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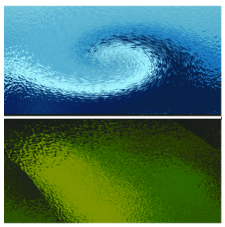

RESEARCH ARTICLE

A patch use behaviour approach to model leaf litter breakdown in aquatic environment

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Abstract

1 - We present a mechanistic model of reed leaves decomposition in a Mediterranean coastal lagoon (Lake Alimini Grande, Puglia, Italy). Our aim is to assess the importance of the heterogeneity of leaf detritus and of the different rules of patch colonization by macroinvertebrates on reed detritus processing.

2 - To this end, we propose two versions of the model (homogeneous and heterogeneous detritus model) where the microflora is supposed to complete all the life cycle on a leaf patch, while the macroinvertebrates move towards or left the patch according to patch attractiveness.

3 - The threshold of patch attractiveness and the number of colonizers are the behavioural sources of variation in the model. The effects of the behaviour of invertebrate consumers on detritus mass loss are tested by a multi-factorial ANOVA design. A field study on reed leaf decomposition in Lake Alimini Grande is used as reference to set a number of biological parameters.

4 - Simulated leaf detritus loses weight according to a negative exponential model. The comparison between simulated and experimental data selects the heterogeneous detritus model for describing reed leaf decomposition. Behaviourally–related characteristics of invertebrate consumers also affect decomposition rates, which are directly related to invertebrate abundance and inversely to resource attractiveness threshold. The model results suggest that reed leaf decomposition in Lake Alimini Grande is probably driven by microbial activity.

Keywords: decomposition, *Phragmites australis*, behavioural approach, patch dynamics, model simulations.

Introduction

Reed stands are among the most productive ecosystems of temperate zones, but a large portion of the annual plant production is not consumed by herbivores and enters the detrital pool in the form of litter (Mann, 1988). In such aquatic ecosystems, decomposition of dead organic matter is a key process regulating the regeneration of carbon and nutrients and represents an important link between primary and secondary production in detritus-based food web (Fenchel and Jørgernsen, 1977).

Litter decomposition in aquatic ecosystems is mainly a biological process involving bacteria, fungi, and invertebrates. On a temporal scale, it proceeds in three distinct stages: i) leaching, i.e. the rapid weight loss due to the washing out of dead leaf soluble constituents; ii) conditioning, i.e. the modification of leaf matrix by microorganisms due to enzymatic activities; iii) fragmentation, i.e. the physical break up from the coarse detritus mostly mediated by shredder feeding (Graça, 2001 and literature cited). However, these three processes are not easily separable, since one influences the others. An example of this is that fungi and bacteria convert a portion of detrital organic matter into microbial biomass transforming the detrital

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substrate into a more nutritious food source for detritus feeders (Bärlocher and Kendrik, 1975; Suberkropp 1992). At the same time, shredders fragmenting the detrital matrix promote microbial activity increasing the available detrital surface for colonisation (Hargrave, 1970; Howe and Suberkropp, 1994) and spreading microfungal spores (Rossi, 1985). The rate of plant litter decomposition can vary considerably depending on environmental factors such as temperature, nutrients, and oxygen, and internal factors such as leaf quality (Webster and Benfield, 1986). Among factors depending on leaf quality, the concentration of nutrients, especially nitrogen, and the content of fibre such as lignin, cellulose, and hemicellulose are the most important factors that affect breakdown rates (e.g. Valiela et al., 1979). In particular, reed (*Phragmites australis*) leaf detritus is predominantly composed of structural polymers that are resistant to decay (Dinka et al., 2004).

