

Influence of Detritus on the Structure of the Invertebrate Community in a Small Portuguese Stream

key words: benthic invertebrates, detritus, community structure, substrate, CPOM stocks

Abstract

This study tests if the coarse particulate organic matter (CPOM) mass was related to the invertebrate community structure in riffles and sandy pools of a fourth-order reach of a stream after partialling out the effects of physical characteristics of the sampled patches. Diversity and structure of the assemblages differed between habitats. In both, CPOM mass was positively correlated with total density and with all functional feeding groups excepting filterers. Redundancy analyses and variance partitioning procedures indicated that (1) CPOM stocks influenced the assemblage structure in both habitats, and (2) most of those effects were unrelated to sampling date and measured physical characteristics (water depth in sandy pools, Froude number and substrate composition in riffles) of the patches.

1. Introduction

Streams can be viewed as mosaics of microhabitats nested within larger-scale habitats with differing environmental conditions (PRINGLE *et al.*, 1988). This hierarchical structure dictates that both large and small-scale environmental patterns affect invertebrates within a given patch (see MALMQVIST, 2002 for a review). As a consequence, the relationship between the habitat characteristics at a given site and their associated stream invertebrate communities may be studied at spatial scales ranging from ecoregions (CORKUM, 1989; PARSONS *et al.* 2003) to patches within riffles (DOWNES *et al.*, 1993; GRAÇA *et al.*, 2004).

Environmental factors such as flow variability (POFF and WARD, 1989; AGUIAR *et al.*, 2002), and water chemistry (TIERNEY *et al.*, 1998; REECE and RICHARDSON, 2000) influence the composition and structure of stream invertebrate communities. These factors change over broader spatial scales than those of the reach (MINSHALL, 1988), and may constrain the species pool available at smaller spatial scales (POFF, 1997). Other habitat characteristics important for stream invertebrates may change at smaller scales within the reaches of a stream. Examples include flow conditions (MÖBES-HANSEN and WARINGER, 1998; NELSON and LIEBERMAN, 2002), substrate composition (ROBSON and CHESTER, 1999; PHILLIPS, 2003), and the nature and amount of food resources (MURPHY and GILLER, 2000; GONZÁLEZ *et al.*, 2003).

In a previous paper GRAÇA *et al.* (2004) investigated the environmental factors associated with invertebrate abundance and diversity analysing a large number of Surber samples (area = 0.09 m², n = 639) taken in riffles of 12 low-order streams from North to South Portugal on two occasions within one year. They found that the variables that explained best the large-scale variation in invertebrate communities were water temperature, pH and mini-

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imum particle size. However, when they compared the invertebrates found in each Surber sample, they observed that the number of animals and taxa were functions of organic matter accumulation in the patch.

Our objective here is to investigate two questions emerging from the results of GRAÇA *et al.* (2004). Firstly, if organic matter stocks explain some differences among invertebrate communities in different patches across many rivers and reaches, can they also explain some of the temporal patterns at a particular location?

Secondly, if seasonal variation on organic matter affects temporal patterns in invertebrate assemblages is this effect specific to riffles, or does it also exist in other habitats? To test this, we analysed the relationship between detritus stocks and benthic assemblages in riffles and pools. Previous work of GONZÁLEZ and GRAÇA (2003) has shown that in the studied site, detritus mass in pools was 4× those in riffles. Thus, we are studying invertebrate assemblages coping with very different environmental conditions including resources mass.

For addressing these issues, we sampled benthic assemblages in riffles and sandy pools at a single site and monthly intervals for one year. Firstly, we compared the abundance, richness, diversity, and functional and taxonomical structure of the invertebrate community in riffles and pools. We aimed to test whether the invertebrate assemblages from the riffles of the studied reach were indeed different from those found in sandy pools. Secondly, we evaluated the influence of coarse particulate organic matter stocks on community attributes in both habitats, correcting for the effects of important physical characteristics of the environment and those of the sampling date.

