# Decomposition of *Spartina anglica, Elytrigia pungens* and *Halimione portulacoides* in a Dutch salt marsh in association with faunal and habitat influences

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**Abstract**

Decomposition of *Spartina anglica, Elytrigia pungens* and *Halimione portulacoides* was studied for 20.5 months in situ in two habitats on a salt marsh in The SW Netherlands. Litter bags of three different mesh sizes were used to exclude meio- and/or macrofauna. The middle-marsh habitat was flooded more frequently than the plant-debris habitat in the highest marsh zone. Decomposition of the three species followed an exponential pattern of decay: instantaneous decay rates varied from 0.0026 to 0.0054 per day. Decay rates were significantly influenced by habitat factors and fauna, while there was a significant interaction between plant species and habitat. In case of a significant meio- and/or macrofauna effect, this became noticeable 12–16 weeks after the start of decomposition and resulted in a difference of 5–10% ash-free dry weight remaining after 20.5 months. Nematodes were the dominant microfaunal group in the plant litter. Densities were influenced by habitat conditions but not by resource quality, season and meio- and/or macrofauna. Only initial C/N and C/P ratios were correlated with differences in decomposition rates between the plant species. During the later stages of decomposition N and P concentrations of the plant litter were higher in the plant-debris habitat than in the middle-marsh habitat, probably as a result of fluctuating detritivores densities. The course of the decomposition process differed per plant species and per habitat. The results of this study underline the importance of knowledge of long-term decomposition rates.

## Introduction

Temperate salt marshes are considered to be among the worlds' most productive natural plant communities (Odum, 1971; Long & Mason, 1983). In North America, many studies have appeared on the production and decomposition of salt-marsh plants (Teal, 1962; see reviews by Turner, 1976; Pomeroy & Wiegert, 1981; Nixon, 1980; Marinucci, 1982). Since many American estuaries have become heavily industrialized, decomposition processes of marsh-plant detritus have received special attention because of reported PCB and heavy metal accumulation in plant litter (Pellenbarg, 1978; Breteler & Teal, 1981; Drifmeyer & Rublee, 1981; Marinucci, 1982; Marinucci & Bartha, 1982a).

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In contrast to North America, primary production and energy flow within European salt marshes have been investigated in a few cases only (Hussey & Long, 1982; Wolff *et al.*, 1979; Groenendijk, 1984). European information on decomposition of halophytes is even more rare (Hussey, 1980). Results of studies in North America have only limited significance for European marshes because of floristic differences (Chapman, 1974), and differences in geomorphological features and tidal regimes. On the other hand there is a great lack of information on European salt marsh functioning (Long & Mason, 1983), while according to a recent inventory of the Council of Europe member states many of these salt marshes are strongly threatened as a result of man's activities (Dijkema *et al.*, in press).

In the absence of large herbivores, only a few percent of the aboveground plant production of North American salt marshes is assumed to be consumed as live tissue (Teal, 1962). This probably also applies to most European salt marshes. The majority of the plant material becomes detritus which is either washed out of the marsh by tidal action or decomposes on the marsh surface. Literature data on the quantities of exported organic matter out of the marshes greatly vary (Nixon, 1980). According to Gallagher *et al.* (1980) this variation is mainly caused by differences in hydrological regime and other characteristics of the sites. However, in cases of a net export of aboveground production it seems that mainly fine particulate organic matter is transported out of the marsh. For a salt-marsh-dominated estuarine ecosystem in South Carolina, Dame (1982) found that less than 1% of the aboveground production was exported as floating macrodetritus from the marshes through the creeks to the Atlantic Ocean. For the Stroodorpepolder salt marsh in the Oosterschelde (SW Netherlands) Wolff *et al.* (1979) estimated indirectly that by storm tides at most 10% of the aboveground production is washed from the marsh and piled up against the bordering sea wall. For the Dollard marshes in the N Netherlands Dijkema & Dankers (1983) estimated that 5-6% of the aboveground production is exported to the sea walls by storm tides. It seems clear that large amounts of macrodetritus remain in the marsh to be decomposed in situ.

In Dutch salt marshes the aboveground biomass of a number of dominant halophytes dies back in part from November onwards. However, when winter is mild, like in 1979/1980, the plants are still predominantly green in early spring. The bulk of the dead plant parts becomes separated from the stems or culms in March and April. This often takes place during one or more storm tides. During such perturbations dead plant material is relocated over the middle marsh and deposited in belts on the higher parts of the marsh along the edge of the bordering sea wall (marsh zonation terminology follows Long & Mason, 1983). The surface of the middle marsh and the plant-debris belts on the higher-marsh locations are the main terrestrial habitats in which decay of plant litter occurs. Dead plant material can be found in these locations the whole year round.

Locally the rates of decay depend on environmental characteristics (e.g. flooding), the composition of the decomposer community (bacteria and fungi, micro-, meio- and macrofauna), and the nature of the plant material (plant morphology, chemical composition of the plant tissues) (Swift *et al.*, 1979; Lee, 1980; Marinucci, 1982; Valiela *et al.*, 1982; Long & Mason, 1983).

This paper reports on the history of in situ decomposition of aboveground material of the grasses *Spartina anglica* Hubbard and *Elytrigia pungens* (Pers.) Tutin (=*Elymus pycnanthus* (Godron) Melderis) and the dwarf shrub *Halimione portulacoides* (L.) Aellen, three dominant halophytes of estuarine salt marshes in SW Netherlands. This was achieved by measuring from early spring onwards decomposition rates, changes in chemical composition of the detritus, and the effects of site differences and of different faunal groups on decomposition rates. Abundance patterns of the major faunal groups in decaying plant material were monitored over the 20.5-month study period.

## The study area

The study area is situated in front of the Stroodorpepolder along the Oosterschelde, 15 km W of Bergen op Zoom (SW Netherlands). The marsh measures ca 30 ha and is situated between high tide level at neap tides and that at spring tides. It is backed by a sea wall, and extensive mud flats are

lying in front of it. The mean tidal range is about 375 cm. The salinity of the Oosterschelde water is about 25 to 30‰ *S*.

Four main vegetation types can be distinguished on the marsh: 1. a *Spartina anglica* vegetation on the lower marsh and the lowest parts of the middle marsh, completely dominated by this grass species; 2. a relatively species-rich vegetation dominated by *Triglochin maritima, Puccinellia maritima* and *Limonium vulgare* on the middle marsh; 3. a dense *Halimione portulacoides* vegetation also on the middle marsh, but on the creek levees raised above the adjacent marsh flat; 4. an *Elytrigia pungens* vegetation on the highest creek levees. There is no proper higher marsh zone. Apart from the creek levees, the middle marsh reaches its highest level near the sea wall, where in an about 10 m wide zone plant-debris belts are deposited. The debris belts are maximal 40 cm thick and about 80 cm wide.

## Material and methods

Experiments were carried out in a *Triglochin–Puccinellia–Limonium* vegetation, further indicated as M (marsh) habitat, and in the debris-belt zone, further indicated as PD (plant-debris) habitat. Flooding frequences at the two locations were determined by measuring the M and PD elevation level and using readings taken from a water-level recorder operating permanently in the Oosterschelde estuary nearby the salt marsh.

Decomposition of the plant material was studied using the litter bag technique (Mason, 1977; Swift *et al.*, 1979). Even though this technique has deficiencies, one of its greatest benefits is that it allows a manipulative approach. Ketner (1972) and Hussey (1980) found that for decomposition studies in a salt marsh environment this technique is preferable to the paired-plots method (Wiegert & Evans, 1964).

