<i>Ampumixis dispar</i> (C)	0	498	39	221	28	1.6
<i>Hydropsyche</i> (T)	0	182	34	127	48	1.4
<i>Antocha</i> (D)	0	234	33	129	48	1.3
<i>Ameletus</i> (E)	0	134	31	94	48	1.3
<i>Heterlimnius</i> (C)	0	301	29	221	34	1.2

TABLE 4. Variation among the 45 sites (49 observations) in population biomass (mg dry mass/m²) of the 16 most common taxa. E = Ephemeroptera, P = Plecoptera, T = Trichoptera, C = Coleoptera, and D = Diptera. CV = coefficient of variation (%). No. of streams = the number of streams from which a taxon was collected. Values in the % column represent a taxon's abundance relative to the combined abundances of the 16 taxa across all sites.

Taxon	Min.	Max.	Mean	CV	No. of streams	%
<i>Baetis tricadatus/bicaudatus</i> (E)	9.3	183.1	51.0	67	49	15.2
<i>Calineuria californica</i> (P)	0	144.9	42.6	98	45	12.7
<i>Hydropsyche</i> (T)	0	438.6	36.0	214	48	10.7
<i>Doroneuria baumanni</i> (P)	0	259.3	30.3	159	34	9.0
<i>Epeorus</i> (E)	0	116.2	28.2	100	48	8.4
<i>Rhyacophila</i> (T)	3.1	69.0	27.5	58	49	8.2
<i>Drunella coloradensis/flaxalimia</i> (E)	0	114.3	21.6	137	38	6.4
<i>Optioservus gradrimaculatus</i> (C)	0	309.6	16.3	282	41	4.8
<i>Dicosmoecus</i> (T)	0	251.2	14.5	270	27	4.3
<i>Pteronarcys</i> (P)	0	110.0	12.0	217	24	3.6
<i>Arctopsyche</i> (T)	0	86.9	11.6	166	32	3.5
<i>Hexatoma</i> (D)	0	59.6	10.7	119	45	3.2
<i>Cinygmula</i> (E)	0	171.2	8.7	289	41	2.6
<i>Psychoglypha</i> (T)	0	179.5	8.7	335	31	2.6
<i>Wormaldia</i> (T)	0	158.9	8.1	302	27	2.4
<i>Rhizelmis nigra</i> (C)	0	108.4	7.7	239	23	2.3

2 were positively, although weakly, related to sampling date for all 3 data sets.

Contour plots showed how temperature, date of sampling, latitude, and elevation varied across the 2-dimensional ordination space (Fig. 4). Sampling date, latitude, and elevation were strongly associated with NMDS 1 for ordinations based on densities (canonical correlations ranged from 0.51 to 0.68). In contrast, a weak temperature gradient (canonical correlation of 0.34) ran diagonally across the density-based or-

dination. Sierra Nevada sites with low NMDS 1 and NMDS 2 scores were associated with the highest temperatures, whereas KM sites were associated with the lowest temperatures.

Ordinations based on biomass and presence or absence were related in the same way to temperature, date, latitude, and elevation, and these patterns contrasted sharply with the patterns observed for the density ordinations (Fig. 4). Gradients in all 4 factors ran diagonally across the ordination space. Two patterns emerged. First, the temperature gradient across presence or absence and biomass ordinations was much stronger than for density data (canonical correlations = 0.50 for presence or absence and 0.62 for biomass data), and the direction of the temperature relationship was shifted ~90° from that observed for density data. These results imply that variation in assemblage structure based both on presence or absence and biomass data was associated with temperature and that this relationship was largely independent of ecoregion. Second, sampling date, latitude, and elevation all varied similarly and defined a strong gradient spanning low-latitude, high-elevation SN sites that were sampled early, and high-latitude, low-elevation KM sites that were sampled late (canonical correlations ranged from 0.67 to

TABLE 5. Results of the multivariate regression analyses of taxon abundance (density and biomass) on temperature (MDT15J = mean daytime temperature on 15 July) and sampling date. Lower values of Wilks' λ imply higher statistical significance. Degrees of freedom for all tests were 16 and 31. All tests were significant at $p < 0.001$.

