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The effect of macrofauna, meiofauna and microfauna on the degradation of *Spartina maritima* detritus from a salt marsh area

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Abstract — Decomposition of salt marsh plants results from physical, chemical and biological processes including abiotic and biotic fragmentation, microbial decay and chemical transformation. According to literature data, only a few species have the ability to feed directly on living plant material, so fungi and bacteria seem to be the principal competitors for the organic substrates. Nevertheless, by consuming bacteria, protists and fungi associated to the detritus, macrofauna and meiofauna recycle the incorporated nutrients. Moreover, this nutrient regeneration may be seen as an effective factor in maintaining and stimulating bacterial production. In fact, it is well known that many detritus feeding species have very low assimilation efficiencies. The objective of the present study was to compare the nutrient mass balance of carbon; nitrogen and phosphorus in *Spartina maritima* covered areas and bare bottom sediment, with and without contribution of macrofauna, meiofauna and microbial populations. Nutrients mass balance was studied taking into account the initial and final nutrient concentrations in the sediment, water and plant material. Faunal activity was measured as a function of remineralised carbon, nitrogen and phosphorus. The experimental set-up included sixteen sub-experiments, which varied with respect to type of fauna, plant biomass and oxic status. Each sub-experiment was performed in small glass containers (3 L) containing about 900 g wwt sediment and 2.5 L estuarine water. Plant material, cut from intact plants, sediment cores and estuarine water were brought from the southern arm of the Mondego estuary (Portugal). The results showed that although the bacterial activity was responsible for the *Spartina maritima* degradation, the presence of meiofauna and macrofauna significantly enhanced the process. Moreover, the presence of *Spartina maritima* positively affected the mineralisation of the sediment carbon and nitrogen, especially when the three faunal components were present, and denitrification rates were highest in the presence of the macrofauna and meiofauna. The present study suggests that macrofauna and meiofauna have an important role on the ecosystem nutrient flux and that fauna might function as a sink for excess nutrients, that otherwise could be exported to the coastal waters.

***Spartina maritima* / decomposition / fauna / nutrient mass balance**

1. INTRODUCTION

Salt marshes are often considered as very productive aquatic ecosystems, where rooted macrophytes such as *Spartina* sp. are able to reach high biomass during the growing season [4, 5, 19, 20, 21].

Several studies on aquatic and terrestrial plants have shown that the decay of plant detritus depends on the availability of the plant nutrients [5, 6, 7, 12, 21]. The amount of structural parts, such as lignin and cellulose, and the nutritional C:N:P ratio of the plant, affect the overall mineralisation rates [5]. Several authors have shown that only a small fraction of the plant production is consumed by herbivores [5, 20]; instead the leaves are sloughed with ageing, or the tide motion mechanically fractionates them. So, most of the *Spartina* production enters the detritus pathway and remain within the marsh area, or is exported to the coastal waters [7, 18, 19]. As a result of the nutrient balance and the amount of structural tissue, *Spartina* has a relatively low mineralisation rate.

Degradation includes several different temporal phases [9] that can be resumed in three steps: 1) initial leaching of easy degradable low molecular cellular substances; 2) decomposition of the structural parts; and 3) slow degradation of the more structural plant material. In the initial stages of decomposition, the impact of the macrofauna and meiofauna seems to be negligible, but the effect increases with time [21]. Although, organic matter is primarily degraded by

Table I. *Spartina maritima* laboratory experiment set-up. Plant biomass is expressed in g of wet weight.

Items	Leaves	Roots	Oxic State	Macrofauna	Meiofauna	Bacteria
Bare sediment	0.000	0.000	+	+	+	+
Bare sediment	0.000	0.000	+	+	+	+
Bare sediment	0.000	0.000	–	–	–	+
Bare sediment	0.000	0.000	–	–	–	+
Spartina maritima	2.012	0.507	+	+	+	+
Spartina maritima	4.021	1.003	+	+	+	+
Spartina maritima	8.031	2.069	+	+	+	+
Spartina maritima	2.028	0.510	+	–	+	+
Spartina maritima	4.011	1.059	+	–	+	+
Spartina maritima	8.017	2.014	+	–	+	+
Spartina maritima	2.030	0.506	+	–	–	+
Spartina maritima	4.029	1.033	+	–	–	+
Spartina maritima	8.017	2.071	+	–	–	+
Spartina maritima	2.030	0.510	–	–	–	+
Spartina maritima	4.013	1.003	–	–	–	+
Spartina maritima	8.006	2.081	–	–	–	+

micro-organisms, their presence also enhances the nutritional quality of leaf litter for the macro invertebrate [10]. This was verified after temporal measurements showing that litter had a lower C:N ratio due to heterotrophic bacteria colonisation [16].