2. Materials and Methods

2.1. Study Site

The study was conducted at a 50 m long fourth-order reach of the São João stream (40° 6' N, 8° 14' W) which drains an 18 km² siliceous area of the Lousã Mountains (central Portugal). This subcatchment is covered mainly by shrubland and *Eucalyptus globulus* LABILL., *Pinus pinaster* AITON, *Acacia dealbata* LINK and *Castanea sativa* MILL. plantations and seminatural forests. There are neither human settlements nor agriculture upstream the study site. Some *Populus x canadensis* MOENCH, *Salix* spp., *C. sativa* and *A. dealbata* grow on the river banks, but some banks are bare, steep rock.

The reach studied included two pools (depth up to 0.8 m) and two shallow riffles (depth up to 0.35 m). The annual mean water temperature during the study year was 12.4 °C, with minimum daily mean water temperatures in January (3.6 °C) and maximum values in August (19.9 °C; GONZÁLEZ and GRAÇA, 2003). Water conductivity and pH were low at the site (mean annual values were 50 µS cm⁻¹ and 6.6, respectively). More information on the study site is given in GRAÇA *et al.* (2001) and GRAÇA *et al.* (2004). CANTO and GRAÇA (1998) and GONZÁLEZ and GRAÇA (2003) made additional descriptions of the studied reach; the former provided also information on retentiveness of this reach, and the latter included also information on CPOM stocks at riffles and sandy pools during the same study period of the present work.

2.2. Sampling

Benthos samples were taken simultaneously from riffles and pools at monthly intervals between November 2000 and October 2001. In total, 60 benthos samples were taken in riffles and 50 in pools. On each date, 5 random samples were taken in riffles using a Surber net (0.09 m² area, 250 µm mesh). The percentages of boulders (rocks with diameter >256 mm), cobbles (diameter, 64–256 mm), pebbles (diameter, 16–64 mm), and gravel (diameter, 2–16 mm) in the sampling quadrates were visually estimated using intervals of 5% and annotated before disturbing the stream bed. After collecting the sample, depth and mean velocity of the water column at the sampling point were recorded.

Sampling procedure in pools differed from that followed in riffles. Due to low water velocity, a Hess sampler (0.025 m² area, 250 µm mesh) was used, a procedure that allowed us to take samples only in

the sandy portions of the pools. The sampling program aimed to take 5 samples per date in this habitat. However, this was only possible from November to February because in March and October high water velocity and depth allowed us to take only 3 samples per date; moreover, from April to September the area covered by sandy pools was reduced due to low water flow, and only 4 samples per date were taken. Water depth at the sampling point was measured after taking each sample.

Samples were transferred to plastic bags, brought to the laboratory in a cooling box, stored at 4 °C (<48 hours), and washed through a series of nested sieves (smallest mesh size, 0.5 mm). All invertebrates were sorted and stored in 70% alcohol for further identification. Later, the ash free dry mass of organic matter retained by 20 and 1 mm sieves (hereafter, CPOM) was determined (see methods in GONZÁLEZ and GRAÇA, 2003).

The invertebrates were counted and identified to family or genus except oligochaetes and mites, which were determined to order. The fauna was assigned to functional feeding groups (filterers, gatherers, predators, scrapers and shredders) from information gathered in TACHET *et al.* (2000).

2.3. Data Analysis

Froude numbers (F) were calculated for the riffle samples using the equation: $F = \frac{U}{\sqrt{g \times W}}$ where

U is water velocity (m s⁻¹), g is the acceleration due to gravity (m s⁻²), and W is water depth (m). Invertebrate diversity (D) of each sample was calculated by the inverse of the Simpson index as:

$$D = 1 - \sum_i \frac{N_i \times (N_i - 1)}{N \times (N - 1)},$$

where S is the number of taxa, N_i is the density of taxon i and N is total invertebrate density at the sample. We recorded the total number of taxa collected in each sample (hereafter, "observed richness"). However, because samples from riffles and pools differed both in number and size, rarefied richness was also calculated for estimating the number of taxa in hypothetical samples containing the same number of animals (40, the minimum value recorded at one sample). These values of rarefied richness should not be used for comparing communities sampled with differing collecting techniques, but allow to estimate the richness of assemblages at a common abundance level (see MAGURRAN, 2004, for a review).

