Temporal and Spatial Patterns of Coarse Particulate Organic Matter and Macroinvertebrate Distribution in a Low-Order Apennine Stream

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ABSTRACT

We described the microdistribution of benthic macroinvertebrates in a 50 m riffle segment of the Rio del Giovo (Sassello, NW Italy) during a period of rapid loss of leaf mass, from March to May 2003. We analyzed the relationship between the taxonomic composition and functional organization of benthic communities and the availability of coarse particulate organic matter (CPOM), as well as the influence of micro-environmental characteristics (water velocity, depth, and substratum). Patches without CPOM hosted specialized communities. The temporal variation of CPOM influenced the distribution of functional feeding groups in the riverbed. In particular, shredder assemblages were widespread in the riverbed when CPOM was abundant, but when this resource became scarce and localized, their density was related to the availability of allochthonous organic detritus.

INTRODUCTION

The structural and functional composition of macroinvertebrate communities is closely related to habitat conditions such as physical and chemical characteristics (Giberson and Hall 1988, Sandin 2003), substratum composition (Lemly and Hildebrand 2000, Wright et al. 2003), hydrodynamics (Malmqvist and Mäki 1994), biological interactions (Dudley et al. 1990), stream vegetation (Heino et al. 2003), and food availability (Richardson 1993). The last factor is very important in explaining small-scale variations of benthic communities (Dobson and Hildrew 1992), especially in low-order segments in which primary production is least and heterotrophic pathways are of greatest importance (Cummins 1974, Vannote et al. 1980). Forested headwater streams rely on terrestrial autotrophic production as allochtonous inputs of coarse particulate organic matter (CPOM) (Wallace et al. 1997).

Aquatic decomposition of deciduous leaves is a complex process involving fungi, bacteria, and macroinvertebrates (Bärlocher and Kendrick 1975, Hieber and Gessner 2002). It has long been known that autumn-shed leaves are the most important source of organic material in temperate streams (Kaushik and Hynes 1971, Murphy and Giller 2000). The detritus is retained and degraded by a combination of physical and biological processes (Richardson 1992) so that the large autumnal inputs disappear over time. Bärlocher and Rosset (1981) reported that the CPOM in a Swiss Jura stream reached a maximum of 60 g/m^2 in November and then declined to 4 g/m^2 in July.

The comminution of plant litter inputs by invertebrate shredders generates fine particulate organic matter utilized by other functional feeding groups (FFG) such as collector-filterers and collector-gatherers (Wallace et al. 1977, Mullholland et al. 1985, Merritt and Cummins 1996, Merritt et al. 2002). An elegant study by Webster (1983) underlined the importance of stream invertebrates in the dynamics of organic detritus. A computer simulation, based on data from Coweeta streams, revealed that the activity of shredders decreased the efficiency of detritus processing in low-order streams because it increased transport loss; however, on a longer time scale, this activity prevented substantial accumulation of organic material and represented a main component of the longitudinal linkage of lotic systems, as described by the river continuum concept (Vannote et al. 1980). Macroinvertebrates usually account for only a small portion of detritus consumption and convert benthic detritus into transported detritus; thus downstream communities are structured to capitalize on upstream inefficiencies (Vannote et al. 1980).

In temperate streams, the macroinvertebrate distribution in the riverbed is probably strongly related to the variation of CPOM availability (Beisel et al. 1998). However, few data are available about the temporal variation of CPOM and its relationship with benthic communities. Many early studies examined correlations between invertebrate numbers and detritus quantity, reporting positive (Ciborowski and Clifford 1983), neutral (Williams 1980), and negative (Barber and Kevern 1973) associations. Some aspects of the relationship between the distribution of invertebrates and detritus in rivers remain unclear and largely depend on the feeding mechanisms of invertebrates (Corkum 1992).

The aim of our study was to relate structural community epiphenomena (taxonomic richness, diversity, and abundance) to the availability of CPOM in an Apennine stream in spring, a period in which loss of leaf mass is most rapid. We tested the hypothesis that temporal variation of CPOM influences the small-scale distribution of some functional feeding groups, particularly the shredders.