Source	Wilks' λ	F
Density data:		
MDT15J	0.320	4.114
Date	0.193	8.116
Biomass data:		
MDT15J	0.297	4.580
Date	0.171	9.401

TABLE 6. Insect taxa that showed strong responses to variation among sites in mean daytime temperature on 15 July (MDT15J) and sampling date. Taxa are ranked in terms of the value of the univariate *F*-tests associated with each test. Degrees of freedom for these tests were 1 and 46. E = Ephemeroptera, P = Plecoptera, T = Trichoptera, C = Coleoptera, and D = Diptera. *Drunella coloradensis* includes individuals that may be *D. flavilinea*. Signs (+/-) describe whether a taxon's abundance increased (+) or decreased (-) with date and temperature.

Variable	Density			Biomass		
	Taxon	<i>F</i>	+/-	Taxon	<i>F</i>	+/-
Sampling date	<i>Rhyacophila</i> (T)	27.57	+	<i>Drunella coloradensis</i> (E)	41.39	-
	<i>Cleptelmis</i> (C)	22.95	-	<i>Arctopsyche</i> (T)	29.02	+
	<i>Drunella doddsi</i> (E)	18.43	+	<i>Hydropsyche</i> (T)	26.66	-
	<i>Ampumixis</i> (C)	18.02	+	<i>Epeorus</i> (E)	20.50	-
	<i>Heterolimnius</i> (C)	14.86	+	<i>Cingmula</i> (E)	13.75	+
	<i>Optioservus</i> (C)	8.12	-	<i>Doroneuria baumanni</i> (P)	12.50	+
	<i>Epeorus</i> (E)	6.38	+	<i>Calineuria californica</i> (P)	11.86	+
	<i>Micrasema</i> (T)	5.38	+	<i>Optioservus</i> (C)	4.16	-
	<i>Ameletus</i> (E)	4.73	+	<i>Dicosmoecus</i> (T)	4.07	-
	<i>Agapetus</i> (T)	4.54	+			
	MDT15J	<i>Drunella doddsi</i> (E)	11.10	-	<i>Doroneuria baumanni</i> (P)	10.29
<i>Rhyacophila</i> (T)		5.72	-	<i>Hexatoma</i> (D)	10.08	+
<i>Epeorus</i> (E)		5.70	-	<i>Epeorus</i> (E)	9.26	-
<i>Agapetus</i> (T)		5.50	+	<i>Cinygmula</i> (E)	8.71	-
<i>Hydropsyche</i> (T)		3.51	+	<i>Ptychoglypha</i> (T)	8.63	+
				<i>Dicosmoecus</i> (T)	8.11	+
				<i>Calineuria californica</i> (P)	7.05	+
				<i>Wormaldia</i> (T)	6.21	+

0.82 for biomass data and 0.49 to 0.58 for presence or absence data). These trends were nearly orthogonal to the relationship between assemblage structure and temperature.

Summary of analyses.—Results from the multiple multivariate regressions, NMDS regressions, and ordination plots were generally consistent with one another. All analyses showed that assemblage structure was strongly related to date (and its geographic correlates), although analyses differed somewhat in the interpretation of how assemblage structure varied with temperature among sites. In general, the regression analyses appeared to provide only partial descriptions of underlying relationships between assemblage structure and temperature, date, latitude, or elevation because the axes of variation in assemblage structure relevant to these factors ran diagonally to the 2 primary NMDS ordination axes. Although regressions led to slightly different interpretations of the data, ordinations based on the 3 response variables, especially those of presence or absence and biomass, were generally similar.