Standing live and partly dead plant material was collected from the marsh early in March 1980. *Spartina* and *Elytrigia* material was clipped near ground level, *Halimione* material about 5 cm above the ground to exclude the thick, woody stem parts. *Halimione* leaves die back from midsummer onwards, however, the bulk of the leaves dies in spring. Thus, collected *Halimione* material consisted of dead and partly dead leaves and stems as well as living stems. The plant material was brought to the laboratory, washed with tap water and oven-dried for one week at 40 °C. About 20 g of dried plant material was cut into 20 cm sections and placed into 20 × 25 cm tagged and weighed nylon net litter bags. The bags were sewn shut with nylon thread and re-weighed; the exact weight of the enclosed material was obtained by subtraction. Additional replicate plant material was oven-dried at 80 °C to a constant weight to obtain 40–80 °C dry weight ratios allowing conversion of all data to 80 °C dry weight equivalents. Faunal effects on decomposition were investigated by using bags of three different mesh sizes to exclude certain portions of the fauna, grouped in terms of their body size (Swift *et al.*, 1979; Vossbrinck *et al.*, 1979). The sizes chosen were: 300 μm, 1 mm, and 1 mm with 0.5 cm perforations at an interspace of 3 cm. The coarsest mesh size allowed access of the entire soil and litter community: the microflora (fungi and bacteria) and the micro-, meio- and macrofauna. (The used classification of the fauna according to their body diameter was: microfauna 0.064–0.3 mm, meiofauna 0.3–1 mm, and macrofauna >1 mm (Swift *et al.*, 1979).) The medium sized mesh excluded the adult stages of the macrofauna and the fine mesh both the adult stages of the meio- and macrofauna.

### *Sampling*

In each of the two habitats 15 series of 27 litter bags were placed on 31 March 1980. The series were set out in rows with bags at 60 cm intervals. At least a 2 m border was left around each series. All bags were fastened to the soil surface with nails to prevent them from being washed away. In the PD habitat plant debris was re-installed on top of the bags. On 15 subsequent dates at each location one series of bags, with three replicates of each plant species and each mesh size, was collected at random. Until January 1981 samples were collected and brought to the laboratory every four weeks, thereafter every six weeks, and from May 1981 until November 1981 every 12 weeks. On every other sampling date and also on the last but one sampling date, the fauna was collected from the contents of one of the replicates of each litter bag type (18 altogether). In case the fauna was not collected, the bag

contents were transferred to a 300 μm mesh sieve (fine mesh bags) or a 1 mm mesh sieve (medium and coarse mesh bags) and gently rinsed with tap water for a few minutes until all adhering sediments were removed. Any root growth into the litter bags was removed. Visible animals were removed also. The plant litter was oven-dried at 80 °C for at least three days, weighed, ground in a rotary mill and chemically analyzed.

### *Fauna analysis*

To separate the fauna from the plant litter several methods were tried. However, none of these methods proved to be sufficiently accurate for all animal groups. Only handpicking gave satisfactory results, but this was time-consuming. In order to make sorting by hand easier a wet-sieving apparatus was designed for dividing litter plus fauna in three fractions (Wolf & Buth, 1981). The apparatus consists of three 'three-dimensional' sieves which fit into each other. The inner one is the coarsest sieve (1 mm mesh size), the outer one the finest sieve (64 μm mesh size). The contents of a litter bag were placed in the inner sieve and after rinsing them with tap water for a few minutes litter plus fauna were divided over the three sieves. From the fraction in the inner sieve the macrofauna was collected by handpicking and stored in 5% formalin or 70% alcohol for identification and enumeration. The 0.3–1 mm and the 0.064–0.3 mm sized fractions (dry weight only a few mg) were preserved in 5% formalin completely. Meio- and microfauna of volumetrical subsamples were identified and enumerated with the aid of a binocular microscope. Animals were identified to Class, Order or Family level. Population densities were calculated as numbers of animals per gram dry weight of litter remaining in the bags at time of sampling. Only the most relevant faunal data in relation to decomposition are reported here. The plant material was handled as mentioned before.

### *Chemical analyses*

Samples for chemical analysis were kept at a workable number by analyzing pooled samples of three replicates of each kind of litter for each sampling date. Ash-free dry weight (AFDW) of the litter was calculated from net weight changes in re-dried subsamples, each of about 100 mg dry weight, combusted at 550 °C for 1 hr in a muffle furnace. Carbon was determined by gravimetric measurements of absorbed $CO_2$ after combustion with oxygen at 580 °C in a Coleman CH analyzer Model 33. Nitrogen was measured by semimicro-Kjeldahl digestion (Allen, 1974) and phosphorus by colorimetric analysis. Percent carbon, nitrogen and phosphorus were calculated on an ash-free dry weight basis. The C/N and C/P ratios were calculated by dividing percent carbon by percent nitrogen, c.q. percent phosphorus.

### *Data analysis*

Decomposition of the plant litter was measured as a function of organic weight loss from the litter bags. To compare the 18 decomposition curves overall decomposition rates were calculated by using the exponential decay model (first order decay function), $W_t = W_0\, e^{-kt}$, where $W_t$ is the weight of material left from the initial $W_0$ quantity after time $t$, $k$ is the decay constant (instantaneous decay rate) (Swift *et al.*, 1979; Wieder & Lang, 1982). The decay constants were calculated by fitting a linear regression to $\ln(W_t/W_0)$ by the least-squares method and the coefficients of determination ($r^2$) were calculated for each regression. The half-life was calculated using the equation $\ln 2/k = t_{1/2}$. The results were tested by an analysis of covariance (test for parallelism between the regression lines) and a factorial scheme with three variables.

## Results and discussion

### *Environmental factors*

The difference in elevation between the M and PD habitats was 44 cm, and flooding frequency during the sampling intervals ranged from 32–82% for the M and 0–35% for the PD habitat (Table 1). Inundation was always longer in the M habitat. Flooding frequency of the PD habitat was relatively high during winter and low during summer, while no seasonal pattern existed for the M habitat. A few months after the start of the experiment, especially in the M habitat, the litter bags became covered by a thin layer of sediment deposited during flooding. At the end of the experiment the last M bags were covered by a layer of 2–4 mm silty sediment. The PD bags became less covered by sediment. In the M habitat the litter bags were sheltered by a dense plant canopy from May till November–December, but during the winter months that plant canopy disappeared nearly completely. In the PD habitat large amounts of macrodetritus were sometimes deposited or replaced by tidal action, especially during winter and early spring.

Undoubtedly these specific circumstances caused distinctive differences in the physico-chemical environment determining the activities and distribution of decomposer organisms and the rate of

*Table 1.* Flooding frequencies of the two decomposition habitats on the salt marsh, calculated for the periods between litter bag sampling dates, from 1980-03-31 to 1981-10-26.

| Habitat | Relative flooding frequency, %[a] | |
|---|---|---|
| | Marsh | Plant-debris |
| Height of habitat cm + N.A.P.[b] | 216 | 260 |
| *Period* | | |
| M.31 - A.29 | 53.6 | 21.4 |
| A.30 - M.27 | 32.1 | 0 |
| M.28 - J.24 | 64.3 | 0 |
| J.25 J.22 | 75.0 | 17.9 |
| J.23 - A.19 | 64.3 | 3.6 |
| A.20 - S.16 | 71.4 | 21.4 |
| S.17 - O.14 | 82.1 | 28.6 |
| O.15 - N.11 | 57.1 | 10.7 |
| N.12 - D.9 | 71.4 | 35.7 |
| D.10 J.6 | 78.6 | 28.6 |
| J.7 - F.17 | 59.5 | 21.4 |
| F.18 - M.31 | 52.4 | 14.3 |
| A.1 - M.12 | 64.3 | 14.3 |
| M.13 - A.4 | 72.6 | 9.5 |
| A.5 - O.26 | 63.1 | 15.5 |

[a] Flooding frequency = No. of days that the habitat floods once or twice between sampling dates/total No. of days between sampling dates.

[b] Nieuw Amsterdams Peil, i.e. Dutch Ordnance Level, corresponding approximately with mean sea level.

decomposition in the two habitats (Kirby & Gosselink, 1976; Kruczynski *et al.*, 1979; Montagna & Ruber, 1980; Frasco & Good, 1982; Reice & Stiven, 1983). In the M habitat environmental conditions probably were more constant, while in the PD habitat debris belts could dry out completely for days or weeks. According to Gallagher *et al.* (1984) especially the moisture status, regulated by the frequency of wetting and drying, influences the respiration of most dead plant material. Changes in salinity seem less important. Besides tidal and meteorological events, the moisture status of dead plant material is also determined by shoot morphology and anatomy. They recorded different drying curves for dead material of different plant species.

*Decomposition rates*

Figure 1 shows the percentages AFDW remaining of the *Spartina, Elytrigia* and *Halimione* litter enclosed in the fine, medium and coarse mesh bags layed out in the M and PD habitat. Data points ($n = 3$) from the M litter bags had in most cases a standard deviation of 3-15%, at the last two sampling dates of 30%. About the same applies for PD, but SD values were in some cases as high as 60-95% (see also Table 5). The higher variability of weight loss of PD samples may be attributed to environmental fluctuations. The increasing variability in time for both habitats was probably caused by cumulative effects of microhabitat variation.