METHODS AND MATERIALS

The study took place in the Rio del Giovo, a small tributary of the Erro River, NW Italy (44° 29' N, 8° 28'E). This lotic system presents good environmental quality, reaching First Class in the I.B.E. system (Ghetti 1997), corresponding to an environment without human alteration. In a 50 m stretch, we collected 40 random quantitative samples on three dates (14 in March, 13 in April and 13 in May 2003). Benthic macroinvertebrate and CPOM samples were taken using a Surber sampler (0.06 m^2), with a 250 μm mesh. The macroinvertebrates in each sample were preserved in ethyl alcohol (70 %). In the laboratory, all organisms were counted and identified to the genus level, except for Chironomidae, Simuliidae, and early instars of some Trichoptera and Diptera which were identified to the family level. According to Merritt and Cummins (1996), each taxon was assigned to a functional feeding group (FFG: Scrapers-Sc, Shredders-Sh, Collectors-gatherers-Cg, Collectors-Filterers-F and Predators-P). To analyze the structure of stream assemblages, we utilized taxonomic richness (number of taxa), invertebrate density (ind./m^2), biological diversity (Shannon index), and relative FFG composition (%).

To quantify the CPOM, leaves and other plant detritus (diameter > 1 mm) were collected from each Surber sample. In the laboratory, this material was air dried for 24 h, oven dried (105 °C) for 24 h, and then weighed with an electronic balance (accuracy 0.01 g).

We measured four physicochemical parameters (temperature, pH, dissolved oxygen, conductivity) with an Eijkelkamp 13.14 multidata sampler and we measured current velocity with an Eijkelkamp 18.28 portable instrument. We also measured water depth and distance from the nearest riverbank (i.e., position in the riverbed). Percentages of different substratum sizes (boulders 25 - 45 cm, cobble 6 - 25 cm, gravel 6 - 60 mm, sand 0.06 - 6 mm, silt < 0.06 mm) were recorded at each point by using a gravelometer.

Comparisons of mean CPOM amounts and mean invertebrate densities on different dates were performed with ANOVAs. Invertebrate abundances were log(x+1) transformed prior to statistical analysis to normalize and stabilize the variance.

Correlations between habitat and biotic variables and between amount of CPOM and relative abundance of FFG were performed with Spearman's tests.

To examine the relationships between taxa and environmental variables we conducted a canonical correspondence analysis (CCA). CCA is a direct ordination technique, commonly used in studies of modern ecology to express the main relations between species and environmental variables by combining ordination and regression (Podani 2000). In the CCA biplots, the first and second axes represent the most important environmental gradients along which taxa are distributed.

RESULTS

In total, we collected 3,373 macroinvertebrates belonging to 69 taxa (Table 1). The mean (± SE) density in the riverbed was 1,410.0 ± 188.5 individuals/m^2, with no significant differences between sampling dates (ANOVA $F_{2,37} = 1.27$, P = n.s.)

Water velocity had no effect on either abundance (Spearman r; r=0.43, P=n.s.), taxonomic richness of invertebrate assemblages (r =0.17, P=n.s.), or on the amount of CPOM (r =0.23, P=n.s.). The position in the riverbed (i.e., the distance from the nearest bank) was not related to the local density (r =0.12, P=n.s.), richness (r =0.16, P=n.s.), or amount of CPOM (r =0.14, P=n.s.). The water depth also had no influence on the density (r=0.46, P=n.s.), richness (r =0.31, P=n.s.), or amount of CPOM (r=0.37, P=n.s.).

The CPOM availability was an important parameter influencing the benthic invertebrate communities (Fig. 1). Areas with higher amounts of organic detritus always presented greater taxonomic richness (r=0.563; P<0.001), invertebrate density (r=0.390; P<0.05), and biological diversity (r=0.450; P<0.005). The patches without CPOM were very different from the rest of the riverbed; these environments were dominated by a few specialized taxa of scrapers, mainly Diptera Blephariceridae.

Canonical correspondence analysis (Fig. 2) showed clear differences among patches. In particular, ordination axis 1 pinpointed the strong difference of environmental characteristics between strongly erosive sites with high water velocity and rocky riverbed and the rest of the riverbed. Ordination axis 2 separated the patches with high sand percentage from patches with high amount of CPOM.

