ANALYSIS OF PLECOPTERAN ASSEMBLAGES ALONG AN ALTITUDINAL GRADIENT IN THE GREAT SMOKY MOUNTAINS, TENNESSEE

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ABSTRACT—Immature Plecoptera were qualitatively sampled from the Little Pigeon River and its tributaries Ramsay Prong, Middle Prong, and Porter's Creek in the Great Smoky Mountains, Tennessee. The samples were collected from 12 sites along an 864-m altitudinal gradient from September 1977 to August 1978. Relative abundance of Plecopteran taxa along the altitudinal profile was examined by cluster analysis and correspondence analysis. The Plecopteran community at the upper five sites was dominated by shredder euholognathous taxa, while the community at the lower seven sites was dominated by predaceous systellognathous taxa. The differences in community structure between the upper five and the lower seven sites were related to physico-chemical parameters (temperature, pH, alkalinity, hardness, and turbidity) and food.

Although changes in the community structure of Plecoptera along an elevational gradient have been studied earlier in North America (Dodds and Hisaw, 1925; Knight and Gaufin, 1966; Alan, 1975; Donald and Anderson, 1977; Ward, 1982), little work has been done in the southern Appalachian mountain region. Stoneburner's (1977) study of longitudinal distribution of aquatic invertebrates in the Great Smoky Mountains of North Carolina included a limited number of stonefly taxa and was confined to June. Sheldon's (1985) recent study of Plecoptera in the Little River in the Great Smoky Mountains of Tennessee was restricted to the family Perlidae and limited to August and September. The objective of the present study was to describe the spatial patterns of Plecoptera along an altitudinal gradient in a mountain stream of Tennessee as disclosed by the techniques of classification and ordination as well as correlate these patterns with physico-chemical variables and food.

STUDY SITES

The study was conducted in the Great Smoky Mountains National Park, Sevier Co., Tennessee, located in the Blue Ridge physiographic province of the southern Appalachian mountains (Fenneman, 1938). The Great Smoky Mountains National Park is one of the wettest areas in the continental United States receiving an annual rainfall ranging from 123.24 cm at low elevations to 254.00 cm at high elevations. Area vegetation consists of mixed hardwoods including rhododendron (*Rhododendron*), oaks (*Quercus*), hickories (*Carya*), and yellow poplar (*Populus*). The bedrock geology consists of Precambrian sedimentary sandstone comprising the Ocoee Series (King et al., 1968).

Twelve rhithral (Ward, 1992) sampling sites, representing varying stream orders, were located along the Little Pigeon River (35°42'N, 83°22'W) and its tributaries Ramsey Prong, Middle Prong, and Porter's Creek (Fig. 1). Sites 1 and 2 were second-order sections, sites 3-5 third-order sections, sites 6-9 fourth-order sections, and sites 10-12 fifth-order sections. From site 1 on the Ramsey Prong at an altitude of 1,284 m to site 12 on the Little Pigeon River at an altitude of 420 m, there is a drop in elevation of 864 m over a 10-km distance. The stream bed at each site is composed of a heterogeneous mix of gravel, pebbles, cobble, and boulders.

METHODS

The 12 sites were sampled monthly from September 1977 through August 1978 using a fine-mesh net with openings of 363 μm. Samples were taken from a riffle area and a pool area at each site using procedures suggested by Frost et al. (1971). Material was preserved in the field with 20% formalin and transported to the laboratory where it was sorted. Plecoptera were identified to the lowest taxonomic level possible and placed in vials containing 70% ethanol. Physico-chemical parameters measured at the time of the benthic collections were pH, water temperature, dissolved oxygen, velocity, turbidity, conductivity, alkalinity, and hardness (Table 1). Silsbee and Larson (1982) provide additional information about water quality in streams of the Great Smoky Mountains National Park.

Abundance of Plecoptera at each site was converted to percentages and then transformed using an octave scale that, in essence, is logarithmic to the base 2 (Gauch, 1982). The classification technique of cluster analysis using the chord distance and the flexible strategy (with $\beta = -0.25$) arranged the sites into a hierarchy on the basis of shared taxonomic composition (Ludwig and Reynolds, 1988). The ordination technique of correspondence analysis ordered the sites and taxa into an objective arrangement (Ludwig and Reynolds, 1988). In this analysis, those sites with similar taxonomic composition are grouped most closely together, and those taxa with similar relative abundance at each site are grouped most closely together.

