Detritus formation from eelgrass (*Zostera marina* L.): The relative effects of fragmentation, leaching, and decay

P. G. Harrison[1,2]

Department of Oceanography, Dalhousie University, Halifax, Nova Scotia

K. H. Mann[3]

Department of Biology, Dalhousie University

Abstract

In laboratory decomposition experiments dead eelgrass leaves lost a maximum of 35% of the original dry weight in 100 days at 20°C. Whole leaves lost 0.5% of their organic content per day whereas particles smaller than 1 mm lost 1% per day. Sterilization of leaves by dry heat or potassium cyanide showed that leaching accounted for 82% of the total loss of organic matter from predried material and 65% of the loss from undried material. Bacteria acting alone increased the nitrogen content of the detritus but only slowly degraded the leaf material. When protozoa were introduced, they grazed on the bacteria, maintained the bacterial population in an active metabolic state, and hastened the rate of decay. The C : N ratio of incubated detritus decreased from over 20 : 1 to as low as 11 : 1, indicating an increase in its potential food value. The overall slow rate of decomposition could enable the eelgrass detritus system to continue functioning during periodic short term fluctuations in eelgrass primary production by ensuring that a reservoir of slowly decomposing material is always present.

In studies of marine detritus, saprophytic decay has been considered the most important process in relation to both rates of decomposition and changes in nutritional value of the detritus (Fenchel 1972), but the situation is not well understood. We have determined the relative contributions of the processes of decomposition in a series of laboratory experiments.

Eelgrass detritus, as here defined, consists of both the nonliving leaf debris and the associated, living microorganisms. The processes forming detritus from leaves include: fragmentation, mechanical breakdown by physical or biological grinding; autolysis, the release of cell contents due to the action of the plant's enzymes; leaching, the removal of water-soluble components; and microbial decay, digestion of the debris by bacterial or fungal extracellular enzymes. The combined effect of these processes in reducing particulate detritus to a subparticulate form is here called decomposition.

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Materials and general methods

Eelgrass leaves were collected from a submarine meadow in St. Margaret's Bay on the Atlantic coast of Nova Scotia as described previously (Harrison and Mann 1975). SCUBA divers collected material for laboratory experiments and also observed the fate of leaves which dropped off the plants in autumn or were torn off by storms. Leaves of various ages were used: young, green leaves; old leaves with brown or black areas; and dead leaves collected from the sediment surface.

The experiments consisted of incubations of *Zostera* leaf material, of various ages and sizes, in flasks with seawater which had been filtered through a Millipore HA (0.45 μm) membrane. Flasks were kept in the dark at 20°C or 2°C, approximately the maximum and minimum temperatures observed in the field. The leaf material was weighed at the start of each experiment, and

[1] Present address: Department of Botany, University of British Columbia, Vancouver.

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after incubation the contents of each flask were filtered with a 0.8-μm Millipore membrane. The particulate material on the filter was rinsed with a 3% (w/v) solution of ammonium formate in distilled water to remove sea salts, dried at 100°C to constant weight, and reweighed. In addition, before and after incubation in some experiments the leaf material was analyzed for organic matter, expressed as loss of dry weight on ashing at 520°C for 8 h, and for carbon and nitrogen, using a CHN analyzer (Hewlett Packard F & M 185) calibrated with cyclohexanone-2, 4-dinitrophenyl hydrazone. Experiments were performed to show that incubation of eelgrass leaf material in flasks did not inhibit bacterial activity.

Experiments and results

Effect of the age of the leaf material—Most eelgrass leaves mature and age on the plant before dying and dropping off. Some green and aging leaves, however, are seen in autumn floating on the sea surface after being torn off by storms. Leaves of various ages differ in total organic matter and nitrogen contents (Harrison and Mann 1975) and might be expected, therefore, to decompose at different rates.

Exp. 1: Two 10-g fresh weight (1.8-g dry wt) samples of green leaves collected in January were incubated in 2 liters of seawater for 28 days at 20°C.

Exp. 2: Two 30-g fresh weight (5.1-g dry wt) samples of old leaves collected in August were incubated in 3 liters of seawater for 25 days at 20°C.

Exp. 3: Three 1.5-g fresh weight (0.2-g dry wt) samples of dead leaves collected in November were incubated in 100 ml of seawater for 20 days at 20°C.