Decomposition of the plant material of all three species displayed a typical negative exponential course in both habitats. In general, decomposition was rapid during the first month, decreased during the first summer, was slow to nearly zero during the winter months, and increased again a little during the second summer, resulting in a 80-97% loss of AFDW after 20.5 months. Rapid initial decomposition is usually attributed to the physical process of leaching of water-soluble compounds (Swift *et al.*, 1979; Frasco & Good, 1982; McKee & Seneca, 1982). Habitat and animal effects were of no importance during this initial phase. However, *Halimione* decomposed significantly faster ($p < 0.05$) during this phase (AFDW loss about 38%) than the two grass species (AFDW loss 13-20%).

Table 2 shows the regression parameters calculated from the data presented in Figure 1, including the calculated half-life of the three plant litter types under the different circumstances. The high values of the correlation coefficient, $r^2$, and the highly significant $t_k$ values of the Student's $t$-test indicate a reasonable fit between the data and the negative exponential for all litter types. In most cases $r^2$ values are lower for the PD decomposition curves. The $r^2$ values for the *Halimione* decomposition curves are mostly lower than those for the two grass species. One by one comparison of the instantaneous decay rates per plant species, habitat and mesh bag type gave a significant difference in only five cases (Table 3). *Spartina* litter in fine mesh bags decomposed faster in the M habitat, while *Halimione* litter in coarse mesh bags decomposed faster in the PD habitat. In the PD habitat *Spartina* litter decomposed faster in coarse mesh bags than in fine mesh bags, while in the M habitat *Elytrigia* litter decomposed faster in medium and coarse mesh bags than in fine mesh bags.

The variables and the interactions between them were also tested by a factorial analysis on the half-

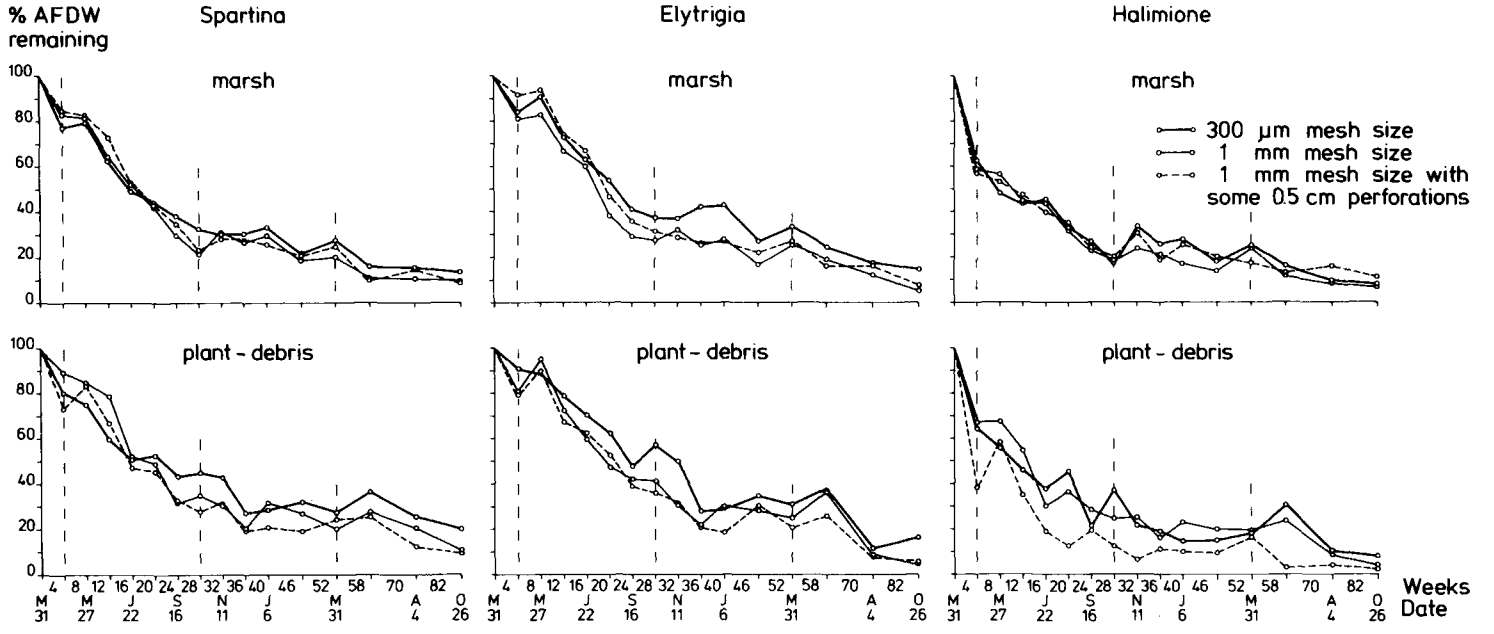


*Fig. 1.* Relative changes in ash-free dry weights (AFDW) of decomposing *Spartina, Elytrigia* and *Halimione* litter in litter bags of three different mesh sizes layed out in two salt marsh habitats during 82 weeks, from 1980-03-31 to 1981-10-26. Each point represents the average of triplicate treatments. Vertical dashed lines indicate different decomposition periods.

*Table 2.* Summary of a first-order decay analysis of organic weight loss of three species of plant litter in fine, medium and coarse mesh litter bags in two salt-marsh habitats.

| Species | Habitat Litter bag | $k \times 10^{-4}$ (day$^{-1}$) | Half-life (days) | $r^2$ | $t_k$[a] |
|---|---|---|---|---|---|
| *Spartina* | marsh | | | | |
| | fine | 35 | 198.0 | 0.92 | 13.2 |
| | medium | 42 | 162.9 | 0.90 | 11.7 |
| | coarse | 42 | 165.1 | 0.90 | 10.9 |
| | plant-debris | | | | |
| | fine | 26 | 270.5 | 0.85 | 8.6 |
| | medium | 35 | 195.6 | 0.85 | 8.9 |
| | coarse | 38 | 180.6 | 0.88 | 10.0 |
| *Elytrigia* | marsh | | | | |
| | fine | 33 | 207.2 | 0.94 | 15.1 |
| | medium | 46 | 149.7 | 0.92 | 12.5 |
| | coarse | 43 | 161.8 | 0.92 | 13.7 |
| | plant-debris | | | | |
| | fine | 35 | 198.0 | 0.88 | 10.3 |
| | medium | 47 | 147.9 | 0.86 | 9.6 |
| | coarse | 48 | 143.5 | 0.92 | 12.3 |
| *Halimione* | marsh | | | | |
| | fine | 36 | 189.1 | 0.86 | 9.3 |
| | medium | 40 | 170.8 | 0.86 | 9.8 |
| | coarse | 33 | 209.9 | 0.83 | 8.2 |
| | plant-debris | | | | |
| | fine | 37 | 187.0 | 0.77 | 7.1 |
| | medium | 44 | 156.0 | 0.86 | 9.9 |
| | coarse | 54 | 127.6 | 0.79 | 7.2 |

Note: $r^2$ is the coefficient of determination, $t_k$ is the test value for significance of regression, $k$ is the decay constant.

[a] All $t_k$ values are highly significant ($p < 0.001$).

*Table 3.* Analysis of covariance of the instantaneous decay rates listed in Table 2. (M is marsh, PD is plant-debris habitat).

| Objects | | | | F | df 1 | df 2 | |
|---|---|---|---|---|---|---|---|
| *Plant species* | | | | | | | |
| for the species per bag type and habitat | | | | | | | ns |
| *Habitat* | | | | | | | |
| *Spartina* | | | | | | | |
| M | fine | - PD | fine | 5.538 | 1 | 28 | * |
| | medium | - | medium | 1.742 | 1 | 28 | ns |
| | coarse | - | coarse | 0.435 | 1 | 28 | ns |
| *Elytrigia* for all bag types | | | | | | | ns |
| *Halimione* | | | | | | | |
| M | fine | - PD | fine | 3.019 | 1 | 28 | ns |
| | medium | - | medium | 0.397 | 1 | 28 | ns |
| | coarse | - | coarse | 6.173 | 1 | 28 | * |
| *Bag type* | | | | | | | |
| *Spartina* M for all bag types | | | | | | | ns |
| *Spartina* | | | | | | | |
| PD | fine | - PD | medium | 3.880 | 1 | 28 | ns |
| | medium | - | coarse | 0.280 | 1 | 28 | ns |
| | fine | - | coarse | 6.894 | 1 | 28 | * |
| *Elytrigia* | | | | | | | |
| M | fine | - M | medium | 8.895 | 1 | 28 | ** |
| | medium | - | coarse | 0.511 | 1 | 28 | ns |
| | fine | - | coarse | 5.972 | 1 | 28 | * |
| *Elytrigia* PD for all bag types | | | | | | | ns |
| *Halimione* M and PD for all bag types | | | | | | | ns |

* $P$ 0.05; ** $p < 0.01$; ns = not significant.