The physico-chemical values, except pH, were transformed to approximate normality. Relationships between the cluster analysis and measured stream physico-chemical parameters were examined by *t*-tests using SYSTAT (Wilkinson, 1989). Product-moment correlation, also with SYSTAT, was used to assess relationships between ordination scores and environmental variables for each site.

The assignment of a taxon to a functional feeding group followed Merritt and Cummins (1984). The four groups used in this study were

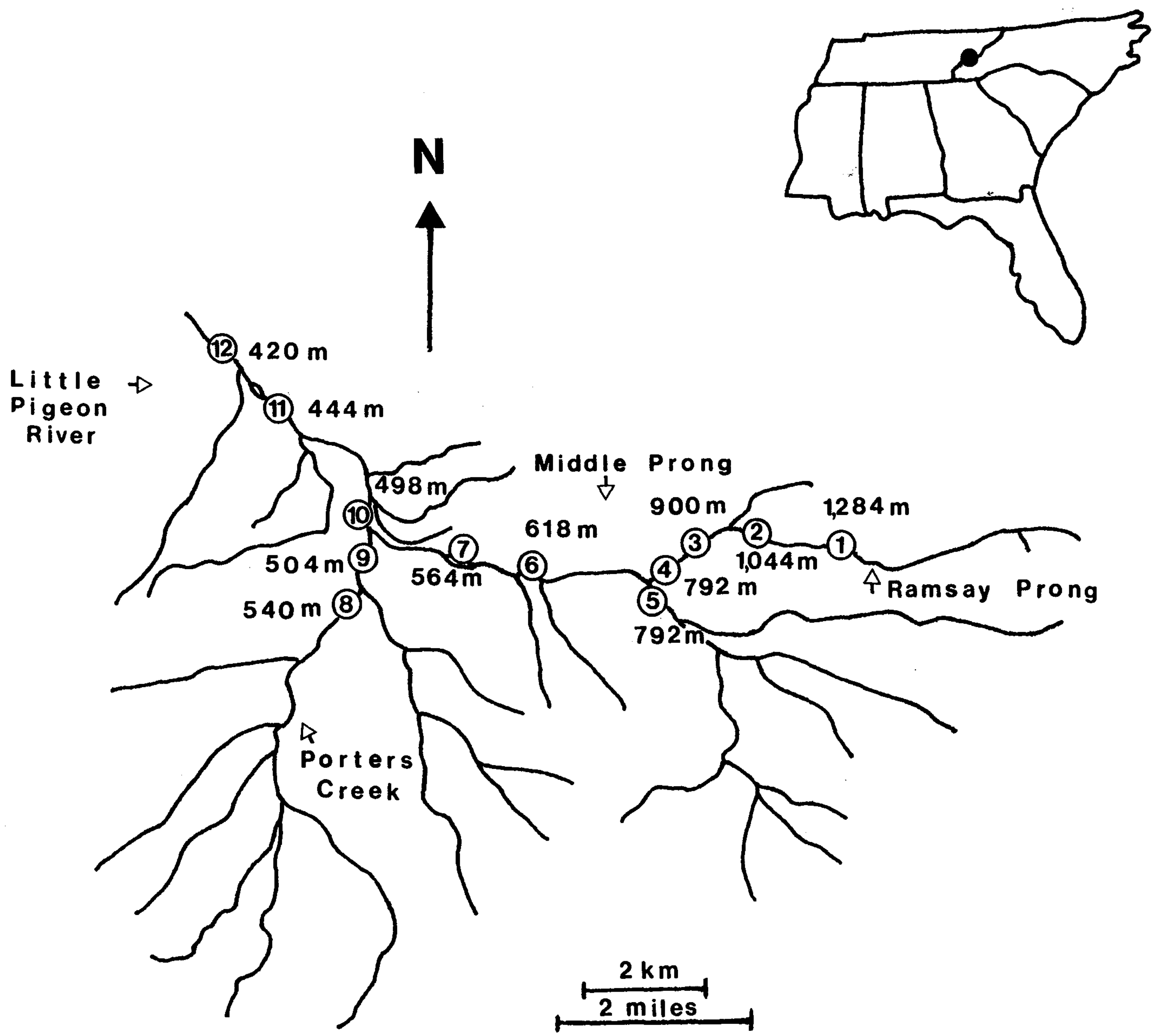

FIG. 1. Location of the study area and sampling sites in the Great Smoky Mountains, Tennessee.

