Hydrobiologia **435:** 127–134, 2000.

Effects of macro-detritivores density on leaf detritus processing rate: a macrocosm experiment

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Received 6 December 1999; in revised form 28 April 2000; accepted 27 May 2000

Key words: Detritus processing, Macroinvertebrate density

Abstract

The effect of macroinvertebrate detritivore density on the mass loss rates of leaf litter of *Alnus glutinosa* (alder) was assessed. Experimental freshwater macrocosms, with increasing densities of four species of macroinvertebrate detritivores belonging to two functional groups (shredders and scrapers), were set up outdoors. The litter bag technique was used to assess decomposition rates of alder leaves. Indirect effects of increasing density of macroinvertebrates on phytoplankton standing crop in the water column were investigated by analysing Chlorophyll *a* concentration. Decomposition rate increased as animal density increased, although a continuous increase in detritivores density resulted in a discrete, step-wise increase of the decomposition rates. Animal colonisation followed an exponential pattern in low-medium density treatments versus a typical 'bell-shape' curve in high density treatments; animals started to leave the consumed patches when about 60% of the initial leaf mass was lost (35th day in high-density treatments). Diversity (Hs) of the simplified detritivore community decreased as decomposition proceeded, with a dominance of shredders during the last phase of decomposition. Faster decomposition rate of detritus in the benthic compartment lead to a higher microalgae standing crop in the water column emphasising the role of allochthonous detritus as a source of nutrients for algae primary production in coastal freshwater ecotones.

Introduction

Decomposition of plant litter plays an important role in nutrient cycling in aquatic systems. Vascular plant litter takes up and releases nutrients as it decomposes. As decomposition proceeds, mineralization predominates over immobilisation and the litter gradually releases nutrients (Jordan et al., 1989). Environmental characteristics that increase decomposition rates also accelerate the release of nutrients, which become directly available to the primary production compartment (Ligetta et al., 1999). The decomposition process of plant organic matter is strongly related to intrinsic leaf chemical-physical characteristics and environmental biotic and abiotic characteristics. Detritus origin and quality as well as the 'enzymes concentration' (micro and macro detritivores) represent the most critical biotic factors that affect the pattern and rate of the decomposition process (Saunders, 1976).

The importance of detritivorous macroinvertebrates in speeding up leaf decomposition has been widely recognised (Cummins, 1973; Lopez et al., 1977; Briggs et al., 1979; Webster & Belfield, 1986; Graça, 1993) although a clear interpretative model on the relationship between leaf decomposition rates and macroinvertebrates guild structure is far from being fully established (Wallace et al., 1970; Hassage et Harrel, 1986). The relation between decomposition rates and macroinvertebrates density becomes even more complex owing to the fact that beside the direct effects of macroinvertebrates on decomposition, animals may stimulate the activity of heterotrophs at lower trophic levels, thus increasing the rate of decomposition process and the metabolic activity of the system as a

whole (Berrie, 1976; Graça, 1993). Microbial colonisation of detritus is strongly affected by animals. The trophic activity of the macroinvertebrates increases the surface–volume ratio of detritus, influences the growth rate and the population dynamics of the microorganisms and speeds up their dispersion (Lopez et al., 1977; Swift et al., 1979; Lee et al., 1980).

A direct relation between decomposition rate and macroinvertebrates density has often been found in case of large differences in macroinvertebrates density (i.e. inter-habitat comparisons: Valelia et al., 1985), but this relation is more difficult to highlight when differences in detritivore density are smaller (i.e. intra-habitat comparison). This could suggest that the relation between macroinvertebrate density, decomposition rate and, by extension, the pattern of nutrient release are not continuous. We tested this idea by studying the pattern of the decomposition rates under seven different densities of four detritivore species and noted relative increases of primary production in outdoor simplified freshwater systems.

Materials and methods

Field animals collection and micro-fungi isolation from leaf detritus

Detritivorous macroinvertebrates were collected in Bracciano lake (Central Italy) using traps constituted by large mesh bags filled with *Alnus glutinosa* leaves. These traps were left for 1 week on the lake bottom. After collection, the content of the traps was immediately sieved (0.5 mm) and the collected macroinvertebrates placed in 10 l aerated containers filled with filtered lake water and maintained under controlled temperature (13–14 °C) and light (12 h per day).

Leaves from the lake bottom were collected and transferred to the laboratory in UV-sterilised plastic containers with the overlying bottom water. In the laboratory, fungus strains were isolated from the leaves and a mixed suspension of spores and hyphal fragments of the eight dominant fungus strains was prepared following the techniques described in Rossi et al. (1983).