*Table 4.* Factorial analysis on the half-life data listed in Table 2.

| Variable | SS | df | var | F | |
|---|---|---|---|---|---|
| Species | 2538.00 | 2 | 1269.00 | 5.580 | ns |
| Habitat | 3.25 | 1 | 3.25 | 0.014 | ns |
| Bag type | 7756.00 | 2 | 3878.00 | 17.050 | *** |
| Species × habitat | 4209.00 | 2 | 2104.00 | 9.254 | * |
| Species × bag type | 1080.00 | 4 | 270.00 | 1.187 | ns |
| Habitat × bag type | 1872.00 | 2 | 936.20 | 4.117 | ns |
| Exp. error | 909.60 | 4 | 227.40 | | |

* $p < 0.05$; *** $p < 0.001$; ns = not significant.

life data (Table 4). There was a significant difference between the mesh bag types. The significant interactions between plant species and habitats are illustrated by Figure 2. Decomposition of *Spartina* litter was much slower in the PD habitat than in the M habitat, for *Halimione* it was the reverse. Habitat differences seem to be less important for the decomposition of *Elytrigia* litter.

Effect of detritivores in the decomposition process could be the increase in the surface-volume ratio of particles through comminution during feeding, regulating growth and population structure of the microbial community by grazing pressures, or redistribution of microbial inoculum because of their locomoter activities (Lopez *et al.*, 1977; Swift *et al.*, 1979; Lee, 1980). The results show that the use of litter bags of various mesh sizes to exclude different groups of animals from the de-

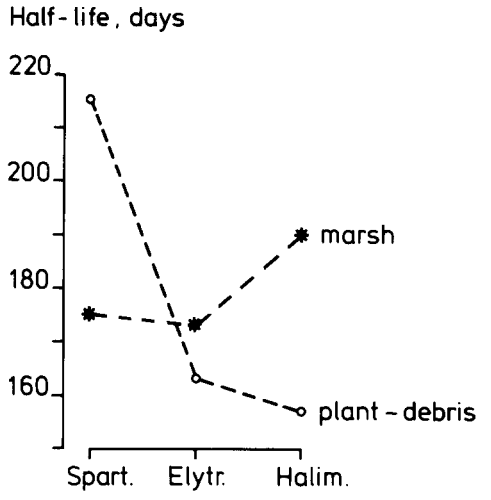


*Fig. 2.* The significant interaction between plant species and habitat. Values calculated from data listed in Table 2.

composition processes was justifiable. Extra loss of small particles from the medium and coarse bags only because of the greater mesh sizes was of no importance. In case of such an extra loss this would be especially noticeable in the more frequently flooded M habitat, however, the *Spartina* and *Halimione* M curves show a more or less interwoven pattern (Fig. 1). In general, meio- and macrofaunal impact on decomposition rates does not seem to be of major importance. Factorial analysis (Table 4) showed a significant mesh bag effect. However, tested separately (Table 3), only decomposition of *Elytrigia* in the M habitat and of *Spartina* in the PD habitat was significantly accelerated by meiofaunal or meio- plus macrofaunal influences, resulting in a difference of respectively 8% and 10% remaining AFDW after 82 weeks. The presence of macrofauna seemed to be of minor importance for decomposition of the two grass species (Fig. 1). Considering the course of the PD decomposition curves and the sometimes high PD data variability, which caused lack of significance, meio- and/or macrofauna also seemed to have some impact (5–10%) on the decomposition of *Elytrigia* and *Halimione* litter in the PD habitat. For *Halimione* this was indirectly indicated by the significant difference between the instantaneous decay rates of the litter in the M and PD coarse mesh bags (Table 3). Macrofaunal impact seemed to be of some importance for decomposition of *Halimione* litter in the PD habitat. Meio- and macrofaunal impact on decomposition of *Spartina* and *Elytrigia* litter was probably initially very small and did not become noticeable until 16 weeks after the start of the decomposition processes (Fig. 1). For *Halimione* litter in the PD habitat macrofaunal impact was presumably of importance earlier in the process of decay.

According to Tenore *et al.* (1982) litter of vascular marsh plants is only available to meio- and macro-detritivores after a certain period (i.e. months) of 'aging' and related bacterial and fungal activity causing nutritional enrichment of the detritus. In the literature data concerning influences of various groups of animals on in situ decomposition of salt-marsh plants are scarce (Lee, 1980). Reice & Stiven (1983) found that meio- and macrofauna did not have a major impact on the decomposition rates of *Spartina alterniflora* in a North Carolina salt marsh. Valiela *et al.* (1982) reported, however, differences of 30–50% in the amount of remaining *Spartina alterniflora* material induced by macrofauna after about a year in litter bag experiments in a Massachusetts salt marsh. They also concluded that impact of macro-detritivores was initially small but increased in the course of time.

Factorial analysis did not show a significant habitat effect (Table 4), but in combination with plant species there were differences in decomposition rates (Fig. 2). *Spartina* litter without meio- and macrofaunal influences (fine mesh bags) decomposed at a slower rate, and *Halimione* litter under the most natural circumstances (coarse mesh bags) at a faster rate in the PD than in the M habitat. The relatively modest role of meio- and macrofauna in the decomposition processes (see also Reice & Stiven, 1983) suggests that the action of microflora and -fauna as well as physical and chemical factors are far more important. Notably the moisture fluctuations in the PD habitat are probably less favourable for microbial activity, especially during the summer. Only decomposition of *Spartina* litter was strongly inhibited by these less optimal environmental conditions (fine bags), though, this was partly compensated by the greater meio- and macrofaunal impact in the PD habitat (medium and coarse bags). But also under the most natural conditions (coarse bags) *Spartina* seemed to decompose at a slower rate in the PD habitat (Table 2). Decomposition of *Halimione* and *Elytrigia* litter

(fine bags) was not inhibited by the environmental conditions in the PD habitat. Because of the greater macrofaunal impact *Halimione* litter decomposed even at a faster rate in the PD habitat (coarse bags) than in the M habitat.

Several studies have focused on spatial variations in decomposition rates, but nearly all only concern *Spartina* species (e.g. *S. alterniflora*). Lower decomposition rates of *Spartina* litter situated higher in the tidal range were found by Kirby & Gosselink (1976), Frasco & Good (1982), Marinucci & Bartha (1982), Valiela *et al.* (1982) and Reice & Stiven (1983), while Kirby & Gosselink (1976) and Reice & Stiven (1983) reported that differences in decay rates became smaller or disappeared in the course of the decomposition processes. Montagna & Ruber (1980) did not find tidal influences on *Spartina* decomposition rates. In all these studies no habitats similar to the PD habitat (extra meio- and macrofaunal impact) were included. Marinucci (1982) and Long & Mason (1983) have summarized half-life values for decomposition of *Spartina alterniflora* tissue from various litter bag studies in marshes on the east coast of the United States. For higher marsh locations values were 100–200 days, and for mid-and lower-marsh locations 30–70 days. For *Spartina* litter in the present study these values are respectively 180 days (coarse mesh bags) and 165 days. Since size and configuration of *Spartina* species differ between marshes, and decomposition studies often differ in condition of the starting material and methods used, comparison of such data has only an indicative value.