Table 1 compares the rates of decomposition and shows that young green leaves and old darkening leaves decomposed more quickly than dead leaves. Since the rate of decomposition did depend on the age of the leaf material, and since most leaves die naturally before beginning to decompose, further work concentrated on the fate of dead leaves.

Table 1. Loss of total dry weight and organic matter from eelgrass leaves incubated with microorganisms, to show differences with the age of the leaf material. Values are means ±1 SD.

Exp	Age of leaves	% loss of: Dry Wt	Organics	Organics/day
1	Young	27±4	39.5±0.7	1.4
2	Old	23±3	27.0±1.4	1.1
3	Dead	15±7	7.3±7.2	0.4

Effect of drying the leaf material before incubation—Decomposing eelgrass leaves were observed in the field both intertidally and subtidally. Winter storms deposit some leaves on shore where they are alternately dried and wetted before being washed back into the sea. Most leaves, however, drop from the plant to the sediment surface and decompose in situ. It was desirable, therefore, to compare rates of decomposition using dried and undried leaf material. Dried samples were inoculated with seawater containing a natural microbial community.

Exp. 3: Three 1.5-g samples of fresh, dead leaves collected in November were incubated in 100 ml of seawater for 20 days at 20°C.

Exp. 4: Three 0.2-g samples of dried, dead leaves collected in November were incubated in 100 ml of seawater for 20 days at 20°C.

Exp. 5: Three 0.4-g samples of fresh, dead leaves collected in March and ground into pieces of 250–1,000 μm were incubated in 2 liters of seawater for 26 days at 20°C.

Exp. 6: Three 0.25-g samples of dried, dead leaves collected in November and ground into pieces of 250–1,000 μm were incubated in 100 ml of seawater for 20 days at 20°C.

Experiments 5 and 6 used leaves collected at the start and end of winter, but the leaves had similar chemical compositions (Harrison and Mann 1975).

Table 2 shows that predried leaf material lost organic matter only slightly more quickly than did fresh leaf material of comparable size. However, organic matter was actually a smaller proportion of the total losses in predried material. Table 3 shows that during decompositon of fresh leaf material both carbon and nitrogen decreased

Table 2. Loss of organic matter and its relation to total loss of dry weight from eelgrass detritus, both in large pieces and finely ground, incubated with microorganisms, to show differences between dried (D) and undried (F) material. Values are means ±1 SD.

Exp	Size of particles	Fresh (F) or Dried (D)	% loss of organics	t-test of diff.	Organic loss as % of total wt loss
3	2–4 cm	F	7.3 ± 7.2	t_4>2.8	34.4
4		D	9.3 ± 1.4	ns	28.8
5	0.25–1 mm	F	15.9 ± 12.4	t_4>2.8	58.8
6		D	20.5 ± 2.2	ns	41.0

(as percentage of remaining dry weight) whereas with predried leaf material carbon and nitrogen levels rose. The C : N ratios also showed opposite trends.

Effect of particle size in unsterilized material—

Exp. 4: Dried, dead leaves in pieces 2–4 cm long were incubated as described earlier.

Exp. 6: Dried, dead leaves of 250–1,000 μm were incubated as described earlier.

Exp. 7: Three 0.25-g samples of dried, ground, dead leaves less than 250 μm were incubated in 100 ml of seawater for 20 days at 20°C.

Figure 1 shows that a reduction in size of leaf material from more than 1 cm to less than 1 mm doubled the rate of loss of organic matter. With further reduction in size the rate of decomposition appeared to decrease.

Effect of sterilizaton of leaf material— By eliminating microorganisms from the detritus complex it should be possible to measure the effect of autolysis and leaching from the debris. Two sterilizing agents were used: dry heat (100°C for 60 h, sufficient to kill bacteria and protozoa) and potassium cyanide. We checked the effectiveness of the sterilizing agents periodically by spreading aliquots from the treated flasks on plates of ZoBell's 2216e medium (Jannasch and Jones 1959) and incubating the plates at 20°C for several days. Although this procedure is not absolutely reliable, we feel that in all flasks called sterile the bacterial populations were, at the very least, reduced substantially from control levels.

Exp. 8: 0.5-g samples of dried, ground, dead leaves less than 420 μm were heat-sterilized and incubated in 100 ml of autoclaved seawater for 35 days at 20°C. Some flasks were inoculated with bacteria and protozoa obtained from sediment and eelgrass leaves.

