Salinity Stresses Along a Complex River Continuum: Effects on Mayfly (Ephemeroptera) Distributions

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Ecology, Vol. 65, No. 5 (Oct., 1984), 1662-1672.

Ecology, 65(5), 1984, pp. 1662–1672

SALINITY STRESSES ALONG A COMPLEX RIVER CONTINUUM: EFFECTS ON MAYFLY (EPHEMEROPTERA) DISTRIBUTIONS[1]

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Abstract. The saline-stressed Washita River in western Oklahoma was evaluated to test the River Continuum Concept (RCC). Physical, chemical, and biological variables were monitored at six sites in the river over 14 sampling periods during 1980 and 1981. Physical parameters represented stream discharge, sediment particle sizes, organic content of the sediment, and related factors. Chemical variables were conductance, pH, and concentrations of major salts (calcium, sulfate, sodium, and chloride). Biological variables were densities of mayfly genera from dredge samples.

Two-dimensional ordinations were produced for the physical, chemical, and biological groups of variables using the ALSCAL model of three-way nonmetric multidimensional scaling. The ALSCAL model summarized variation over the 14 sampling periods. Rank correlations of the dimensions from all ordinations suggest that both river gradient and local effects influence the structure of the benthic community. River gradient dimensions for physical and chemical variables were highly correlated with one biological dimension. The remaining biological dimension was correlated with local salinity effects.

Benthic community structure is influenced by physical gradients. Saline effects, although governed by geomorphological processes, do not conform to the typical river gradient. This localized saline impact influences the benthic community structure. Therefore, the RCC must be modified to allow for multiple gradients if it is to be useful in the generation of ecological models in regions with high river salinity.

Key words: benthos; community structure; Ephemeroptera; ordination; River Continuum Concept; salinity; stress ecology.

INTRODUCTION

Stream morphology creates linear patterns of variation in many ecologically important variables (Leopold et al. 1964). Biological communities in streams are thought to show distinct linear gradients in terms of species composition in response to the influence of these variables (Hynes 1970, Pennak 1971, Hawkes 1975, Vannote et al. 1980). Vannote et al. (1980) proposed the River Continuum Concept (RCC) as a means of predicting community development along linear stream gradients. This concept stresses the close interrelationships among physical factors such as flow rates, substrates, and the habitat requirements of benthic invertebrates by treating the stream community at a given site as a material-processing unit controlled by the basinal morphology of the stream. The RCC relates directly to other recent, generalized theories for streams such as those pertaining to the spiraling of nutrients (Webster and Patten 1979, Elwood et al. 1981). However, there are common situations where these generalized models may not apply. Minshall (1978) has pointed out that organic inputs from outside the stream may be of little importance to community organization in streams with high rates of internal, autotrophic production. These streams are often encountered in drier regions in the western United States.

Streams in arid regions often develop complex salinity gradients. Previous studies have usually ignored or infrequently measured the impact of these complex gradients on the community structure of benthic invertebrates. These chemical parameters may well be more important for many algae (Blinn et al. 1981) and benthic consumers (Magdych 1979*b*) than are the variable flow rates, sources of detritus, or substrates that change dramatically on a seasonal basis. The localized geological distribution of salt deposits (Johnson et al. 1972) and the fluctuations in discharge due to variable rainfall and groundwater inputs (Carr and Bergmann 1976) create a complex mosaic of salt concentrations (Oklahoma State Department of Health 1977) in the Washita River in western Oklahoma. Unlike many streams (Woods 1965), the major dissolved ions vary independently and in a nonlinear manner along the Washita River's downstream flow (Fig. 1). This mosaic chemical development produces a spatial-temporal landscape that could create major barriers for species dispersal and affect community function. The present study tests the relationship among benthic community structure, mosaic saline development, and the river gradient.

MATERIALS AND METHODS

Six sites over a 150-km reach of the Washita River were chosen to monitor biological, chemical, and phys-

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[1] Manuscript received 23 August 1982; revised 20 May 1983; accepted 24 June 1983.

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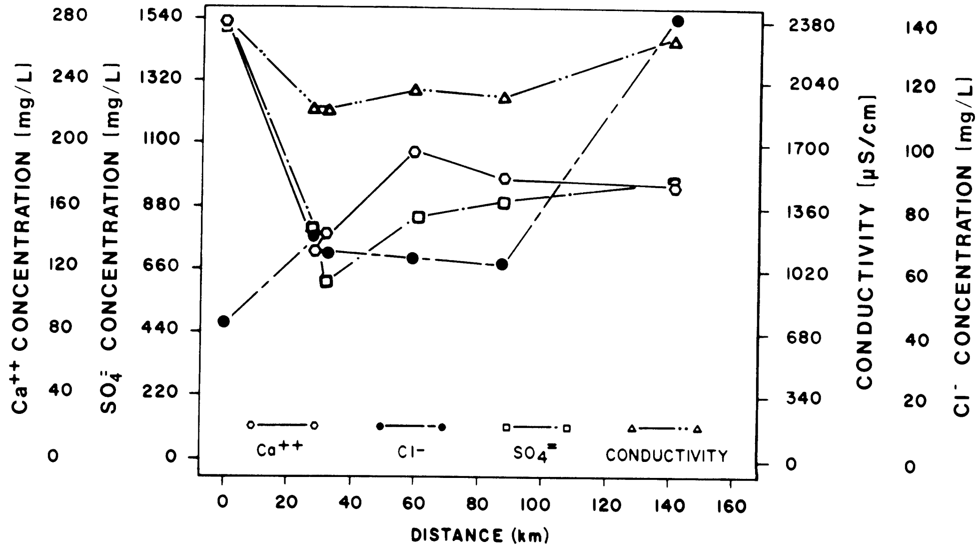

FIG. 1. Mean October concentrations of certain salts in the Washita River.

ical parameters from June 1980 to December 1981 (Fig. 2). These sites ranged from the river headwaters (which are intermittent during drought conditions) to fourth-order streams (Strahler 1957). Site 1 (first order) had a broken tree canopy produced by willows, and sandy substrate. Site 2 (third order) was located below the discharge of Foss Reservoir. This site had no canopy and a silty substrate. The third (third order) and fourth (third order) sites had canopies similar to site 1 and substrates of silt and sand. Site 5 (fourth order) had a light tree canopy, and site 6 (fourth order) was open. These latter two sites had sandy substrates.