Experimental design

Tanks containing 75 l of filtered lake water were set up outdoor (30 × 50 × 100 cm, water depth 15 cm). Leaves of *Alnus glutinosa* were washed and dried for 3 days at 60 °C. Leaves (15 g dry weight – DW) and 2 l of the mixed fungus strains suspension were introduced in each tank.

The decomposition of detritus was assessed by mass loss in litter bags (Cummins et al., 1989). Thirty five litter bags with 1 g DW leaf material each were introduced in each tank. Mass loss from litter bags was assumed to be the result of the decomposition process. Simultaneously 0, 50, 100, 200, 400, 800 and 1600 individuals of four major species of detritivorous macroinvertebrates were introduced in each tank with three replicates for each treatment (shredders: *Proasellus coxalis* and *Gammarus veneris*; scrapers: *Planorbarius corneus* and *Bithynia tentaculata*). The distribution of the four species reproduced the natural distribution found in Bracciano lake (*P. coxalis* 45%, *P. corneus* 35%, *B. tentaculata* 15%, *G. veneris* 5%).

Taking into account that the amount of dead leaves introduced in each tank was 50 g DW (35 g in litter bags + 15 g of free leaves), the initial animal density was of 0, 1, 2, 4, 8, 16 and 32 number of invertebrates (ni) per gram, respectively.

At days 7, 14, 21, 28, 35, 48 and 77 (from March to May), 5 litter bags were randomly collected from each tank taking special care to avoid losing animals. In the laboratory, the plant detritus was gently washed to separate all the animals. The collected animals were identified, counted and carefully re-introduced in the tanks. Detritus in the litter bags was dried (72 h, 60 °C), weighed and the ash content determined (6 h, 500 °C) in order to estimate the Ash Free Dry Weight (AFDW).

The decomposition rates were estimated using the exponential decay

$$W_t = W_0 \, \mathrm{e}^{(-kt)},$$

where W_t is the remaining weight at time t, W_0 the initial weight and k the decay coefficient (Olson, 1963; Petersen & Cummins, 1974). The decay coefficients were calculated by fitting a negative exponential regression and the coefficients of regression (r) were calculated for each regression. The litter half-life was calculated as $t_{1/2} = \ln 2 / k$ (Gallardo & Merino, 1993). Regression lines (ln transformed data) were compared by Analysis of Covariance (F-test). One-way ANOVA was used to compare weight losses due to leaching. The animal contribution to the detritus mass loss (hereafter named animal consumption) was calculated as the difference between the litter weight in the treatments with and without animals. Animal colonisation was analysed in terms of total density

Table 1. Remaining biomass (AFDW g) in litter bags at the end of the experiment (SE = Standard Error), decay constants (k) and litter half-life in the seven treatments with increasing animal density. No significant differences were found among experimental treatments grouped by square brackets (ANCOVA test, $p>0.05$)

Initial invertebrate density: number of invertebrates (ni) per gram of dead leaves	Biomass after 77 days		Exponential model		
	Mean (g)	SE	K	r	Half-life (days)
0	0.437	±0.047	0.0092	0.975	67.61
1	0.359	±0.042	0.0114	0.986	60.78
2	0.290	±0.050	0.0144	0.992	48.12
4	0.246	±0.051	0.0164	0.990	42.25
8	0.278	±0.063	0.0161	0.991	43.04
16	0.115	±0.050	0.0262	0.992	26.41
32	0.123	±0.057	0.0258	0.997	26.86

(number of invertebrate per gram of detritus – ni/g) and diversity (Shannon index).

Measurement of Chlorophyll a *concentration*

At the end of the experiment (77 days), Chlorophyll *a* concentration was evaluated. Samples of water (6 ml, five replicates for each tank) were filtered through cellulose acetate filters (0.45 μ). Each filter was dissolved in 5 ml of acetone (90%) and homogenised for 7.5 min. The sample was left for 24 h in the dark, centrifuged (5 min at 3000 rotation/minutes) and then analysed by a spectrophotometer. Following Strickland & Parsons (1965) Chlorophyll *a* concentration was evaluated as:

$$\text{Chlorophyll } a = (11.6\ D_{665} - 1.31\ D_{645} - 0.14\ D_{630})$$

where D is the assorbance of the pigment at three different wavelength (665, 645 and 630); the results were expressed in mg/l.

