Jing + Holly: Thanks for your support of this and other aspects of our research in the FC Wilderness and especially on Big Creek!

This was the study that started our collaboration with Taylor Ranch

Macroinvertebrate community structure in relation to measures of lotic habitat heterogeneity

Wayne

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With 4 figures and 3 tables in the text and 1 appendix

Abstract: We examined the relationship between habitat heterogeneity and benthic macroinvertebrate assemblages in thirty-two 2nd to 6th order wilderness streams in central Idaho. Twenty-one environmental measures were evaluated for each stream with their heterogeneity expressed in terms of coefficients of variation (CV's). Although the annual range in water temperature was greater in the larger (5th and 6th order) streams, most other habitat measures showed greater variation among smaller streams (2nd order) than larger streams. Mean habitat-CV's also were about 20 % greater for smaller (2nd order) than larger (5th and 6th order) streams, suggesting a homogenizing influence of stream size on habitat heterogeneity. Multivariate analyses of the habitat measures clearly separated 5th and 6th order streams from ≤4th order streams, further indicating major environmental differences between larger and smaller stream systems. Multiple regression and canonical correspondence analysis revealed that some biotic properties, e.g. % shredders, were associated with stream size, reflecting longitudinal changes in food resource availability or annual variation in temperature, while others, e.g. Shannon's diversity, were more dependent on measures of within-reach habitat heterogeneity.

Introduction

Southwood (1977, 1988) posited that the habitat strongly influenced population distributions and community assembly by providing the evolutionary conditions from which life history attributes and community properties are derived. Southwoods ideas subsequently have been developed for flowing water ecosystems (Vannote et al. 1980, Minshall 1988, Poff & Ward 1989, Townsend & Hildrew 1994). For example, geomorphic features of stream channels were conceived as the habitat templet for biota along the stream con-

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tinuum and resident biota were viewed functionally in terms of ecological equivalents and feeding guilds (VANNOTE et al. 1980, MINSHALL et al. 1985). Recent focus has turned to individual species and the predominance of species traits in relation to differences in environmental characteristics among lotic habitats (SCARSBROOK & TOWNSEND 1993, TOWNSEND & HILDREW 1994, POFF & ALLAN 1995, TOWNSEND et al. 1997).

Although channel geomorphology still is viewed as an important component of the habitat templet, within-site factors (biotic and abiotic) also are recognized as important in defining the niche space of individual species. For instance, important biotic components of lotic habitats that can affect community assembly include food resources, competitors, and predators (e.g. HART 1983, PECKARSKY 1984, POWER et al. 1988). Abiotic factors consist of a variety of physical and chemical measures, such as temperature, flow, and substratum, that impose different frequencies and intensities of disturbance (WARD & STANFORD 1983, RESH et al. 1988) or differences in inter-habitat characteristics (BROWN & BRUSSOCK 1991, ANGRADI 1996). In addition, biotic and abiotic factors can interact to accentuate the spatial heterogeneity of lotic habitats (sensu HART 1992).

SOUTHWOODS (1977, 1988) model predicts that the structural attributes of benthic assemblages are associated with the heterogeneity of aquatic habitats. For example, streams having more physically-heterogeneous environments should contain a greater diversity of species than streams with less heterogeneous habitats (MINSHALL 1988, POFF & WARD 1990). Further, habitat heterogeneity differs not only among streams of similar size (e.g. see POFF & WARD 1989, 1990), but also longitudinally along a river (VANNOTE et al. 1980, MINSHALL et al. 1983). In general, the habitat heterogeneity for any particular stream system is a function of several interacting factors (e.g. MINSHALL et al. 1985, QUINN & HICKEY 1990, RICHARDS et al. 1993), and thus multiple measures must be analyzed for comparisons among-streams (PRINGLE et al. 1988). In this study, we examined a number of specific properties of the habitat templet and their relationship to benthic assemblages in mountain streams ranging from 2nd through 6th order in size in the Frank Church Wilderness of central Idaho.

Methods

Study streams

Thirty-two streams located in the Frank Church River-of-No-Return Wilderness in central Idaho, USA were used for analysis (Fig. 1). This wilderness encompasses over 950,000 hectares of rugged roadless terrain (FINKLIN 1988) and provided a set of streams relatively unaffected by anthropogenic influences. The Middle Fork Salmon
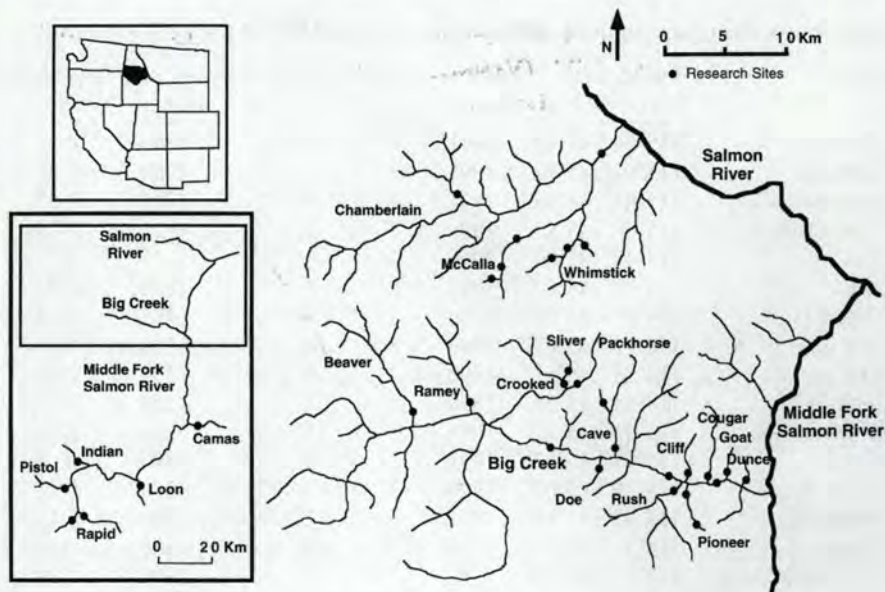
Fig. 1. Map of study site locations in central Idaho, USA.