Here, the relevance of leaf quality and biological agents on the decomposition of P. australis leaves in a coastal lagoon of Southern Italy has been studied through model simulations. There are many possible approaches for modelling decomposition processes. In fact, depending on the desired degree of analytical complexity, generality, and predictive power, the model can or cannot include the effect of abiotic factors, resource quality, and decomposer dynamics. Two major groups of models can be identified: models focused on transformation of detrital mass (Webster, 1983; Moran et al., 1988; Gessner et al., 1999; Asaeda et al., 2002) and models focused on decomposer population dynamics (Van Wensen et al., 1997; Hieber and Gessner, 2002; Schimel and Weintraub, 2003). Most of decomposition models do not take into account the behavioural constraints affecting the colonization of decaying detritus by benthic macroinvertebrates. Recently, a relevant role of short-term space use mechanisms that regulate the colonization of invertebrates on decaying detritus and detritus decomposition rates has been emphasised (Mancinelli et al. 2005). Detritivores are known to ignore patches until some threshold of resource availability is attained and to abandon them after a partial depletion of the resources (Basset 1995 and literature cited). In the present study, we designed a simple mechanistic model of leaf decomposition in aquatic systems to evaluate: 1) the influence of resource quality and 2) the importance of behavioural aspects of macroinvertebrate foraging habits in modelling decomposition processes. To this end, we designed two versions of the model; one model which considers a chemically homogeneous detrital matrix and another model where the detritus is heterogeneous, being partitioned into a labile and a refractory fraction. In both versions the behavioural components of leaf patch colonisation by macrofauna were explicitly included in order to increase the realism of the model accounting for the short-term space use of detritivore consumers.

Methods

Outline of the model

The model simulates the transfer of dry mass through a tri-trophic food chain composed of coarse particulate organic matter (CPOM) leaf detritus, bacteria (BAC), fungi (FUN), and detritivores (DET) (Fig. 1A and 1B). Specifically, it describes the degradation process of *Phragmites australis* [(Cave.) Trin. ex Steud.] leaves as the result of leaching, microbial mineralization, and macroinvertebrate consumption. In what follows, the basic assumptions of this model are explained. CPOM is a non-renewable resource and it is considered to be a homogeneous matrix for the homogeneous detritus model ("HOD" model hereafter) and a heterogeneous matrix for the heterogeneous detritus model ("HED" model). In the latter model, a fast-decomposing sub-compartment has been included in the CPOM pool accounting for the decomposition of the most labile particulate organic matter (L-CPOM). In both models, fungi and bacteria are assumed to grow on CPOM (and L-CPOM in the "HED" model) and to derive all carbon for sustaining their growth from the leaf detritus itself. The growth of fungi and bacteria is

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governed by the logistic equation while the uptake, supporting standing biomass, is limited by the Michaelis–Menten equation. Mass losses from the microbial compartments are due to intrinsic mortality and to detritivore grazing; two different terms accounting for respiratory costs, one related to maintenance and another associated to growth, are also included.