Results

Decomposition

In all experimental treatments, weight loss pattern over time (after adjustment to 100% at t=0) fits with a negative exponential model ($r>0.97$ Figure 1, Table 1). Differences in breakdown rates were significant (ANCOVA; $P<0.05$) among treatments with low animal density (0–1 ni/g, average K = 0.0103), medium animal density (2–4–8 ni/g, average K = 0.0156), and high animal density (16–32 ni/g, average K = 0.0260) (Table 1). In high animal density treatment, the half-life of the detritus of *A. glutinosa* decreased to about 60% of that in tanks without animals (Table 1). The three major groups (low-medium-high animal density) were also separated by cluster diagram cut at 0.22 according to cophenetic correction (Sneath & Sokal, 1973) (Figure 2).

No significant differences in detritus weight loss were observed between the experimental treatments during the first phase of the decomposition process (ANOVA test, $P>0.05$ – 7 days F = 2.87 – 14 days F = 1.45); differences became significant after 21 days (ANOVA, $P<0.05$).

Animal colonisation

Animal colonisation of leaf packs followed an exponential pattern in low-medium density treatments while a typical bell-shape pattern in high density treatments with the maximum around the 35th day when about 60% of the leaf mass was lost (Figure 3).

The average animal density, at the end of the experiment, shows a significant linear correlation with the animal density introduced at the starting ($y = 0.99x + 4.04$; $R^2 = 0.97$; $p<0.05$).

Invertebrate diversity (Hs) in litter bags increased with increasing densities of invertebrates in the macrocosms. At the beginning of the experiment, the simplified community had a diversity of Hs = 1.2 and it decreased with time; it went down to 0.4 in low density treatment, to 0.1 in medium density treatments and to 0.9 in high density treatments (Table 2).

Grouping the four species in trophic groups, we obtained a prevalence of the scrapers (*P. corneus* and *B. tentaculata* – max values 66–70%) during the first phase of decomposition while shredders (mainly *P. coxalis* – max.values 72–98%) were predominant during the second phase (after 28th day).

The relation between total invertebrate consumption at the end of 77 days and invertebrate density in the experimental treatments follows a logarithmic curve (Figure 4).

Chlorophyll a

Chlorophyll *a* concentration at the end of the experiment showed a significant relation with animal density (Figure 5); its concentration increases from 210 mg/m^3 in the low density treatment to 754 mg/m^3 in the high density treatment.

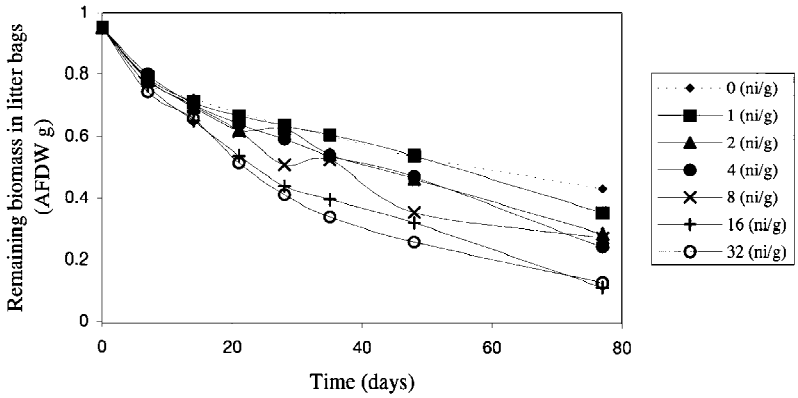

Figure 1. Remaining biomass (AFDW) in alder litter bags through time exposed to several densities of invertebrates.

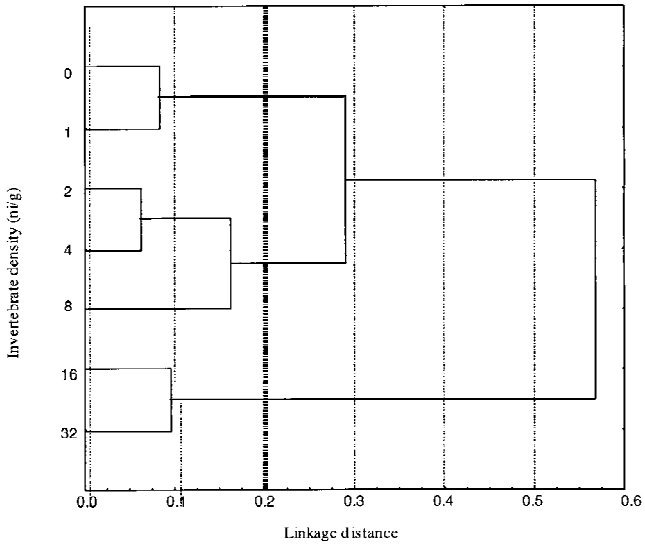

Figure 2. Results of the cluster analysis among remaining biomass (AFDW) in alder litter bags through time exposed to several densities of invertebrates. The dashed line indicates the value of cophenetic correlation cutting-off the dendrograms.