River is the primary catchment in the wilderness. In the United States, the term wilderness identifies legally designated areas which are roadless, devoid of permanent human inhabitants, generally pristine and representative of pre-settlement conditions. The primary activity imposed by humans is recreational: river floating, backpacking and horsepacking, fishing, and hunting. Mining occurs in the headwaters of some sites, e.g. the Big Creek drainage, but with little influence on stream biota during the time of study.

In order to acquire this relatively large sample size from remote wilderness areas, stream site collections were restricted to the most accessible period (summer baseflow) and pooled across several years (1988 through 1992). RICHARDS & MINSHALL (1992) found little variation in biotic assemblage structure within undisturbed wilderness streams in this region that were sampled annually over five years during summer baseflow conditions. Streams ranged in size from 2nd through 6th order and from 4 (Sliver Creek) to 1018 (Middle Fork Salmon River) links (Table 1). Streams ranged in elevation from 1065 m (Dunce Creek) to 1915 m (East Fork McCalla Creek) and had gradients from <1.0 to about 18 percent. Most of the large (≥5th order) study streams are tributaries of the Middle Fork Salmon River except for Chamberlain Creek which flows into the mainstem Salmon River.

The climate of the area is semi-arid with less than 30 cm of precipitation annually (FINKLIN 1988). The majority of precipitation occurs as snowfall during winter, thus peak runoff is associated with spring snowmelt. Primary vegetation on forested side-slopes is Ponderosa pine (*Pinus ponderosa* LAWS), Douglas fir (*Pseudotsuga menziesii* (MIRB.) Franco.), and aspen (*Populus tremuloides* MICHX.), with sagebrush (*Artemisia*)-grass communities predominant on south-facing slopes. However, bare soil/rock

Table 1. Location, year sampled, and general site characterisitcs for study streams.

Stream	Coordinates	Sample Year	Order	Link	Slope (%)	Elevation (m)	Discharge (m³/s)
Sliver	115′04″; 45′13″	1991	2	4	5	1880	0.04
Packhorse	115′02″; 45′12″	1991	2	5	4	1780	0.04
EF Whimstick	115′01″; 45′18″	1991	2	6	2	1745	0.02
EF McCalla	115′08″; 45′17″	1991	2	6	2	1915	0.05
Goat	114′48″; 45′07″	1990	2	6	18	1125	0.01
Dunce	114′47″; 45′07″	1990	2	6	15	1065	0.02
Pioneer	114′51″; 45′05″	1990	2	9	6	1485	0.13
Cliff	114′51″; 45′07″	1988	2	10	13	1196	0.04
WF Cave	114′58″; 45′11″	1990	2	9	6	1365	0.01
Doe	114′58″; 45′08″	1990	3	7	16	1260	0.02
SF Whimstick	115′01″; 45′17″	1991	3	11	2	1730	0.04
McCalla	115′08″; 45′17″	1991	3	12	2	1890	0.05
Cougar	114′49″; 45′07″	1990	3	14	12	1095	0.11
Crooked	115′02″; 45′18″	1991	3	17	3	1780	0.17
Pioneer	114′51″; 45′06″	1990	3	18	3	1165	0.16
WF Chamberlain	115′11″; 45′24″	1992	3	22	1.5	1806	0.20
Beaver	115′14″; 45′10″	1988	3	26	4	1537	1.17
Cave	114′57″; 45′08″	1990	3	41	6	1220	0.31
Whimstick	115′01″; 45′17″	1991	4	26	1	1710	0.10
McCalla	115′06″; 45′18″	1991	4	38	2	1820	0.13
Ramey	115′10″; 45′11″	1988	4	47	3.5	1440	0.74
Indian	115′06″; 44′46″	1992	5	89	1.5	1450	1.31
Rush	114′51″; 45′07″	1988	5	223	1	1171	1.61
Pistol	115′10″; 44′43″	1992	5	812	1.8	1548	1.81
Camas	114′44″; 44′53″	1992	5	834	1	1226	2.92
Chamberlain	114′58″; 45′25″	1992	6	296	3.5	1032	2.43
Big Creek @ Coxey	115′02″; 45′08″	1988	6	414	1.5	1305	5.23
Big Creek @ Rush	114′51″; 45′07″	1988	6	627	1.5	1174	8.04
Rapid	115′10″; 44′40″	1992	6	794	2.5	1613	1.11
Loon	114′47″; 44′48″	1992	6	903	1	1291	3.29
Big Creek @ Gorge	114′47″; 45′07″	1988	6	912	1	1122	8.83
MF Salmon River	115′10″; 44′40″	1992	6	1018	1	1613	5.47

often dominates (ca. 20–30 %) this region, especially on south-facing slopes. Primary riparian woody-vegetation consists of water birch (*Betula*), alder (*Ulnus*), willow (*Salix*), and dogwood (*Cornus*).

Field and laboratory procedures

Variables measured included major physical, chemical, and biological components of the stream ecosystem. "Point" sampling was used to obtain data from a specific location or where one measurement was sufficient to characterize an entire stream reach (e.g. temperature and chemical measures of pH, specific conductance, alkalinity and

hardness). "Transect" sampling was used for factors that were expected to vary across a stream in a regular manner (e.g. width, discharge). Width was measured at five transects at each site with each transect being 50 m from another. "Random" samples were used where a number of samples are required to characterize an entire reach (e.g. substrate size and embeddedness, depth, near-bed velocity, benthic macroinvertebrates, and periphyton). Substrate size, embeddedness, depth, and near-bed velocities were recorded at 100 random locations within the study reach. These sample locations were about 1 m equidistant, beginning at the first downstream transect and moving upstream, and with relative distance (in 10 % increments) from the stream bank derived from a random numbers table.

Ten benthic samples were collected from each stream sampled in 1988, and five samples collected for each stream sampled in the other years using a standard Surber net (0.10 m^2, 250 µm mesh) and preserved in the field with 4 % formalin (PLATTS et al. 1983). In the laboratory, macroinvertebrates were handpicked from each sample using a dissecting microscope at 10×. Invertebrates were identified to at least genus, except for Chironomidae, counted, and dried at 60 °C for biomass determinations. Macroinvertebrates were examined in terms of density, biomass, species richness (PLATTS et al. 1983), Simpsons' dominance index (C), Shannons' diversity (H') (BARBOUR et al. 1987), functional feeding groups (MERRITT & CUMMINS 1984), and species-trait groups (after COLINVAUX 1993, PIANKA 1994, STEARNS 1992).