Discussion

Channel morphology, hydrology, and water temperature

Our data suggest that channel morphology may play an important role in regulating the summer temperature of small streams. The % of the channel as pools appears to be especially important, affecting stream temperature in 2 offsetting ways. First, increasing pool depth appears to reduce the rate of warming in streams, a conclusion consistent with many previous studies. Deep pools tend to maintain cooler temperatures in streams by reducing the area of stream exposed to the air relative to the volume of water in the stream (reviewed by Bartholow 1989). Second, we suggest that pools can increase summer stream temperatures by increasing the residence time of water in the channel and increasing area of water exposed to air relative to stream volume (e.g., large, shallow pools will have large surface to depth ratios). This idea is consistent with several empirical studies, which show that beaver ponds usually

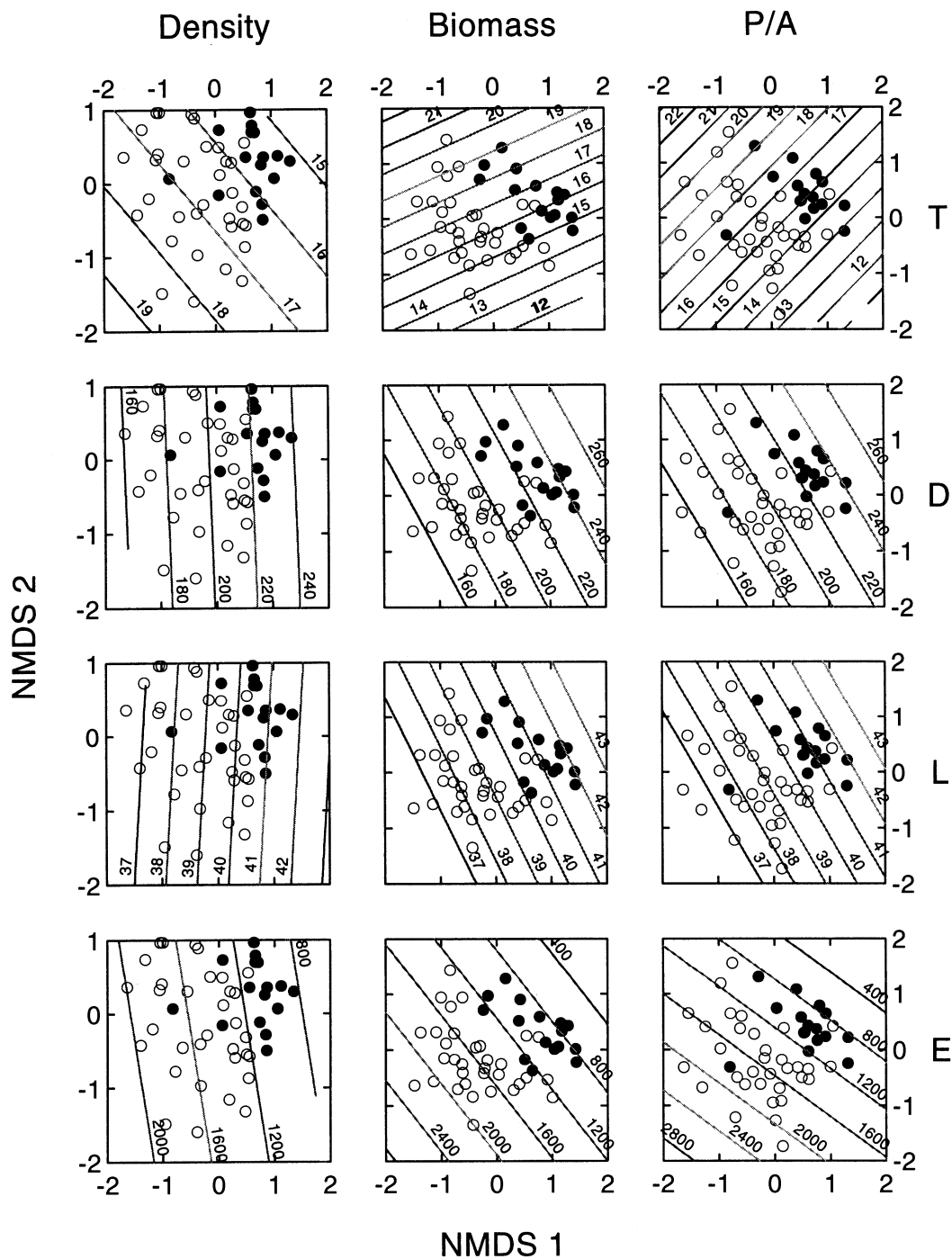


FIG. 4. Ordinations of the 45 study sites (49 observations) in non-metric multidimensional scaling (NMDS) space based on densities of the 16 most common taxa, biomasses of the 16 most abundant taxa, and presence or absence of 182 taxa. For each ordination, contours show how 15 July temperature (T), date of sampling (D), latitude (L), and elevation (E) vary with respect to site positions within the ordination space. Klamath Mountain Ecoregion sites are black; Sierra Nevada sites are white.