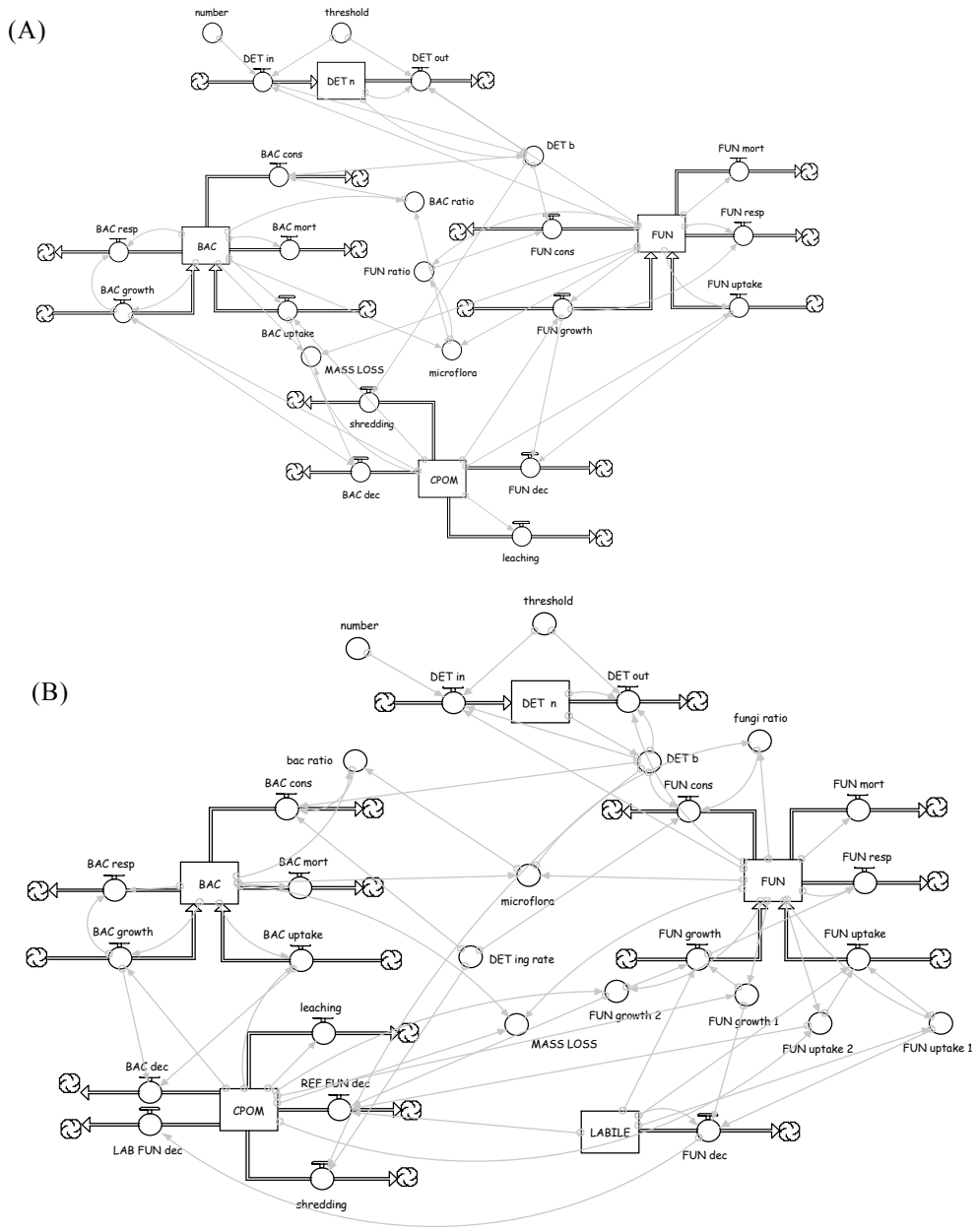

Figure 1.Conceptual diagram of STELLA® of the HOD Model (A) and the HED Model (B).

Detritivore consumers are expected to colonize and abandon the leaf patch according to patch profitability. When the resource (fungal biomass) increases up to a threshold level the detritivores enter the patch. Conversely, under the threshold, they abandon it. The threshold level is estimated on the base of the relationship between fungal biomass and macroinvertebrate biomass, while the number of invertebrates is randomly selected from within a fixed range. Detritivore growth is not modelled and the individual mass of invertebrates is assumed to be constant throughout the simulations. Moreover, invertebrates consume the microflora

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together with the leaf matrix in different proportions, according to the assumption that they prefer microbial resources.
The above illustrated biological processes are translated into mathematical equations while the description of the behavioural aspects of detritivore colonization and the leaching process is carried out using logical functions (i.e., if, then, else) (Tab. 1).

Table 1. List of mathematical and logical functions used in the Models.

n° mathematical functions

(1) Coarse Particulate Organic Matter (CPOM) temporal variation :

HOD model

$$\frac{dCPOM}{dt} = -I \cdot CPOM - g_{fun} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max}}\right) - u_{fun} \cdot FUN \cdot \frac{CPOM}{(k_{fun} + CPOM)} - g_{bac} \cdot BAC \cdot \left(1 - \frac{BAC}{BAC_{max}}\right) - u_{bac} \cdot BAC \cdot \frac{CPOM}{(k_{bac} + CPOM)} - F_{leaf} \cdot i_{det} \cdot DET_b$$

HED model

$$\frac{dCPOM}{dt} = -I \cdot CPOM - g_{fun} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{maxL}}\right) - u_{fun} \cdot FUN \cdot \frac{LPOM}{(k_{funL} + LPOM)} + g_{funR} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{maxR}}\right) +$$
$$-u_{fun} \cdot FUN \cdot \frac{CPOM}{(k_{fun} + CPOM)} - g_{bac} \cdot BAC \cdot \left(1 - \frac{BAC}{BAC_{max}}\right) - u_{bac} \cdot BAC \cdot \frac{CPOM}{(k_{bac} + CPOM)} - F_{leaf} \cdot i_{det} \cdot DET_b$$

(2) Labile-Coarse Particulate Organic Matter (L-CPOM) temporal variation :

HED model

$$\frac{dL - CPOM}{dt} = g_{fun1} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max1}}\right) - u_{fun1} \cdot FUN \cdot \frac{L - CPOM}{(k_{funL} + L - CPOM)}$$

(3) Fungal biomass (FUN) temporal variation:

HOD model

$$\frac{dFUN}{dt} = g_{fun} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max}}\right) + u_{fun} \cdot FUN \cdot \frac{CPOM}{(k_{fun} + CPOM)} - r_{fun} \cdot g_{fun} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max}}\right) - mr_{fun} \cdot FUN - m_{fun} \cdot FUN - F_{micro} \cdot \frac{FUN}{FUN + BAC} \cdot i_{det} \cdot DET_b$$

HED model

$$\frac{dFUN}{dt} = g_{fun} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max}}\right) - u_{fun} \cdot FUN \cdot \frac{LPOM}{(k_{funL} + LPOM)} + g_{funR} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{maxR}}\right) +$$
$$-u_{fun} \cdot FUN \cdot \frac{CPOM}{(k_{fun} + CPOM)} - r_{fun} \cdot g_{fun/funR} \cdot FUN \cdot \left(1 - \frac{FUN}{FUN_{max/maxR}}\right) - mr_{fun} \cdot FUN - m_{fun} \cdot FUN - F_{micro} \cdot \frac{FUN}{FUN + BAC} i_{det} \cdot DET_b$$

(4) Bacterial biomass (BAC) temporal variation:

$$\frac{dBAC}{dt} = g_{bac} \cdot BAC \cdot \left(1 - \frac{BAC}{BAC_{max}}\right) + u_{bac} \cdot BAC \cdot \frac{CPOM}{(k_{bac} + CPOM)} - r_{bac} \cdot g_{bac} \cdot BAC \cdot \left(1 - \frac{BAC}{BAC_{max}}\right) - mr_{bac} \cdot BAC - m_{bac} \cdot BAC - F_{micro} \cdot \frac{BAC}{FUN + BAC} \cdot i_{det} \cdot DET_b$$

(5) Detritivores (DET_n) numerical abundance temporal variation:

$$\frac{dDET_n}{dt} = (DET_{n\_in}) - (DET_{n\_out})$$

a) DET_{in} = if $(FUN > T \cdot DET_b)$ then $\{round\ [random\ (0, N)]\}$ else (0)

b) DET_{out} = if $(FUN < T \cdot DET_b)$ then $\{round\ [random\ (DET_n)]\}$ else (0)

(6) Detritivores biomass (DET_b) temporal variation:

$$\frac{dDET_b}{dt} = DET_{ib} \cdot DET_n$$

Calibration

The model was calibrated using data from both experiments and literature. Specifically, data about leaching, invertebrate individual average mass, and initial weight for leaf packs were taken from a study on the decomposition of *P. australis* leaf detritus in Lake Alimini Grande (Apulia, Italy) (Mancinelli et al., 2005), while for the ingestion rate of detritivores, data from a laboratory experiment carried out on the two

marine detritivores *Gammarus insensibilis* and *Lekanesphaera monodi* was used (Manganelli and Rossi, 1996). Other parameters used in the model were taken from literature. All microbial metabolic rates were obtained by works focused on *P. australis* breakdown (Komínková et al., 2000; Buesing and Gessner, 2005). The saturation constants of the HED model (k_{bac} and k_{funL}) were assumed to be a little percent (0.1%) of the initial resource (Hieber and Gessner, 2002) while that of the HOD (k_{fun}) was estimated according to the percent of lignin content of *P. australis* leaves (Dinka et al., 2004). On the other hand, initial values for the microbial state variables were obtained from literature data (Findlay and Arsuffi, 1989). All parameters and initial values are shown in Tab. 2. The models were programmed using Stella 8.0® (HPS System, Inc. 2003) simulation software with runs of 8 weeks and time steps of 1 day.

Table 2. List of state variables (A) and parameters (B) used in the Models

A) Symbols, description, units and values for the state variables

Symbols	Descriptions	Units	Values
BAC	Bacterial Biomass	mg dry mass	0.025
CPOM	Coarse Particulate Organic Matter	mg dry mass	3000
L–CPOM	Labile–Coarse Particulate Organic Matter	mg dry mass	870
DET_b	Detritivore Biomass	mg dry mass	0.69
DET_n	Detritivore Number	number	0
FUN	Fungal Biomass	mg dry mass	5