The final aquatic instar of all collected taxa from each stream was characterized using estimates regarding the potential evolutionary selection of generalized species traits: relative size, morphology, voltinism, mobility, and dispersal ability (after SOUTHWOOD 1977, RESH et al. 1994). Relative size was based on whether final instar larvae were greater than or less than 1 cm long. Body morphology was characterized as being streamlined, flattened, cylindrical, or spherical (USSEGLIO-POLATERA 1994). Voltinism simply referred to a taxon as being multivoltine or univoltine (or longer). Mobility was based on whether an organism was considered mobile or sedentary. Mobile taxa were defined as being active swimmers or crawlers and lacking cases or retreats, whereas sedentary taxa were inactive (e.g. burrowers) or have cases or retreats (HAWKINS & FURNISH 1987). Disperal ability referred to organisms typically found in the drift or known to have fast colonization rates, such as the mayfly *Baetis* (ANDERSON 1992).

Factor analysis (3 factor with varimax rotation) was employed to display taxa along a gradient of so-called opportunistic to equilibrium species (sensu STEARNS 1992, PIANKA 1994). Binary values (i.e. 0 or 1) for each species trait were used in the analysis (see Appendix). The resulting three factor scores for each taxon were summed and taxa assigned, based on this summed value, to one of five species trait groups: obligate opportunists, facultative opportunists, obligate equilibrium taxa, facultative equilibrium taxa, and mixed-trait taxa. The name for each group was selected to descriptively characterize the species traits that comprised, based on the factor analysis, a particular group of taxa. Similar approaches have been used for classifying lotic macroinvertebrates (GROWNS & DAVIS 1994, USSEGLIO-POLATERA 1994) and fishes (POFF & ALLEN 1995).

The remaining material from each benthic sample was dried at 60 °C, weighed, ashed at 550 °C, rewet, redried at 60 °C, and reweighed for determination of benthic or-

ganic matter (BOM) as ash-free dry mass (APDM). Periphyton was collected from individual rocks in each stream using the method described in ROBINSON & MINSHALL (1986), with sample size the same as for benthic macroinvertebrates. Samples were immediately frozen in a Union Carbide 3DS Dry Shipper saturated with liquid nitrogen and returned to the laboratory. In the laboratory, samples were extracted for chlorophyll-a in 100 % methanol for 24 h and then measured using a Gilford (model 2200) spectrophotometer (APHA 1989). Periphyton AFDM also was determined from these samples as described above for BOM (LORENZEN 1966, STOCKNER & ARMSTRONG 1971).

Initially, most physical and chemical data were summarized as means and coefficients of variation (CV). In addition, these data were log(X+1) or arcsin(sqrt(X)) transformed to normalize the data, eliminate the dependence of the variance on the mean, and ensure that the components of the variance were additive (ELLIOTT 1977, ZAR 1984). Subsequent analyses employed a variety of multivariate techniques. The physical and chemical data were analyzed inititially using principal components analysis (PCA), following varimax rotation, to identify general characteristics for streams of different size. ANOVA and PCA were used to test for differences in community properties among streams of different size. Multiple stepwise regression and canonical correspondence analysis (CCA) were used to determine relationships between the physical and chemical properties of each stream with respective biotic components (TER BRAAK 1987a, b). CCA is a nonlinear technique used to relate variation in biotic properties to measured variation of the environment (TER BRAAK 1986).

Results

Habitat characteristics and heterogeneity

Smaller order streams displayed greater, although nonsignificant ($F = 1.67$, $p = 0.201$), average variation in habitat measures (mean habitat CV's) than 5th-6th order (large) streams (Fig. 2 a). Habitat measures that displayed $2-3 \times$ more variation among 2nd order streams than among large streams included periphyton chlorophyll-a, the difference between bankfull and baseflow water depths, and ion concentrations (alkalinity, hardness, conductivity) (Table 2). Coefficients of variation (CV) in annual water temperature range (CV = $18-22$ %) and average substratum size (CV = $42-56$ %) were relatively low among streams of similar size.

Principal components analysis (PCA) of physical and chemical variables separated the streams along PCA-1(x-axis) primarily by size (Fig. 2 b). PCA clearly distinguished 2nd–4th order streams from 5th–6th order streams suggesting major shifts in habitat conditions with change in stream size. For example, PCA-1 showed that chlorophyll-a, annual temperature range, water depth, and hydraulic sheer stress (tau) increased and benthic organic matter (BOM) decreased with stream size. PCA-2 (y-axis) separated streams based
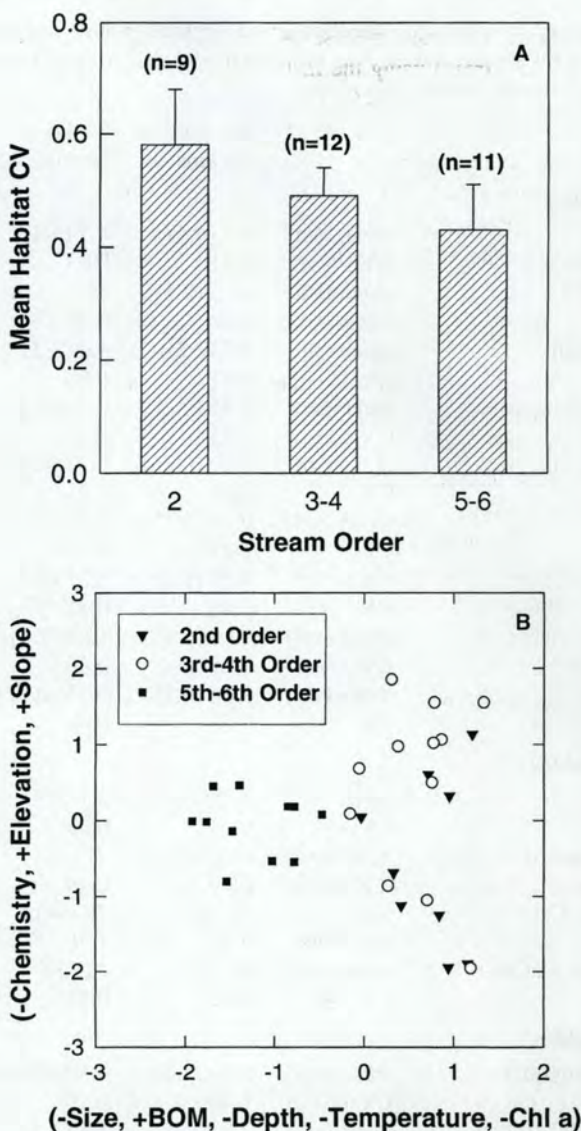
Fig. 2. a) Mean coefficients of variation (CV's) for habitat measures among streams of different size. Bars represent mean +1 standard deviation. Sample size is number of streams in each size class (in parentheses). **b**) Principal components scatterplot of study sites based on physical and chemical measures recorded for each site. Variables for each axis had factor loading scores that were greater than 0.60 for that axis. Signs in front of each variable indicate relationship of that factor with axis.