It is known that benthic fauna can feed on detritus formed by bacterial decomposition of *Spartina* and macroalgae [4, 19, 20, 21], but not much is known about the role of different fauna levels on *Spartina maritima* detritus degradation, or to what extent the macrofauna and meiofauna affect the nutrient dynamics during the decay process. Therefore, this study focuses on the nutrient mass balance during *S. maritima* decomposition, and the role of the macrofauna and meiofauna compared with an oxic and anoxic microbial degradation of *Spartina* detritus.

2. MATERIALS AND METHODS

Sediment, water, *Spartina maritima* and macrofauna were collected in the southern arm of the Mondego estuary (Portugal) (see also [2, 15]). The laboratory set-up made it possible to measure the aerobic and anaerobic degradation of plant material and sediment organic matter, simulating in situ high tide conditions. The experimental set-up included sixteen sub-experiments, that were performed in small glass containers of 3 L (Ø: 14.0 cm), each containing about 900 g (wwt) of sediment, composed namely by silt and clay, and 2.5 L GF/F filtered estuarine water (20 ‰). The sediment was previously sieved (1-mm mesh size) and mixed to improve the homogeneity among containers.

All plant material was gently washed with estuarine water and weighed (g wwt) before being placed in containers. Different plant biomass, as outlined in *table I*, were chosen to represent realistic values for the salt marsh area of the Mondego estuary. *Spartina maritima* leaves were still green, when cut from intact plants, and placed vertically on the sediment surface, while roots were buried at 3-cm depth. Macrofauna was carefully sorted from the sediment and each individual used in the experiment was previously measured (mm) or weighed (g wwt). Previous studies on macrofauna population dynamics in the Mondego estuary provided the regression models to calculate the initial biomass values in AFDW (ash free dry weight) [13, 14, 17].

The effect of the bacterial degradation was measured by isolating their activity, from the faunal activity, by adding the eukariotic toxin cyclohexamide into the relevant containers. In other containers, macrofauna representing real field abundance was added to the sieved sediment (*table II*), while meiofauna and bacteria only affected the plant degradation in other. Bubbling with atmospheric air ensured oxic conditions, while the anoxic conditions were formed during the first day of the experiment, due to the oxygen consumption in the closed containers.

Table II. Macrofauna species composition and total initial biomass (g AFDW).

Species composition	Items	Macrofauna (g AFDW)
Scrobicularia plana	Bare sediment	0.2825
Nereis diversicolor	Bare sediment	0.2822
Hydrobia ulvae	*Spartina maritima* (2 g AFDW)	0.2636
Cyathura carinata	*Spartina maritima* (4 g AFDW)	0.2753
Oligochaeta sp.	*Spartina maritima* (8 g AFDW)	0.2821

All containers were incubated in darkness at 20 °C, to avoid primary production. Samples were taken for nutrient analysis of plant, water and sediment, corresponding to the initial and final conditions of the experiment. Plant material (leaves and roots) subsamples were used to analyse plant dry weight, loss on ignition (3 h, 450 °C) and C, N and P content. All water samples were filtered (GF/F) and kept frozen until analysis. The removed water was replaced with filtered estuarine water with known concentrations of nutrients. In the budget, this removal of nutrients and dilution were taken into account. Sediment triplicate sub-samples were analysed for dry weight, loss on ignition (8 h, 450 °C), total nitrogen and phosphorus.

At the end of the experiment, *Spartina* leaves and roots were easily identified and separated from the sediment and analysed for total C, N, P and loss on ignition. Sediment sub-samples from each container were removed, homogenised and analysed for total N, P and loss on ignition. Macrofauna was carefully sorted from the sediment (1-mm mesh sieve) and the biomass quantified (g AFDW).

2.1. Analytical procedure

Analyses for dissolved reactive phosphate, ammonia and nitrate were measured on a rapid flow autoanalyser (RFA 300 Alpkem) and performed according to Alpkem methodologies [1]. Before elementary analyses, all plant material was dried to constant weight at 105 °C, and analysed for carbon and nitrogen content (CHN-analyser, Carlo Erba), while total phosphorus was measured according to standard methods. Organic carbon in the sediment was estimated as 40 % mass of the loss on ignition (8 h, 450 °C). Denitrification was calculated considering the difference between the initial and the final amounts of nitrogen in the oxic systems, assuming a steady state in the bacterial biomass, during the experiments [6].