shredder, gatherer, scraper, and predator. Taxa that used more than one feeding strategy were divided among the relevant functional groups. Identified as shredders were species belonging to *Allocapnia*, *Paracapnia*, *Amphinemura*, *Leuctra*, *Tallaperla*, and *Pteronarcys*. Scrapers were composed of species of *Strophopteryx* and *Oemopteryx*, and gatherers were composed of species of *Amphinemura* and *Isoperla*. Predators were comprised of species belonging to *Taeniopteryx*, *Alloperla*, *Sweltsa*, *Haploperla*, *Suwallia*, *Acroneuria*, *Agnetina*, *Eccoptura*, *Paragnetina*, *Perlesta*, *Isoperla*, and *Yugus*.

RESULTS AND DISCUSSION

A total of 12,710 individuals representing a minimum of 29 species belonging to 21 genera and nine families was collected. It was not possible to distinguish between the nymphs of species belonging to *Alloperla* (*A. atlantica*, *A. caudata*, *A. chloris*, *A. neglecta*, and *A. usa*), *Sweltsa* (*S. lateralis*, *S. mediana*, and *S. urticae*), and *Tallaperla* (*T. elisa* and *T. maria*), and, therefore, they are considered together.

Abundances of species collected are given in Table 2. Species frequently showed one of three distributional patterns: 1) one indicating peak abundance upstream decreasing in the downstream direction (e.g., *Oemopteryx limata*, *Amphinemura wui*, *Allocapnia stannardi*, *Paracapnia angulata*, and *Leuctra ferruginea*); 2) one indicating peak abundance downstream decreasing in the upstream direction (e.g., *Alloperla* spp., *Isoperla* spp., *Leuctra tenella*, and *Sweltsa* spp.); 3) uniform distribution (e.g., *Haploperla brevis* and *Acroneuria abnormis*).

Cluster analysis of the transformed values of relative abundance of taxa for each of the 12 sites yielded two major clusters, one comprising five sites at or above 792 m and the other comprising seven sites below

TABLE 1. Values for measured physico-chemical parameters of Little Pigeon River and tributary sites.

Site	Mean pH	Mean temperature (C°)	Mean dissolved oxygen (ppm)	Width (m)	Mean velocity[1] (m/sec)	Mean turbidity[2] (NTU)	Mean conductivity[2] (umhos/cm)	Mean alkalinity[2] (mg/l $CaCO_3$)	Mean hardness[2] (mg/l $CaCO_3$)
1	4.63	5.75	11.9	6	0.49	0.49	16.6	3.51	5.41
2	5.00	6.71	11.4	8	0.48	0.45	14.0	3.30	5.27
3	5.86	7.63	11.6	10	0.56	0.52	14.2	4.47	5.40
4	6.14	8.01	11.3	13	0.31	0.48	12.0	3.80	5.13
5	5.73	8.09	11.3	15	0.45	0.49	12.5	3.66	5.17
6	6.06	8.84	11.3	20	0.38	0.62	13.7	3.60	5.06
7	6.22	8.93	11.4	10	0.41	0.64	13.9	4.11	5.09
8	6.10	8.72	11.5	15	0.49	0.67	16.2	4.07	6.50
9	6.10	8.58	11.8	7	0.51	0.69	15.3	5.00	6.06
10	6.37	8.75	11.1	25	0.50	0.57	14.3	4.97	6.17
11	6.42	9.01	11.2	17	0.47	0.55	14.7	5.09	6.06
12	6.66	9.32	10.9	25	0.44	0.64	14.4	5.20	5.66

[1]Means for February to August 1978.
[2]Means for October 1977 to June 1978.

this elevation (Fig. 2). An identical partitioning of the sites is indicated by correspondence analysis (Fig. 3A). Stoneburner (1977) found a similar pattern for the aquatic invertebrates comprising seven sites along an elevational gradient in the Great Smoky Mountains. In his study, the sites were separated into two distinct groups depending on whether they were above or below 830 m, an elevation comparable to that identified in the present study.