B) Symbols, descriptions, units and values for the parameters

Symbols	Descriptions	Units	Model values	Literature values	Ref.
BAC_{max}	max BAC biomass	d^{-1}	0.003	0.5% CPOM	1
DET_{ib}	Detritivores individual biomass	mg	0.69	0.69	9
F_{micro}	Fraction of microflora ingested	d^{-1}	0.75		10
F_{leaf}	Fraction of leaf detritus ingested	d^{-1}	0.25		10
FUN_{max}	max fungal biomass	d^{-1}	0.075	5-8.5% CPOM	1
FUN_{maxR}	max fungal biomass	d^{-1}	0.075	5-8.5% ref. fract.	1
g_{bac}	bacterial max growth rate	d^{-1}	3	3.4	2
g_{fun}	fungal max growth rate	d^{-1}	1.5	2.56	3
g_{funR}	fungal max growth rate on ref. fract.	d^{-1}	0.007	0.007	1
i_{det}	detritivores max ingestion rate	d^{-1}	0.37	0.17–0.57	4
k_{bac}	CPOM half-saturation constant for BAC	mg	3	0.1% CPOM	5
k_{fun}	CPOM half-saturation constant for FUN	mg	300	10% CPOM	8
k_{funL}	L–CPOM half-saturation constant for FUN	mg	9	0.1% LPOM	5
l	leaching rate	d^{-1}	0.02	8% CPOM	9
m_{bac}	bacterial mortality rate	d^{-1}	0.2	0.24-0.72	6
m_{fun}	fungal mortality rate	d^{-1}	0.02		11
mr_{bac}	bacterial maintenance respiration rate	d^{-1}	0.1	0.15	7
mr_{fun1}	fungal maintenance respiration rate	d^{-1}	0.1	0.15	7
r_{bac}	bacterial respiration rate	d^{-1}	0.7	0.7	1
r_{fun}	fungal respiration rate	d^{-1}	0.7	0.39-0.88	1
u_{bac}	bacterial max uptake rate	d^{-1}	0.1	0.15	7
u_{fun}	fungal max uptake rate	d^{-1}	0.1	0.15	7

1) Kominkova, 2000; 2) Buesing, 2006; 3) Van Wensen, 1997; 4) Manganelli, 1996; 5) Hieber, 2002; 6) Servais, 1985; 7) Moran, 1989; 8) Dinka, 2004; 9) Field experiment; 10) Estimated from various literature data 11) Estimated on the basis of bacterial mortality rates.

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Factorial design

A factorial design was developed in order to select the best agreement between observed and simulated data and to evaluate the influence of different rules of patch colonization and of the chemical quality of detrital matrix on decomposition rates. Specifically, we investigated the effects of the number of invertebrates entering the leaf patch, the threshold level of patch attractiveness (defined as "Number" and "Threshold", respectively), and the quality of leaf detritus resource ("Resource"). Three level were chosen for "Number" (10, 30 and 50) and "Threshold" (1, 5 and 20), and two for "Resource" (HED and HOD). The "Number" and "Threshold" values were chosen according to various literature data and simulation results. Then, parallelism tests based on ordinary least square correlative analyses between observed and simulated mass loss were carried out in order to select the best agreement between observed and simulated data. Finally, two- and Three-Way ANOVAs were performed to test the effects of the different levels of both "Threshold" and "Number" factors on decomposition rates.

Field experiment

The study was undertaken in Lake Alimini Grande, a coastal brackish lagoon located in Puglia (South-East Italy) in the Adriatic Sea. The lagoon is 3.03 km long and has a maximum width of 1.34 km. The maximum depth is 3.5 m, and the water surface is ~1.26 km^2, depending on tidal cycles and freshwater inflows (see Mancinelli et al. 2005 for further information on the study site). An experimental site was located on the western coast of the lagoon, close to a reed stand. Senescing leaves of *Phragmites australis* were collected from Lake Alimini Grande reed stands and air dried. Aliquots of leaf fragments were weighed to the nearest mg after drying at 60°C for at least 72 h ('leaf packs': 3.000 ± 0.001 g dry mass) and enclosed in ballasted net bags (0.5 cm mesh size) to facilitate their manipulation and retrieval. A total of 164 leaf packs were placed at each experimental site on October 17th, 1998. 4 leaf packs per site were immediately used for determinations of the initial mass at t = 0. Subsequently, 4 leaf packs per site were collected after 4 days from the start of the experiment; pack collection was carried out daily for the following 39 days. In the field, leaf packs were singularly enclosed underwater in plastic bags and transferred at 4°C to the laboratory, where they were washed with tap water to remove invertebrates. Leaf fragments were subsequently dried and weighed according to the aforementioned procedures. Invertebrates were recognized and enumerated. Their individual dry mass was determined after drying at 60°C for at least 72 h. Nonlinear regressions were carried out to calculate the decay rate coefficient of reed leaf detritus according to a single negative exponential model $m_t = m_0 * e^{-kt}$ (Olson, 1963) where m_0 is the initial dry mass, m_t is the leaf pack dry mass at time t (both expressed in mg) and k is the decomposition constant.