Populations of mayflies were monitored at each site with Ekman dredge samples. The Ephemeroptera represented the most abundant members of the river's benthic community. Dredge samples were collected at intervals not <1.0 m along cross-sectional transects at each site. These samples were collected in a section of uniform stream velocity (pools were excluded). These sections were similar to riffle habitats, with respect to flow conditions. True riffles are rare in the Washita River due to the scarcity of larger substrates (gravel and cobble). Four replicate samples were dredged at each site from June 1980 to July 1981. Sample sizes were increased to 12 replicates per site from August 1981 through December 1981 to lower sampling variance. The number of transects taken at each site was a function of stream width and the number of replicates. The dredge samples were washed through a 0.59-mm (20-mesh) sieve and preserved in 10% formaldehyde in the field. Final separation of organisms from the substrate was performed by elutriation (Magdych 1981).

Sediment samples were collected at the position of each dredge by removing a core 10 cm deep × 5 cm in diameter. These samples were stored frozen until analysis, when they were thawed and dried at 100°C. A subsample was removed for measurement of organic content by loss of mass upon ignition at 500° (Cox 1976). The remaining sample of mineral particles was then passed through standard sieves of 4.0 mm (5 mesh), 2.0 mm (10 mesh), 1.0 mm (18 mesh), 0.5 mm (35 mesh), 0.25 mm (60 mesh), 0.125 mm (120 mesh), and 0.0625 mm (230 mesh) to determine percentages of particle size distributions (Hynes 1970, Carver 1971). Particles larger than 4.0 mm (5 mesh) were combined, and particles <0.0625 mm (230 mesh) were also combined in a silt-clay fraction. Stream velocity was measured at each dredge position with a Teledyne-Gurley digital flow meter (Model 645). Stream discharge was calculated from these data. Turbidity was measured with a Hach meter (Model DR-EL). These parameters

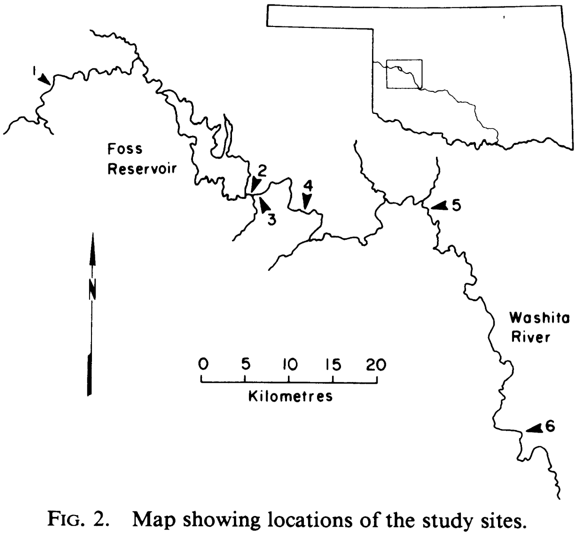

FIG. 2. Map showing locations of the study sites.

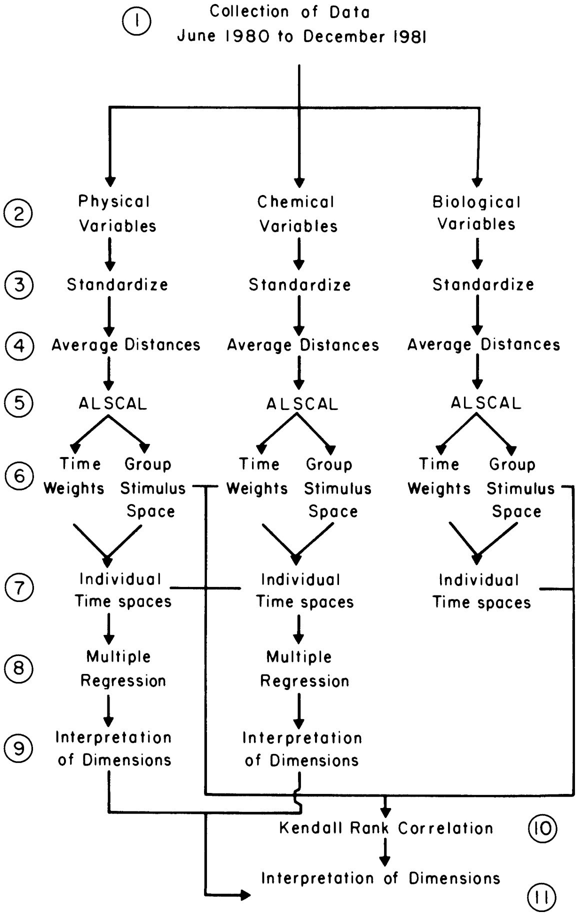

FIG. 3. Flow chart of techniques used in data analysis. A detailed discussion of the techniques of analysis is given in the text.

summarized the major physical variation along the stream gradient.

Chloride, sodium, and calcium were measured in the laboratory with an Orion specific ion meter (Model 407). Sulfate was assessed using Hach chemicals and a Bausch & Lomb Spec 70 spectrophotometer as described by Lind (1974). A Yellow Springs Instruments meter (Model 33) was used in the field to determine conductivity and temperature. The pH was measured with an Extech meter (Model 651). Dissolved oxygen was measured by Winkler titration (Lind 1974).