Results of the correspondence analysis of the taxa are shown in Fig. 3B. The 29 taxa are positioned along component II as a gradient ranging from those taxa with highest abundances at one or more of the five upper sites (*Strophopteryx limata, Oemopteryx contorta, Soyedina carolinensis, Amphinemura nigritta, A. wui, Leuctra grandis, L. ferruginea, L. tenella, L. sibleyi, L. truncata, Allocapnia stannardi, Paracapnia angulata, Tallaperla* spp., *Eccoptura xanthenes*, and *Perlesta frisoni*) to those taxa with highest abundances at one or more of the seven lower sites (*Taeniopteryx maura, Leuctra tenuis, Alloperla* spp., *Sweltsa* spp., *Haploperla brevis, Suwallia marginata, Acroneuria abnormis, A. carolinensis, Paragnetina marginata, Agnetina capitata, Yugus bulbosis, Isoperla* species 1, *Isoperla similis*, and *Pteronarcys scotti*). Four taxa (*Soyedina carolinensis, Leuctra tenella, L. truncata*, and *Eccoptura xanthenes*) are present only within the five upper sites, while seven taxa (*Taeniopteryx maura, Acroneuria carolinensis, Paragnetina marginata, Agnetina capitata, Yugus bulbosis, Isoperla* species 1, and *Pteronarcys scotti*) are present only within the seven lower sites.

Classification and the ordination of the sites indicate that taxa belonging to the family group Euholognatha (Taeniopterygidae, Nemouridae, Capniidae, and Leuctridae) dominated the stonefly community (ca. 72-93%) in the five upper sites (Fig. 4). Contrastingly, taxa belonging to the family group Systellognatha (Pteronarcyidae, Peltoperlidae, Perlidae, Perlodidae, and Chloroperlidae) were most abundant (ca. 70-89%) in the seven lower sites (Fig. 4).

Numerous workers have concluded that the composition of the stonefly community along an altitudinal gradient can be attributed to various environmental parameters (Dodds and Hisaw, 1925; Knight and Gaufin, 1966; Ward, 1982; Uchida, 1990). Stoneburner (1977) suggested that temperature changes associated with decreasing altitude at sites in the Great Smoky Mountains, North Carolina, was responsible for the decline in taxa comprising *Nemoura* and *Leuctra*. In the present study, the cluster-analysis classification could be related to differneces between the two major clusters of sites in temperature, acid-related factors (pH, alkalinity, and hardness), and turbidity (t-values = -3.228, -2.731, -2.647, -2.382, and -3.254; all t-values significant at $P < 0.05$). Results of t-tests for dissolved oxygen (1.203), width (-1.876), velocity (-0.140), and conductivity (-1.271) were not significant at $P < 0.05$. Product-moment correlation of the site ordination coordinates to measured physico-chemical parameters also indicates a strong relationship to these same environmental variables (Table 3). Generally, the five upper sites had lower values for temperature, acid-related factors, and turbidity than did the seven lower sites.

The stonefly trophic composition of the Little Pigeon River and tributary sites examined in this study consisted primarily of shredders and predators (Fig. 5). In the five upper sites, shredders dominated (ca. 57-75%) the stonefly community and were composed primarily of taxa belonging to the Euholognatha. Predators, however, were the most important functional group (ca. 69-84%) in the seven lower sites and were comprised largely of taxa belonging to the Systellognatha. Scrapers were at their highest abundance in the five upper sites but poorly represented in the lower sites. The low relative abundance of gatherers remained fairly constant at each site. These results are consistent with Stoneburner's (1977) observation that, with decreasing altitude, there is a shift in the trophic structure in the stonefly community of the Great Smoky Mountains from herbivore-detritovore to carnivore. The dominance of winter- and spring-emerging euholognathous shredders in the stonefly community at the second- and third-order stream sections represented by the five upper sites suggest that the major energy input at these sites is most probably autumnal, allochthonous coarse particulate, organic matter, such as leaves, twigs, and logs. Change in the trophic pattern in the generally wider fourth- and fifth-order stream sections represented by the seven lower sites may reflect either a reduction of this coarse particulate organic matter per unit area or

TABLE 2. Relative abundance of each Plecopteran taxon per site.