Table 2. Summary of physical, chemical, and organic matter resources for study streams grouped by stream size. CV is the coefficient of variation using the average values from each stream within each group.

		2 order streams	3–4 order streams	5–6 order streams
Physical variables				
Slope (%)	mean (std)	9.2 (6.5)	4.7 (4.4)	1.5 (0.8)
	CV	0.71	0.93	0.50
Temperature (°C)	mean (std)	11.5 (2.5)	12.0 (2.6)	16.3 (3.0)
	CV	0.22	0.22	0.18
Bankfull width (m)	mean (std)	2.7 (2.2)	4.4 (2.2)	26.1 (11.8)
	CV	0.81	0.50	0.45
Bankfull depth (hiz; m)	mean (std)	0.35 (0.2)	0.51 (0.2)	1.02 (0.4)
	CV	0.55	0.34	0.34
Base flow depth (loz; m)	mean (std)	0.09 (0.06)	0.17 (0.06)	0.35 (0.08)
	CV	0.68	0.33	0.23
hiz-loz (m)	mean (std)	0.52 (0.77)	0.33 (0.15)	1.44 (0.81)
	CV	1.47	0.46	0.56
hiz/loz	mean (std)	4.05 (1.9)	3.21 (1.3)	2.92 (1.0)
	CV	0.48	0.42	0.34
Substrata (cm)	mean (std)	12.0 (5.4)	12.5 (7.0)	26.0 (10.8)
	CV	0.45	0.56	0.42
Velocity (cm/s)	mean (std)	0.34 (0.18)	0.35 (0.17)	0.34 (0.23)
	CV	0.53	0.49	0.68
Chemical variables				
pH	mean (std)	8.1 (0.3)	8.1 (0.3)	8.3 (0.2)
	CV	0.04	0.03	0.03
Conductivity (umhos @ 20°C)	mean (std)	80 (31)	71 (35)	85 (20)
	CV	0.39	0.49	0.24
Hardness (mg/L $CaCO_3$)	mean (std)	58 (26)	78 (94)	39 (6)
	CV	0.45	1.20	0.14
Alkalinity (mg/L $CaCO_3$)	mean (std)	51 (21)	42 (30)	35 (9)
	CV	0.41	0.71	0.24
Resource variables				
Chlorophyll-a (mg/m^2)	mean (std)	8.1 (11.3)	4.9 (3.9)	10.0 (5.8)
	CV	1.40	0.79	0.58
Periphyton AFDM (g/m^2)	mean (std)	2.0 (0.9)	1.8 (1.2)	2.3 (2.8)
	CV	0.45	0.68	1.19
Benthic Organic Matter (g/m^2)	mean (std)	68.4 (61)	26.0 (15.4)	12.7 (12.1)
	CV	0.89	0.59	0.94

on water chemistry, site elevation and stream gradient, with 2nd–4th order streams displaying much greater variation, i.e. range in factor scores, among sites than 5th–6th order streams along this axis. These first two axes explained 80 % of the variation among sites.

Spatial patterns in macroinvertebrate community structure

Most of the total-community indicators (Table 3, top block) were similar for 2nd through 4th order streams, but were notably greater (total density, total biomass, species richness) or lower (Shannon's diversity) in the 5th–6th order streams than in the smaller streams. Further, most of the total community-indicators were similar for 1st–2nd and 3rd–4th order streams, but many of the individual community-indicators showed intermediate values for the mid-sized streams. Only Simpson's index showed no difference among stream sizes. Of these observed differences, however, only Shannon's diversity was statistically different among stream sizes (p = 0.0001). Likewise, the relative densi-

Table 3. Means, standard deviations (SD), and coefficients of variation (CV) for attributes of the macroinvertebrate assemblages in streams grouped by size. P-values from ANOVA results on means and attributes significantly different among stream sizes in bold.