2.2. Data analysis

Statistical treatment (one-way ANOVA: 95 % Tukey's HSD intervals method) was performed with MINITAB 10.1 software package. All data were previously transformed as arcsine $(\sqrt{\text{value}})$, according to Zar [23].

3. RESULTS

In the present study, abiotic processes were assumed irrelevant. Available information from a similar set-up, concerning *Zostera marina* and *Ulva* sp. degradation, showed that mineralisation of plant material was purely biotic [6].

During the study period of 99 d, the degradation of *S. maritima* leaves was significantly different (Tukey's test; one-way ANOVA, $n = 3$, $P = 0.001$) when the three fauna levels were present, corresponding to 92 % of the initial biomass. With the decrease in faunal complexity, there were no significant differences among the fauna levels, which corresponded to 74 % when meiofauna and bacteria were present and 67 % when just bacteria were present (*figure 1A*). During degradation of roots, 67 % of the root biomass were degraded in the presence of bacteria, when both meiofauna and bacteria were present, the degradation rose up to 77 % (*figure 1B*). For the same experiment, the role of macrofauna was not so conclusive and there were no significant differences among the experiments. Results concerning *S. maritima* degradation under anoxic conditions were very similar to the oxic conditions in the presence of bacteria, and bacteria and meiofauna.

In the *S. maritima* decomposition process, the mineralisation followed the order C < N < P. Although there was always carbon conservation, carbon mineralisation increased with the increase of fauna complexity. Considering the three elements (C, N, P), the highest mineralisation rates of leaves occurred when macrofauna, meiofauna and bacteria were present: 93 % C, 96 % N and 97 % P (*figure 2A*). In fact, the presence of the three fauna levels was significantly different from the other containers in respect to mineralised carbon (Tukey's test; one-way ANOVA, $n = 3$; $P = 0.001$), and nitrogen (Tukey's test; one-way ANOVA, $n = 3$; $P = 0.001$). But the mineralised phosphorus was just significantly different from anoxic conditions (Tukey's test; one-way ANOVA, $n = 3$, $P = 0.022$). The other fauna levels were not statistically different from each other. At the end of the experiment, 61 % of the initial C content of leaves were already mineralised in the presence of bacteria, 72 % when both meiofauna and bacteria were present, and 92 % when the three fauna levels were present (*figure 2A*). These relationships were not so clear

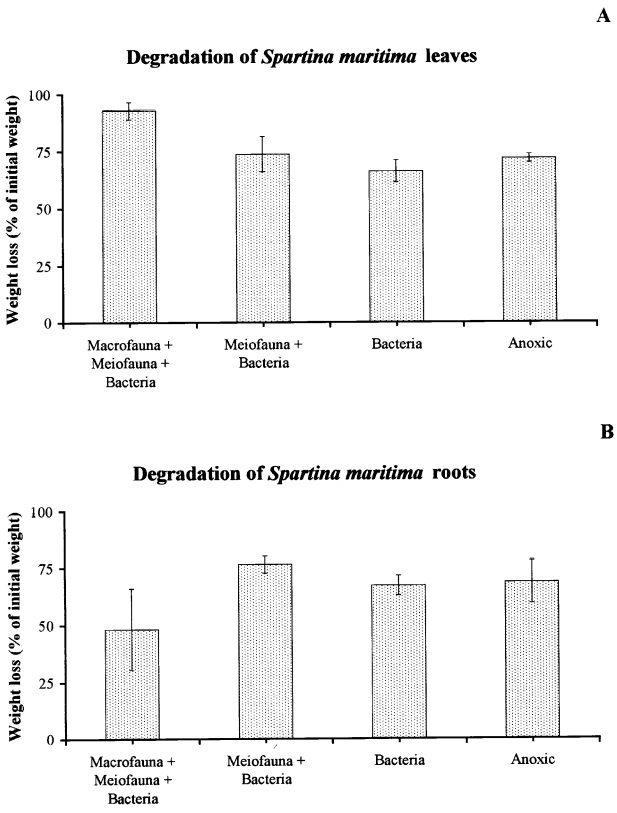

Figure 1. Weight loss of *Spartina maritima*, during 99 d of degradation, in the presence of just bacteria, under anoxic and oxic conditions; bacteria and meiofauna, and bacteria, meiofauna and macrofauna (mean ± standard deviation, $n = 3$). A: Leaves; B: roots.