Taxon	Sites 1	2	3	4	5	6	7	8	9	10	11	12	Total
Allocapnia stannardi	195	99	18	12	21	1		8	4	2		5	365
Paracapnia angulata	183	431	105	107	176	17	13	40	25	4	9	3	1,113
Taeniopteryx maura						1		8	13	11	4	3	40
Oemopteryx contorta	108	90	37	29	6	1			3	3	2	5	284
Strophopteryx limata	457	425	278	28	14	1		4	1				1,208
Soyedina carolinensis	1												1
Amphinemura nigritta	21	6	3	1	3					1	3		38
Amphinemura wui	306	253	72	40	40	7	1	5	5	2		4	735
Leuctra grandis	16	103	86	54	127	10	3	4	9	3	4	3	422
Leuctra sibleyi			3		16	2							21
Leuctra ferruginea	1,064	1,236	511	424	872	82	25	49	39	23	19	21	4,365
Leuctra tenella				1									1
Leuctra tenuis			3			5	5	7	17	23	66	23	149
Leuctra truncata					1								1
Pteronarcys scotti						1		1	1				3
Tallaperla ssp.	26	17	36	13	16	9	2	12	5	9	2	4	151
Alloperla spp.	20	54	67	91	95	127	77	106	163	27	126	166	1,119
Sweltsa spp.	59	44	27	55	84	58	91	80	191	87	271	196	1,243
Haploperla brevis			3	8	4	30	8	9	7	19	7	7	102
Suwallia marginata		4	13	13	63	44	70	21	78	30	34	36	406
Isoperla sp. 1						2	2	31	40	25	47	101	248
Isoperla similis	136	60	17	5	6	4	5	4	2	1	2		242
Yugus bulbosis								2					2
Agnetina capitata									6		3	2	11
Paragnetina immarginata									1			2	3
Perlesta frisoni	1	5	52	80	98	46	13	18	31	15	29	24	412
Eccoptura xanthenes			2	1									3
Acroneuria abnormis		1	1	2		2		2	3	1		1	13
Acroneuria carolinensis						1	1	1	2	1	3		9
Total	2,593	2,828	1,334	964	1,642	451	316	412	642	287	631	606	12,710

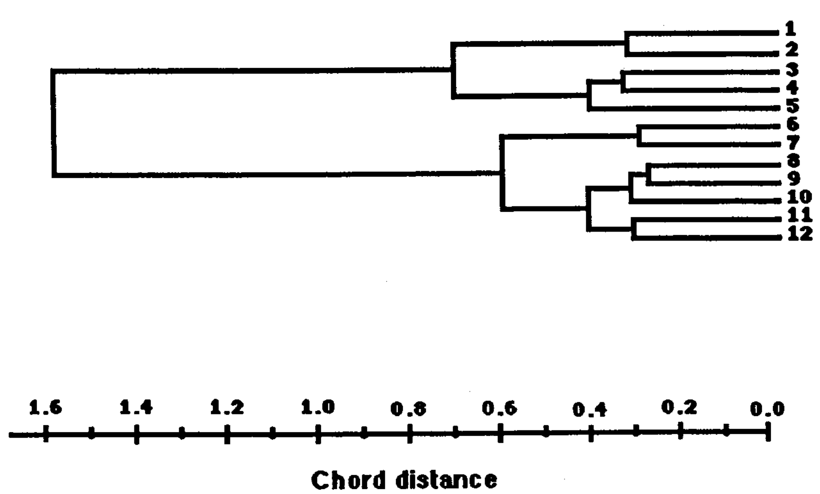

FIG. 2. Dendrogram resulting from cluster analysis of transformed data of abundance of taxa from 12 sites in the Great Smoky Mountains, Tennessee. Clustering was accomplished using the chord distance measure and flexible clustering strategy (β = -0.25).