So far, mainly overall decomposition rates were discussed. Dividing the period of decomposition in artificially chosen time spans gives a better understanding of the course of the processes. The vertical dashed lines in Figure 1 divide the curves in four parts corresponding with the leaching-dominated period, the first summer period, the winter period and the second summer period. For clarity the means of the remaining percentages AFDW and standard deviations of the medium mesh bags contents at the end of these four periods are given in Table 5. Instantaneous decay rates for these four periods did not differ significantly in all cases. However, considering the course of all the decomposition curves and the consistent pattern in differences between habitats per plant species, it is probably that differences in habitat impact on decomposition change per period. During the first 4 weeks habitat impact did not cause differences in decomposition rates. At the end of the first summer PD decomposition rates lagged behind the M ones for all plant species. However, at the end of the winter period they were approximately equal again. During the second summer decomposition rates again did not differ between the habitats. Thus during the winter period decomposition in the PD habitat is catching up with decomposition in the M habitat. During the winter, decomposition rates were nearly zero in the M habitat, probably because of the low temperatures (temperature of the estuarine water during that period was 2.5–5 °C, mean monthly air temperature 2–10 °C above zero). In the PD habitat however, decompo-

*Table 5.* Means and standard deviations ($n = 3$) of percent remaining ash-free dry weight (AFDW) of *Spartina*, *Elytrigia* and *Halimione* litter in 1 mm mesh bags on the sampling dates indicated in Figure 2 by vertical dashed lines. Columns refer to % AFDW after 4, 28, 52 and 82 weeks respectively.

| Species<br>Habitat | 4 w | 28 w | 52 w | 82 w |
|---|---|---|---|---|
| *Spartina* | | | | |
| marsh | 82.4 ± 4.5 | 20.8 ± 1.8 | 20.0 ± 0.9 | 9.8 ± 2.1 |
| plant-debris | 88.4 ± 3.7 | 34.5 ± 9.7 | 19.9 ± 5.6 | 10.5 ± 6.2 |
| *Elytrigia* | | | | |
| marsh | 80.4 ± 1.9 | 27.3 ± 9.7 | 24.9 ± 1.7 | 4.5 ± 1.2 |
| plant-debris | 80.4 ± 6.5 | 41.3 ± 8.1 | 24.9 ± 7.9 | 4.5 ± 3.6 |
| *Halimione* | | | | |
| marsh | 58.4 ± 3.2 | 17.3 ± 1.4 | 24.1 ± 0.3 | 6.9 ± 1.9 |
| plant-debris | 66.5 ± 2.0 | 24.3 ± 0.6 | 18.1 ± 1.9 | 4.0 ± 3.8 |

sition continued slowly. The plant-debris belts were flooded more frequently (Table 1) and dried out more slowly, while interior temperatures were probably higher and more constant than air temperatures, similar to those in a compost heap.

As to the individual plant species, decomposition changed during the four periods. *Halimione* litter decomposed fastest during the first 4 weeks and *Spartina* litter at a slightly faster rate during the first summer (Fig. 1, Table 5). During the winter especially *Halimione* litter decomposed slowly in the PD habitat and during the second summer *Elytrigia* litter decomposed at the fastest rate. So, although at the end of the 20.5-month period remaining AFDWs of the different treatments did not differ much, there were distinct differences between species and habitats during the successive phases of decomposition.

Most litter decomposition studies described in the literature have been conducted for six months to one year. Considering the temporal patterns pointed out it can be doubted whether short-term results can be extrapolated. In this study for instance, after 12 months *Elytrigia* had the highest remaining AFDW values, but after 20.5 it had the lowest values. Mathematical models are often used for calculations of detritus half-life. However, as shown here and also by De Lyon *et al.* (1983), this can be erroneous when these moments are not situated within the time span of the experiments.

*Chemical changes*

Percents carbon content of the litter material remained essentially constant throughout the study period (Table 6). Differences in carbon content between the habitats and between the mesh bag types were insignificant.

Initial total nitrogen contents of *Halimione*, *Spartina* and *Elytrigia* litter were 2.13, 1.40 and 1.14% respectively. Figure 3 shows the changes in percentage nitrogen in the decomposing litter. Considering the interwoven pattern of the curves, it is safe to conclude that there were no differences between the mesh size types. Percentage nitrogen decreased during the first 4–8 weeks. Especially initial loss from *Halimione* litter was rapid. Thereafter nitrogen levels of the *Spartina* and *Elytrigia* litter increased in both habitats. Nitrogen content of *Halimione* litter in both habitats remained more or less constant until the 24th week and increased from then on. For all three plant species litter nitrogen content was mostly higher in the PD habitat after the 28th week. C/N ratios are summarized in Table 6. Initial differences between the litter material diminished in the course of time.

Initial phosphorus contents of *Halimione*, *Spartina*, and *Elytrigia* litter were 0.20, 0.18 and 0.11% respectively. These values declined more sharply than the nitrogen contents during the first 4 weeks (Fig. 4). Thereafter phosphorus contents showed similar changes as nitrogen contents: an increase in the *Spartina* and *Elytrigia* litter, a delayed increase in the *Halimione* litter, and for all species higher levels in the PD habitat from the 28th week onwards. For *Spartina* and *Elytrigia* litter there was no noticeable mesh bag effect, but *Halimione* litter in the fine mesh bags often had the highest phosphorus contents in both habitats. C/P ratios are summarized in Table 6. As with C/N ratios initial differences between plant species diminished in the course of the first summer.

It is often observed that after the rapid increase of the C/N and C/P ratios at the start of decomposition, which is due to differential loss of N and P relative to C, the concentrations of N and P increase over time (Odum & de la Cruz, 1967; Fenchel, 1970; de la Cruz, 1975; Josselyn & Mathieson, 1980; Kruczynski *et al.*, 1979; Marinucci & Bartha, 1982b). Although some nutrient increase may be partly due to preferential loss of carbon, changes are mainly attributed to an increase in the proportion of bacteria and fungi with time. Nutrient concentrations, particularly N concentration when C/N is greater than 20, are usually limiting factors to decomposer organisms (Swift *et al.*, 1979). P is probably less limiting than N to the rate of decomposition of halophytes (Marinucci *et al.*, 1983). The idea that the nutritional quality of detritus for decomposer organisms increases with increasing nitrogen content has recently been questioned (Rice & Tenore, 1981; Rice, 1982; Tenore *et al.*, 1982). Estimates of bacterial and fungal biomass showed that the living cells of these microbes account for only a minor part of the increase in N (Christian & Wetzel, 1978; Lee *et al.*, 1980). According to Rice (1982) increasing N is mainly due to proteinaceous materials exuded by microbes being bound to carbohydrates and phenolic plant constituents. During this humification process N is

*Table 6.* Summary of changes in the carbon concentration and the carbon to nitrogen, and carbon to phosphorus ratios (ash-free dry weight) and standard deviations of *Spartina, Elytrigia* and *Halimione* litter during decomposition in two salt-marsh habitats. Data represent averages of the fine, medium and coarse mesh bags. Each set of five values refer to measurements at 0, 4, 28, 52, and 82 weeks.

