

## Decomposition of *Spartina alterniflora* in Different Seasons and Habitats of a Northern Massachusetts Salt Marsh, and a Comparison With Other Atlantic Regions

**ABSTRACT:** Packets of freshly harvested live *Spartina alterniflora* were placed on the marsh surface, in a tidal ditch, in a pool contacting sides and bottom, and in the center-bottom of the same pool in September 1972. Rates of loss were the same for all four sites through day 242. After that packets on the marsh surface decomposed slower. A second experiment was begun in July only at the marsh surface and pool side sites. These lost dry weight much more rapidly than packets started in September.

Populations of bacteria, fungi, diatoms, flagellates, ciliates and nematodes within the packets peaked within 60 days then decreased proportionately with the loss of dry weight in packets through day 242. After this, bacterial numbers decreased more rapidly presumably in response to a qualitative change in the packet material. Populations of flagellates and ciliates also declined rapidly after day 300. This decline occurred in new packets at around this date as well.

In a limited set of samples 12 taxa were analyzed for date or detritus-age dependent occurrence. Of these, eight were date dependent, two were dependent on packet age, and two could not be determined from the data.

### Introduction

For a number of years we have been studying various aspects of the ecology of the Rowley Marsh (Montagna 1975; Deegan 1976; Gillis 1977; Murray 1978; Ruber and Murray 1978; Ruber, Gillis and Montagna, unpublished). The present study had two sets of objectives, (1) To compare rates of decomposition of *Spartina alterniflora* with those obtained previously to the south of us (Burkholder and Bornside 1957; Odum and de la Cruz 1967; Ustach 1969; Kirby 1971; Gessner and Goos 1973); to compare rates at different sites on our marsh; and to compare rates of material loss from packages established at different seasons. (2) To determine abundance patterns of major organismic groups on these decaying plants, in order to assess whether there was a sequential invasion of species, and whether such colonization was primarily regulated by the qualitative content of the packet, or by the season.

### Materials and Methods

The study was conducted at the Parker River National Wildlife Refuge (Rowley, Massachusetts) about 60 km north of Boston. The salt marsh drains into Broad Sound which is the lagoon-like portion of the Parker River Estuary, formed by Plum Island (72°45'N, 70°48'W).

Live, clean, dwarf *Spartina alterniflora* leaves were collected, wet-weighted (15.00 g/packet) and sealed in plastic bags of a diamond shaped mesh (4.5 mm × 11 mm). We used live leaves because these give consistent ash-free dry weights while dead materials were variable (Ruber, Gillis, and Montagna, unpublished). Five randomly selected bags were oven dried at 90 °C for 48 hours to establish an appropriate wet weight to dry weight conversion factor. Fifty such bags were placed in each of 4 locations: on the surface of the marsh in the original *Spartina* stand (SS), in an adjacent tidal ditch (TD), and in contact with the side and bottom of a salt marsh pool (PS), and in the center-bottom in the same pool (PC). Bags were loosely packed in hardware cloth boxes (mesh of 10 mm<sup>2</sup>) for protection.

The bags were placed in the field on 8 September 1972, and pairs were collected on 20 subsequent dates, 19 over the first year and one after two years had elapsed. Similar studies were begun in July 1973 and again in July 1974, but packets were placed only in the SS and PS habitats.

On each date replicate samples from each site were censused in three ways. Bacteria and fungi were sampled by the following method modified from Witkamp (1963). The decomposing grass was placed in an erlenmeyer flask with 1,000 ml of sterile artificial sea water made from Rila Marine Mix at a salinity of 25‰. The grass was agitated by magnetic stirrer for 20 minutes to suspend all organisms. Colony densities were determined by serial dilution plating on Difco nutrient agar for bacteria and Difco Sabouraud agar for fungi, again using artificial sea water. The second phase of censusing began by concentrating the 1,000 ml supernatant with organisms down to 25 ml. Densities of protists, diatoms, and nematodes were determined by live counts from the concentrate. At the beginning of the study the grass was subjected to 2 stirring cycles. The second stirring resulted in increased population estimates of only 1–5% giving us confidence that the organismal separation from the grass and subsequent census was accurate. During the third and last census phase macroinvertebrates were hand-picked from the grass remnants, after which the grass was recovered by filtration through plankton netting of 178 µm mesh, oven dried at 90 °C and weighed.