Discussion

Alder leaves belong to the fast processing category (Petersen & Cummins, 1974). In accordance with other authors, who found that alder leaves lose 50% of their initial weight in 30–60 days (Sedell et al., 1975; Bärlocher, 1991; Pozo, 1993), the half-life of alder leaves in our study ranged between 27 and 68 days.

Comparing the leaves half-life in the 'no animal' with the 'high animal density' (32 ni/g) treatments, we can establish that the animal contribution reduces the detritus half-life by 60%. Among others, while comparing the invertebrate colonised and non-colonised detritus half-life in nature, Menendez et al. (1989) found a difference of 23%, Buth & de Wolf (1985) of 16–32% and Fazi (1994) of 64%. Moreover, our results are in agreement with literature data on the weak role played by animal activities during the first phase of decomposition (Swift et al., 1979; Valiela et al., 1982; Buth & de Wolf, 1985). In the first 2 weeks of study, no differences were found in detritus weight loss between treatments with and without animals. Beside the weight loss due to leaching, as animals mainly feed upon the microflora attached to leaf matrix, the delay in the effect of the animal metabolism could be due to the pattern of fungal colonisation. Canhoto & Graça (1996) found that the number of fungal species on submerged alder leaves, reached its maximum between the 14th and the 21st day of submersion.

In our simplified experimental treatments, the decomposition rates increased with detritivores density although a continuous increase in detritivores density

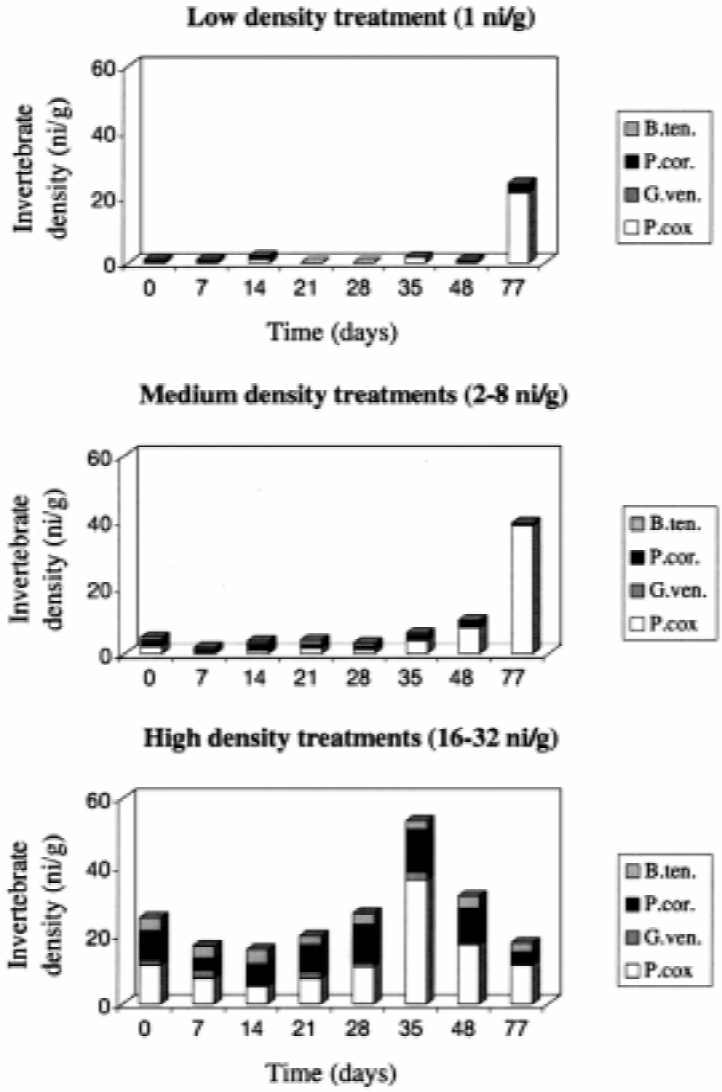

Figure 3. Macroinvertebrate density (ni/g) through time in the different experimental treatments. Experimental treatments were grouped based on the significant differences in leaves decomposition rates: I Treatment (1 ni/g), II–IV Treatments (2–8 ni/g), V–VI Treatments (16–32 ni/g). P.cox = *Proasellus coxalis*, P.cor = *Planorbarius corneus*, B.ten = *Bithynia tentaculata*, G.ven = *Gammarus veneris*.