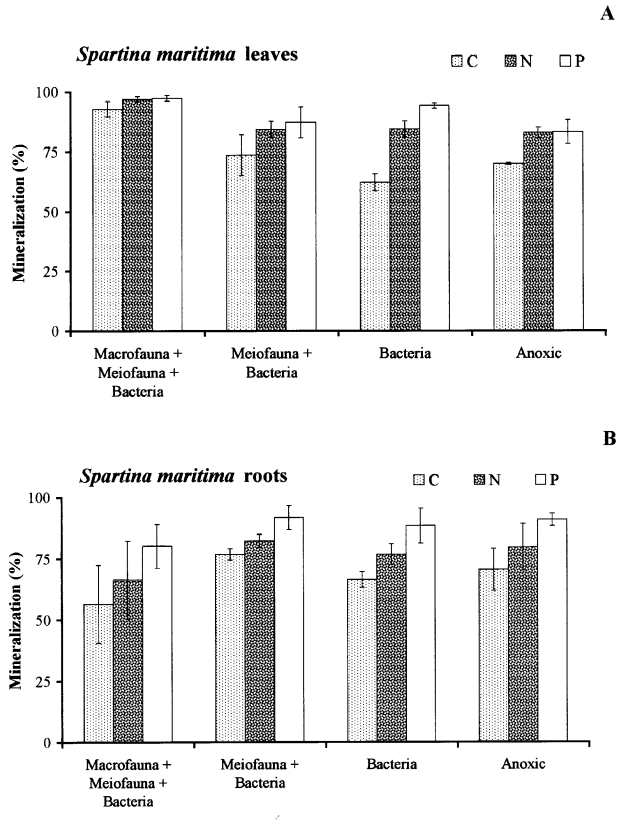

Figure 2. Comparison of the initial percentage of *Spartina maritima* mineralisation, during 99 d, in the presence of bacteria only under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna (mean ± standard deviation, $n = 3$). A: Leaves; B: roots.

during the mineralisation of root and there were no significant differences among the fauna levels. Nevertheless, mineralisation rates were slightly higher in the presence of meiofauna and bacteria (*figure 2B*). The initial C/N, C/P and N/P values, for leaves and roots, are shown in *table III*.

Regarding the mineralisation of POM in the sediment pools, the addition and degradation of *Spartina maritima* enhanced the mineralisation of carbon, nitrogen and phosphorus, when compared to the bare bottom containers (*figure 3*). Mineralisation was also higher in the containers with *S. maritima* under oxic conditions. The highest mineralisation occurred when plant material and macrofauna, meiofauna and bacteria were present. Nitrogen mineralisation increased from anoxic to oxic conditions and with the increase of fauna complexity.

Table III. *Spartina maritima* initial C/N, C/P and N/P value in leaves and roots.

Spartina maritima	C/N	C/P	N/P
Leaves	16.22	94.92	5.85
Roots	24.54	78.58	3.24

Considering mineralisation on a mass balance scale, very different amounts of mineralised dissolved nutrients appear in the water column during the experiment. Under oxic conditions, organic carbon and nitrogen concentrations were lower at the end of the experiment (*figure 4A, B*), while phosphorus to some extent was reformed as phosphate in the water-phase (*figure 4C*). Regarding nitrogen mass balance in the water-phase, results show that in the anoxic experiments, all mineralised sediment particulate organic nitrogen and plant component nitrogen were re-found as an increase

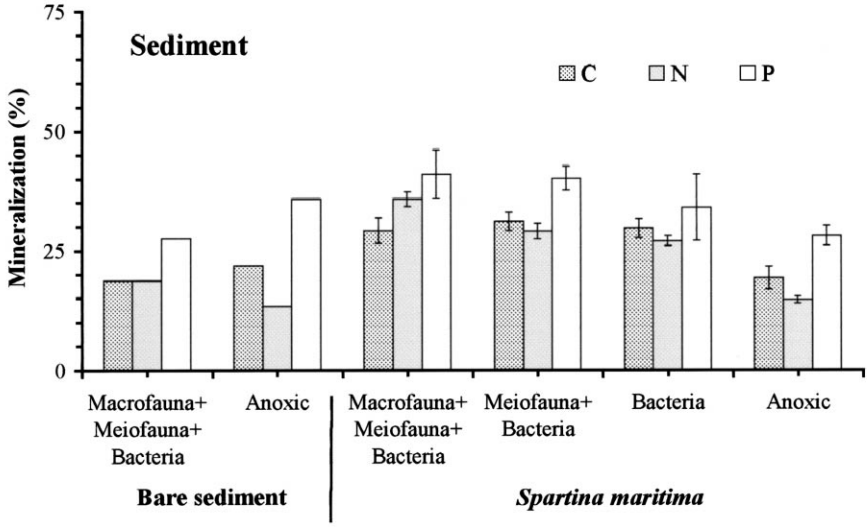

Figure 3. Comparison of the initial percentage of POM in the sediment mineralised, during 99 d, in bare bottom and in presence of *Spartina maritima*, and in the presence of bacteria only under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna (mean ± standard deviation, $n = 3$).

in the ammonia pool (*figure 5A*); while in the oxic experiments, there was an increase in the nitrate pool (*figure 5B*). The highest nitrate concentrations were found in the containers with bacteria, meiofauna and macrofauna. At the end of the experiment and regarding phosphorus mass balance in the water-phase, concentrations in the water column clearly increased (*figure 5C*).