TABLE 7. Pearson product-moment correlations between log₁₀ abundances of the 16 most common taxa (densities and biomasses) and non-metric multidimensional scaling (NMDS) ordination scores based on density (Den), biomass (Bio), and presence or absence (P/A) data. Values in bold identify taxa with correlation coefficients ≥0.4, an arbitrary value above which the correlation was considered moderate to strong. E = Ephemeroptera, P = Plecoptera, T = Trichoptera, C = Coleoptera, and D = Diptera. *Baetis* includes individuals of *B. bicaudatus* and *B. tricaudatus*. *Drunella coloradensis* includes individuals that may be *D. flavilinea*. na = not applicable.

Taxon	Densities						Biomasses					
	NMDS 1			NMDS 2			NMDS 1			NMDS 2		
	Den	Bio	P/A	Den	Bio	P/A	Den	Bio	P/A	Den	Bio	P/A
<i>Ameletus</i> (E)	0.11	0.16	0.12	-0.08	0.49	0.25	na	na	na	na	na	na
<i>Baetis</i> (E)	0.21	0.11	0.16	-0.18	-0.20	0.14	0.12	0.01	0.24	-0.37	-0.28	-0.14
<i>Deiphator lugeni</i> (E)	-0.38	-0.10	0.03	-0.12	0.17	0.46	na	na	na	na	na	na
<i>Epeorus</i> (E)	0.24	0.41	0.46	0.34	0.01	0.27	-0.16	-0.19	-0.01	0.05	-0.56	-0.32
<i>Cinygmula</i> (E)	na	na	na	na	na	na	0.41	0.54	0.60	0.03	-0.22	-0.07
<i>Drunella doddsi</i> (E)	0.72	0.63	0.75	0.01	-0.24	-0.22	na	na	na	na	na	na
<i>Drunella coloradensis</i> (E)	na	na	na	na	na	na	- 0.43	- 0.56	-0.36	0.02	- 0.65	- 0.40
<i>Paraleptophlebia</i> (E)	- 0.44	-0.21	-0.16	0.02	0.05	0.18	na	na	na	na	na	na
<i>Pteronarcys</i> (P)	na	na	na	na	na	na	-0.06	0.07	-0.04	0.38	0.03	0.24
<i>Calineuria californica</i> (P)	na	na	na	na	na	na	0.25	0.36	0.25	0.00	0.58	0.57
<i>Doroneuria baumanni</i> (P)	na	na	na	na	na	na	0.44	0.70	0.67	0.20	-0.39	-0.11
<i>Hydropsyche</i> (T)	-0.23	0.06	-0.03	0.29	0.20	0.42	- 0.53	- 0.56	- 0.48	0.09	-0.37	0.01
<i>Arctopyche</i> (T)	na	na	na	na	na	na	0.56	0.81	0.60	0.34	0.16	0.17
<i>Rhyacophila</i> (T)	0.44	0.59	0.65	-0.02	-0.06	0.15	0.16	0.25	0.27	-0.21	0.06	0.14
<i>Agapetus</i> (T)	0.01	0.03	0.13	- 0.65	0.25	0.60	na	na	na	na	na	na
<i>Wormaldia</i> (T)	na	na	na	na	na	na	- 0.45	-0.35	-0.33	-0.06	0.39	0.46
<i>Dicosmoecus</i> (T)	na	na	na	na	na	na	-0.22	- 0.44	-0.37	-0.25	0.14	0.28
<i>Psychoglypha</i> (T)	0.03	0.32	0.35	0.59	-0.02	0.30	-0.36	- 0.42	- 0.45	na	0.20	0.11
<i>Micrasema</i> (T)	0.17	-0.02	0.15	- 0.78	0.12	0.19	na	na	na	na	na	na
<i>Apatania</i> (T)	-0.13	-0.07	-0.04	-0.17	0.17	0.34	-0.38	-0.39	-0.33	-0.31	0.39	0.18
<i>Antocha</i> (D)	na	na	na	na	na	na	na	na	na	na	na	na
<i>Hexatoma</i> (D)	na	na	na	-0.14	0.27	0.47	na	na	na	na	na	na
<i>Ampumixis</i> (C)	0.52	0.47	0.46	-0.14	0.27	0.47	na	na	na	na	na	na
<i>Cleptelmis</i> (C)	- 0.75	- 0.55	- 0.47	0.27	-0.20	-0.03	na	na	na	na	na	na
<i>Heterimmius</i> (C)	0.40	0.44	0.47	0.11	0.11	0.30	na	na	na	na	na	na
<i>Optiserosus</i> (C)	- 0.68	- 0.52	-0.31	-0.19	0.13	0.35	- 0.63	- 0.47	-0.27	-0.20	0.24	0.39
<i>Rhizelmis</i> (T)	na	na	na	na	na	na	0.39	0.54	0.40	0.16	-0.27	-0.16