| Species<br>Habitat | Carbon<br>% AFDW | C/N ratio | C/P ratio |
|---|---|---|---|
| *Spartina* | | | |
| marsh | 47.36 ± 0.20 | 33.71 ± 0.03 | 270.90 ± 12.12 |
| | 47.30 ± 0.46 | 43.40 ± 6.12 | 515.98 ± 84.40 |
| | 49.40 ± 1.28 | 24.96 ± 0.39 | 274.44 ± 7.09 |
| | 47.13 ± 1.17 | 23.13 ± 1.95 | 249.68 ± 49.67 |
| | 50.23 ± 0.80 | 22.27 ± 2.70 | 272.37 ± 34.04 |
| plant-debris | 47.36 ± 0.20 | 33.71 ± 0.03 | 270.90 ± 12.12 |
| | 46.47 ± 1.36 | 40.46 ± 3.06 | 370.03 ± 40.12 |
| | 49.00 ± 1.74 | 23.30 ± 2.10 | 232.92 ± 34.32 |
| | 48.03 ± 1.93 | 18.44 ± 1.69 | 190.94 ± 27.86 |
| | 51.57 ± 0.50 | 16.24 ± 1.26 | 173.95 ± 5.15 |
| *Elytrigia* | | | |
| marsh | 47.66 ± 1.07 | 42.00 ± 1.20 | 433.31 ± 9.71 |
| | 48.90 ± 1.47 | 55.93 ± 11.39 | 676.94 ± 96.66 |
| | 48.23 ± 1.84 | 32.00 ± 7.65 | 296.69 ± 102.62 |
| | 46.60 ± 0.95 | 28.23 ± 2.34 | 282.71 ± 37.91 |
| | 49.83 ± 0.64 | 22.95 ± 0.89 | 228.04 ± 43.59 |
| plant-debris | 47.66 ± 1.07 | 42.00 ± 1.20 | 433.31 ± 9.71 |
| | 45.23 ± 1.53 | 45.56 ± 6.06 | 582.05 ± 117.20 |
| | 48.83 ± 0.93 | 29.12 ± 5.08 | 293.65 ± 55.45 |
| | 47.23 ± 1.03 | 20.10 ± 1.59 | 185.49 ± 22.38 |
| | 51.07 ± 0.42 | 16.73 ± 0.27 | 182.60 ± 26.65 |
| *Halimione* | | | |
| marsh | 47.40 ± 0.64 | 22.25 ± 0.20 | 237.00 ± 10.50 |
| | 50.03 ± 2.14 | 38.13 ± 2.06 | 405.84 ± 82.18 |
| | 48.77 ± 2.17 | 27.85 ± 3.52 | 274.02 ± 41.77 |
| | 51.27 ± 0.55 | 29.52 ± 3.81 | 275.32 ± 16.58 |
| | 50.43 ± 0.87 | 24.37 ± 1.93 | 253.92 ± 55.87 |
| plant-debris | 47.40 ± 0.64 | 22.25 ± 0.20 | 237.00 ± 10.50 |
| | 47.10 ± 0.55 | 31.81 ± 9.30 | 417.75 ± 97.87 |
| | 48.20 ± 3.11 | 26.88 ± 1.36 | 258.05 ± 9.52 |
| | 47.63 ± 2.16 | 20.92 ± 1.56 | 203.26 ± 32.59 |
| | 48.87 ± 3.78 | 18.53 ± 1.03 | 208.92 ± 27.55 |

gradually transformed to progressively less assimilable forms. For decomposition of halophytes the percentage N becomes probably a poor index of nitrogen availability after 20–30 days (Rice, pers. comm.). Marinucci *et al.* (1983) found a significant increase in overall decomposition rate of *Spartina alterniflora* litter when initial nitrogen levels were higher. In the present study *Halimione, Spartina* and *Elytrigia* litter differed in initial N and P content. Although besides C/N (and C/P) ratio other differences in the chemical and structural composition of the plant species may have affected initial decomposition (Swift *et al.*, 1979), maximum weight loss during the first 8 weeks of the study decreased in the order: *Halimione, Spartina, Elytrigia.* This corresponds with the order of initial C/N (and C/P) ratios from low to high. Probably not all of this weight loss was due to leaching; also microbial activities may have played a role. Fine mesh bags treated with an antibiotic showed lower initial weight losses than non-treated fine mesh bags (data not presented here), while in another decomposition experiment respiration rates of litter samples measured at weekly intervals showed a

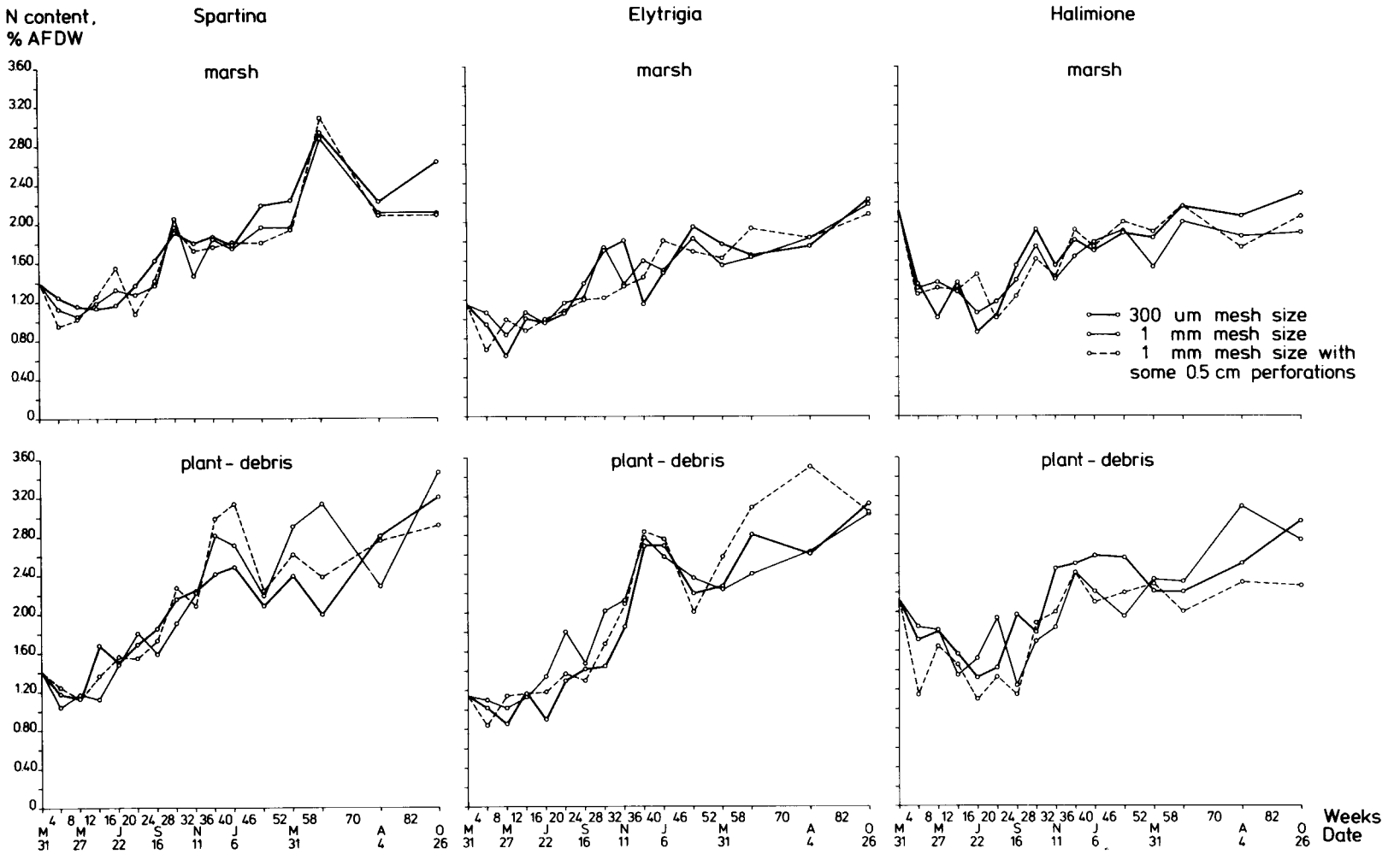


*Fig. 3.* Percent nitrogen content (ash-free dry weight) of material remaining in the mesh bags vs. time (weeks).