The highest nitrification processes occurred when macrofauna, meiofauna and bacteria were present (*figure 5B*). This increase in nitrate production may allow denitrification to take place. In fact, denitrification rates were much higher under aerobic conditions and in the presence of the three fauna levels (*figure 6*). Considering the relative denitrification rates, it is clear that it was higher in the experiments with *S. maritima*, and that it increases with the increase of fauna complexity (*figure 7*). In the anoxic experiment with plant material, the not-shown values corresponded to negative denitrification rates that will be discussed further.

4. DISCUSSION

For the same period of time (99 d), although microbial activity was responsible for at least 67 % of *Spartina maritima* degradation, the increase in fauna complexity increased the degradation process. In fact, macrofauna detritus feeding activity may change the microbial flora and stimulate the microbial activity [21]. In this experiment, macrofauna species, such as *Hydrobia ulvae*, might by their feeding activity on leaves' surfaces [3] contribute to the fragmentation of the plant material and stimulate the microbial activity. Moreover, meiofauna may also enhance the use of detritus by macrofauna [21]. The role of macrofauna in root degradation is not well defined, probably because most of the individuals belong to the epibenthic groups and roots were placed at 3 cm depth. Nevertheless, the presence of meiofauna enhanced the degradation of roots by 9 %. The higher bacterial degradation recorded under anoxic conditions (without cyclohexamide), may result from the presence of anaerobic flagellates, that could enhance the degradation processes by 5 %, when compared to the aerobic microbial degradation for the same period of time.

Although it seems that in the initial stages of decomposition the impact of meiofauna may be negligible, it tends to increase in the course of time [21]. In fact, the highest mineralisation rate of *Spartina* leaves occurred when macrofauna, meiofauna and bacteria were present, and in root material, mineralisation rates were slightly higher in the presence of meiofauna. It seems that meiofauna and macrofauna do not compete for bacteria as food resource since meiofauna species are able to support a bacterial production, by recycling nutrients and inducing their activity [4]. Furthermore, micro-organisms' activity may enrich the nutrient palatability and nutrient quality of leaf litter for macro-invertebrate consumption [10]. Other studies showed that polychaetes can incorporate significantly more carbon from detritus of *Spartina* and *Zostera* when meiofauna is present [21].