An outline of the steps involved in the data analysis is provided in Fig. 3. The data were first tabulated for the 14 sampling periods. In the second step, the data were divided into three major groups of physical, chemical, and biological variables as previously mentioned. Each of the three groups was treated identically in steps 3 through 7. The physical, chemical, and biological groups consisted of 14 matrices representing sampling dates between June 1980 and December 1981. Each matrix contained values for each measured variable at six sites. In step 3, the values for each variable were standardized to a mean of zero and a variance of one across sites for each sampling date. This standardization was performed to allow the comparison of variables which were measured on different scales (Austin and Noy Meir 1971, Gauch et al. 1977). A matrix of average taxonomic distances (Sneath and Sokal 1973) among the six sites was then calculated for each sampling date in step 4. The formula for average taxonomic distance is:

$$\sqrt{\left[\sum_{i=1}^{n} (X_{ij} - X_{ik})^2/n\right]},$$

where n is the number of variables, i is the variable being compared, j and k are the sites compared, and X is the value of the variable. The standardization and calculation of distances was performed using NT-SYS (Rohlf et al. 1979).

The average distance matrices for each group of variables was analyzed by the ALSCAL (alternating least squares scaling) model of three-way nonmetric multidimensional scaling (Takane et al. 1976, Kruskal and Wish 1978). A program from SAS implementing this technique was used (Young and Lewyckyj 1979). The ALSCAL model produced an ordination of the six sites for each group of variables, which is a composite accounting for the variation among the 14 distance matrices (representing sampling dates). This composite ordination is the group stimulus space (GSS) in step 6. ALSCAL also produced time weights for each sampling date (distance matrix). The time weight is a point in the time space which has the same dimensionality as the GSS. Individual spaces in step 7 were calculated by multiplying the coordinates of the sites in the GSS by the square root of the coordinates of the time weights. Individual time spaces represent ordinations for each sampling period.

The original variables were regressed onto the individual time spaces in step 8 to provide an interpretation of the physical and chemical groups in step 9. The GSSs for all groups were compared by rank correlations of dimensions within each space in step 10. These correlations lead to interpretation of the biological groups in step 11.

RESULTS

Physical analysis

The results of the ALSCAL ordinations are shown in Figs. 4 and 5. Rankings of the sites along the first dimension of the physical GSS do not correspond to the position of the sites along the actual river gradient (Fig. 4). Site 1 is far removed from the other sites. Sites 4, 5, and 6 are identical on this axis. Sites 2 and 3 are further removed from the other sites. Dimension 1 is positively correlated with medium to coarse sands (as retained by 0.25- and 0.5-mm [60- and 35-mesh] sieves)

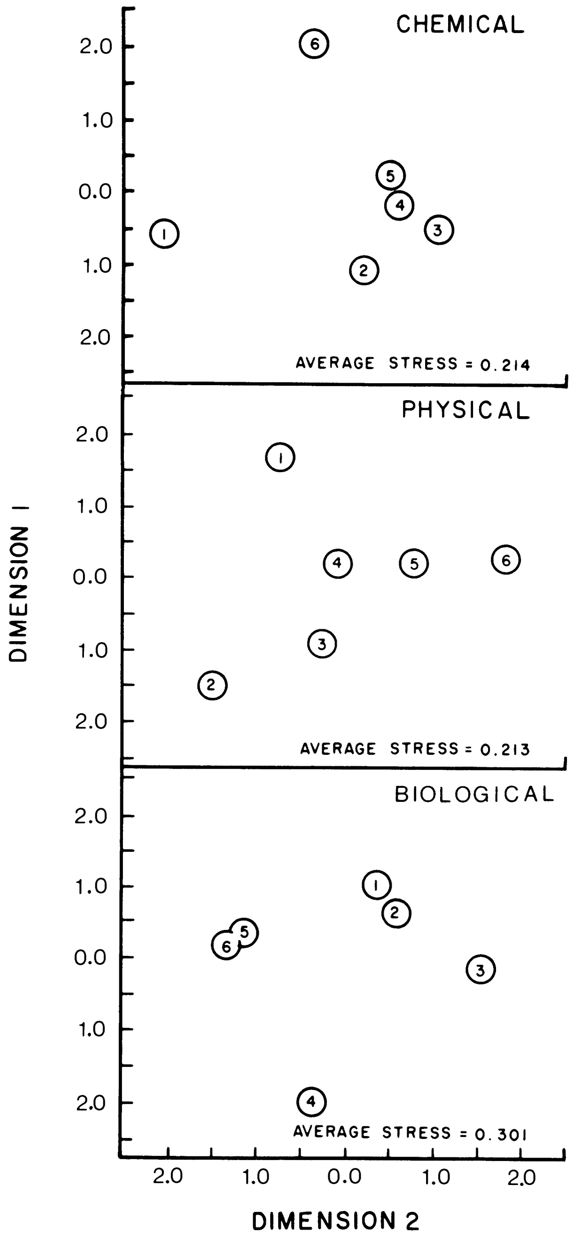

FIG. 4. Plots of the group stimulus spaces for the physical, chemical, and biological ordinations. The dimensions are scaled in relative units. Circled numbers indicate the sampling sites. Average stress is the disparity between rankings in the Group Stimulus Space and the average taxonomic distance.

in the individual time spaces. This dimension is negatively related to organic content of the sediments and to turbidity (Table 1). Sediments at site 1 are composed largely of coarse to medium sand. Sites 5 and 6 are very similar with respect to these factors (Fig. 6). Sites 2 and 3 are composed of finer sediments in a zone of deposition with high organic content and increasing turbidity during spates (Figs. 6 and 7).

The second dimension of the physical GSS reproduced the position of sites on the river gradient with one exception; sites 1 and 2 are reversed (Fig. 4). Foss Reservoir is located between these two locations. This dimension is positively correlated with stream velocity, discharge, and fine sands (as retained by 0.125- and