TABLE 8. Results of the regressions on non-metric multidimensional scaling (NMDS) dimensions 1 and 2 used to test the hypothesis that assemblage structure was a function of differences among streams in date of sampling and mean daytime temperature on 15 July (MDT15J). NMDS dimensions 1 and 2 represent different patterns of variation in assemblage structure among streams. Results based on taxa presence or absence, density, and biomass. Raw regression coefficients describe variation in the dependent variable with respect to the measured units of the independent variables and are useful for prediction. Standardized regression coefficients show the relative importance of an independent variable after standardizing the values of all independent variables.

Source	SS	df	MS	F	p	Regression coefficients		R ²
						Raw	Standardized	
Presence or absence (182 taxa)								
NMDS Dimension 1:								
Regression model	19.086	2	9.543	60.377	<0.001			0.72
Constant					<0.001	-0.756	0.000	
MDT15J					<0.001	-0.164	-0.526	
Sampling date					0.011	0.017	0.669	
Residual	7.270	46	0.158					
NMDS Dimension 2:								
Regression model	8.262	2	4.131	13.213	<0.001			0.37
Constant					0.190	-4.052	0.000	
MDT15J					<0.001	0.138	0.478	
Sampling date					<0.001	0.009	0.370	
Residual	14.382	46	0.313					
Density (16 taxa)								
NMDS Dimension 1:								
Regression model	14.200	2	7.100	24.884	<0.001			0.52
Constant					0.004	-2.315	0.000	
MDT15J					0.023	-0.077	-0.241	
Sampling date					<0.001	0.018	0.667	
Residual	13.125	46	0.285					
NMDS Dimension 2:								
Regression model	1.219	2	0.610	1.371	0.264			0.18
Constant					0.318	0.961	0.000	
MDT15J					0.107	-0.067	-0.235	
Sampling date					0.838	0.001	0.029	
Residual	20.456	46	0.445					
Biomass (16 taxa)								
NMDS Dimension 1:								
Regression model	20.919	2	10.460	47.158	<0.001			0.67
Constant					0.001	-2.474	0.000	
MDT15J					<0.001	-0.108	-0.317	
Sampling date					<0.001	0.021	0.756	
Residual	10.203	46	0.222					
NMDS Dimension 2:								
Regression model	6.842	2	3.421	14.262	<0.001			0.38
Constant					<0.001	-3.588	0.000	
MDT15J					<0.001	0.138	0.536	
Sampling date					0.011	0.006	0.309	
Residual	11.035	46	0.240					

increase stream temperatures (Sayler 1935, Evans 1948, Patterson 1951, Rupp 1954, Avery 1992, McRae and Edwards 1994).