| Attribute	2 Order			3–4 Order			5–6 Order			p-value
	mean	SD	CV	mean	SD	CV	mean	SD	CV	
Density (no./m²)	5266	3585	68	5659	2721	48	8542	4277	50	0.113
Biomass (mg/m²)	869	373	43	821	349	43	1054	679	64	0.561
Taxa richness	22.8	4.7	20	24.8	6.3	25	27.0	3.4	13	0.184
Diversity (H′)	3.0	0.1	4	3.0	0.4	12	2.3	0.3	13	**0.000**
Simpson's Index	0.2	0.0	17	0.2	0.0	22	0.2	0.1	25	0.092
% Predators (no.)	22.3	10.2	46	10.6	3.4	32	13.8	6.0	43	**0.004**
% Gatherers (no.)	14.8	9.2	62	15.0	9.1	61	13.7	7.0	51	0.963
% Scrapers (no.)	18.1	13.9	77	19.9	8.3	42	16.4	7.0	43	0.758
% Shredders (no.)	10.0	9.0	90	5.7	6.3	109	0.7	0.9	124	**0.011**
% Filterers (no.)	13.8	11.4	83	8.4	8.5	101	10.1	11.3	112	0.538
% Miners (no.)	22.1	13.3	60	37.3	15.6	42	44.7	11.4	25	**0.004**
% Predators (mg)	23.9	10.4	44	25.0	12.3	51	32.6	9.7	30	0.182
% Gatherers (mg)	13.5	5.9	43	13.5	7.0	52	14.1	7.4	52	0.973
% Scrapers (mg)	23.1	18.1	78	27.1	9.0	33	17.4	8.5	49	0.254
% Shredders (mg)	16.7	16.3	98	12.2	15.0	123	4.2	6.2	147	0.129
% Filterers (mg)	6.2	3.9	63	8.2	7.5	91	12.2	10.7	87	0.265
% Miners (mg)	14.5	15.0	104	12.0	10.7	89	18.7	4.4	24	0.406
% Obligate opportunists (no.)	46.6	20.1	43	61.6	13.2	21	63.4	9.1	14	**0.017**
% Facultative opportunists (no.)	30.3	21.4	71	17.4	10.6	61	18.9	11.5	61	0.132
% Obligate equilibrialists (no.)	1.9	1.6	82	2.2	2.1	96	4.8	2.7	55	**0.001**
% Facultative equilibrialists (no.)	9.8	4.6	47	8.6	1.8	21	6.6	3.4	52	0.082
% Mixed-trait (no.)	11.4	8.0	71	10.1	7.0	69	6.3	3.8	60	0.201
% Obligate opportunists (mg)	26.2	9.8	37	25.9	12.2	47	29.1	9.7	33	0.766
% Facultative opportunists (mg)	14.8	12.6	86	11.1	8.3	75	10.6	6.3	59	0.581
% Obligate equilibrialists (mg)	14.7	11.1	76	17.7	13.3	75	37.4	18.4	49	**0.004**
% Facultative equilibrialists (mg)	23.7	16.3	69	31.4	23.3	74	16.2	11.5	71	0.179
% Mixed-trait (mg)	20.6	17.1	83	13.9	14.3	103	6.7	8.7	131	0.101
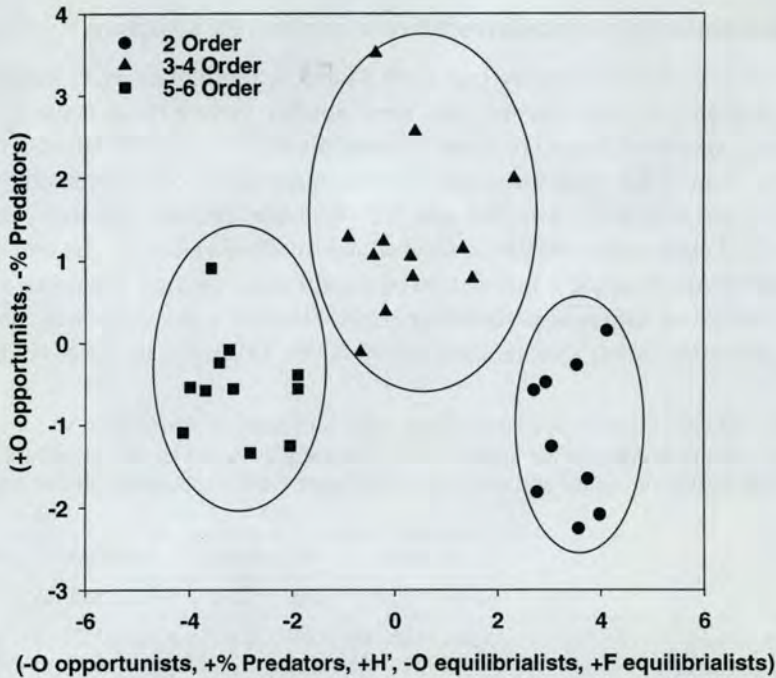
Fig. 3. Principal components scatterplot of study sites based on community properties. Variables for each axis had factor loading scores that were greater than 0.60 on that axis. Signs in front of factors indicate relationship of that variable to axis. Circles arbitrarily drawn to enhance clarity of presentation.

ties of most functional feeding groups, except miners, were greater in the 2nd order streams than in the 5th–6th order streams, with 3rd–4th order streams having intermediate values (Table 3). However, only the small versus large stream differences for predators, shredders, and miners were statistically significant (p < 0.05). Relative biomass of the functional feeding groups also showed a general trend, but it was the reverse of that for relative densities: biomass values were lower in the 2nd order streams than in the 5th–6th order streams for all groups but scrapers and shredders, although no differences were statistically significant.

The relative density of obligate opportunists (p = 0.017) and obligate equilibrium taxa (p = 0.001) was significantly greater in 5th–6th order streams (Table 3). In contrast, the relative density of facultative equilibrium taxa was lower in 5th–6th order streams than in 2nd through 4th order streams (p = 0.082). The absolute biomass of mixed-trait taxa was significantly greater in the smaller than in the 5th–6th order streams (p = 0.068); whereas the absolute and relative biomass of obligate equilibrialists was greater in these larger systems (p = 0.013, p = 0.004; respectively).
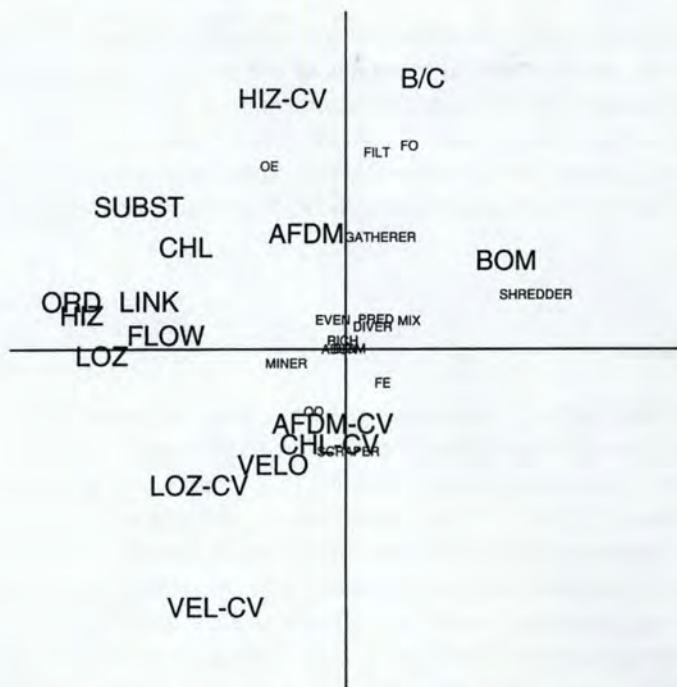
Fig. 4. Results of canonical correspondence analysis relating environmental measures to biotic community indices. Community attributes notated as diver = H′ diversity, even = Simpson's index, rich = species richness, prd = predators, filt = filterers, abun = abundance, biom = biomass, FO = facultative opportunist, FE = facultative equilibrialist, OO = obligate opportunist, OE = obligate equilibrialist, and mix = mixed-trait (see text for explanation of community groups).