Results and Discussions

Reed leaf pack in Lake Alimini Grande lost mass according to a negative exponential model ($r = 0.9181$, d.f.= 42, $P < 0.001$). At the end of the study period, which lasted 56d, the dry weight of the reed leaf packs was on average the 43.5% ±2.8% of the dry weight at the start of the field experiment.

In Fig. 2 simulated patterns of detritus breakdown, according to the factorial design, are compared each others and with that observed in the field experiment of Lake Alimini Grande. Both the resource quality and the behavioural components significantly affect reed leaf decomposition processes in simulation models (Tab. 3). In particular, as regards the influence of resource quality, reed leaf decay rates in the "HOD" model are on average 66.7% faster than in the "HED" model ($k = 0.011 \pm 0.0002$ and $k = 0.018 \pm 0.0014$, respectively). This result is consistent with the differences of the biological assumptions underlying the two models. The "HOD" model is developed without any constraints regarding the chemical complexity of detrital matrix, while the "HED" model takes account of highly decomposable

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and more recalcitrant components of detrital matrix. The comparison between observed and simulated data clearly points out that the "HOD" model over-estimates the decay rate of reed leaves and produces an almost-linear pattern of decay, while the "HED" simulations are in good agreement with observed data (Fig. 2.). Our results are also consistent with a number of investigations that have identified, beside the species-specificity of leaf detritus decomposition pattern in terms of quality (e.g., nutrient contents, relative abundance of structural components etc.; Webster and Benfield, 1986), an overall bi-compartmented structure of the detrital matrix constituted by a labile and a recalcitrant carbon pool (Dinka et al., 2004) with different decay rates.