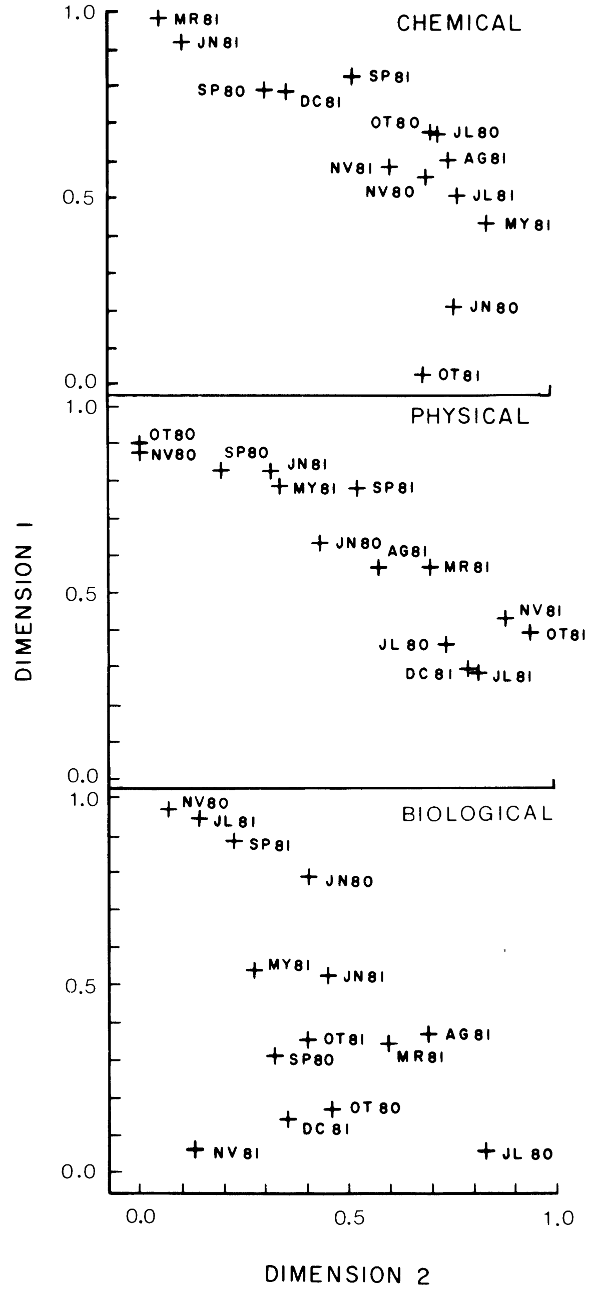

FIG. 5. Graphs of the time weights for each dimension in the time space for the ALSCAL ordinations of sites for physical, chemical, and biological parameters. Projections of sites (individual time spaces) for a specific time are obtained by multiplying the coordinate values of each GSS dimension by the square root of the respective time weight. The dimensions are scaled in relative units.

TABLE 1. Multiple regression of physical variables on time-space dimensions D1 and D2 for representative sampling times for individual time spaces. The regression weights are normalized to equal direction cosines.

Variable	28 July 1980			19 May 1981			21 July 1981			16 November 1981		
	D1	D2	R^2	D1	D2	R^2	D1	D2	R^2	D1	D2	R^2
Turbidity	0.950	0.313	0.45	−0.372	−0.928	0.96	−0.994	−0.111	0.88	−0.552	0.834	0.71
Water temperature	−0.884	−0.468	0.50	−0.102	−0.995	0.78	−0.752	0.664	0.02	−0.945	−0.336	0.97
Mean velocity	−0.113	0.993	0.67	−0.500	0.861	0.83	−0.758	0.652	0.98	−0.270	0.963	0.96
Surface velocity	−0.169	0.986	0.63	−0.519	0.857	0.88	−0.781	0.624	0.97	−0.288	0.958	0.98
Bottom velocity	−0.044	0.984	0.73	−0.488	0.878	0.72	−0.730	0.683	0.91	−0.245	0.970	0.91
Discharge	−0.432	0.902	0.78	−0.258	0.966	0.95	−0.841	0.541	0.97	−0.276	0.962	0.83
Organic content	−0.979	−0.205	0.66	−0.914	−0.405	0.54	−0.752	−0.659	0.23	−0.798	−0.603	0.92
Substrate particles retained by												
4.0-mm mesh	−0.916	0.401	0.06	−0.999	0.040	0.13	−0.996	0.089	0.08	−0.988	0.155	0.14
2.0-mm mesh	−0.882	0.472	0.25	−0.912	0.125	0.03	−0.925	0.380	0.00	−0.945	0.328	0.13
1.0-mm mesh	−0.645	0.764	0.19	0.995	−0.104	0.09	0.983	0.182	0.16	0.520	0.854	0.17
0.5-mm mesh	0.906	0.423	0.26	0.955	−0.297	0.80	0.997	0.082	0.37	0.963	0.267	0.76
0.25-mm mesh	0.998	0.062	0.83	0.870	0.493	0.80	0.978	0.207	0.79	0.925	0.379	0.95
0.125-mm mesh	0.278	0.961	0.75	0.026	1.000	0.80	0.512	0.859	0.59	0.864	0.504	0.89
0.0625-mm mesh	−0.087	0.996	0.84	0.075	0.997	0.34	0.432	0.902	0.53	−0.895	−0.446	0.94
0.0625-mm mesh	−0.851	−0.525	0.62	−0.537	−0.843	0.63	−0.931	−0.364	0.78	−0.995	0.104	0.50

0.0625-mm mesh sieves). It is negatively correlated with organic content and turbidity (Table 1).

An inverse relationship exists between the two dimensions in the time space (Fig. 5). When values of the time weights are high on dimension 1, they are low on dimension 2. This pattern follows temporal changes in rainfall.

Chemical analysis

Chemical GSS dimension 1 produced rankings of the sites which are identical to those of physical GSS dimension 2. Sites 1 and 2 are reversed on the lower end of this saline dimension. Sites 3 to 6 then follow in increasing order. Chemical dimension 1 (in the individual time spaces) is consistently correlated with chloride (Table 2). This dimension is also associated with sodium during 1980 and calcium during 1981. The actual patterns of salinity development are shown in Fig. 8.

Rankings of the sites along dimension 2 do not correspond to the river gradient. Sites 2, 3, 4, and 5 form a cluster to the right of this dimension. Site 6 is to the left of this cluster, and site 1 is far removed from these sites. Chemical dimension 2 is consistently correlated with sulfate in the individual time spaces (Table 2). It is also correlated with calcium during 1980. The re-

TABLE 2. Multiple regression of chemical variables on time-space dimensions D1 and D2 for representative sampling times for individual time spaces. The regression wieghts are normalized to equal direction cosines.