### Results

In the first experiment, begun in September, packets from all 4 sites lost weight at about the same rate except SS which lost weight more slowly after 242 days. The

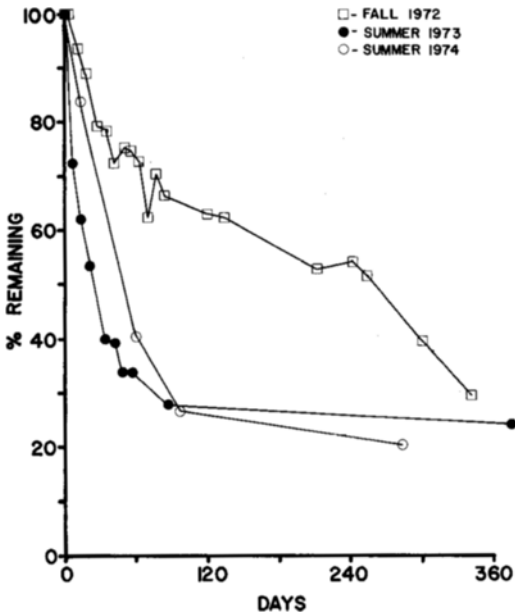


Fig. 1. Remaining dry weight of *Spartina alterniflora* litter for experiments begun Sept. 8, 1972, July 13, 1973, and July 9, 1974. Each point is the mean for all 4 sites. Standard errors range from 1 to 4% of the mean for all but 3 data points of the 1972 and 1973 runs; data were insufficient to assess the 1974 run statistically.

average monthly loss rates could be divided into three phases (Fig. 1). Decomposition was rapid the first 3 months (12%). The rate of loss decreased the next 5–6 months (2%) and then increased the following 3 months (7%). After 342 days, 30% of the original dry weight remained. Only one-half of this was lost during an additional year in the field.

In the experiments begun in July, site differences were again slight. Early loss rates were much greater (23% per month for the first 3 months). Only 30% of the original material remained after this interval, compared with 65% in the first experiment (Fig. 1).

In order to assess whether the presence of a taxonomic group was related to season or to sample age the co-occurrence of 12 taxonomic categories was compared for the dates 13 October 1972 (a 35 day-old packet) and 16 August 1973 (a 34 day and a 342 day packet). Season-dependent occurrence (34 vs. 342 day packet) was found in 8 cases. The abundance of the diatoms *Amphora*, *Nitzschia*, *Pleurosigma*, and *Synedra*; the flagellate *Euglena*; the ciliates *Paramecium*, and *Uronema* (?) and the gastropod *Hydrobia* was dependent on the season. Age-dependent occurrence (34 vs. 35 day packet) was found in the flagellate *Astasia*, and the ciliate *Euplotes*. The diatom *Navicula* and the phylum Nematoda occurred in all packets. Of the 10 genera examined, eight were season-dependent and two were age-dependent. The binomial test (Zar 1964) of the hypothesis that this distribution pattern is independent of season was rejected ( $p = .05$ ). Many other taxa were

censused but did not occur in packets of critical date and age and so could not be tested.

Population densities relative to remaining packet dry weights were calculated for various groups that occurred in the tidal pool (Fig. 2). Since these data are presented as numbers of organisms per gram of dry weight remaining in the packets a slope of zero means that organismal numbers are decreasing proportionately with the decrease of dry weight.

Relative densities generally peaked within the first 60 days for the study begun in September. Thereafter, the populations of all groups remained more or less constant at or were slightly below their maxima through day 242 (May 8). Diatom, nematode, and fungal populations remained relatively constant through the last sample on day 342 (Aug. 16). Bacterial populations declined steadily after day 242 while the numbers of flagellates and ciliates declined rapidly between day 301 (July 6) and day 342 (Fig. 2). Fig. 2 was constructed from the PS and PC packets and represented the trends in the other packets.

A different situation was noted in the packets begun in July, i.e., bacteria did not decline in July or August. However, flagellates and ciliates did show population decreases in August which were similar to those occurring at the same time in packets of the September experiment which were now over 10 months old, therefore, we do not attribute these changes to packet age.