results in a step-wise increase of the decomposition rates. Significant differences in decomposition rates were found only between the treatments with 1 and 2 individual per gram of detritus (ni/g) and between the treatments with 8 ni/g and 16 ni/g. This discontinuity in the relation between animal density and decomposition rates could be understood if we consider the trophic differences among individuals within a population. Increasing the size of the population, the trophic variability within the population increases as well as the potentiality for resource exploitation. As the phenotypic variability of the population increases non-continuously with its size, the potentiality for resource exploitation will also increase non-continuously, resulting in a step-wise increase in detritus utilisation and decomposition rates.

Analysing animal colonisation, individuals born during the running of the experiment were not taken into consideration. Because of their small body size, we assume juveniles had a very small impact on the decomposition rate of detritus.

In all treatments, simplified animal community diversity decreases as decomposition proceeds. This pattern is mainly due to *P. coxalis* dominance at the

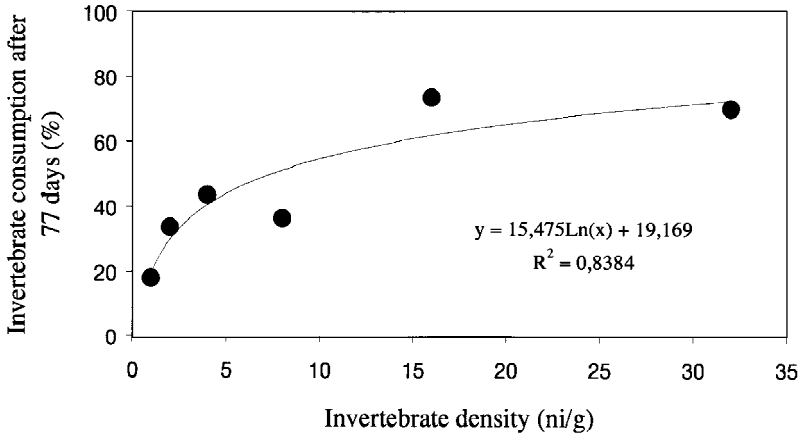

Figure 4. Average percentage of animal consumption in the different experimental treatments over 77 days.

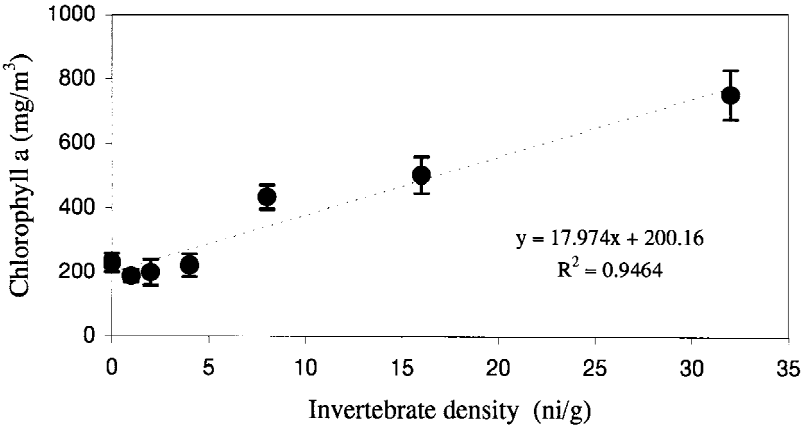

Figure 5. Relation between Chlorophyll *a* concentration in water columns and invertebrate density. Vertical bars = ± SE.

end of the experiment. Our results show a dominance of scrapers (*P. corneus* and *B. tentaculata*) during the first phase of decomposition versus a dominance of shredders (mainly *P. coxalis*) during the second phase. These changes of the trophic groups dominance during decomposition process fully agrees with some field observations (i.e. Cummin et al., 1989) and may be attributed to the groups' feeding behaviours.