The amount of CPOM declined from March to May (Fig. 3); the total CPOM was significantly different among the dates (ANOVA $F_{2,37} = 4.22$, P=0.022). The functional composition of the assemblages differed in relation to the temporal change in CPOM availability. The most affected FFG was shredders. In late winter, when leaves were abundant in the streambed, shredders were widespread and their relative proportion in each Surber sample was not related to the amount of CPOM (r=0.26; P=n.s.). After two months, when CPOM was more localized and scarce, the shredder abundance was related to the CPOM availability (r=0.54; P<0.05).

DISCUSSION

Stream invertebrates respond to both spatial and temporal variation in habitat heterogeneity (Vinson and Hawkins 1998). Small-scale variations in substratum composition shape the composition and density of invertebrate assemblages. Sand seems to be a poor substratum, probably because of its instability and because tight packing of the sand grains reduces the trapping of fine organic detritus and limits the availability of oxygen. On the other hand, boulders are a peculiar microhabitat in terms of ecological and faunal characteristics. These patches do not depend on organic detritus; they are strongly erosive systems dominated by a few taxa of scrapers (Diptera Blephariceridae and a few Ephemeroptera Heptageniidae) that rely exclusively on epilithic autochthonous primary production.

Table 1. Taxonomic list and percent relative abundance (ind./m^2) for macroinvertebrates collected in the natural riverbed in March, April and May 2003. (FFG: P=predators, SH=shredders; SC=scrapers, F=filterers, CG= collector gatherers).

Taxon	Sampling date			FFG	Reference number
	March	April	May		
Plecoptera					
Brachyptera sp.	6.45	1.22	0.00	SH	1
Amphinemura sp.	0.08	0.20	0.00	SH	2
Chloroperla sp.	0.00	1.22	0.00	P	3
Leuctra sp.	0.49	1.52	14.74	SH	4
Nemoura sp.	0.00	0.30	0.00	SH	5
Perla marginata	0.00	0.00	0.24	P	6
Isoperla sp.	0.16	0.10	0.00	P	7
Dinocras cephalotes	0.00	0.00	0.08	P	8
Protonemura sp.	5.07	7.40	1.11	SH	9
Ephemeroptera					
Baetis sp.	17.57	13.17	11.49	CG	10
Caenis sp.	0.25	0.41	1.66	CG	11
Epeorus sylvicola	0.65	1.32	0.40	SC	12
Ephemera danica	0.08	0.91	0.24	CG	13
Electrogena sp.	1.47	3.24	1.58	SC	14
Ecdyonurus sp.	2.61	0.91	3.72	SC	15
Serratella ignita	0.00	0.20	9.83	CG	16
Habroleptoides sp.	5.72	2.13	1.03	CG	17
Habrophlebia sp.	0.00	0.41	0.32	CG	18
Rhithrogena sp.	4.25	0.51	1.35	SC	19
Torleya major	1.55	0.00	0.16	CG	20
Trichoptera					
Allogamus sp.	0.00	0.10	0.00	SH	21
Beraeidae	0.57	0.51	1.35	SC	22
Cheumatopsyche lepida	2.37	0.20	0.48	F	23
Glossosoma sp.	0.08	0.41	0.00	SC	24
Diplectrona felix	0.00	0.30	0.00	F	25
Hydropsyche sp.	13.07	3.24	8.72	F	26
Hydroptile sp.	0.33	0.00	0.08	SC	27
Hyporhyacophila sp.	0.65	0.20	0.00	P	28
Chimarra marginata	0.25	0.00	0.00	F	29
Philopotamus sp.	0.08	0.10	3.01	F	30
Polycentropus sp.	0.00	0.10	0.24	F	31
Lepidostoma hirtum	0.49	0.10	0.08	SH	32
Rhyacophila sp.	0.25	0.41	0.40	P	33
Sericostoma pedemontanum	0.25	0.00	0.24	SH	34
Coleoptera					
Elmis sp.	5.64	16.51	7.21	CG	35
Gyrinus sp.	0.65	0.00	0.16	P	36
Esolus sp.	0.74	1.62	7.61	CG	37
Hydraena sp.	1.96	1.11	1.19	SC	38
Dytiscidae	0.00	0.00	0.08	P	39
Pomatinus substriatus	0.16	0.10	0.00	SH	40
Limnius sp.	3.68	0.41	7.45	CG	41
Halesus sp.	0.08	0.00	0.00	SH	42
Scirtes sp.	0.08	0.00	0.32	SH	43
Helodidae	0.00	0.81	0.00	SH	44
Diptera					
Athericidae	0.74	0.81	0.24	P	45
Liponeura sp.	0.49	0.71	0.63	SC	46
Dicranota sp.	0.65	0.00	0.00	P	47