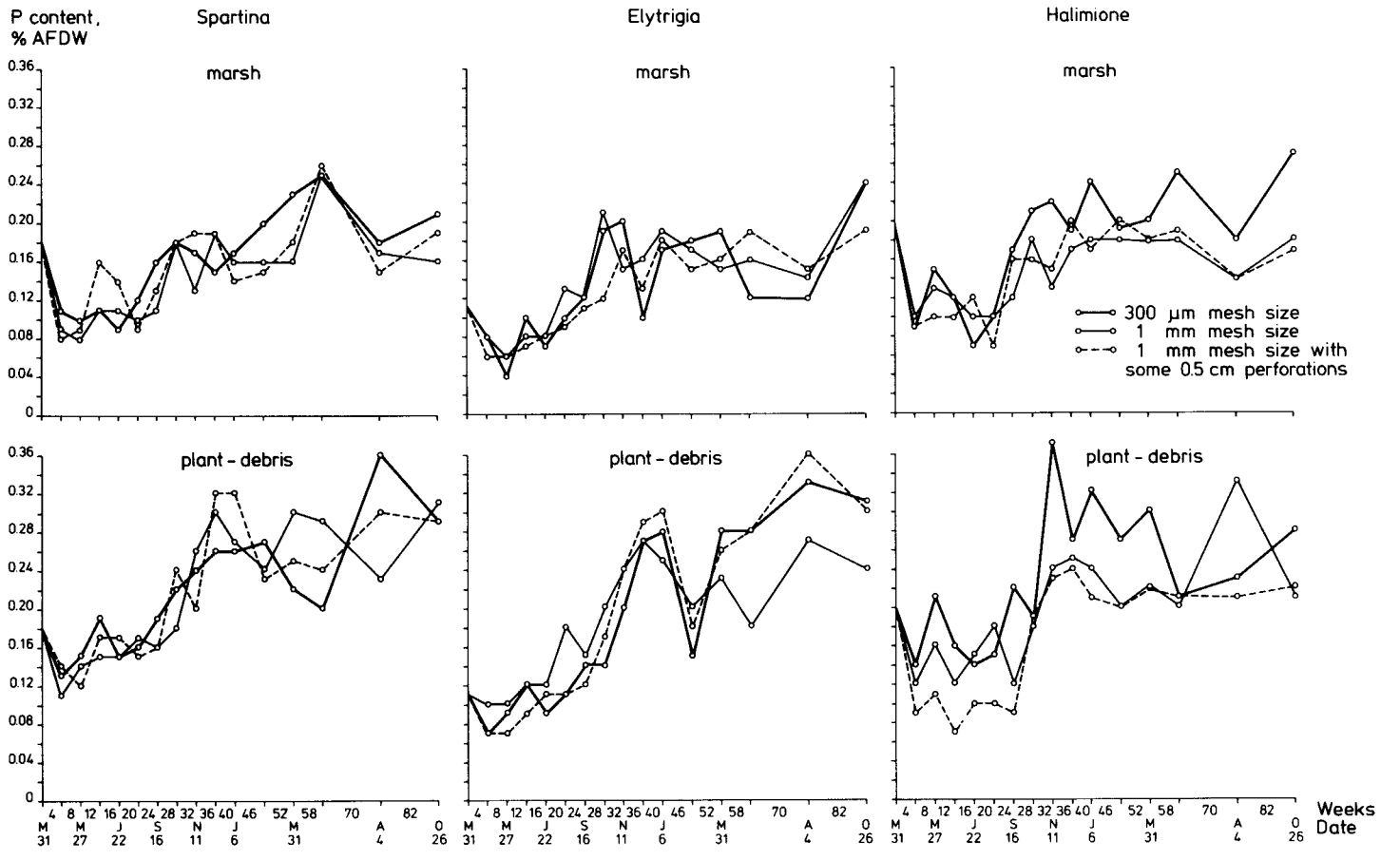


*Fig. 4.* Percent phosphorus content (ash-free dry weight) of material remaining in the mesh bags vs. time (weeks).

peak at two weeks after the experiment began (Buth, in prep.; Voesenek, unpubl.). Lee *et al.* (1980) and Marinucci *et al.* (1983) also found a rapid increase in respiration during the first weeks after the start of a *Spartina alterniflora* decomposition experiment.

The higher N and P content of the PD litter during the later stages of decomposition was probably caused by higher numbers of microbes, which could probably be reached because of lower flooding frequency. Less tidal flushing caused less removal of microbial biomass. Likewise, irregular desiccation reduced or eliminated populations of faunal grazers, which would in turn allow a larger total microbial biomass.

The delayed N and P increase in the *Halimione* litter may be caused by a difference in decomposability between leaves and stems. After 28 weeks, when the increase started, no leaf material could be distinguished in the litter anymore. Nutrient contents in the leaves were probably much higher than in the stems. It is possible that during decomposition net mineralization of N and P from leaves roughly balanced net immobilization of N and P from stems and when most leaf material was decomposed immobilization became dominant.

*Changes in microfauna*

Because decomposition rates of the three plant species are strongly determined by physical processes and activities of microflora, only the results of microfauna countings are given here.

With a mean percentage of 61.5% for all sampling dates, Nematodes formed the dominant group (Fig. 5). Other important groups were Oligochaeta (Annelida), Foraminiferida (Protozoa) and, only in the M habitat, Harpacticoida (Crustacea). Nematodes were present in high densities: hundreds to thousands per gram DW remaining in the litter bags (Fig. 6). Densities were neither influenced by plant species nor by meio- and macrofauna. However, there was a clear habitat effect. Densities fluctuated strongly in the PD habitat, while they remained relatively constant after an initial increase in the M habitat (Figs. 5 and 6). This indeed confirms the earlier supposition that irregular desiccation can reduce or eliminate faunal grazer densities and can eventually lead to higher microbial biomass values. Densities of other taxa were also influenced by habitat differences (Fig. 5).

A number of nematode samples from August, December and February were identified to genus or species level. According to Wieser (1959) marine nematodes can be divided into four groups of feeding types, based on the structure of their buccal cavities. The group of animals without a true buccal cavity, probably selective deposit feeders, was lacking or nearly lacking in both habitats. Between the other three groups, the non-selective deposit feeders, the epigrowth feeders and the predators, c.q. omnivores, there was no constant difference in dominancy. Nematode species composition differed temporally and spatially. For the Ems estuary in The N Netherlands Bouwman *et al.* (in press) found that nematodes with a non-selective way of feeding were dominant on the surface of decaying *Spartina anglica* material. He concluded that in the debris biotope, in contrast to the sediment biotope, this way of feeding is appropriate to survive because food is abundant and food organisms (bacteria) are hardly mixed with similar sized inedible particles.

After the colonization phase nematode densities did not show a relation to season or litter age. Total numbers of nematodes were decreasing proportionally to the decrease of DW. This indicates two possible mechanisms (Montagna & Ruber, 1980):

- The nematodes exist as a community, the size of which is regulated by quantitative and/or qualitative changes of the substrate available for decomposition.
- The substrate provides shelter or sites for attachment, regardless of nutrient contents.

It is not possible to conclude from these data whether either or both mechanisms apply. However, since nematodes are so abundant, they probably play a direct or indirect role in the decomposition of marsh plants (Lee, 1980). Activities of microfauna, and especially of nematodes, may improve the release of nutrients immobilized in fungal and bacterial tissues, eliminate fungiostasis and bacteriostasis, while bioturbation can improve oxygen penetration in the detritus and distribution of spores. Findlay & Tenore (1982) showed that nematodes increased mineralization of *Spartina* litter. Coull & Bell (1979) and Findlay & Tenore (1982) stated that nematodes are an important component of the decomposition subsystem of the salt-marsh ecosystem, because of their high abundancy and metabolic rates and their functioning at temporal