The different responses of mean, maximum, and minimum DT and DT range to different environmental variables provides some additional insight into how a suite of factors may jointly influence stream temperature. Latitude, elevation, stream gradient, and riparian shading have all been identified as factors affecting stream temperature (Brown 1969, Smith 1975, Smith and Lavis 1975, Crisp and Howson 1982, Crisp et al. 1982, Hockey et al. 1982, Webb and Walling 1986, Beschta et al. 1987). Although none of these factors was related to mean DT in our study, riparian shading was related to maximum DT and DT range, implying that shade plays a role in reducing the daily variance in stream temperature but not average daily temperature. Minimum DT was the only temperature measure associated with geographic gradients, implying that streams at higher elevations and latitudes lose more heat at night than streams at lower elevations and latitudes. In general, 1 or more aspects of summer stream temperature appear to increase with riffle width and the % of the channel present as pools. In contrast, temperature appears to decrease with increasing latitude, elevation, pool depth, riparian shade, and stream gradient.

Percent channel as pool was probably the single best predictor of mean DT in our study because it integrates several geomorphic and hydrologic attributes that directly influence the rate of heating of water within a reach of headwater stream. Although pools are usually deeper than riffles, they have less steep slopes, have slower current speeds, and are often wider than riffles. These factors affect both the flow retention time and the area of water exposed to solar radiation and air.

As water flows downstream from headwater source areas that are either cool (groundwater) or cold (snowmelt), stream waters will warm and eventually attain a near thermal equilibrium with the air (Brown 1969, Crisp et al. 1982, Theurer et al. 1984, Bartholow 1989). The distance water must flow before attaining equilibrium is a function of local heating and cooling fluxes largely governed by air temperature and the quantity (discharge) of water in the channel (Smith and Lavis 1975, Hockey et al. 1982, Theurer et al. 1984, Bartholow 1989, Stefan and

Preud'homme 1993). During seasons when air and stream temperatures strongly differ, any mechanism that reduces the rate of downstream movement of water (e.g., pools or obstructions within headwater channels) should act to shorten the distance water travels before reaching thermal equilibrium and, as a consequence, increase the amount of heat accumulated or released at any given distance downstream from a stream's source.

Our observations of high variance in the % channel as pool among streams are also consistent with the observation that small, mountainous stream channels appear to be much more chaotically and complexly structured than lowland, alluvial streams (Keller and Swanson 1979, Grant et al. 1990)—i.e., pools do not occur at regular intervals and the ratio of pools to riffles is not constant. If streams generally exhibit large differences in the % channel as pool, a mechanism exists by which strong thermal differences in otherwise similar neighboring streams may arise. To our knowledge, no previous empirical study has shown variation in channel form to be such a potentially critical factor affecting summertime stream temperature.

Relationships between channel units and water temperature are almost certainly transitory in nature and may only emerge during summertime low-flow conditions because the absolute and relative abundances of riffles and pools in a stream change seasonally and annually. During periods of high discharge, the riffle-pool organization of streams deteriorates, flow is rapid, and retention of water is low. Furthermore, in much of the western United States, air temperatures and the rate of stream heating are low during high-discharge periods. Summer thermal regimes may also vary randomly between years because of annual changes in channel form. Such changes in channel morphology occur in response to discharge events that differ in magnitude each year (Wolman and Miller 1960, Andrews 1980).

Variation in assemblage structure of aquatic insects at landscape spatial scales

Stream ecologists often relate assemblage structure of insects and other invertebrates to variation in environmental attributes among streams. Such analyses are used to generate and test hypotheses about the causal factors thought

to influence assemblage structure in streams and to model biotic response to natural and human-caused changes in the environment. Landscape-level analyses of assemblage structure are becoming increasingly common as natural resource managers recognize the need to assess biotic conditions across entire ecoregions. However, assessing structure at such large spatial scales takes time, and the effects of date of sampling (or correlated factors) may confound our ability to detect relationships between assemblage structure and factors of primary interest. Furthermore, inferences about how streams differ in assemblage structure may vary depending on the type of data used in analyses, although few studies have examined this potential problem in much detail (but see Marchant et al. 1995).