(continued)

Table 1 (continued)

Taxon		Sampling date			FFG	Reference number
		March	April	May		
Diptera						
	Ceratopogonidae	0.16	0.20	0.32	P	48
	Empididae	0.08	0.20	0.00	P	49
	Chironomidae	5.39	10.33	4.99	CG	50
	Simuliidae	4.00	13.98	2.46	F	51
	Tabanidae	0.00	0.61	0.08	P	52
	Tanypodinae	0.74	0.00	0.48	P	53
	Tipulidae	0.90	0.30	0.00	SH	54
	Limoniidae	0.33	2.03	0.08	P	55
	Orthocladinae	1.80	0.00	0.00	CG	56
	Rhagionidae	0.00	0.00	0.16	P	57
	Hexatoma sp.	0.00	0.00	0.16	P	58
Hemiptera						
	Micronecta sp.	0.08	0.10	0.00	P	59
Odonata						
	Cordulegaster boltoni	0.00	0.10	0.00	P	60
	Onychogomphus sp.	1.23	0.20	0.71	P	61
Crustacea						
	Austropotamobius pallipes	0.16	0.00	0.00	SH	62
Gastropoda						
	Ancylus fluviatilis	2.37	0.30	0.16	SC	63
Oligochaeta						
	Eiseniella tetraedra	0.16	0.30	0.00	CG	64
	Lumbricidae	0.74	0.41	0.79	CG	65
	Lumbriculidae	0.25	1.32	0.32	CG	66
Tricladida						
	Dugesia sp.	0.82	0.30	0.08	P	67
Nematomorpha						
	Gordius sp.	0.08	0.00	0.00	P	68
Arachnida						
	Hydracarina	1.06	6.38	1.82	P	69

Within the natural range of the measured parameters, neither water velocity nor water depth significantly affected the density or composition of the riverbed communities. It is well known that small low-order streams are mostly heterotrophic, depending on allochthonous energy inputs, mostly leaves (Webster and Benfield 1986). In these environments, the amount of coarse organic detritus is a key factor influencing the structural and functional composition of the benthic coenosis. At our study site, microhabitats with a high availability of CPOM had more abundant and richer communities, while areas with less CPOM seemed to have a simpler and poorer coenosis.

A main point of our study was the temporal reduction of CPOM. Autumnal leaf fall is a major source of allochthonous detritus in Apennine streams. The amount of allochthonous organic material in temperate lotic systems is variable, being extremely abundant in fall-winter and declining after this period. In fall, organic detritus may be so abundant that it no longer influences the distributional patterns of invertebrates (Minshall 1984), but this picture changes over time. Our results agree with this finding, confirming that shredders have a stronger correlation with detritus than do other feeding groups (Peckarsky 1980). When CPOM was abundant and widespread in the riverbed (e.g., in late winter and early spring), shredders were present in all patches, and their abundance was not strongly conditioned by the local amount of CPOM. But when

CPOM was scarce in May, the distribution of shredders became resource-dependent, with a clear tendency to aggregate in patches with high CPOM availability.

Our study confirms that preserving high spatial heterogeneity in riverbeds and riparian areas is essential to maintain high biodiversity in lotic systems. Indeed, habitat heterogeneity is a main element enhancing the taxonomic richness and diversity of faunal communities (Beisel et al. 1998). Moreover, it is important to maintain high functional efficiency in headwater streams because linkages among various components