### Discussion

We had expected that the different sites would yield different loss rates as reported by Kirby (1971). It may be that the placement of SS bags, which was expected to yield the lowest rates was too close to the tidal ditch (3 m) and the pool (1 m). This would permit a greater effect by migrating invertebrates such as *Palaemonetes pugio* which Welsh (1975) found to be important in the fragmentation of *Spartina*, and which was probably present in Burkholder and Bornside's (1957) crates. Such proximity also resulted in flooding during mean high tides, which affects breakdown rates (Teal 1962; Blum 1968; and Kirby 1971).

The difference between the summer and autumn series is striking. Odum and Fanning (1973) and Hardisky and Reimold (1977) have shown that there is a continual loss of leaves from the culms of *Spartina* species during their growing season. Such early losses are probably subject to much more rapid degradation at all latitudes studied than is the main crop in autumn. However, since we used healthy leaves and the continued loss is of senescing leaves, we cannot be certain of this.

Despite the differences in latitudes and in packaging of materials in these studies two patterns of loss seem to occur. First, a slow group characterized by studies done in Louisiana, Georgia, Rhode Island, and Massachusetts and which began in the autumn, winter, or spring, and second, a fast group done in Louisiana, North Carolina, and Massachusetts which began in the summer (Fig. 3).

It appears that when experiments are begun in the summer, the high prevailing temperatures result in a rapid loss of material (70% after 3 months). Those begun in other seasons are exposed to more moderate temperatures in the early stages of the experiment resulting in a slower loss of material (35% after 3 months),