Effect of type of data on inferences.—Although slightly different patterns emerged from use of density, biomass, and presence or absence data, similarities in most aspects of the different ordinations suggest they were generally robust in describing real differences in assemblage structure among sites. Presence or absence and biomass ordinations were remarkably similar in spite of the different types of data used, different numbers of taxa involved in the calculation of site similarities, and different similarity measures used for the 2 analyses. Results based on densities tended to differ from those of biomass or presence or absence data. It is likely that density and biomass produced different patterns for at least 2 reasons. First, densities and population biomasses show different temporal trajectories within the same stream as a consequence of schedules of recruitment, growth, and mortality. On 1 date, a taxon may have many small individuals but little population biomass; on a later date the same taxon will have fewer individuals but biomass may be proportionately much higher. Because we sampled over such a long time period, it is not surprising that we observed differences between these 2 measures. Densities appear to be especially variable over time compared to biomasses.

Analyses based on abundance and presence or absence data may lead to similar interpretations of how assemblages are structured. For example, Marchant et al. (1995) found that density and presence or absence data in Australian streams led to similar interpretations of ordinations. Our results contrast slightly with Mar-

chant et al. (1995) in that presence or absence and biomass rather than presence or absence and density produced similar results. We were surprised to find that biomass and presence or absence data led to such similar interpretations given that we know of no obvious mechanisms linking the 2 assemblage properties. Nonetheless, if the similarity between presence or absence and biomass analyses is a general one, the use of presence or absence data may be of even greater use than argued by Marchant et al. (1995) because biomass is a better predictor than is density of the productive capacity of stream insects (Benke 1993). However, the relationship between presence-or-absence- and biomass-based analyses needs to be examined across more stream ecosystems before we can generalize about it.

Influence of sampling date on assemblage structure.—Although confounded with potential effects of latitude and elevation, date of sampling appeared to have a stronger influence on assemblage structure than temperature differences among streams. The effect of date of sampling on assemblage structure seems readily interpretable given that most insect taxa in streams are known to complete their life cycles in ≤ 1 y, taxa differ in their timing of life-history events, and many stream insects emerge as adults sequentially over the period of early to late summer (Hynes 1970, Sweeney 1984, Newbold et al. 1994). It is therefore likely that many taxa would not have been detected in the benthos during some part of the period we sampled. As such, taxonomic composition and relative abundances of taxa would have been expected to change over the time period of our sampling.

The magnitude of effect on assemblage structure associated with date was so large that it could have easily obscured other relationships had we not included it in our analyses. Considering that many monitoring programs rely on samples collected at 1 time over the course of summer, we believe it would be wise to routinely include date of sampling as a covariate whenever testing for effects of other factors.

Water temperature and assemblage structure.—At 1 level, our results corroborated a phenomenon we have understood for decades: distributions of ectothermic organisms such as insects are influenced by ambient thermal environments. Two mechanisms probably account for the relationships we observed between assemblage

structure and thermal differences among streams: 1) temperature-mediated effects on rates of seasonal (phenological) shifts in taxon abundances (Newbold et al. 1994), and 2) spatial differences among streams in taxon composition and abundance associated with taxon-specific differences in thermal optima or tolerances (e.g., Rossaro 1991).

Geographic variation in stream invertebrate assemblages.—Analysis of geographic trends in species distributions can provide insight into the factors most strongly limiting the distribution of taxa. Furthermore, where strong geographic trends exist, location along the geographic gradient can be used as a surrogate to predict both the environmental conditions and the biotic assemblage most likely to occur at an unstudied site. Such relationships can be extremely useful for predicting the consequences of large-scale alterations in either the landscape or climate (e.g., Sweeney et al. 1992).