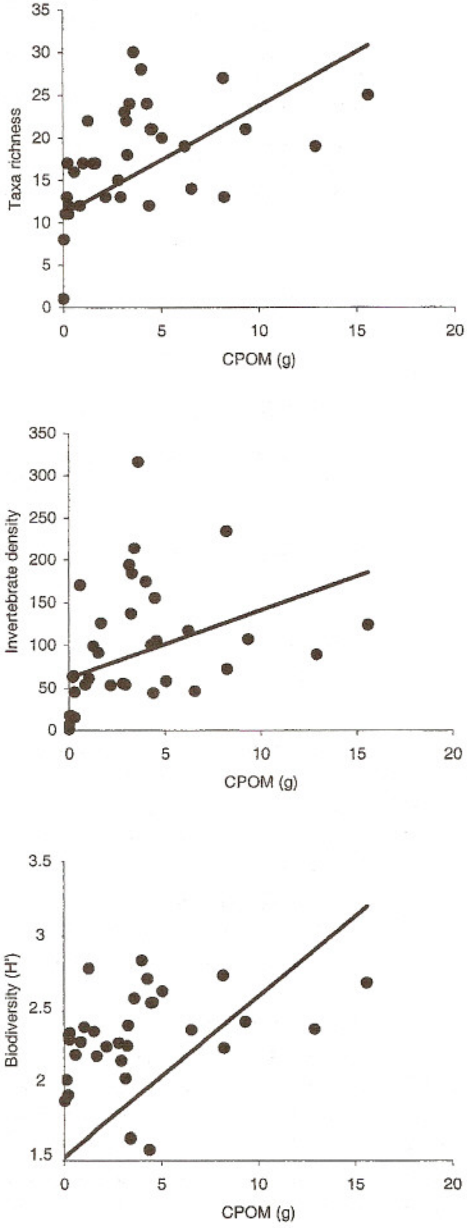

Figure 1. Relationships between CPOM availability and invertebrate density taxonomic richness, and biological diversity.

of stream networks act as important energy pathways, contributing energy to systems with low production (Malmqvist and Wotton 2002).

Our data indicate the importance of considering the variation of allochthonous CPOM availability in analyses of the abundance of stream invertebrates in Mediterranean streams, particularly the functional composition of their communities in different microhabitats. It may be important to consider the strong spatio-temporal diversity of invertebrate assemblages in routine biomonitoring programs. When assessing the biological quality of rivers, environmental operators must analyze all the microhabitats, since there could be clear faunal diversity among nearby patches or within the same area in different seasons.

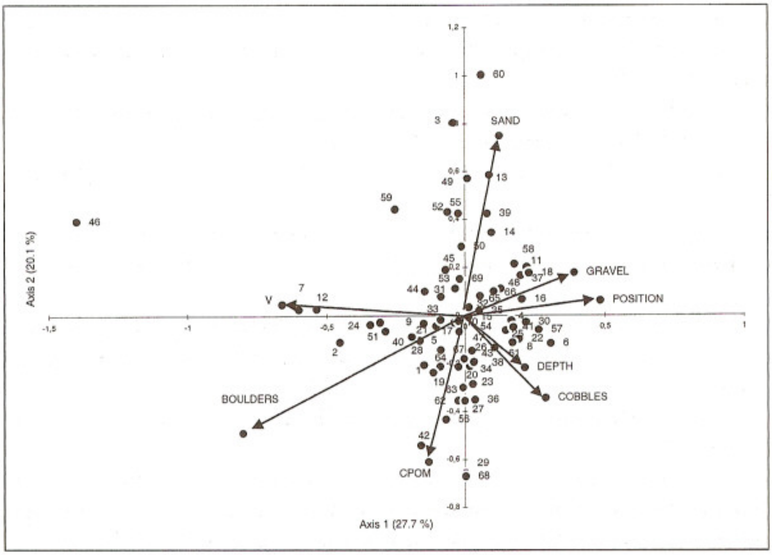

Figure 2. Biplot of the first and second CCA axes for the macroinvertebrate taxa in the Rio del Giovo.

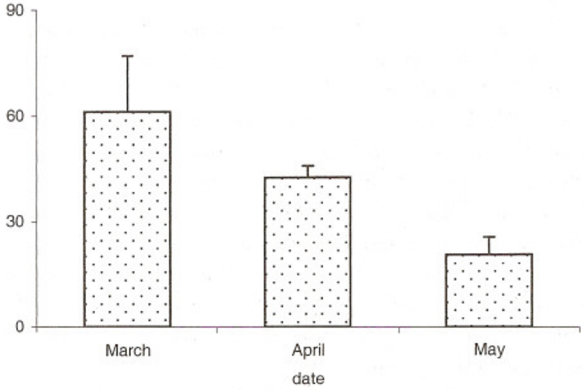

Figure 3. Temporal variation of CPOM (mean and SE).

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