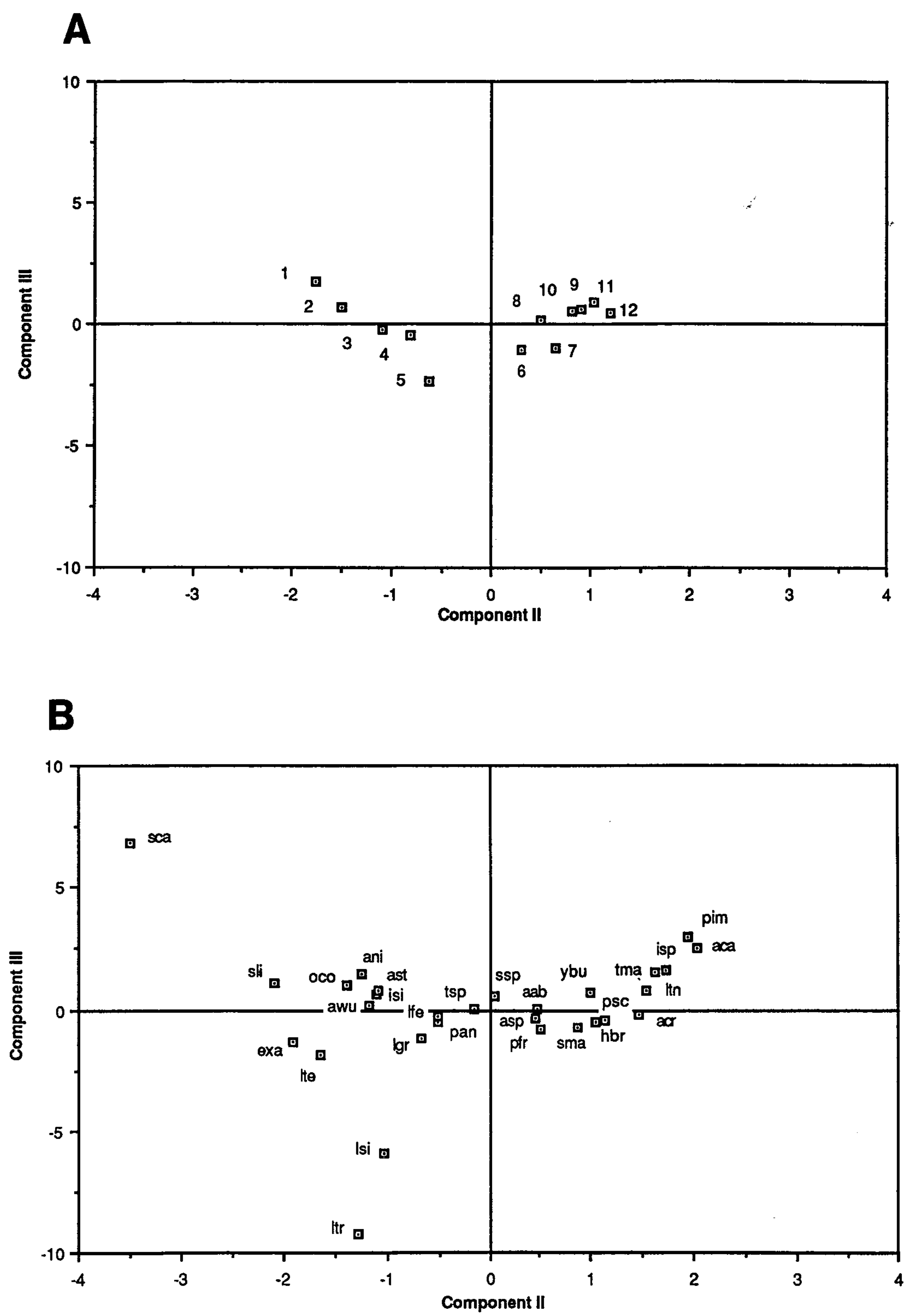

FIG. 3. Correspondence analysis of transformed data of abundance of taxa from 12 stream sites in the Great Smoky Mountains, Tennessee. Ordination of the sites (A) and taxa (B) shown separately for clarity. Sca = *Soyedina carolinensis*, sli = *Strophopteryx limata*, oco = *Oemopteryx contorta*, ani = *Amphinemura nigritta*, awu = *Amphinemura wui*, isi = *Isoperla similis*, ast = *Allocapnia stannardi*, tsp = *Tallaperla* species, ltr = *Leuctra truncata*, lsi = *Leuctra sibleyi*, lte = *Leuctra tenella*, exa = *Eccoptura xanthenes*, lgr = *Leuctra grandis*, pan = *Paracapnia angulata*, lfe = *Leuctra