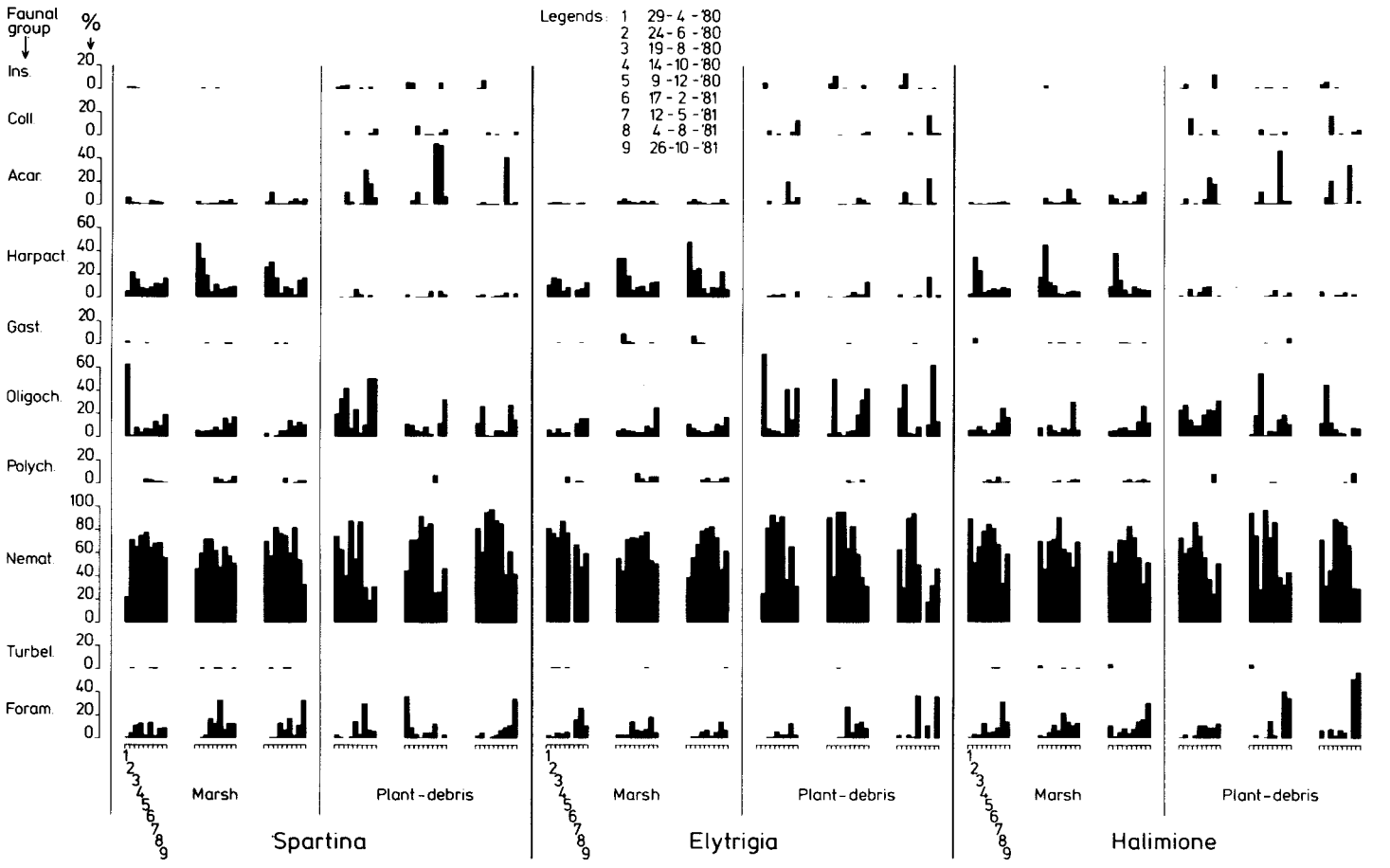


*Fig. 5.* Percentages of the different microfaunal groups per gram dry weight of material remaining in the mesh bags vs. time in the salt marsh for all treatments. Faunal groups are: Insecta, Collembola, Acarina, Harpacticoida, Gastropoda, Oligochaeta, Polychaeta, Nematoda, Turbellaria, Foraminiferida.

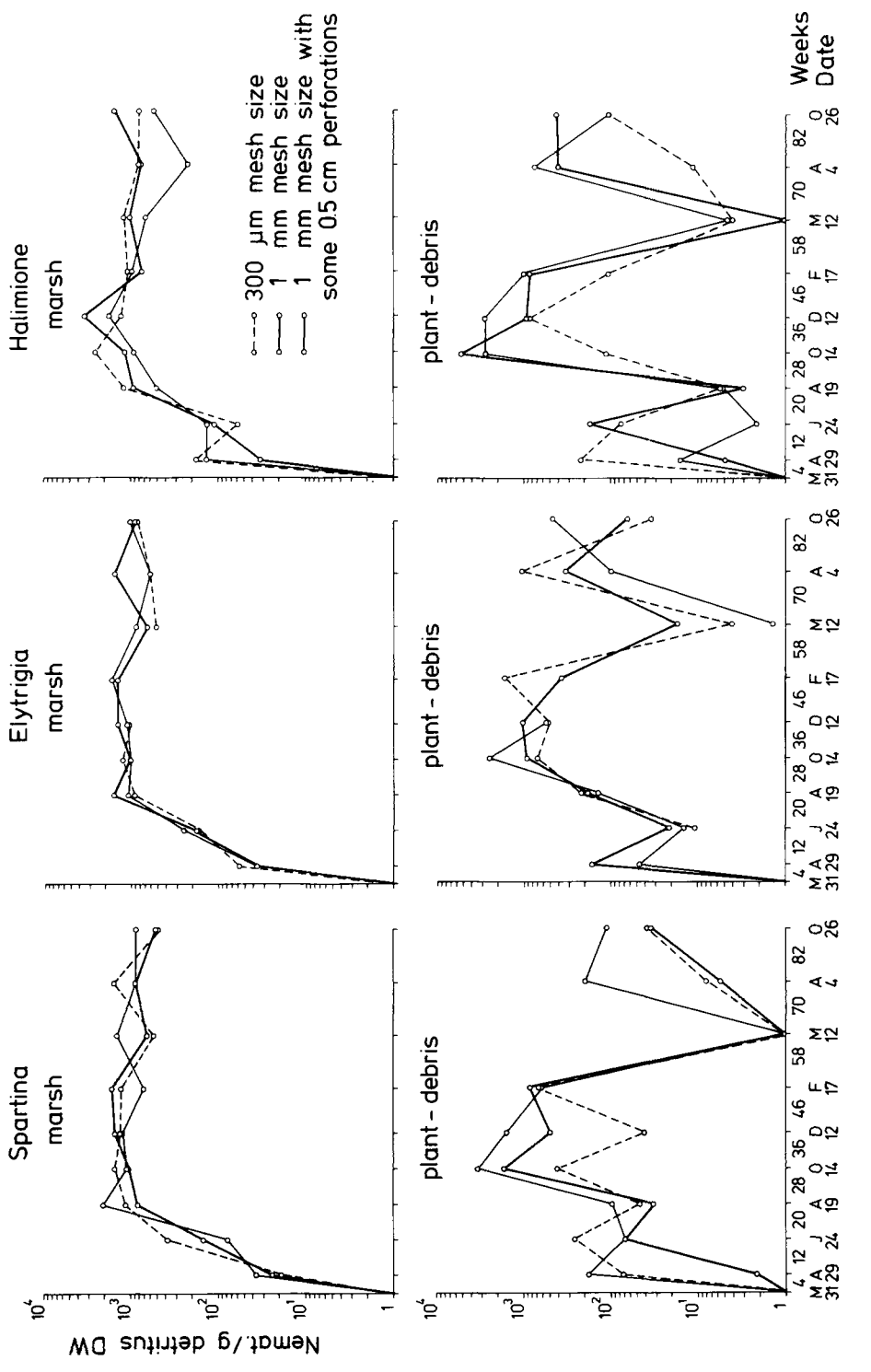


*Fig. 6.* Log of numbers of Nematoda per gram dry weight of material remaining in the mesh bags vs. time (weeks) in the salt marsh for all treatments.

and spatial scales similar to microbes, allowing a close coupling with them.

## Conclusions

The exponential decay model proved to be convenient for comparing the decomposition rates of *Spartina, Elytrigia* and *Halimione* litter enclosed in fine, medium and coarse mesh bags, located in the middle-marsh and plant-debris habitats. Decomposition was clearly influenced by plant species, habitat factors and fauna, while there was a significant interaction between plant species and habitat. Habitat- and species-determined differences changed during the successive phases of decomposition. Faunal influences became noticeable 12–16 weeks after the start of decomposition, while habitat- and species-determined differences were becoming smaller or disappearing in the course of the process. The results of this study underline the importance of knowledge of long-term decomposition rates and show that extrapolation of results of studies of relatively short duration can easily lead to false conclusions.

Decomposition of *Spartina* and *Halimione* litter was significantly accelerated by meio- and macrofaunal influences in the PD habitat, resulting in a 5–10% difference in AFDW remaining after 20.5 months. The same probably applied to *Elytrigia* litter, however, differences were not significant. In the M habitat only decomposition of *Elytrigia* was significantly accelerated by meio- and macrofauna, resulting in a 8% difference in AFDW after 20.5 months.

*Halimione* decomposed faster in the PD habitat than in the M habitat because of macrofaunal influences. In comparison to the M habitat, decomposition of *Spartina* was inhibited by PD environmental conditions, though this was partly compensated by meio- and macrofaunal influences in this habitat. Decomposition rates of *Elytrigia* hardly seemed to be influenced by differences in habitat conditions.

Differences in decomposition rates between the plant species were correlated with differences in C/N and C/P ratio only during the first 8 weeks. *Halimione* showed the fastest initial decomposition rates, *Spartina* had the fastest rates during the first summer, while after a year *Elytrigia* decomposed fastest.

Nematodes formed the dominant microfaunal group. Densities were not influenced by resource quality, season or meio- and macrofauna, but there was a strong habitat effect.

Decomposition of all species was slower in the PD habitat during the first 28 weeks. However, during the winter period decomposition continued slowly in the PD habitat, while there was a nearly standstill in the M habitat. Patterns of N and P content of the litter and of nematode densities also indicated that decomposition processes followed different coarses in the two habitats.

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