Most density data and community descriptors were not normally distributed and could not be normalised. Therefore, differences between riffles and pools were analysed with the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (hereafter, SRH test), as described in SOKAL and ROHLF (1995). This is a non-parametric test analogous to two-way Anova and allows comparing simultaneously (1) habitats (i.e., riffles vs. pools) and (2) sampling dates (time). The degrees of freedom for the factor "habitat" and for the factor "time" were 1 and 11, respectively. Three sets of comparisons were performed: (1) community descriptors: diversity, total invertebrate density and density of each functional feeding group, (2) density of the most abundant taxa, and (3) proportions of the functional feeding groups. In these comparisons, the probability of falsely rejecting null hypotheses was kept at 0.05 using the False Discovery Rate procedure (hereafter, FDR, BENJAMINI and HOCHBERG, 1995; GARCÍA, 2004).

Inter-habitat differences in the taxonomical structure of invertebrate assemblages were tested by an indirect ordination. Densities of invertebrate taxa were square root-transformed, and a similarity matrix among samples was calculated using the BRAY-CURTIS algorithm (BRAY CURTIS, 1957). Subsequently, the similarities among the samples were represented in a plot with non-metric multidimensional scaling (MDS; SHEPHARD, 1962) using the PRIMER 5 software (PRIMER-E Ltd, Plymouth). To check the performance of the ordination, the stress value was inspected, and the groups resulting from the MDS were compared with those defined by a hierarchical clustering using group-average linking constructed from the same similarity matrix derived in PRIMER 5. Differences between the macroinvertebrate samples from riffles and pools were evaluated with a permutation test (CLARKE and GREEN, 1988) following the ANOSIM routine of the PRIMER 5 software.

The relationships between CPOM mass from each sampling unit were inspected against the following biological parameters: total invertebrate density, diversity, observed richness, rarefied richness, and densities of each functional feeding group. These relationships were checked, using SPEARMAN rank correlation (ZAR, 1996), and were conducted separately for riffles and pools, with the FDR correction for Type I errors. Since some CPOM samples were lost while ashing, these correlations were performed with 57 samples in riffles and 46 samples in pools.

Direct ordination was used to evaluate the relationship between environmental conditions, transformed sampling date (see below), and invertebrate density separately for riffles and pools. Environmental conditions in the samples were classified into (1) physical characteristics: water depth in pools, Froude number and percentage of boulders, cobbles, pebbles and gravel in riffles, and (2) CPOM stocks. First, detrended correspondence analyses (HILL and GAUCH, 1980; TER BRAAK, 1987) were used to determine the type of response of biotic data to environmental gradients. Because the responses were monotonic, redundancy analyses (RDAs; RAO, 1964) were selected to perform the direct analyses. RDA is a technique that selects the linear combination of environmental variables explaining the greatest portion of the total variance in the species data (TER BRAAK, 1987).

The effect of sampling date on the invertebrate communities was also considered in the RDAs. Rather than treating this variable as linear, we assumed it to be circular (i.e., we expected that samples from November 2000 to be more similar to those from October 2001 than to those from May 2000). Thus, we included two surrogates of sampling date as explanatory variables in the RDAs: sine(D), and cosine(D), where D was the product of 2π and number of days from the first sampling divided by 365.

A forward selection procedure was followed to retain only those environmental variables that were significant for the analysis of each habitat ($p < 0.05$ as tested through 1000 Monte Carlo simulations). Three pool samples had very high CPOM mass and had much influence on the results of the ordination, and they were thus excluded from the analysis. Therefore, the RDAs were performed with 60 samples for riffles and 47 from pools.