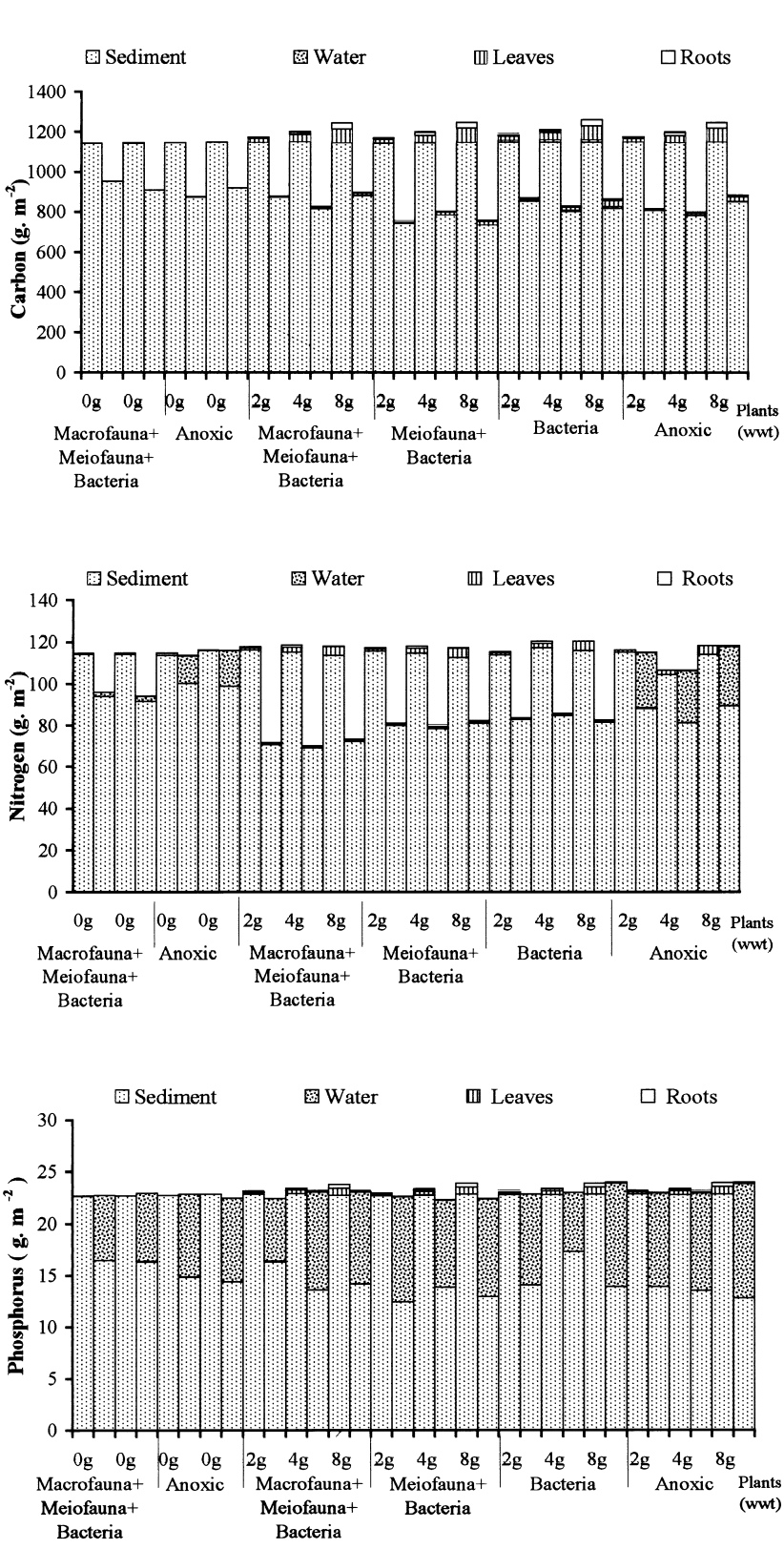

Figure 4. Mass balance of carbon, nitrogen and phosphorus in bare bottom and in presence of *Sparina maritima*, and in the presence of bacteria only under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna. The two bars per experiment represent the initial and final amounts of the element in the sediment, water column and plant material, respectively. A: Carbon; B: nitrogen; C: phosphorus.