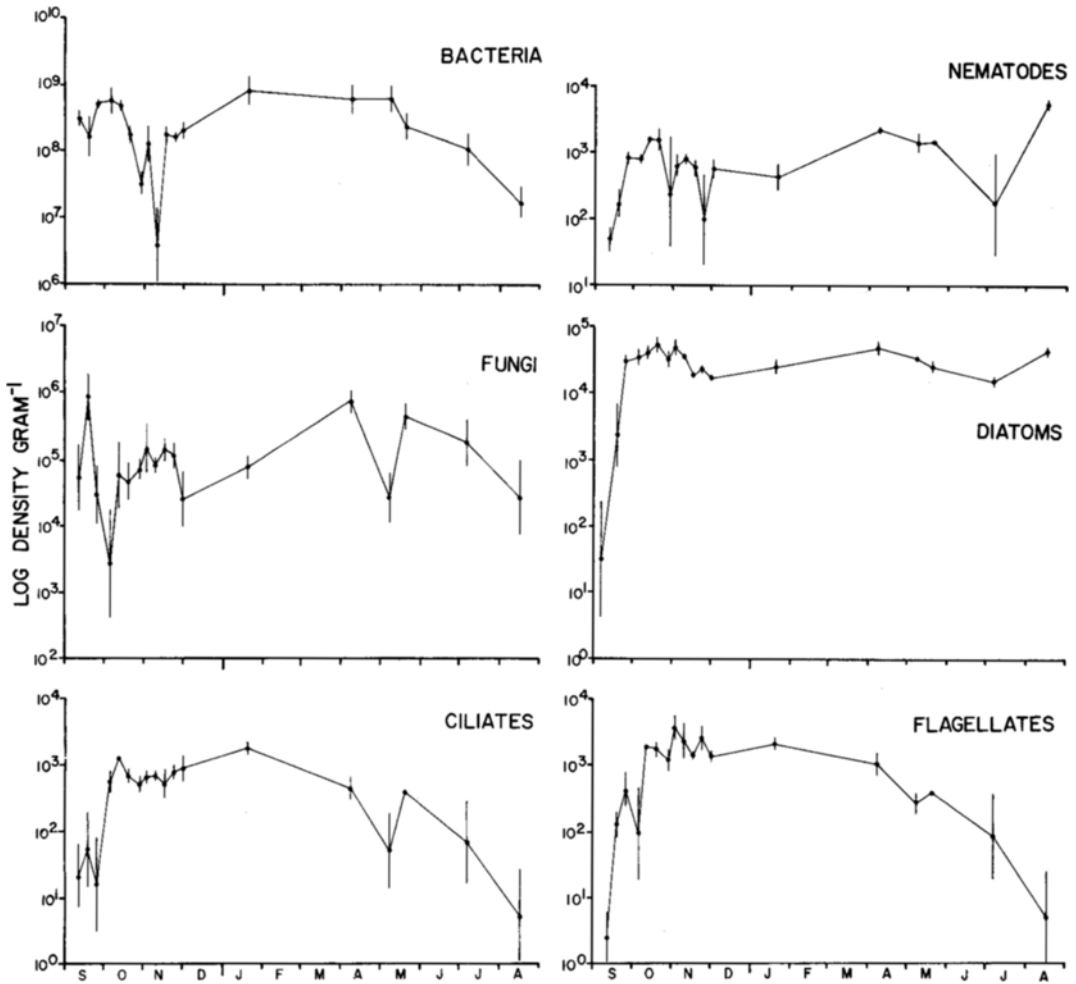


Fig. 2. Temporal variability of dominant organisms for the 2 pool sites. Log of population density per gram dry weight of grass remaining in packets during different months. Mean of 4 samples, vertical bars represent 1 standard error. Packets started Sept. 8; age at last sample 342 days.

and in most cases reduced rates of loss for the remainder of the experiment.

There are a number of other known or presumed variables which might influence loss-rates: mesh size of bags, location of bags, major geographical and perhaps faunal differences, grass composition with season and the condition of the grass selected for packaging, which ranged from healthy-live through newly dead in different studies. Despite this the high correlation of season with loss-pattern gives evidence of the great importance of temperature.

This study does not show significant decomposition related patterns of succession for most taxa (8 of 10) which could be tested. Total group densities did show a decline proportional to the reduction in packet material. This suggests two possible mechanisms: (1) That these organisms exist as a community, the size of which is regulated by the remaining substrate available for decomposition (probably cellulose). (2) The substrate

contribution is that of a shelter or a site of attachment regardless of any nutritional content. We cannot differentiate these mechanisms from the data but one or both appears to apply to diatoms, nematodes and fungi. Bacterial declines in the later stages may indicate a third possibility, a decline due to the changing quality of the packet substrate, since their decline exceeded packet loss rates during the period after day 242. Since these bacterial decreases were not noted in the experiment begun in the summer it is reasonable to conclude that these changes were not merely reflections of events in the adjacent habitats. Decreases of flagellate and ciliate populations in old packets were roughly paralleled in the fresh packets on the same dates so these changes must have reflected ambient events.

#### ACKNOWLEDGMENTS

This work was done on a portion of the Parker River National Wildlife Refuge, Newburyport, Mass. under

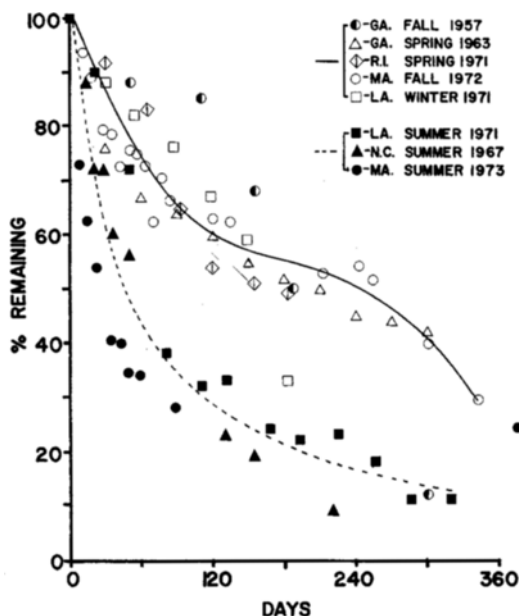


Fig. 3. Remaining dry-weight vs. time for experiments from a number of workers and locales. Georgia (Burkholder and Bornside 1957); Georgia (Odum and de la Cruz 1967); North Carolina (Ustach 1969); Louisiana (Kirby 1971); Rhode Island (Gessner and Goos 1973); Massachusetts, 1972, 1973 (present study). Curves have been eye-fitted to suggest pattern.

permits 5-PRR-72-14 and 5-PRR-74-14. We are most appreciative of the cooperation and friendship of the late William R. Forward and of Edward S. Moses and George W. Gavutis of the U.S. Fish and Wildlife Service.

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