Table 4 shows that unsterile leaves lost 23% more organic matter than did sterile leaves.

Exp. 9: 4.0-g samples of fresh, ground, dead leaves of 250–1,000 μm were treated 2 h with 100 ml of a 1/500 (w/v) solution of KCN in

Table 3. Carbon and nitrogen content (% of dry wt) and C : N ratio of finely ground eelgrass detritus before and after incubation with microorganisms, to show differences between dried and undried material. Values are means ±1 SD.

Exp	Treatment	% Carbon		% Nitrogen		C:N ratio	
		Before	After	Before	After	Before	After
5	Undried	39.3±0.8	37.1±1.6	3.1±0.1	2.1±0.0	12.8±0.3	17.9±0.4
6	Dried	34.7±3.9	46.4±2.5	1.9±0.4	4.3±0.3	18.8±2.5	10.8±0.6

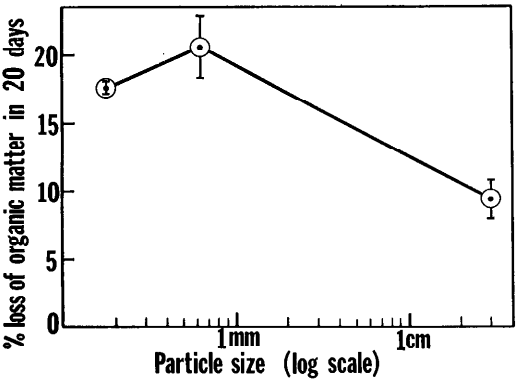

Fig. 1. Loss of organic matter from eelgrass detritus incubated with microorganisms at 20°C, showing the differences with various sizes of particles. Vertical lines indicate ±1 SD.

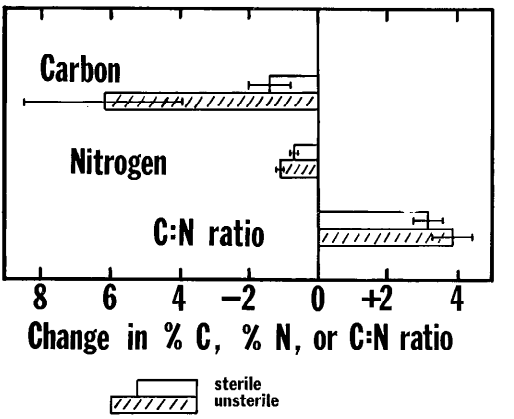

Fig. 2. Changes in carbon and nitrogen content and C : N ratio of undried eelgrass detritus, to show the effect of incubation at 20°C under sterile conditions or with microorganisms. Vertical bars joined by a horizontal line indicate ±1 SD.

seawater or sterile seawater, filtered, rinsed, resuspended in 2 liters of autoclaved seawater, and incubated 26 days at 20°C or 2°C.

Bacteria grew at 20°C and the loss of weight from controls and treated samples was identical. Results for the 2°C series are in Table 4 and indicate an increased rate of decomposition in unsterile material.

Exp. 10: 1.5 g of fresh, dead leaves 2–4 cm long were incubated in 100 ml of a 1/1,000 (w/v) solution of KCN or seawater for 20 days at 20°C. Sterility was maintained.

Table 4 shows once again an increased rate of decomposition in unsterile leaves, but the majority of the losses occurred in the sterile material. Figure 2 indicates that sterile debris lost nearly as much nitrogen as did unsterile detritus but that saprophytic decay resulted in a greater loss of carbon than did leaching. In both cases the C : N ratio increased to a similar extent.

Table 4. Losses of total dry weight and organic matter from eelgrass detritus of various types to show differences between sterile material and material incubated with microorganisms. Values are means ±1 SD.