Variation in community properties among streams of similar size was assessed further using coefficients of variation (CV) (Table 3). Of the 27 community properties assessed, 15 showed higher CV's in the smaller streams than the 5th–6th order streams, including total density, species richness, and the relative densities of gatherers, scrapers, miners, opportunist and equilibrium taxa. Diversity (H′), and the relative abundances of filterers and shredders had higher CV's in 5th–6th order streams than in 2nd streams. Properties that showed no change in CV with stream size included organism biomass, Simpson's index, and the relative biomass of opportunist and equilibrium taxa.

PCA clearly separated streams of different size based on community properties. PCA-1 was determined from the relative density of obligate opportunists, equilibrium taxa, shredders, and miners; whereas PCA-2 was derived from the relative biomass of opportunist and equilibrium taxa (Fig. 3). These first two axes explained 69 % of the variation among sites. Lastly, canonical correspondence analysis was used to determine relationships between environ-

mental variables and macroinvertebrate assemblage structure (after TER BRAAK 1986). Most structural attributes of the benthic assemblage displayed poor relationships with measured environmental variables (Fig. 4). Exceptions were the gatherer group, which showed a strong relationship with periphyton AFDM, and scrapers which were related to near-bed velocities. In addition, shredders were strongly associated with BOM and inversely related to stream size.

Discussion

We found that habitat heterogeneity within this geographic region varied within and among stream sizes, with smaller ($\leq$4th order) streams expressing greater within and among stream variation than larger ($\geq$5th order) streams. In addition, more (1.7 X's) of the coefficients of variation of community measures were greater in the smaller than in the larger streams. The results of the community-level indicators are consistent with the habitat templet hypothesis because they correspond with the differences in spatial habitat factors observed among streams of different size. Smaller streams showed greater among-system habitat heterogeneity, i.e. higher CV's, than larger systems probably because more stream and habitat types can occur within a given unit area for smaller than larger streams. Similar results were found for the mainstem Salmon River (MINSHALL et al. 1985).

Two of the habitat factors that we found to differ in degree of heterogeneity among streams of different size, annual temperature range and change from baseflow to bankfull water depth (an indicator of annual discharge range), are measures of annual temporal variability. We found that both temporal measures were greater in 5th–6th order streams compared to smaller streams. As noted above, these larger streams generally exhibited less overall spatial habitat heterogeneity than did the smaller streams. These results suggest that the lack of spatial heterogeneity within a stream, at least with respect to certain habitat factors, may be compensated for by higher levels of temporal heterogeneity. In the Salmon River, the greatest annual temperature variation was found in 4th–6th order streams than in either larger or smaller streams (MINSHALL et al. 1985). Total species richness followed this pattern directly, as did spring and summer richness values, whereas Shannon's diversity showed an inverse relationship. Based on theoretical considerations (VANNOTE et al. 1980, VANNOTE & SWEENEY 1980), it was suggested that the increased temperature variability in mid-sized systems meets the thermal optima for the greatest number of macroinvertebrate taxa, thus accounting for the higher species richness. In the present study, species richness also increased and Shannon's diversity decreased, albeit only slightly, from 2nd to 5th–6th order

streams, however we lack data for larger (>7th order) streams. Using multiple stepwise regression, we found only Simpson's index (a measure of dominance) to be positively associated and percent shredder density to be negatively associated with annual range in temperature. It could be that our measures of temperature variation or taxa richness, based as they were on limited sampling, were insufficient to adequately test this relationship or that the influence of other factors confounded the results. For example, taxa richness was more related, in the stepwise regression analysis, to CV of near-bed velocity than to annual temperature range, although still displaying a nonsignificant increase with stream size.

Some spatial properties of the habitat templet for lotic systems, notably water chemistry, are thought to regionally differ primarily as a result of differences in geology (EGGLISHAW & MORGAN 1965, MINSHALL & MINSHALL 1978, KOETSIER et al. 1996, RICHARDS et al. 1996). Macroinvertebrate standing crops have been shown to be greater in certain streams in relation to some of these chemical factors, e.g. higher alkalinity or specific conductance (LA PERRIERE et al. 1989, KOETSIER et al. 1996). In this study, the relative biomass of scrapers, miners, and filterers were related more strongly to measures of water chemistry than with other habitat properties, demonstrating their importance even within regional spatial scales. Higher alkalinity or specific conductance may enhance food resources resulting in greater macroinvertebrate standing crops. We also found macroinvertebrate density and biomass, density and biomass of the obligate opportunist trait group, and the relative abundance of scrapers and miners to be associated with food resource levels.

Relating species traits to habitat characteristics can provide important evolutionary insights into the structuring of stream communities (e.g. SCARSBROOK & TOWNSEND 1993, GROWNS & DAVIS 1994, USSEGLIO-POLATERA 1994, POFF & ALLEN 1995, TOWNSEND et al. 1997), although trade-offs among species traits (RESH et al. 1994, TOWNSEND & HILDREW 1994) and between spatial and temporal components of the habitat templet (see above) in response to environmental fluctuations can make data analysis and interpretation difficult. We found that obligate opportunists and obligate equilibrium taxa were significantly more abundant in 5th–6th order streams than in smaller ones, whereas facultative opportunists and mixed-trait groups were more prevalent in smaller than in larger streams. We suggest that each of these groups may be adapted to habitat conditions characteristic of a stream of particular size. For example, mobile taxa, whether multi- or univoltine, may be better suited for the more temporally diverse habitats found in the 5th–6th order streams than are less mobile taxa. Perhaps this is due to the ability of more mobile forms to leave, recolonize, or otherwise actively adjust to rapidly changing temperature or flow conditions that are characteristic of 5th–6th order streams in this region.