The effect of CPOM stocks on macroinvertebrate communities was separated from those of transformed sampling date and the physical characteristics significant for the analyses using the variation partitioning procedure explained in BORCARD *et al.* (1992). This procedure allows discriminating the portion of variance explained in direct ordinations by (1) one set of variables, (2) another group of variables, and (3) interactions between both sets of variables. All DCAs and RDAs were done using the CANOCO 4.5 software (GLW-CPRO, Wageningen).

3. Results

3.1. Inter-Habitat Differences

Overall, invertebrate density did not differ significantly between sandy pools and riffles (Fig. 1). Moreover, the interaction habitat \times time was not significant (Table 1), reflecting the similarity between habitats in invertebrate abundance throughout the study year. The taxa that individually constituted more than 5% of the mean annual invertebrate abundance at either habitat were Chironomidae, Oligochaeta, *Sericostoma*, *Leuctra*, *Baetis* and *Habroleptoides*. They accounted for 70 and 77% of the community at riffles and sandy pools, respectively. Chironomidae, Oligochaeta and *Sericostoma* were more abundant in the studied pools than in riffles, the contrary was true for *Baetis*, *Habroleptoides* and *Leuctra* (Table 2). However, the comparisons for Chironomidae, *Leuctra* and Oligochaeta showed significant habitat \times time interaction (Table 2), indicating that their inter-habitat differences were not consistent throughout the year.

Table 1. Comparisons of community descriptors between habitats and time (Scheirer-Ray-Hare extension of the Kruskal-Wallis test, followed by False Discovery Rate correction test). The habitat with the highest value of community descriptor is indicated (R: riffles; P: sandy pools). N. S.: non significant differences.

Factor	Total density	Filterer density	Gatherer density	Predator density	Scraper density	Shredder density	Diversity
Habitat	N. S.	N. S.	N. S.	N. S.	**** R	* R	**** R
Time	****	N. S.	****	****	****	****	****
Interaction	N. S.	N. S.	N. S.	N. S.	N. S.	N. S.	N. S.

*: $p < 0.05$. ****: $p < 0.001$.

Table 2. Comparisons of density of the most abundant taxa between habitats and time (Scheirer-Ray-Hare extension of the Kruskal-Wallis test, followed by False Discovery Rate correction test). The habitat with the highest value of community descriptor is indicated (R: riffles; P: sandy pools). N. S.: non significant differences.

Factor	<i>Baetis</i>	Chironomidae	<i>Habroleptoides</i>	<i>Leuctra</i>	Oligochaeta	<i>Sericostoma</i>
Habitat	**** R	**** P	**** R	**** R	* P	* P
Time	N. S.	*	****	N. S.	****	*
Interaction	N. S.	*	N. S.	*	*	N. S.

*: $p < 0.05$. ****: $p < 0.001$.

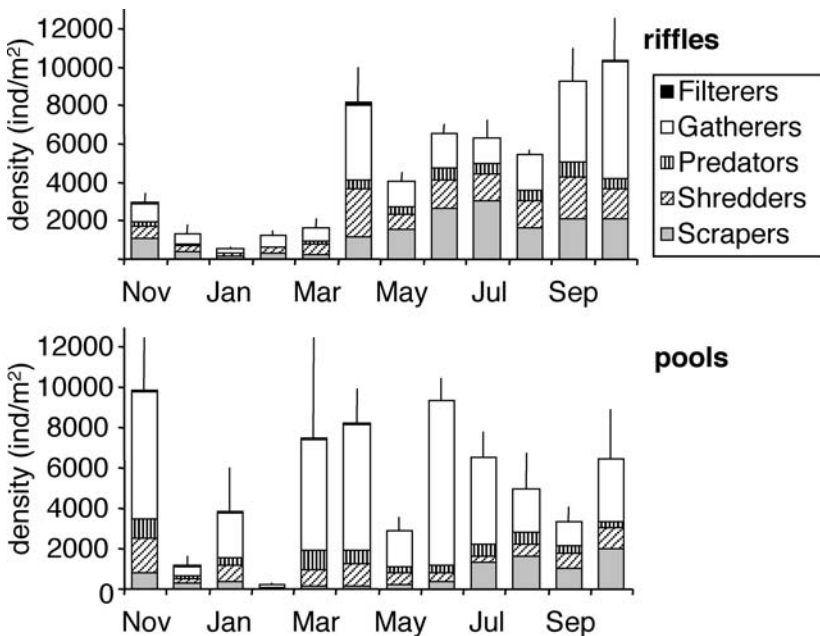


Figure 1. Density of the 5 functional feeding groups at riffles and sandy pools. Vertical lines indicate the standard error of total invertebrate density at each habitat.