Variable	28 July 1980			6 October 1980			29 August 1981			22 September 1981		
	D1	D2	R^2	D1	D2	R^2	D1	D2	R^2	D1	D2	R^2
Calcium concentration	0.392	−0.920	0.88	−0.050	−0.999	0.72	0.983	0.184	0.98	0.975	0.221	0.98
Sulfate concentration	0.052	−0.999	0.79	−0.020	−1.000	0.93	0.395	0.919	0.80	0.513	0.859	0.97
Sodium concentration	0.873	−0.488	0.95	0.988	−0.059	0.83	0.783	0.622	0.75	0.783	0.622	0.75
Chloride concentration	0.929	0.370	0.87	0.991	0.136	0.78	0.856	0.517	0.88	0.978	0.210	0.89
Conductivity	0.846	0.533	0.54	0.450	−0.893	0.98	0.454	0.891	0.96	0.519	0.855	0.99
pH	0.963	−0.271	0.37	−0.614	0.789	0.30	0.925	−0.435	0.38	0.657	−0.754	0.63

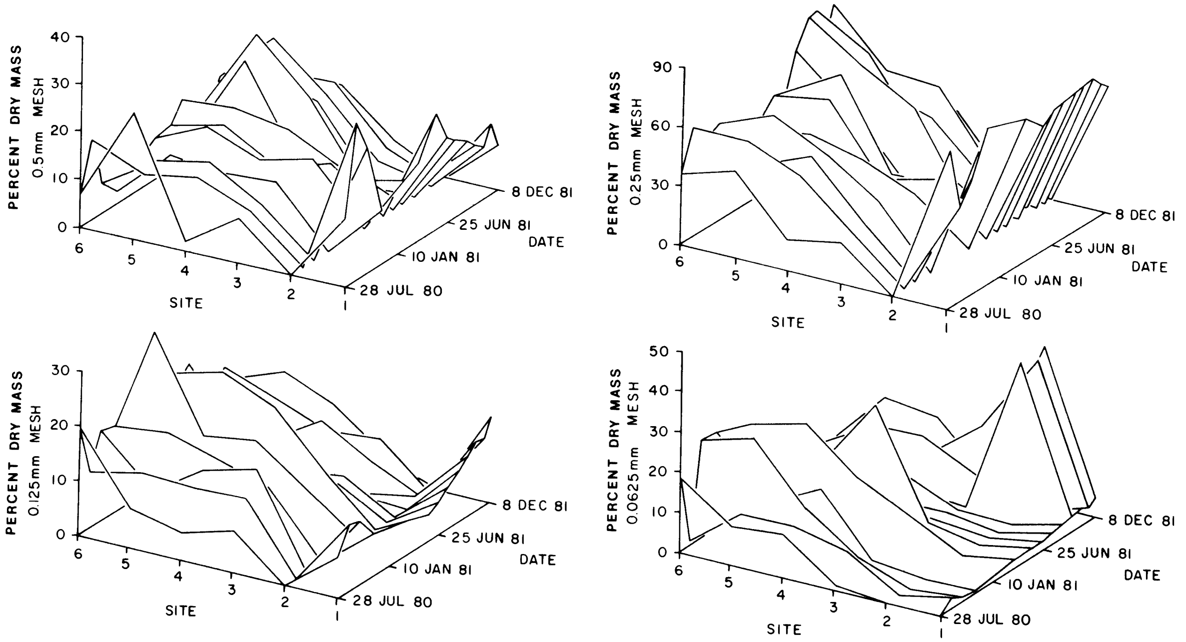

FIG. 6. Variation in percentages of stream-bottom core composed of particles retained by 0.5-mm, 0.25-mm, 0.125-mm and 0.0625-mm mesh sieves among the six sites over sampling time. Dry masses were used to calculate the percentages.

lationships among conductivity, pH, and the two dimensions fluctuate greatly among individual time spaces.

The time weights for the chemical ordination also produce an inverse relationship between the dimensions of the time space (Fig. 5). However, the variation in the chemical distances among sampling times produced a different pattern from that observed in the