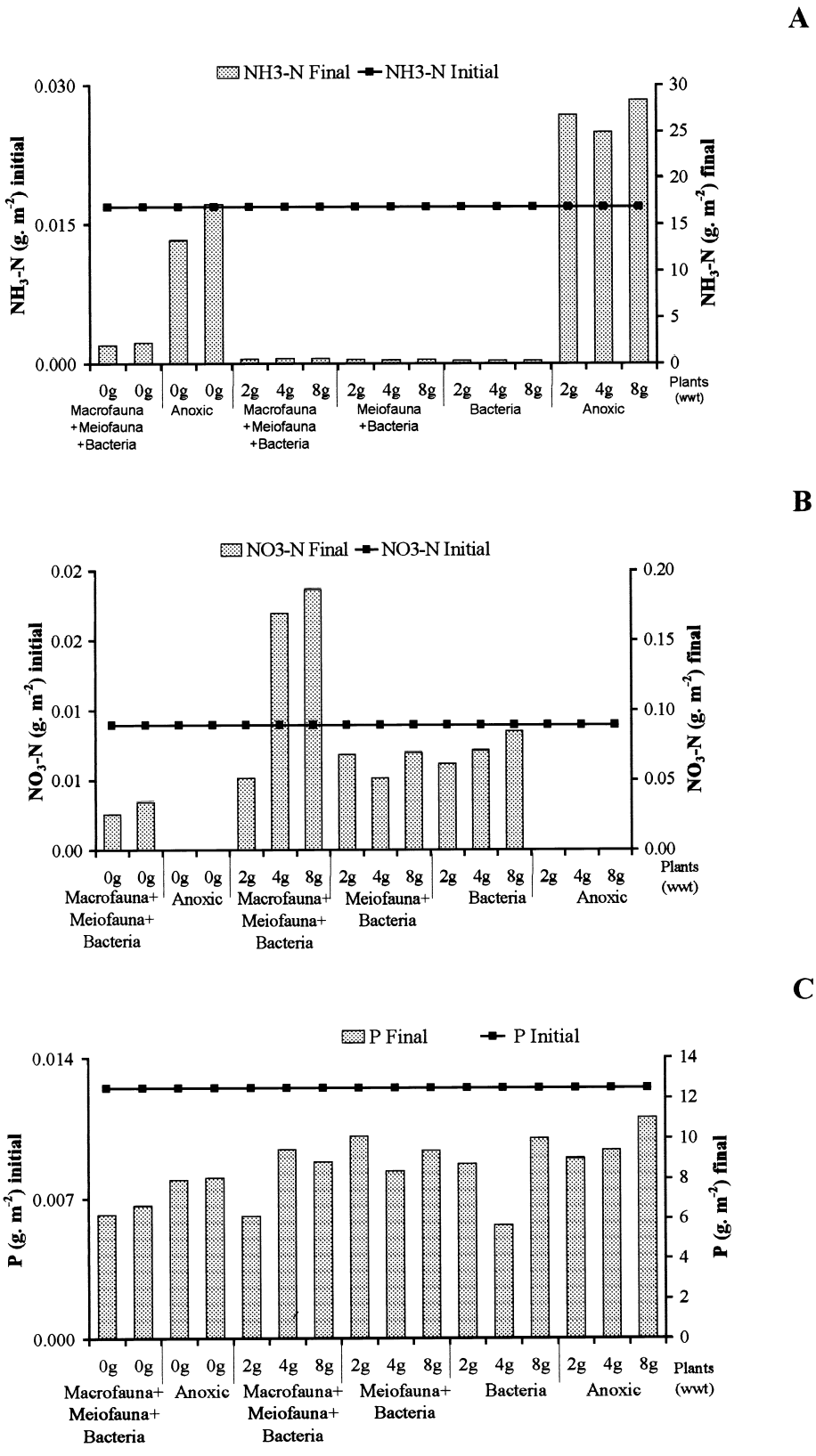

Figure 5. Nitrogen and phosphorus mass balance in the water-phase, in bare bottom and in presence of *Spartina maritima*, and in the presence of just bacteria under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna. The line and the bar per experiment represent, respectively, the initial and final amounts of the element. A: Ammonia; B: nitrate; C: phosphorus.

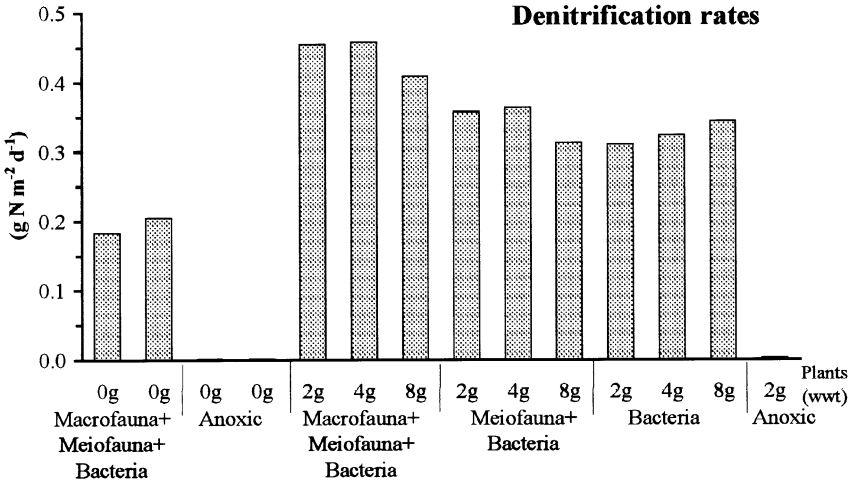

Figure 6. Denitrification rates during the experiments in bare bottom and in presence of *Spartina maritima*, and in the presence of bacteria only under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna.

Although, bacteria are the first catabolisers of organic matter [10], benthic macrofauna feeds on detritus formed by bacterial decomposition activity and both macrofauna and meiofauna may feed directly on bacteria [4].