The invertebrate community in pools was dominated by gatherers (64% of total fauna on an annual average), predators (15%) and shredders (13%) (Fig. 1). Gatherers were also dominant at riffles (41% of total fauna), but scrapers (28%) and shredders (21%) were also important. Proportional abundance of gatherers was higher in sandy pools than in riffles, whereas the reverse was true for scrapers and shredders (Table 3). Such differences disappeared in some months, as showed by the interaction habitat \times time.

Table 3. Comparisons of proportions of functional feeding groups between habitats and time (Scheirer-Ray-Hare extension of the Kruskal-Wallis test, followed by False Discovery Rate correction test). The habitat with the highest value of community descriptor is indicated (R: riffles; P: sandy pools). N. S.: non significant differences.

Factor	Filterers	Gatherers	Predators	Scrapers	Shredders
Habitat	N. S.	**** P	N. S.	**** R	**** R
Time	N. S.	N. S.	***	*	N. S.
Interaction	*	*	N. S.	**	N. S.

*: $p < 0.05$. **: $p < 0.01$. ***: $p < 0.005$. ****: $p < 0.001$.

The only significant between-habitat differences in functional feeding group density were those showed by scrapers and shredders (Table 1), two groups that were more abundant in riffles than in sandy pools. The interactions found in all of the comparisons were non significant.

Invertebrate diversity was higher in riffles than in sandy pools throughout the year (Table 1). The total number of invertebrate taxa recorded in this study was 87, with 79 occurring in riffles and 73 in sandy pools. Fourteen taxa that were found in riffle samples were absent from sandy pool samples, whereas there were 8 taxa recorded in sandy pools but not in riffles. Nevertheless, all these were very scarce (i.e., 12 or less animals found in all the sample set). Our sampling thus failed to detect invertebrates that could be regarded as exclusive to either habitat.

The MDS ordination shows that invertebrate assemblages in sandy pools were different from those in riffles (Fig. 2). Although the stress value of the biplot was 0.16, the groups depicted by the MDS were consistent with those found by a classification dendrogram constructed from the same data (not shown). This indicates that the 2-dimensional ordination represented accurately the affinity among samples. Moreover, the inter-habitat difference observed in invertebrate assemblages was significant ($p < 0.001$ after 1000 permutations; ANOSIM).

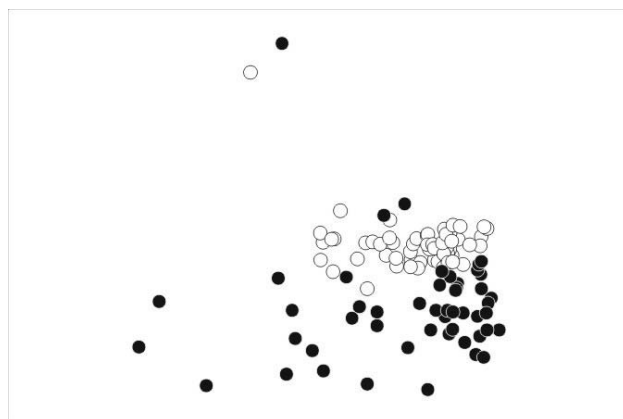


Figure 2. MDS ordination of invertebrate assemblages found in riffles (white points) and sandy pools (black points).

3.2. Ambient Effects

In both habitats, significant positive correlations were found between CPOM stocks and (1) total invertebrate density, (2) density of all functional feeding groups with the exception of filterers, and (3) diversity and observed richness of the assemblages (Table 4). No correlations were however found between CPOM mass and rarefied richness in either habitat.