ferruginea*, acr = *Acroneuria carolinensis*, psc = *Pteronarcys scotti*, hbr = *Haploperla brevis*, sma = *Suwallia marginata*, pfr = *Perlesta frisoni*, asp = *Alloperla* species, aca = *Agnetina capitata*, pim = *Paragnetina immarginata*, isp = *Isoperla* species 1, tma = *Taeniopteryx maura*, ltn = *Leuctra tenuis*, ybu = *Yugus bulbosis*, aab = *Acroneuria abnormis*, and ssp = *Sweltsa* species.

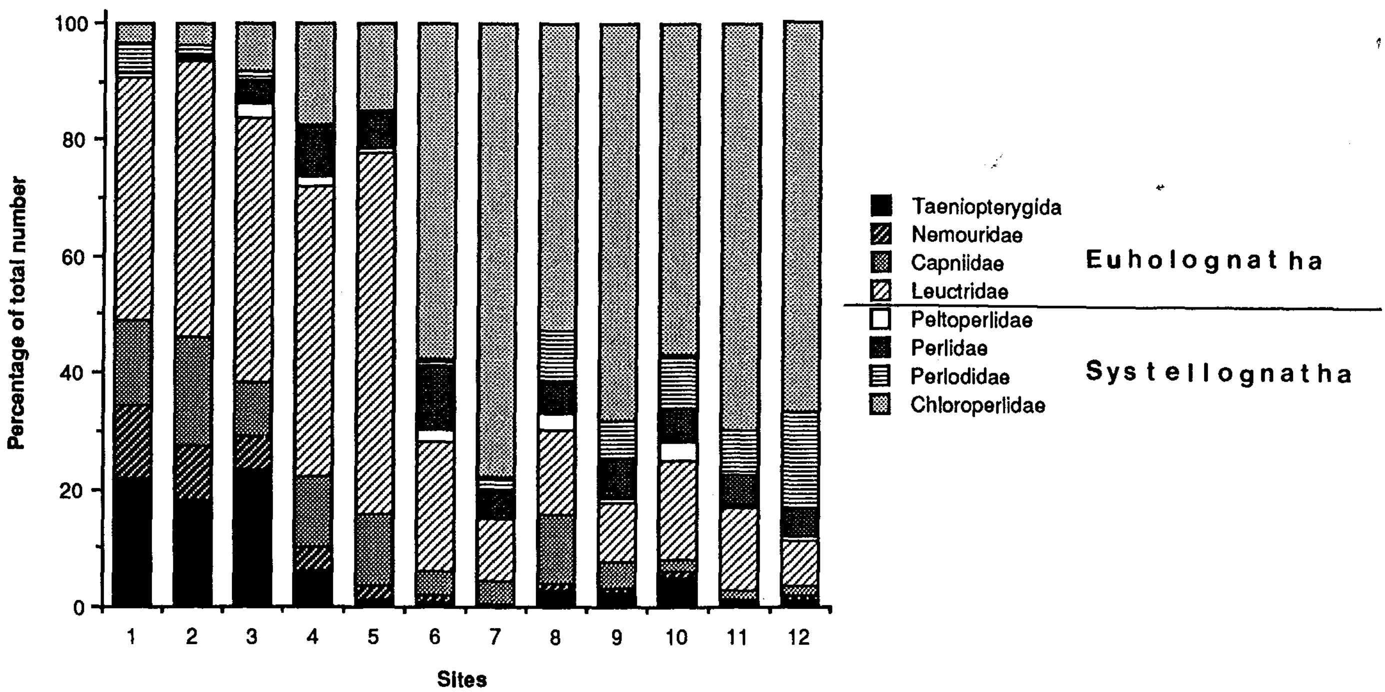

FIG. 4. Relative abundances of families of Plecoptera collected at 12 stream sites in the Great Smoky Mountains, Tennessee.

competitive displacement by shredders belonging to other insect groups or both.