Many studies have examined variation in stream invertebrate assemblage structure across large spatial scales (Furse et al. 1984, Wright et al. 1984, Marchant et al. 1985, 1994, Bunn et al. 1986, Moss et al. 1987, Corkum and Ciborowski 1988, Whittier et al. 1988, Corkum 1989, 1990, 1991, 1992, Quinn and Hickey 1990). Most of these studies reported strong gradients in biotic structure associated with either elevation (Furse et al. 1984, Marchant et al. 1985, 1994, Moss et al. 1987, Corkum and Ciborowski 1988, Corkum 1989, Quinn and Hickey 1990) or latitude (Corkum and Ciborowski 1988, Corkum 1989). However, it is difficult to generalize from these studies about either the nature of geographical patterns in assemblage structure or the factors that produce them. Unfortunately, few studies measured the same environmental variables, and some of the geographically most-extensive studies did not measure temperature (e.g., Furse et al. 1984, Wright et al. 1984, Corkum and Ciborowski 1988, Corkum 1989). Most of the studies that measured temperature found that it was related to variation in assemblage structure (Marchant et al. 1985, 1994, Bunn et al. 1986, Moss et al. 1987, Quinn and Hickey 1990), although in each of these studies temperature was correlated with other factors such as water chemistry (Marchant et al. 1985, Bunn et al. 1986); stream velocity (Bunn et al. 1986); elevation (Quinn and Hickey 1990, Marchant et al. 1994); dissolved oxygen (Marchant et al. 1994); or channel slope,

flow, specific conductivity, chlorophyll, nitrogen in the water column, and land use (Quinn and Hickey 1990). Because many of these factors vary in concert along latitudinal, elevational, or longitudinal gradients, it has been impossible to isolate the factors that most likely produce geographical patterns in biotic structure.

If landscapes could be experimentally manipulated, the factors responsible for geographic gradients in assemblage structure could be determined by manipulating streams so factors of interest varied independently of geographic gradients, and then observing if the geographic gradients in biotic structure persisted or disappeared. The landscape we studied provided a natural experiment that appeared to manipulate temperature independently of elevation and latitude. The existence of nearly random geographic patterns in biotic structure across such a large landscape is of potentially great ecological significance. These patterns suggest that in mountainous landscapes local processes may be strong enough to mask patterns that would have otherwise emerged in more homogeneous landscapes.

Implications for theoretical and applied stream ecology

Our results have significant implication for both our understanding of the factors that influence biotic structure in streams and our ability to either detect human-caused degradation of stream biota or predict the effects of climate change. Although channel form may only influence stream temperature during low-flow conditions, summertime temperature may limit the presence or overall abundances of some species within a stream. Summertime temperature effects may therefore carry over to annual or greater time scales and thus potentially influence long-term and large-scale biogeographic patterns. For example, during this study, we collected at least 1 species, *Caudatella edmundsi*, (Allen and Edmunds 1961, Allen 1980) that had previously been recorded only from streams in the Oregon Cascades and Idaho. We found it in 4 cold-water streams in the central SN ~800 km south of its previously reported range.

If summertime stream thermal environments are highly variable among streams and are not strongly correlated with geographic gradients, it may be difficult if not impossible to predict

assemblage structure within any given stream reach or even within an ecoregion unless detailed data on stream thermal conditions are available. This problem would be heightened if summer thermal regimes varied between years because of annual changes in the abundances of different geomorphic features. Random spatial and temporal variation in summer stream temperature would produce a statistical problem of special concern to ecosystem modelers and resource managers responsible for predicting the consequences of either landscape alteration or climate change on natural ecosystems. If high, thermally induced spatial or temporal variance in biotic structure naturally exists among unperturbed communities, then biomonitoring protocols presently used by several federal and state agencies will be able to detect only the most extreme human disturbances. These methods (Plafkin et al. 1989, Gurtz 1994, Resh et al. 1995) often rely on a single sampling during summer and require comparison of a target stream to a theoretical reference stream (control) that is created from a composite of the biota found in a representative sample of unperturbed streams. Basic statistical theory shows us that as the variance among control samples increases, the differences necessary to discriminate treatment and control means will also increase. Our results suggest that natural variation in biotic structure among streams available as controls may be high enough to limit the effectiveness of some bioassessment methods in morphologically variable mountain streams.

Modeling and predicting the effects of climate change on stream biota in regions with highly variable stream morphology may be equally difficult. We currently have only a crude understanding of the effects climate change might have on aquatic ecosystems (Regier et al. 1990, Carpenter et al. 1992, Hogg et al. 1995, Hogg and Williams 1996). Highly variable effects of the local channel on natural stream temperatures would exacerbate our ability to predict anything but region-wide average responses. Accurate site-specific predictions would require local data describing the geomorphic structure of a stream channel—information that could be obtained only with a considerable investment of time and money.

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