In the treatments with low-medium density, animal colonisation follows an exponential trend while a typical bell-shape relationship was found at the highest density (16 –32 in/g). In the latter case, animals started to leave the patches after 35 days of submersion, when leaves had lost about 60% of their initial weight, looking for a new trophic patch. Cummins et al. (1989) and Sabetta et al. (1999), respectively, found that animals leave detritus when it retains about 30–50% of the initial weight. This pattern could be the result of a reduction in detritus quality. In high density treatments animals overgrazing could reduce detritus quality in terms of increased proportion of refractory substance (i.e. lignin) and of reduced microbial density and diversity (Barlocher, 1980; Picciafuoco & Rossi, 1985; Rossi, 1985). Detritus, thus becoming nutritionally poor, can no longer sustain abundant populations. This upper limit in animal contribution to decomposition is also confirmed by the total animal consumption at the end of 77 days: animal consumption increases with increasing densities of invertebrates in the treatments following a logarithmic relation. It should be noted that the amount of the detritus was not limited: at the end of the experiment, about 2.6 g of detritus (A.F.D.W) remained in the high density treatments. Considering that under these treatments the whole animal community consumes about 0.08 g of detritus per day, any food limitation was not based on absolute amount.

Table 2. Macroinvertebrate species colonising submerged litter bags in the different experimental treatments. Experimental treatments were grouped based on the significant differences in leaves decomposition rates: Treatment I, 1 ni/g; Treatments II–IV, 2–8 ni/g; Treatments V–VI, 16–32 ni/g. On Day 0, the data refers to the macroinvertebrate species introduced in the treatments

	Days								Average
	0	7	14	21	28	35	48	77	
Treatment I									
Proasellus coxalis	x	x	x			x		x	
Gammarus veneris	x	x							
Planorbis corneus	x	x	x				x	x	
Bithynia tentaculata	x	x	x						
Shannon index	1.2	1.4	1.0	-	-	0.0	0.0	0.4	0.4
Treatments II–IV									
Proasellus coxalis	x	x	x	x	x	x	x	x	
Gammarus veneris	x	x			x				
Planorbis corneus	x	x	x	x	x	x	x	x	
Bitynia tentaculata	x	x	x	x	x	x	x		
Shannon index	1.2	1.2	1.0	1.1	1.1	0.6	0.6	0.1	0.8
Treatments V–VI									
Proasellus coxalis	x	x	x	x	x	x	x	x	
Gammarus veneris	x	x	x	x	x	x	x		
Planorbis corneus	x	x	x	x	x	x	x	x	
Bithynia tentaculata	x	x	x	x	x	x	x	x	
Shannon index	1.2	1.3	1.2	1.2	1.1	0.9	1.0	0.9	1.1

A direct link between decomposition rate and primary productivity is shown by the measurement of the phytoplankton standing crop at the end of the experiment. The algal bloom we observed in the macrocosms with high detritivores density suggests that the density of detritivores, speeding up the decomposition rate, affects the rate of nutrient release in the water column and consequently the primary production of the system. Relations between animal density and nutrient release from detritus have previously been hypothesised (Ligetta et al., 1999). Our results emphasise the role of detritivores density on phytoplankton productivity. This should be considered in modelling donor-control systems, where a link between detritus and primary production has not yet been considered (Cerfolli & Rossi, 1995).

Conclusion

Detritivorous macroinvertebrate density is one of the major variables in enhancing the rate of disappearance of coarse organic matter and our results show that significant relations between animal density and decomposition rate can be detectable only when considering large differences in detritivore densities (i.e. between habitat comparisons). In all experimental treatments with different animal densities, animals started to affect decomposition of alder leaf after 21 days of submersion. On the other hand, animal contribution to decomposition showed an upper limit that strongly depends on animal density as animals start to leave the patches when about 60% of the initial mass is lost (35th day in high-density treatments). This is also confirmed by the pattern of the total animal consumption: even if animal consumption increases as the animal density increases, it reaches an upper-limit beyond which it remains constant.

Our results also show that a faster decomposition rate of detritus at the water-sediment interface results in a higher microalga standing crop in the water column. These results could help in clarifying the linkage between grazing and detritus pathways in freshwater ecosystems and emphasise the role of the allochthonous detritus as a source of nutrients for algae primary production.

Acknowledgements

We thank Dr L. Picciafuoco and Dr A. Barra Caracciolo for the collaboration during the experimental phase and two anonymous reviewers for their valuable comments. This study was funded by European Union under the contract ENV4-CT97-0584-CODEPASS and MURST cofinanziamento.

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