Exp	Treatment	% loss of dry wt		Sig.	% loss of organic matter		Sig.
		Sterile	Unsterile	of diff.*	Sterile	Unsterile	of diff.*
8	Dried, ground <420 µm	30.5±0.3	32.5±1.2	ns	15.4±0.5	20.1±1.5	99%
9	Fresh, ground 250–1,000 µm	6.0†	10.7		4.0	7.7	
10	Fresh, whole	3.9±10.0‡	15.1±6.5	ns	5.6±6.9‡	7.3±7.2	ns
11	Dried, whole	21.4±2.9	22.6±1.2	ns	8.6±3.4	9.3±1.4	ns
12	Dried, ground 250–1,000 µm	27.0±3.5	34.5±1.7	95%	15.0±2.9	20.5±2.2	ns
13	Dried, ground <250 µm	24.7±0.7	26.0±0.4	95%	15.0±0.9	17.6±0.4	95%

*Using t-test: ns = not significant; 95% = significant at 95% level; 99% = significant at 99% level.
†Data insufficient to calculate SD.
‡Data highly variable.

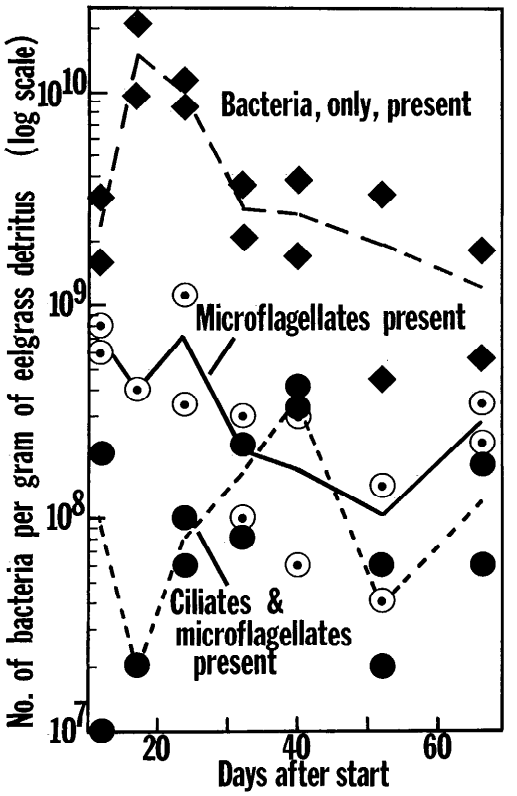

Fig. 3. Numbers of bacteria per gram dry weight in flasks at 20°C containing finely ground eelgrass detritus, to show differences with and without protozoa. Symbols are actual counts in duplicate on each occasion; lines join the means.

Exp. 11–13: 0.2 g of dried, dead leaves were incubated as in exp. 10. In exp. 11 the material was in pieces 2–4 cm long; in exp. 12 it was 250–1,000 μm; and in exp. 13 it was less than 250 μm.

Table 4 shows that the sterile leaves lost 73–92% as much organic matter as did leaves decomposed by microorganisms.

Effect of successive additions of bacteria, microflagellates, and ciliates to sterilized leaf debris—

Exp. 14: 0.25 g of dried, ground, dead leaves of less than 420 μm were sterilized with dry heat, treated as below, and incubated 35 or 102 days at 20°C.

Ten flasks were used for each of four treatments: 1—control, no further treatment; 2—inoculation with bacteria from

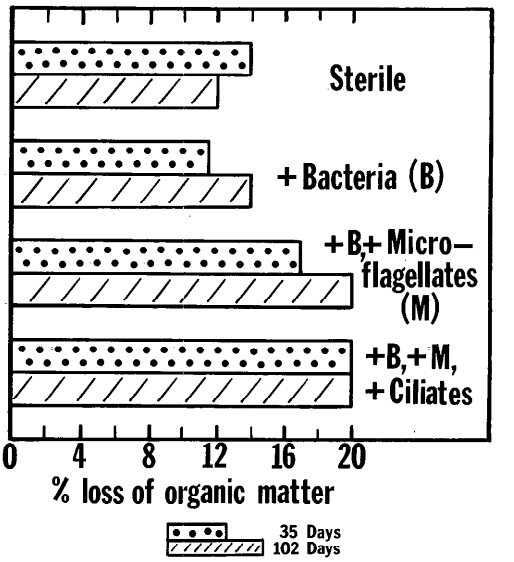

Fig. 4. Loss of organic matter from finely ground eelgrass detritus after 35 and 102 days at 20°C, to show the effect of incubation under sterile conditions or with various microorganisms.

decaying eelgrass leaves and mud; 3—addition of microflagellates, probably a species of *Bodo*, to 2; and 4—addition of ciliates, a species of *Euplotes*, to 3. The maintenance of sterility in controls was checked as before. Bacterial population sizes were monitored with plate counts as follows: 1-ml samples were removed from stirred flasks with a wide bore pipette, diluted to 10^{-3} to 10^{-5} (to give between 30 and 300 colonies per plate), and spread on plates of ZoBell's 2216e medium. Plates were incubated at 20°C initially for up to 5 days but since no new colonies were observed after the first day, 24-h counts were used. Because of the dilutions and conditions of incubation, some populations may have been underestimated. Ciliates were counted live in a 1-ml plankton cell under 50× magnification.