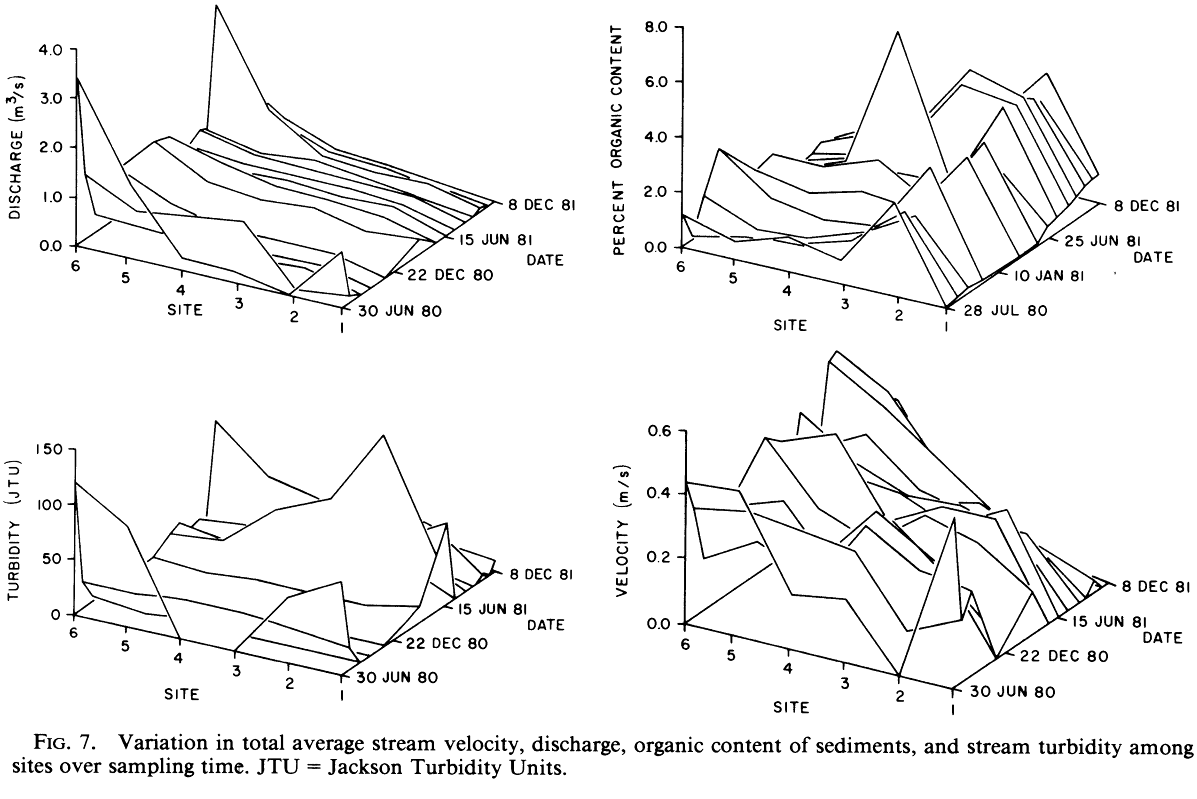

FIG. 7. Variation in total average stream velocity, discharge, organic content of sediments, and stream turbidity among sites over sampling time. JTU = Jackson Turbidity Units.

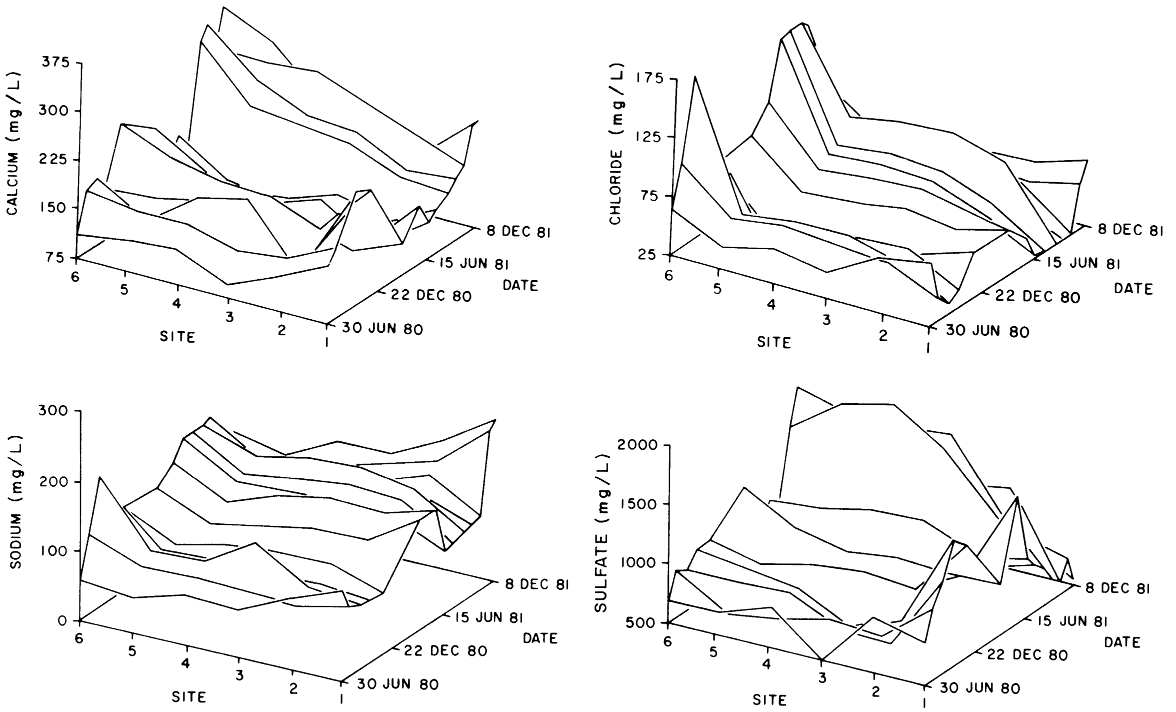

FIG. 8. Variation in the concentrations of major salts in the Washita River among sites over sampling time.

physical time space. The temporal variation of the chemical environment is not identical to the temporal variation of the physical environment.

Biological analysis

Rank correlations of the GSS dimensions from the biological ordination with the GSS dimensions from the physical and chemical ordinations were performed (Table 3). Biological GSS dimension 1 is negatively correlated with chemical GSS dimension 2. This biological dimension is not correlated with any of the physical GSS dimensions. Biological GSS dimension 2 is negatively correlated with chemical GSS dimension 1 and physical GSS dimension 2.

The projections of the dredge time weights in the time space do not present distinct patterns of association between the two dimensions of the time space (Fig. 5). There is no temporal pattern of variation among the time weights either. The parameters associated with each respective time dimension do not appear to be correlated.

DISCUSSION

Average stress (Fig. 4) measured the disparity between the rankings in the GSS and the original average taxonomic distances. Average stress was 0.213 for the physical GSS, but ranged from 0.076 to 0.283 for the individual time spaces. Low values of stress indicate high retention of information from the original data (Fasham 1977, Kruskal and Wish 1978). The interpretability of an *n*-dimensional solution is also very important and must be considered when choosing the number of dimensions in multidimensional scaling (Kruskal 1964). A two-dimensional solution provided a balance between considerations of interpretability and minimization of stress for all three groups of variables.

The rankings of sites along the dimensions of the physical GSS suggest that dimension 2 represents the river gradient. Only site 2 is out of place with respect to the actual linear position along the stream (Fig. 4). The switching of sites 1 and 2 in the ordination with respect to their actual position along the stream gradient represents a physical reset mechanism in the RCC (Vannote et al. 1980). Foss Reservoir is located between these two sites. The discharge of water from the reservoir into site 2 results in the deposition of fine sediments and organic matter (Figs. 6 and 7). Therefore, site 2 has characteristics which would be expected in a hypothetical site upstream from site 1. The high correlations of this dimension with discharge and finer particles of substrate (Table 1) also support this interpretation. Discharge increases predictably downstream, and the small substrate particles are distributed in a manner that conforms to stream hydrodynamics.