This study demonstrates that habitat heterogeneity in wilderness mountain streams occurs across both temporal and spatial (within-, among-, and along-stream) scales. These multiple trajectories and dimensions taken together account more for macroinvertebrate assemblage patterns than does any one dimension alone, either among or within the spatial temporal axes (e.g. WARD 1989). In addition, some environmental factors were seen to have both a temporal and a spatial heterogeneity component. For species richness and mobile taxa, the temporal component seemed more important than the spatial one; species richness and some adaptive traits were primarily functions of annual temperature or discharge that change predictably with stream size. In contrast, macroinvertebrate diversity (H') was a function of habitat heterogeneity measured at the scale of the stream reach, whereas most functional feeding group abundances reflected the spatial distribution of food resources whether at the within-reach level or longitudinally along the river continuum. These patterns suggest that the analysis of community properties are dependent on the spatial or temporal scale of influence (MINSHALL 1993), and emphasize the importance of relating basic questions of community organization to the most relevant scale of influence (see RICHARDS et al. 1996).

Acknowledgements

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Appendix: Binary coding for species traits of taxa identified in the study streams with resultant PCA factor loadings for each trait, and factor scores and summed factor scores for each taxon. Summed factor scores determined the designation of a taxon into a species trait group.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	−0.82	0.14	0.30	−0.12	0.84	−0.46	−0.61	−0.32				
Factor-2 loadings	0.18	−0.62	−0.09	0.33	0.20	0.09	−0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	−0.21	0.34	0.17	−0.74	0.76	0.00	0.08	−0.19	0.06	−0.18				
Coleoptera															
Hydrophilidae	0	0	0	0	1	0	0	1	0	0	1	0.938	0.994	−3.078	−1.146
Heterlimnius	0	0	0	1	0	0	0	1	0	0	1	−0.251	0.644	−0.931	−0.538
Hydrovatus	0	0	0	0	1	1	1	0	0	0	1	−0.029	−0.893	−1.898	−2.820
Narpus	0	0	0	1	0	0	0	1	0	0	1	−0.251	0.644	−0.931	−0.538
Optioservus	0	0	0	1	0	0	0	1	0	0	1	−0.251	0.644	−0.931	−0.538
Oreodytes	0	0	1	0	0	1	1	0	0	0	0	0.006	−2.396	0.424	−1.966
Rhizelmis	0	0	0	1	0	0	0	1	0	0	1	−0.251	0.644	−0.931	−0.538
Diptera															
Antocha	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Atherix variagata	1	0	0	1	0	1	0	0	1	0	1	−1.382	0.419	0.564	−0.400
Blephariceridae	0	0	1	0	0	1	0	0	0	1	1	−0.398	0.019	0.309	−0.071
Ceratopogonidae	0	0	0	1	0	0	0	0	1	0	1	−1.480	0.152	−1.051	−2.379
Chaoboridae	0	0	0	1	0	0	0	0	0	1	1	−1.631	0.192	−0.579	−2.018
Chelifera	0	0	0	1	0	0	0	0	0	1	1	−1.631	0.192	−0.579	−2.018
Chironomidae	0	0	0	1	0	0	0	0	1	0	0	−1.371	−0.733	−0.822	−2.926
Clinocera	0	0	0	1	0	0	0	0	0	1	1	−1.631	0.192	−0.579	−2.018
Dicronota	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441

Appendix: Continued.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	-0.82	0.14	0.30	-0.12	0.84	-0.46	-0.61	-0.32				
Factor-2 loadings	0.18	-0.62	-0.09	0.33	0.20	0.09	-0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	-0.21	0.34	0.17	-0.74	0.76	0.00	0.08	-0.19	0.06	-0.18				
Dixa	0	0	0	1	0	0	0	0	0	1	1	-1.631	0.192	-0.579	-2.018
Empididae	0	0	0	1	0	0	0	0	0	1	1	-1.631	0.192	-0.579	-2.018
Glutops	1	0	0	1	0	1	0	0	1	0	1	-1.382	0.419	0.564	-0.400
Hexatoma	1	0	0	1	0	1	0	0	1	0	1	-1.382	0.419	0.564	-0.400
Pedicia	1	0	0	1	0	1	0	0	1	0	1	-1.382	0.419	0.564	-0.400
Rhabdomastrix	1	0	0	1	0	1	0	0	1	0	1	-1.382	0.419	0.564	-0.400
Simulium	0	0	0	1	0	0	0	0	0	1	0	-1.521	-0.693	-0.351	-2.565
Ephemeroptera															
Ameletus cooki	1	0	0	1	0	1	1	0	0	0	0	-1.128	-1.956	1.150	-1.934
Ameletus siphonuras	1	0	0	1	0	1	1	0	0	0	0	-1.128	-1.956	1.150	-1.934
Attenella	1	0	1	0	0	1	1	0	0	0	1	-0.123	-1.339	0.868	-0.594
Baetis parvus	0	1	0	0	0	0	1	0	0	0	0	-0.500	-2.701	-1.219	-4.420
Baetis tricaudatus	0	1	0	0	0	0	1	0	0	0	0	-0.500	-2.701	-1.219	-4.420
Cinygmula mimus	0	1	0	0	0	1	0	1	0	0	0	0.702	-1.625	-0.516	-1.438
Drunella coloradensis	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	0.630	2.235
Drunella doddsi	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	2.630	2.235
Drunella falvilinea	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	0.630	2.235
Epeorus albertae	0	1	0	0	0	1	0	1	0	0	0	0.702	-1.625	-0.516	-1.438
Epeorus deceptivus	0	1	0	0	0	1	0	1	0	0	0	0.702	-1.625	-0.516	-1.438