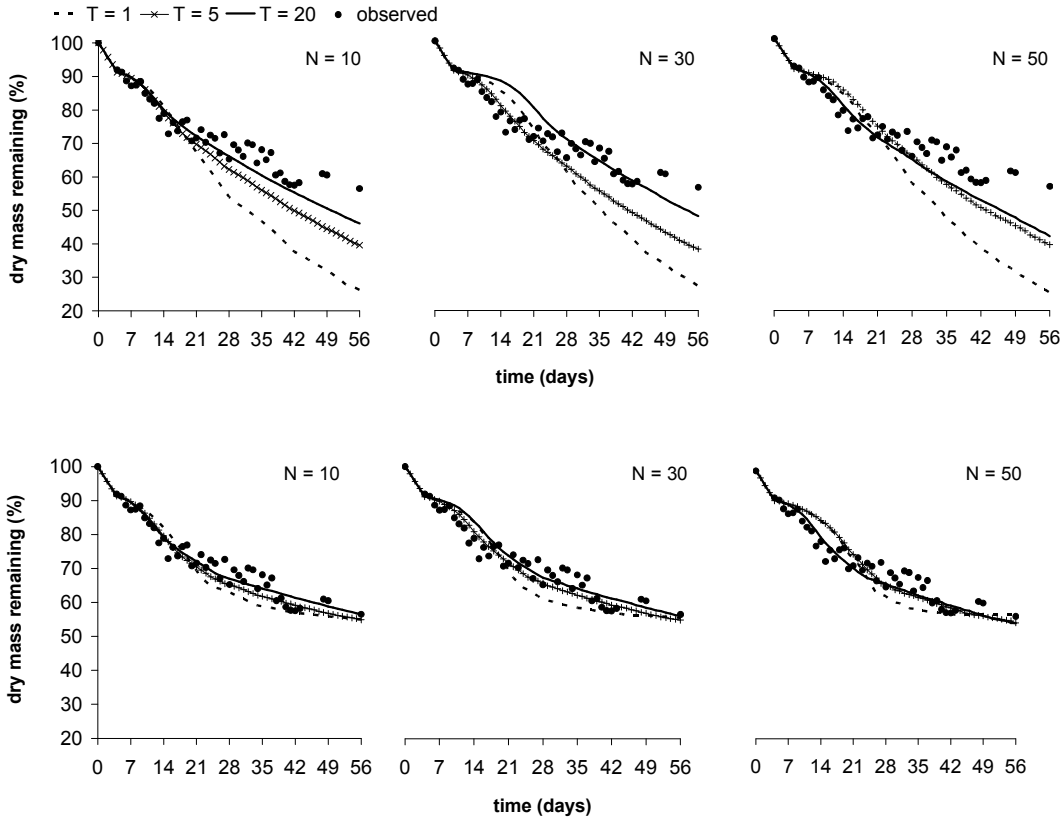

Figure 2. Detritus mass loss simulations of the HOD Model (A) and the HED Model (A) according to the factorial design.

Table 3. Three-Way ANOVA results on simulated decomposition rates k obtained with respects to the different combinations of resource type (two levels: heterogeneous - homogeneous) number of invertebrate consumers (three levels: 10, 30, 50) threshold level of patch attractiveness (three levels: 1, 5, 20).

factors	**d.f.**	**variance**	**F**	***P***
Resource type	1	0.000694	1254.38	0.0000
Number	2	0.000006	10.29	0.0003
Threshold	2	0.000120	216.86	0.0000
Resource × Number	2	0.000003	5.32	0.0094
Resource × Threshold	2	0.000074	133.72	0.0000
Number × Threshold	4	0.000001	1.98	0.1181
Resource × Number × Threshold	4	0.000001	2.19	0.0897
Error	36	0.000001		

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As regards the behavioural components introduced in the models, we evaluate the importance of different rules of patch colonization and of different values of detritivore density on the decomposition rates only for the "HED" model, which has a better fit than the "HOD" model with observations. Nevertheless, in the "HOD" model the behavioural components have even larger effects on leaf decomposition than in the "HED" model (see Fig. 2), determining an increase of decomposition rates up to 84% ($k = 0.0240$ vs. $k = 0.0132$; $N = 30$, $T = 1$ and $N = 30$, $T = 20$, respectively). In the "HED" model, decay rates of reed leaves increase significantly with the density of potential colonisers and decrease as the threshold of reed detritus attractiveness increases (Two-Way ANOVAs, "Number" $F_{2,18} = 28.5$, $P < 0.01$; "Threshold" $F_{2,18} = 78.5$, $P < 0.01$). The influence of density of potential colonisers is clearly non-linear and significant differences of decay rates between density pairs are observed only comparing the condition with 10 potential colonisers per time unit with the other two high-density conditions ($N = 10$ vs. $N = 30$ and $N = 50$; Two-Way ANOVAs followed by HSD tests: $P < 0.001$ for both comparisons; $N = 30$ vs. $N = 50$, $P = 0.35$). A significant interaction factor (Two-Way ANOVAs "Threshold" × "Number" $F_{4, 18} = 4.67$, $P < 0.01$) is also observed, as the differences of decomposition rates among different threshold levels decrease with an increase in consumers' density (Two-Way ANOVAs followed by Tukey HSD tests: $N = 10$ and $N = 30$, P always < 0.05 for all pair-wise comparisons; $N = 50$, $P < 0.05$ only for the comparison $T = 1$ vs. $T = 20$). On these respects, the model synthesizes and extends a set of existing evidences on the role of macro-invertebrates in detritus processing. A relationship between density of macro-invertebrates and decay rate of plant detritus is commonly found in aquatic ecosystems (e.g., Webster and Benfield, 1986). Furthermore, an influence of behavioural constraints on space use and detritus patch colonisation by benthic macro-invertebrates was also recently shown (Mancinelli et al., 2005). Here, applying the behavioural rules of detritus patch use by benthic macro-invertebrates, affecting the time spent on a single patch by individual colonisers and ultimately related to patch use optimisation and energetic constraints, we found that they significantly affected decomposition rates. Our simulations, in contrast with the high inertia which is conventionally expected for the detrital pool towards variations in external constraints (DeAngelis, 1992), indicate that even relatively small changes in consumers' behavioural parameters such as the individual's perception of resource availability within the patch (Basset, 1995), can affect the decay rate of leaf detritus. A number of interacting biological factors potentially affect detritus patch attractiveness determining the individual behaviour of patch colonisation and giving up, including detritus quality and microbial conditioning (Rossi, 1985; Webster and Benfield, 1986; Graça, 2001) as well as individual body size and energetics (Basset, 1995), since the body size has been found to affect the individual perception of both resource quality and quantity (Haskell et al., 2002). The behavioural rules selected for our models are fully consistent with these potential forcing factors and cover a range from high attractiveness of detritus patches and high exploitation efficiency of benthic macro-invertebrates ($T = 1$) to low attractiveness, low efficiency of benthic macro-invertebrates on their microbial resources ($T = 20$).