The present study indicates that the stonefly community structure along an 864-m altitudinal gradient in the Great Smoky Mountains in Tennessee shifts from one that is dominated by shredder euholognathous taxa to one dominated by predaceous systellognathous taxa. These changes probably are influenced by physico-chemical parameters such as temperature, acid-related changes, and turbidity as well as food. The relative importance of these factors in influencing community structure will need to be investigated in future studies.

TABLE 3. Product-moment corelations between (measured physico-chemical parameters) ordination and scores.

	Component	
Parameters	II	III
pH	0.862***	-0.240
Temperature (log)	0.896***	-0.372
Dissolved oxygen (log)	0.488	-0.222
Width (log)	0.590	-0.253
Velocity (log)	0.001	0.398
Turbidity (log)	0.751**	-0.287
Conductivity (log)	0.375	0.306
Alkalinity (log)	0.766**	0.280
Hardness (log)	0.543	0.489

$^{**}P < 0.01$.
$^{***}P < 0.001$.

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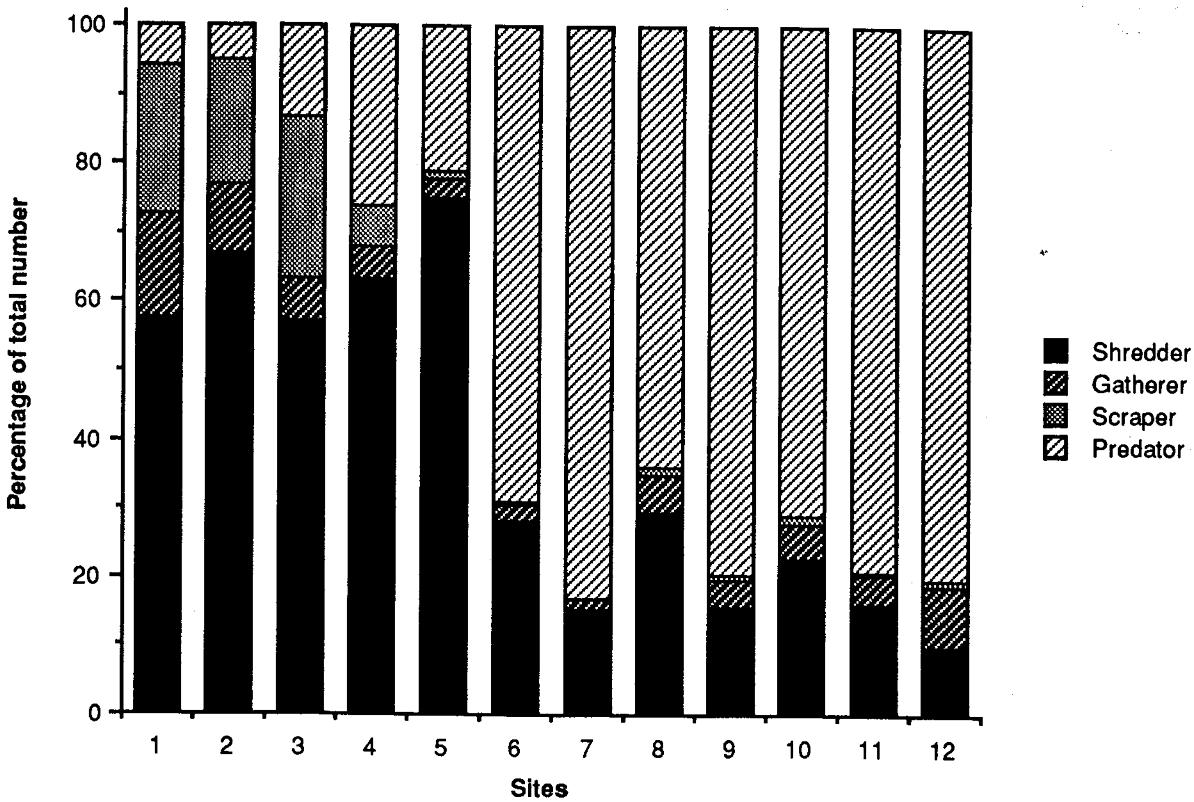

FIG. 5. Relative abundances of the major functional groups of Plecoptera collected at 12 stream sites in the Great Smoky Mountains, Tennessee.

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