The results in Fig. 3 show that when bacteria only were present their population reached 10^{9}–10^{10} cells per gram dry detritus. When protozoa were present there were only 10^{8} bacteria per gram dry detritus. Ciliates maintained populations of 10^{4} per gram dry detritus for 50 days after

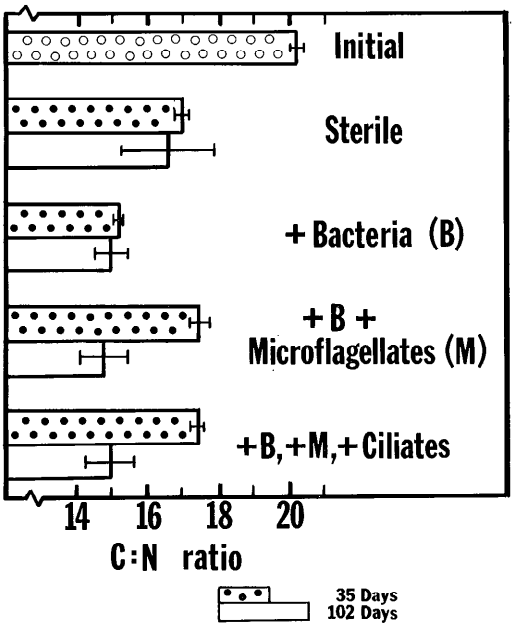

Fig. 5. C : N ratio of finely ground eelgrass detritus before and after incubation at 20°C for 35 and 102 days, to show the effect of incubation under sterile conditions or with various microorganisms. Vertical bars joined by a horizontal line indicate ±1 SD.

which the numbers fluctuated between 10 and 10^3 per gram. Figure 4 indicates that sterile debris lost 12% of its organic matter through leaching; bacterial activity had little effect, but another 6% was lost when protozoa were present. Figure 5 shows that the lowest C : N ratios (15 : 1) were characteristic of detritus with only bacteria present. When protozoa were growing well the C : N ratio was around 17.5 : 1, but this eventually decreased to the level of the bacterial series when the protozoan populations decreased.

Effect of renewal of the medium during incubation—In a static system such as we used in the previous experiments microbial activity may become limited by the supply of nutrients or oxygen or by the buildup of metabolic products. Two different methods were used to renew the seawater during the incubations.

Exp. 15: 10 g of fresh, dead leaves of 2–4 cm were incubated in 2 liters of either seawater flowing with a renewal time of 12 h or standing seawater, for 51 days at 20°C.

Exp. 16: 0.25 g of dried, ground, dead leaves of 250–1,000 μm were incubated in 100 ml seawater for 20 days at 20°C. On days 1, 5, and 10, 50 ml was pipetted off and replaced with fresh, filtered seawater.

Table 5. Loss of dry weight from eelgrass detritus incubated with microorganisms, to show the effect of two different methods used to renew the medium, i.e. continuous flow (exp. 15) and periodic dilution (exp. 16). Values are means ±1 SD.

Exp		% loss of dry wt		Sig. of diff. *
		Static	Renewed	
15		21.7±4.5	9.1±8.9	ns
16	Day 1	34.5±1.7	31.5±1.6	ns
	Day 5		23.9±1.3	99%
	Day 10		22.7±0.03	99%

* Using t-test: ns = not significant; 99% = significant at 99% level.

Tables 5 and 6 show that renewal of the medium generally reduced, rather than enhanced, the rate of decomposition and had little effect on the C : N ratio.

Effect of the addition of inorganic nutrients—Bacteria decomposing organic matter of plant origin may be limited by the low nitrogen or phosphorus levels in the substrate (Richards and Norman 1931).