GSS dimension 1 of the physical ordination is a scale of local variation of some of the physical variables. The rankings of sites along this dimension do not relate to the river gradient. This dimension is correlated with coarser particles of substrate, turbidity, and organic

TABLE 3. Kendall's rank correlation of all dimensions from the group stimulus spaces for the physical, chemical, and biological ordinations. The upper value is Kendall's Tau. The lower value is the probability of a greater $|R|$.

		Biological		Chemical		Physical	
		D1	D2	D1	D2	D1	D2
Biological	D1						
	D2	0.0667 0.8510					
Chemical	D1	−0.3333 0.3476	−0.7333 0.0388				
	D2	−0.6000 0.0909	0.3333 0.3476	−0.0667 0.8510			
Physical	D1	0.2000 0.5730	−0.4667 0.1885	0.4667 0.1885	−0.6000 0.0909		
	D2	−0.3333 0.3476	−0.7333 0.0388	1.0000 0.0048	−0.0667 0.8510	0.4667 0.1885	

content of the sediment. The availability of coarse substrates in this stream is dependent upon geologic distributions of rock strata. The flow in the river is generally not strong enough to produce sorting of larger particles along the river gradient. The increase in turbidity and organic content in the central sites (Fig. 7) indicates that these are areas of deposition in the stream.

The graph of the physical time weights (Fig. 5) demonstrates the variation of the river environment over time. Dimensions 1 and 2 of the time space correspond to dimensions 1 and 2 of the physical GSS, respectively. A high coordinate value for one dimension in the time space indicates greater distances among sites along that dimension in the individual time space for that sampling date. The relationship between the two dimensions of the time space indicates that there is an inverse temporal distribution of the effects of the two dimensions in the GSS. When the river discharge is high, the sediments are better sorted along the river gradient. At times of the year when the discharge is low, the local variation in substrate distribution is more pronounced. The time weights for September, October, and November 1980 have the highest values on dimension 1 of the time space. This was the peak of a long drought during that year when discharge was the lowest. Conversely, October and November 1981 have high values on time-space dimension 2. These were periods of flooding. Local and river-gradient effects can have discernible impacts on the benthic community, because the effects occur at different times of the year and at different sites.

A similar pattern is seen in the chemical ordination. Chemical dimension 1 of the GSS (Fig. 4) also appears to represent the river gradient. The reversal of sites 1 and 2 along this dimension is a chemical reset in the stream gradient caused by Foss Reservoir. The shallow reservoir acts as a salt sink causing a sharp increase in chlorides in its discharge water compared to site 1 (Madden and Morris 1978, Magdych 1979*b*). This dimension is correlated with chloride (Table 2).

Chemical dimension 2 represents local variation in the river's chemical environment. It is correlated with sulfate and calcium. The major source of these salts is from gypsum deposits. These salt deposits are patchily distributed throughout the watershed (Johnson et al. 1972). Rainfall and irrigation cause leaching patterns of these salts that are distinct from the patterns of other salts (Rhoades et al. 1974, Hillman 1981). This effect produces a gradient which is orthogonal (not parallel) to the actual river gradient.

The chemical time space also exhibits an inverse relationship between dimensions. Therefore, the separation among sites is maximized along the dimensions at different times. The temporal variation is distinct from that of the physical time space, and effects of the chemical environment on the benthic community should be discernible from the effects of the physical environment. Since chemical GSS dimension 1 and physical GSS dimension 2 are correlated (Table 4) and represent the river gradient, it would be difficult to separate these effects on the benthic community. However, chemical GSS dimension 2 and physical GSS dimension 1 represent uncorrelated gradients of local variation. Therefore, it should be possible to determine if the benthos conforms to the river gradient, local physical variation, or local chemical variation.

The correlation of biological GSS dimension 1 of the group stimulus space with chemical GSS dimension 2 demonstrates that a portion of the benthic community conforms to the local distribution of salts (primarily sulfates) in the Washita River. Biological GSS dimension 2 is correlated with both chemical GSS dimension 1 and physical GSS dimension 2. This indicates that the distribution of some of the benthos also conforms to the river gradient as predicted by the RCC. The dimensions of the biological time space do not produce an inverse relationship. This lack of relationship between dimensions in the time space suggests that there is an external causal agent affecting the benthic variation over time, supporting the relationship between local chemical environments and the benthic community structure.

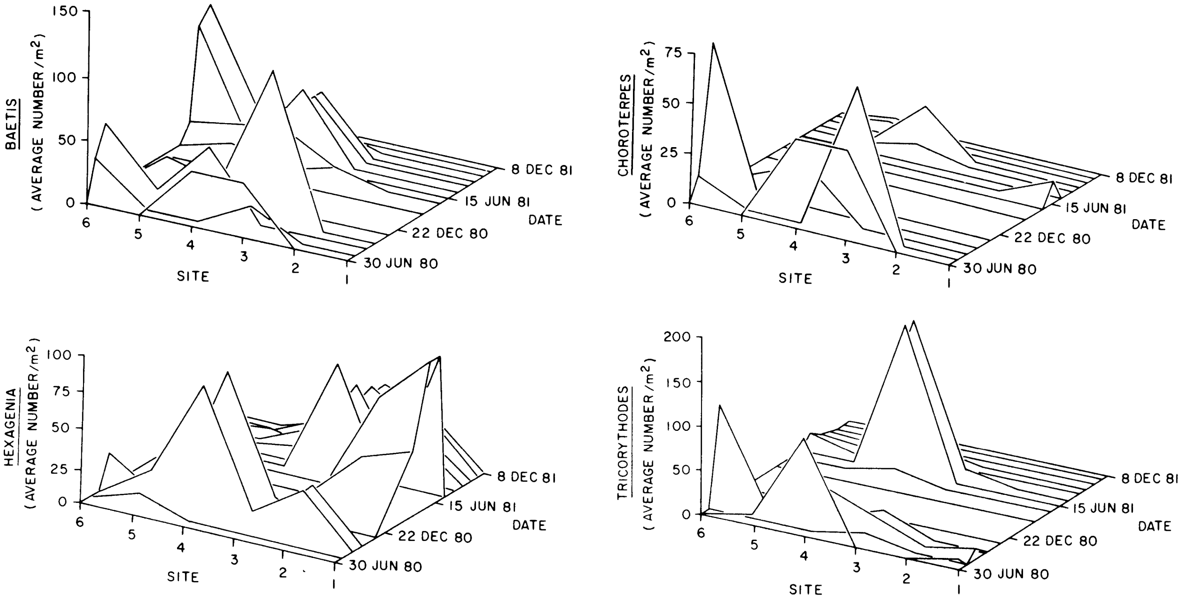

FIG. 9. Variation of faunal densities (no. individuals/m²) of *Baetis, Choroterpes, Hexagenia,* and *Tricorythodes* from dredge samples.