The RDA ordination of sandy pool samples showed that both the transformed sampling date and CPOM mass had significant effects on the invertebrate assemblage, and defined two significant ordination axes ($p = 0.001$ after 1000 permutations). Together, they explained 27.3% of the variability in assemblage structure. Moreover, the variance inflation factors were low (highest value 1.05) indicating that there was not multicollinearity between the variables. When the effect of sampling date was removed, the RDA also revealed that density of all abundant taxa in sandy pools had a positive relationship with CPOM mass (Fig. 3).

The variation partitioning analysis in the sandy pool habitat showed that CPOM mass explained 7.7% of the total variation in the invertebrate assemblages, but 18.2% of such explained variation (i.e. 1.4% of total variation) was also assessed by transformed sampling date. This last variable explained 21% of total variation in taxa matrix of sandy pools.

Table 4. Spearman's rank correlations (r) with the False Discovery Rate corrections between CPOM mass and community invertebrate attributes. N. S.: non significant correlation.

		Total density	Filterer density	Gatherer density	Predator density	Scraper density	Shredder density	Diversity	Observed richness	Rarefied richness
Riffles	r	0.333	0.233	0.292	0.338	0.331	0.319	0.284	0.635	0.068
	p	*	N. S.	*	*	*	*	*	****	N. S.
Sandy pools	r	0.583	0.273	0.519	0.605	0.650	0.637	0.307	0.675	-0.051
	p	****	N. S.	****	****	****	****	*	****	N. S.

*: $p < 0.05$. ****: $p < 0.001$.

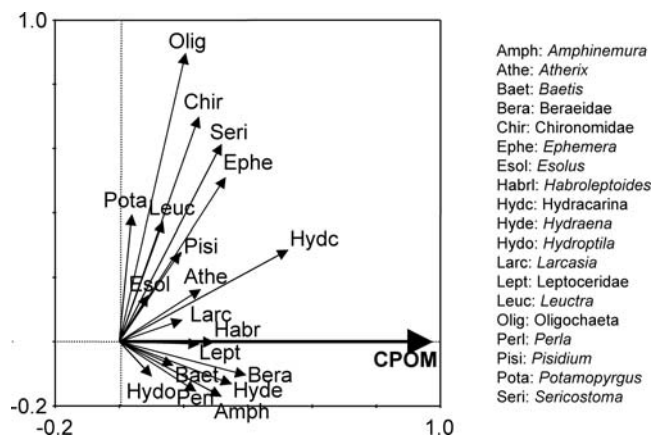


Figure 3. RDA ordination of invertebrate assemblages from sandy pools after removing the effect of sampling date. Coarse vectors represent the environmental variables. Fine vectors represent densities of taxa that constituted at least 10% of total invertebrate abundance in one or more samples from sandy pools.

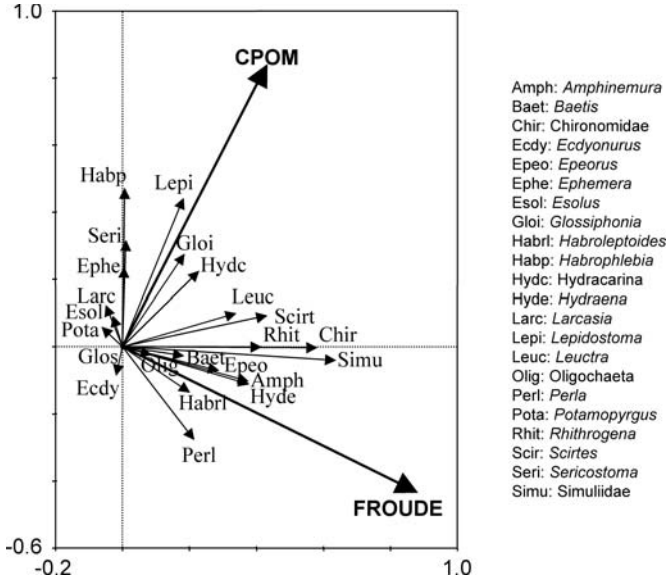


Figure 4. RDA ordination of invertebrate assemblages from riffles after removing the effect of sampling date. Coarse vectors represent the environmental variables. Fine vectors represent densities of taxa that constituted at least 5% of total invertebrate abundance in one or more riffle samples.