The comparison between observed and simulated data shows that the simulated condition with $T = 20$ and $N = 10$ has the strongest agreement with the data collected from the field experiment in Lake Alimini Grande (Tab. 4). This condition corresponds to the low attractiveness of decaying detritus for benthic macro-invertebrates and low exploitation efficiency. Under this condition fungi and bacteria are responsible of the most of reed leaf detritus breakdown: 17% of reed leaf mass loss is attributable to leaching, 82% to microorganisms and only 1% to invertebrate detritivores. These results suggest that reed detritus decay in Lake Alimini Grande would be principally driven by the microbial decomposers. The correspondence between the

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condition T = 20, N = 10 and the decomposition of leaf detritus at Lake Alimini Grande seems to be independent of possible bias in the role of microbial decomposers deriving from the biological framework or the parameterisation of the model.

Table 4. Results of parallelism tests performed between observed vs. simulated detritus mass loss for homogeneous and heterogeneous detritus models (d.f. = 84)

	HOD model	HED model
run simulations	***Significance level***	
T = 1, N = 10	***	**
T = 1, N = 30	***	**
T = 1, N = 50	***	**
T = 5, N = 10	***	*
T = 5, N = 30	***	*
T = 5, N = 50	***	**
T = 20, N = 10	***	**n.s.**
T = 20, N = 30	***	*
T = 20, N = 50	***	*

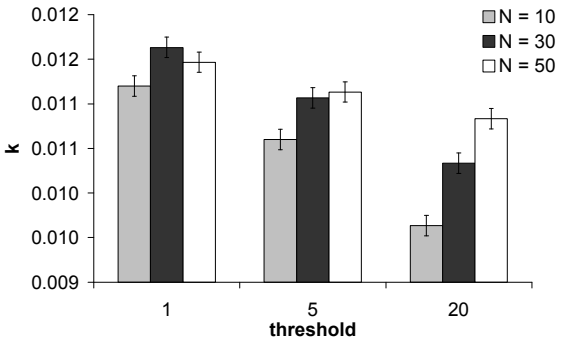

Figure 3. Factorial ANOVA graph of the HED model with decomposition rate (k) as dependent variable and number and threshold as sources of variation. Vertical bars denote 0.95 confidence intervals.

The relative contribution of fungi and bacteria to the weight loss of *P. australis* is 13% and 69% respectively, being the bacterial pool contribution consistent with the results of other authors that found values on saltmarsh macrophytes ranging from 18% to 25% (Mason, 1976; Findlay, 1989). The parameterization of the metabolic parameters regarding the microfungal decomposers is very robust, being based on experimental work carried out on *P. australis* degradation in a lacustrine reed stand (Komínková et al. 2000). Specifically, the fungal growth efficiency (30 %) agrees with other values reported in literature for leaf detritus (Webster, 1983; Moran, et al. 1988; Hieber and Gessner, 2002; Buesing and Gessner, 2005) while the maximum fungal standing stock is consistent to values obtained from a laboratory microcosm experiment (Alemanno, unpublished data) and from the literature (Kominkova et al., 2000). Moreover, a key role of microorganisms in reed decomposition in freshwater and brackish ecosystems is consistent with other studies in lentic habitat (e.g. Sabetta et al. 2000) or specifically focused on the decay of the reed leaves of P. australis (Tanaka, 1991; Komínková et al., 2000; Buesing and Gessner, 2005; Bayo et al., 2005).

In conclusion, in our work we support the relevance of the quality of the detrital matrix on leaf detritus decay and we show that it might also be influenced by behaviorally-related factors characterizing the colonization by detritivores. A linkage between consumers' individual choices and functional processes occurring at an ecosystem level is also suggested by the model results. Our approach can open a new perspective to the study of plant decomposition processes in aquatic ecosystems, relating a functional process to constraints acting at the individual, population and community levels – in other words, characterised by different ecological scales.

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