This interpretation of the relationship between the benthos and both the river gradient and local chemical effects is supported by the distribution of several of the most abundant mayflies (Fig. 9). The generic level of taxonomic identification indicates an ecological type in many aquatic insects (Wiggins and Mackay 1978). This level of identification also provides more information than would be available if the insects were combined into general functional feeding groups (sensu Merritt and Cummins 1978). Changes in the insect community with respect to genera should indicate the ability of the community to utilize microhabitats and process organic material along the stream gradient. Distributions of insect genera that do not conform to the optimal habitat availability along the stream gradient indicate that causal agents other than the river gradient affect their distribution.

Baetis is an open-water form commonly found in clear, flowing water and areas of high autotrophic productivity (Magdych 1979*a*). *Baetis* feeds largely on periphyton. River discharge and velocity are usually greatest in sites 4 through 6. These sites quite often have dense algal mats associated with them and reach high levels of oxygen supersaturation, which suggests high autotrophic production. This trend is controlled by the hydrodynamics of the river gradient, and the distribution of *Baetis* reached greatest densities toward site 6 (Fig. 9), conforming to this trend along the stream gradient.

Hexagenia also appears to be distributed in a manner which conforms to the river gradient (Fig. 9). *Hexagenia* is a burrowing organism that requires fine sediments in areas of low current velocity to build its tubes in the substrate. It feeds primarily by filtering detritus particles from water pumped through its tube. *Hexagenia* reached highest densities in site 4 during the early part of 1980. It then shifted to points of highest densities at the first few sites during 1981. The early part of 1980 experienced heavy rainfall and high volumes of water were released from the reservoir until August of that year. The high densities of *Hexagenia* in the central sites during this time period is probably the result of washout of the organisms from the reservoir. Sites 2 through 4 are zones of deposition, and many of the *Hexagenia* would have settled out of this catastrophic drift at these locations. After August 1980, discharge of water from the reservoir was stopped until the late fall of 1981. During this time the distribution of *Hexagenia* shifted to maximum densities at sites 1 and 2. This latter pattern of distribution is exactly what would be expected along the river gradient without the influence of Foss Reservoir.

Choroterpes is a scraper (feeding primarily on periphyton). It is commonly found on exposed surfaces or submerged wood in open water. Therefore, it should have been abundant in sites 3 through 6. This was the case during the early part of 1980 (Fig. 9). However, its distributions shifted to the central sites (site 4 in particular) after the drought set in during the middle of 1980. From August of 1980 through the fall of 1981, sulfates reached the lowest levels of concentration at site 4. The distribution of *Choroterpes* appears to follow the pattern of sulfate concentration in the river, at least during periods of low discharge.

Tricorythodes follows a pattern of distribution similar to that of *Choroterpes*. *Tricorythodes* is a collectorgatherer (Merritt and Cummins 1978) that is found in a wide range of microhabitats (Magdych 1979*a*). It commonly feeds on periphyton and detritus. It would be expected to reach high densities throughout the stream and highest densities in sites 4 through 6. This distribution is seen from June to August 1980 (Fig. 9). However, the distribution rapidly shifts to a peak at site 4 after August 1980 when the chemical differentiation among sites due to sulfate concentration is the greatest. Therefore, it appears that the distribution of both *Choroterpes* and *Tricorythodes* are affected by the mosaic of sulfate concentrations during periods of low discharge and high chemical stress.

CONCLUSIONS

Cushing et al. (1980) pointed out the difficulty of comparing physical, chemical, and biological parameters. This problem was addressed with the ALSCAL model of multidimensional scaling. The ordinations produced by ALSCAL summarized the relationships among sites over sampling time. These nonmetric ordinations were based on distance coefficients. This greatly reduced many of the problems associated with comparing these very different types of variables. Rankings of sites along the dimensions of the respective ordinations represented the underlying physical, chemical, and biological structure of the river. This allowed the comparison of abstract structures based on these three groups of variables to the structure of the actual river gradient. Congruence in the rankings of sites for each group of variables suggested a close relationship among the associate variables in congruence.

The results of this study support the RCC but also suggest the need to modify it. The RCC was originally described in terms of instream factors, and one gradient was sufficient to explain river structure. The saline effects described in this study are not predicted by the RCC. These saline effects are orthogonal, abstract gradients controlled by complex geomorphological processes. These results still fit into the general framework of the RCC in that the benthic community structure appears to be a function of abiotic parameters. But it also points out that multiple gradients must be considered when developing dynamic management models for similar systems.

ACKNOWLEDGMENTS

I would like to thank Alan Covich, Gary Schnell, Alan Nicewander, Frank Sonleitner, Harley Brown, Paul Risser, Linda Tway, Joy Zedler, Bert Cushing, and the reviewers of *Ecology* for their advice with this manuscript. Linda Tway, John Dumitras, and Jeannie Huggins assisted with some of the fieldwork and sample processing. Dan Hough was of great assistance with computer-related problems. Zenith Marsh drafted the figures. Part of this work was supported by National Science Foundation Doctoral Dissertation Research Grant DEB-8112460. The Oklahoma Biological Survey and Department of Zoology at the University of Oklahoma supplied computer and other technical facilities.

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