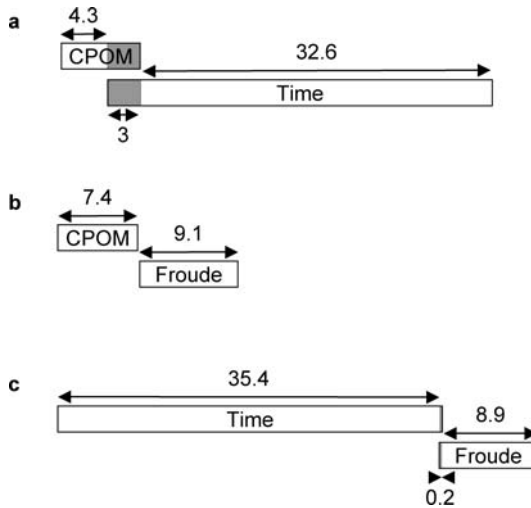


Figure 5. Percentages of variation of riffles data matrix explained by (a) CPOM mass (CPOM) and sampling date (Time), (b) CPOM mass and Froude number (Froude), and (c) sampling date and Froude number. Variance explained by each factor alone is depicted with white, and that explained by the interaction between 2 factors with grey columns.

In riffles, transformed sampling date, Froude number, and CPOM mass (cited in decreasing order of variance explained), accounted for 48.8% of variance in the abundance data (Fig. 4). No multicollinearity among these variables was detected (highest variance inflation factor: 1.12). The relationship between the species and the explanatory variables was highly significant ($p = 0.001$ after 1000 permutations). High CPOM stocks were positively associated to density of most taxa, with the exceptions of *Perla* and *Ecdyonurus* (Fig. 4).

The variance partitioning analyses performed with riffle samples (Fig. 5) showed that more than half of the effect of sampling time and CPOM mass on invertebrate assemblages was independent of sampling time. However, considerable overlap existed between the effects of these two variables, indicating that some of the effect of CPOM on invertebrate communities was time-dependent. In clear contrast, no overlap was detected between the effects of CPOM mass and Froude number on the riffle assemblages.

4. Discussion

4.1. Inter-Habitat Differences

At the studied site in the São João stream, no significant inter-habitat (sandy pools vs. riffles) difference in total density of invertebrates was observed. This result contrasts with other studies that have reported higher densities in riffles than in pools (RAMIREZ and PRINGLE, 1998; CROSA *et al.*, 2002). Nevertheless, other authors have also reported opposite patterns, with greatest invertebrate abundance in pools (HURYN and WALLACE, 1987). In terms of biomass, WOHL *et al.* (1995) found higher values in pools than in riffles at three stream sites, and the opposite in one site. Therefore, it seems that there are no general patterns for inter-habitat comparisons of total invertebrate abundance.

Between-habitat differences were observed in the taxonomic structure of the invertebrate assemblages, a finding that is consistent with other studies in temperate streams (e.g. WOHL *et al.*, 1995; CROSA *et al.*, 2002). Such differences were significant for both the abundance of the main taxa and the MDS ordination of samples. Moreover, riffles and sandy pools also differed in the functional organisation of the invertebrate assemblages. These shifts were mainly a result of scrapers and shredders being more abundant in riffles. MARIDET *et al.* (1998) and RAMIREZ and PRINGLE (1998) also reported this pattern for scraper abundance, but found the opposite result for shredders. LEMLY and HILDERBRAND (2000), however, reported higher density of scrapers and shredders in riffles than in pools.