The faster mineralisation of N and P can be related to the fact that the initial C/N and C/P ratio of the leachate were low [7]. This is a general tendency, because most of the phosphorus is present in the intracellular plant part as ATP, RNA and DNA, and most of the nitrogen is found in the protein pool. All these substances are among the easy leaching components when the plant dies. Although the percentage of

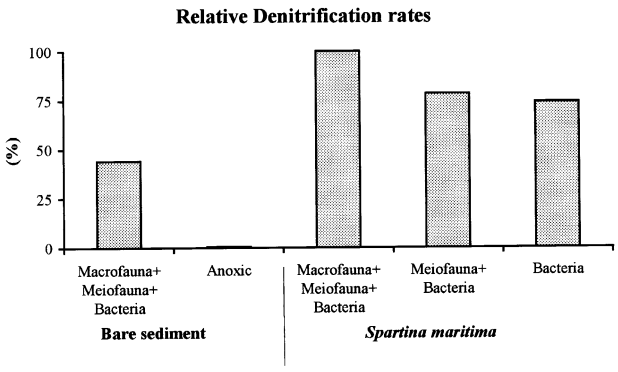

Figure 7. Relative denitrification rates during the experiments in bare bottom and in presence of *Spartina maritima*, and in the presence of bacteria only under anoxic and oxic conditions, bacteria and meiofauna, and bacteria, meiofauna and macrofauna.

S. maritima biomass remaining was much higher in a litter bag field study, the percentage of initial nitrogen and phosphorus mineralised, for the same period is comparable [19]. Several authors have considered that the degradability of plant material is directly proportional to the nitrogen content [9, 12], and mentioned that, during the early mineralisation of plant materials, more nitrogen than carbon is retained, through the action of aerobic micro-organisms [12].

It is well known that decomposition of particulate organic matter is faster under aerobic conditions. It was therefore an open question if the non-degraded plant material, instead of being mineralised, fertilised the sediment organic pool as detritus. As a net result, this did not happen either in the oxic or the anoxic experiment. Sediment organic pools were also mineralised during the experiment and the addition of *S. maritima* positively affected the mineralisation of sediment carbon and nitrogen, as well as the presence of macrofauna, meiofauna and bacteria. These results are consistent with results from other authors, although fauna was not considered [7].

Considering mineralisation on a mass balance scale, very different amounts of mineralised dissolved nutrients appear in the water column. At the end of the experiment, organic carbon and nitrogen presented lower concentrations in the water column, while phosphorus to some extent was reformed as phosphate in the water-phase. Considering Valiela [21], phosphate is mainly regenerated by the decay of particulate organic phosphorus and by animals. In addition, their concentration in water and sediments is to a very large

extent determined by biological activity. Microbe and animal activity can control phosphorus distribution and dynamics, because biological activity can change the redox potential of the sediments and hence, the chemical adsorption properties for phosphorus. Regarding nitrogen, in the anoxic experiments, all mineralised sediment particulate organic nitrogen and plant component nitrogen were found as an increase in the ammonia pool, that diffused upward to the overlying water, and it was more abundant than in aerobic situations. Although the concentration of dissolved inorganic nitrogen was higher in the anaerobic systems, the mineralisation rate of the nitrogen pool was higher in the oxic experiment. This is due to an uncoupling of nitrification and denitrification in the anaerobic systems, which results in high concentrations of ammonia [6, 11]. In the oxic systems, the ammonification supplied the subsequent nitrification and denitrification, and hence, the mineralised nitrogen was transformed to N_2 and lost. This pathway is considered as an important way to export nitrogen, when denitrification rates in salt marshes exceed nitrogen fixation [22]. In this study, the highest nitrification processes occurred when both macrofauna and meiofauna were also present, probably as a result of a better oxygen supply due to bioturbation, better carbon source or higher ammonia concentration. Since, bacterial growth takes place on DOC from the surface water or the sediment porewater [21], in aerobic sediments, most of the ammonium is released near the sediment surface, resulting from the decay and deposition of organic matter in the upper part of the sediment. In this experiment, benthic macrofauna were more abundant near the sediment surface, and their excretions probably contributed to high ammonium concentrations in the upper layers of the sediment [21]. Moreover, nitrifying bacteria convert the ammonium into nitrate, and the feeding activity of the benthos (bioturbation) increases the transport of nitrate down into the deeper anoxic part of the sediment where the denitrification takes place [8, 21]. These may be the reason why denitrification rates were much higher under aerobic conditions and in the presence of macrofauna. These results are probably due to the fact that nitrification was inhibited in the anoxic experiments, and that the only denitrification that took place was the nitrate respiration of the initial nitrate concentration present in the estuarine water. In the anoxic experiment, the negative denitrification could be interpreted as an ongoing nitrogen fixation but, as there are high concentrations of ammonium available that could easily be available as nitrogen source, this result should probably not be taken under consideration since it may result from inadequate methodology.

The present study suggests that macrofauna and meiofauna have an important role in the ecosystem nutrient flux and that fauna might function as a sink for excess nutrients, that otherwise would be exported to coastal waters.

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