Appendix: Continued.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	−0.82	0.14	0.30	−0.12	0.84	−0.46	−0.61	−0.32				
Factor-2 loadings	0.18	−0.62	−0.09	0.33	0.20	0.09	−0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	−0.21	0.34	0.17	−0.74	0.76	0.00	0.08	−0.19	0.06	−0.18				
Epeorus longimanus	0	1	0	0	0	1	0	1	0	0	0	0.702	−1.625	−0.516	−1.438
Ephemerella aurivilli	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Ephemerella infrequens	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Ephemerella margarita	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Heptageniidae	0	1	0	0	0	1	0	1	0	0	0	0.702	−1.625	−0.516	−1.438
Paraleptophlebia	0	0	1	0	0	1	1	0	0	0	0	0.006	−2.396	0.424	−1.966
Rhithrogena	1	1	0	0	0	1	0	1	0	0	0	0.682	−1.452	0.157	−0.613
Serratella inermis	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Serratella tibialis	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Tricorythodes	0	1	0	0	0	0	0	1	0	0	0	0.585	−1.719	−1.457	−2.592
Plecoptera															
Alloperla	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	0.630	2.235
Calineuria	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Capnia	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Claasenia	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Cultus	0	0	1	0	0	1	0	1	0	0	0	1.091	−0.414	0.186	0.863
Hesperoperla pacifica	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Isoperla	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Isoperla pinta	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688

Appendix: Continued.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	−0.82	0.14	0.30	−0.12	0.84	−0.46	−0.61	−0.32				
Factor-2 loadings	0.18	−0.62	−0.09	0.33	0.20	0.09	−0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	−0.21	0.34	0.17	−0.74	0.76	0.00	0.08	−0.19	0.06	−0.18				
Megarcys	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Nemoura	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Perlesta	0	0	1	0	0	1	0	1	0	0	0	1.091	−0.414	0.186	0.863
Perlidae	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Prostoia	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Perlodidae	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Pteronarcys californica	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Skwala	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Suwallia	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Sweltsa	1	0	1	0	0	1	0	1	0	0	0	1.071	−0.242	0.859	1.688
Visoka cataractae	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Yoroperla brevis	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Zapada cinctipes	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Zapada oregonesis	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Trichoptera															
Apatania	0	0	0	1	0	1	0	1	0	0	1	−0.133	0.738	0.011	0.616
Arctopsyche grandis	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Brachycentrus	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Clostoeca	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441

Appendix: Continued.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	−0.82	0.14	0.30	−0.12	0.84	−0.46	−0.61	−0.32				
Factor-2 loadings	0.18	−0.62	−0.09	0.33	0.20	0.09	−0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	−0.21	0.34	0.17	−0.74	0.76	0.00	0.08	−0.19	0.06	−0.18				
Doliphilodes	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Glossosoma	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Helicopsyche	0	0	0	1	0	1	0	1	0	0	1	−0.133	0.738	0.011	0.616
Hydropsyche	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Hydroptila	0	0	1	0	0	1	0	0	0	1	1	−0.398	0.019	0.309	−0.071
Lepidostoma	0	0	0	1	0	1	0	1	0	0	1	−0.133	0.738	0.011	0.616
Limnephilidae	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Micrasema	0	0	0	1	0	1	0	0	0	1	1	−1.513	0.286	0.362	−0.864
Molanna	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Neophylax	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Oligoplectrum	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Onocosmoecus	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Parapsyche elis	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Polycentropus	0	0	0	1	0	1	0	0	0	1	1	−1.513	0.286	0.362	−0.864
Rhyacophila acropedes	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Rhyacophila angelita	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	0.630	2.235
Rhyacophila hyalinata	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Rhyacophila rotunda	0	0	0	1	0	1	0	1	0	0	1	−0.133	0.738	0.011	0.616
Rhyacophila vaccua	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Rhyacophila vagrita	1	0	1	0	0	1	0	1	0	0	1	0.961	0.643	0.630	2.235

Appendix: Continued.

	Size	Streamlined	Flattened	Cylindrical	Spherical	Voltinism	Swimmers	Crawlers	Burrowers	Sedentary	Dispersal	PCA-1	PCA-2	PCA-3	Summed Score
Factor-1 loadings	0.08	0.13	0.68	−0.82	0.14	0.30	−0.12	0.84	−0.46	−0.61	−0.32				
Factor-2 loadings	0.18	−0.62	−0.09	0.33	0.20	0.09	−0.73	0.31	0.05	0.11	0.75				
Factor-3 loadings	0.58	−0.21	0.34	0.17	−0.74	0.76	0.00	0.08	−0.19	0.06	−0.18				
Rhyacophila vepulsa	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Tinodes	1	0	0	1	0	1	0	0	0	1	1	−1.533	0.458	1.035	−0.039
Others															
CLADOCERA	0	0	1	0	0	0	0	0	1	0	1	−0.366	−0.116	−1.104	−1.586
Ostracoda	0	0	0	0	1	0	0	0	1	0	1	−0.292	0.502	−3.198	−2.987
COPEPODA	0	0	0	1	0	0	0	0	1	0	1	−1.480	0.152	−1.051	−2.379
GASTROPODA	1	0	0	0	1	0	0	1	0	0	1	0.917	1.167	−2.405	−0.321
Lymnaea	1	0	0	0	1	0	0	1	0	0	1	0.917	1.167	−2.405	−0.321
Physidae	1	0	0	0	1	0	0	1	0	0	1	0.917	1.167	−2.405	−0.321
AMPHIPODA	1	0	1	0	0	0	1	0	0	0	0	−0.132	−2.318	0.155	−2.294
Hyallela azteca	1	0	1	0	0	0	1	0	0	0	0	−0.132	−2.318	0.155	−2.294
Pisidium	0	0	0	0	1	0	0	0	0	1	1	−0.442	0.542	−2.726	−2.626
Lepidoptera	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
Simyra	1	0	0	1	0	1	0	1	0	0	1	−0.153	0.910	0.684	1.441
COLLEMBOLA	0	0	1	0	0	0	0	1	0	0	1	0.863	0.376	−0.984	0.255
HYMENOPTERA	0	0	1	0	0	1	0	1	0	0	1	0.981	0.471	−0.042	1.410
Hydracarina	0	0	0	0	1	0	0	1	0	0	1	0.938	0.994	−3.078	−1.146
Lumbricus	1	0	0	1	0	0	0	0	1	0	1	−1.500	0.324	−0.378	−1.554
Oligochaeta	0	0	0	1	0	0	0	0	1	0	0	−1.371	−0.733	−0.822	−2.926
NEMATODA	0	0	0	1	0	0	0	0	1	0	1	−1.480	0.152	−1.051	−2.379
TURBELLARIA	1	0	1	0	0	0	0	1	0	0	1	0.843	0.549	−0.311	1.081