In our case, we were comparing two habitats that contrast in flow conditions, water depth and substrate composition. All these traits have the potential to limit algal populations (see ALLAN, 1995), and, hence, grazer abundance. The observed shifts in shredder density are however more intriguing because we found the highest shredder density in riffles despite (1) sandy pools accumulated more (4 \times) CPOM mass than riffles (GONZÁLEZ and GRAÇA, 2003), and (2) shredders are frequently food-limited (DOBSON and HILDREW, 1992; NEGISHI and RICHARDSON, 2003). Again, the observational approach followed in this study does not allow identifying the causes of such pattern.

Thus, the analyses performed here show that, although invertebrate assemblages from riffles and sandy pools had similar densities and estimated taxa richness, they differed in other community attributes such as diversity, and functional and taxonomic structure.

4.2. Ambient Effects

As expected, high CPOM stocks were associated with high densities of total invertebrates, some functional groups and some abundant invertebrate taxa. These associations were shown by riffle- and sandy pool-dwelling assemblages having clear taxonomic and functional differences.

The role of CPOM accumulations providing shredders with food is well-established (RICHARDSON, 1992; ROWE and RICHARDSON, 2001), and it may explain the positive correlation between shredder density and CPOM mass. However, densities of other functional groups that do not ingest leaf litter were also correlated with CPOM abundance in both habitats. We therefore suggest that the positive association between total invertebrate density and CPOM mass was not a mere consequence of shredders aggregating where they found food. Instead, CPOM accumulations seemed to provide additional resources such as refuge, biofilm or fine particulate organic matter that also could benefit other invertebrates apart from shredders (e.g. DUDGEON and WU, 1999; QUINN *et al.*, 2000; but see GJERLØV and RICHARDSON, 2004).

Another explanation of the association observed between CPOM stocks and invertebrate density may be that both invertebrate abundance and CPOM storage responded to the same environmental factors. According to this view, the hydraulic factors responsible for the accumulation of organic matter in patches in a stream may also be responsible for the setting of drifting invertebrates in the same patches. CANHOTO and GRAÇA (1998) found that wood and physical traits, such as water velocity or the presence of shallow margins, enhanced the leaf litter retention efficiency of the patches of the São João stream. Moreover, GRAÇA *et al.* (2004) reported high abundance of organic matter and taxa richness in shallow retentive areas. However, in the present work, water depth had no significant effect on the invertebrate assemblages found in sandy pools. Moreover, no overlap was detected in riffles between the influence of CPOM mass and the single physical trait with a significant effect (Froude number) on invertebrate assemblages. Thus, these results indicate that the physical characteristics measured in this study were not interfering with the observed effect of CPOM stocks on invertebrate abundance.

CPOM mass was also positively correlated with observed taxa richness. This relationship could be interpreted as a consequence of detritus increasing the structural complexity of the habitat, (DOWNES *et al.*, 1998; STEWART *et al.*, 2003; see review in MINSHALL, 1984). However, in both our study and the related work of GRAÇA *et al.* (2004), the relationship between taxa richness and CPOM mass disappeared when the former variable was standardised to a fixed number of invertebrates. These results indicate a low influence of such structural complexity on invertebrate richness, suggesting that the influence of CPOM stocks on invertebrate richness was due to CPOM increasing their density.

The findings of this study highlight the linkages between the stream invertebrate community found at the São João and the surrounding terrestrial ecosystems. Together with sampling date and Froude number, CPOM stocks had a measurable effect on the structure of the invertebrate community. Moreover, the influence of CPOM stocks on invertebrates was roughly independent of those exerted by the variables cited above. Therefore, any of the factors affecting the storage of CPOM on the stream bed, including changes in riparian vegetation (MURPHY and GILLER, 2000; PRICE *et al.*, 2003), leaf litter breakdown rates (BUZBY and PERRY, 2000; ROBINSON and GESSNER, 2000) or in the leaf litter retention efficiency of the stream (LAITUNG *et al.*, 2002; NEGISHI and RICHARDSON, 2003) have the potential to change the invertebrate communities inhabiting this small stream.

5. Acknowledgements

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