Table 6. C : N ratio of eelgrass detritus before and after incubation with microorganisms, to show the effect of periodic renewal of the medium (exp. 16). Values are means ±1 SD.

Treatment	C:N ratio	Sig. of diff. from control *
Initial leaf material	18.8±2.5	-
Static medium (control)	10.8±0.6	-
Renewed-day 1	10.5±0.4	ns
-day 5	9.2±0.7	99%
-day 10	10.3±0.6	ns

* Using t-test: ns = not significant; 99% = significant at the 99% level.

Table 7. Loss of dry weight from finely ground eelgrass detritus incubated with microorganisms, to show the effect of the addition of various inorganic nutrients at the start of the incubation period (exp. 17) or throughout the incubation (exp. 18). Values are means ±1 SD.

Exp	Nutrients added (mg-atoms/liter)	% loss of dry wt	Sig. of diff. from control *
17	None (control)	28.7 ± 1.1	--
	1.0 NH_4 +	28.4 ± 1.3	ns
	1.0 NO_3^-	28.8 ± 0.9	ns
	0.2 PO_4^{3-}	28.9 ± 1.0	ns
	NH_4+ + PO_4^{3-}	26.6 ± 0.8	99%
	NO_3^- + PO_4^{3-}	28.7 ± 0.3	ns
18	None (control)	29.7 ± 1.0	--
	1.0 NH_4^+ + 0.2 PO_4^{3-}	29.0 ± 0.7	ns
	10.0 NH_4^+ + 0.2 PO_4^{3-}	29.4 ± 1.4	ns

* Using t-test: ns = not significant, 99% = significant at p = 0.01.

Exp. 17: 0.25 g of dried, ground, dead leaves of 250–1,000 μm were incubated in 100 ml of seawater containing added nitrate, ammonia, and phosphate in various combinations for 20 days at 20°C.

The water in all flasks became cloudy and brown in 2 days. Gradually the cloudiness disappeared, first in the controls and then in the enriched samples, until by day 12 all were transparent and amber colored. As Table 7 shows, enrichment with nitrogen or phosphorus or both had little effect on the rate of decomposition.

Exp. 18: We repeated exp. 17 but added nutrients initially and every second day for the 10 days of incubation.

Table 7 shows that this treatment also had no effect on the rate of decomposition.

Changes in nitrogen content of detritus—Figure 6 summarizes the data on gains and losses of nitrogen from the eelgrass detritus used in several of these experiments. Published data from previous studies using detritus from eelgrass and other macrophytes (marine, terrestrial, and freshwater) are included for comparison. Large increases in the percent nitrogen content were

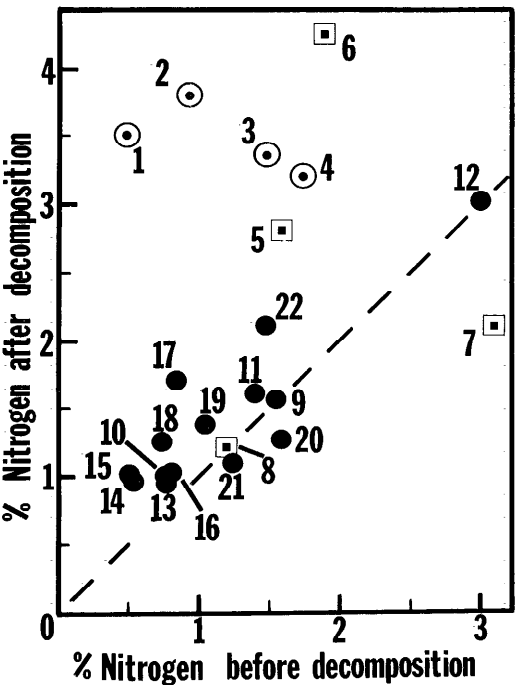

Fig. 6. Changes in the nitrogen content (as % of remaining dry weight) during decomposition of detritus derived from eelgrass and other marine macrophytes as well as terrestrial and freshwater plants.

1–8. Marine macrophyte detritus (1–3, in field; 4–8, in lab): 1—mangrove leaves (Heald *cited in* Mann 1972); 2—marsh grass leaves (Odum and de la Cruz 1967); 3—eelgrass leaves (Jensen 1914); 4—eelgrass leaves (Fenchel unpublished). 5–8—Eelgrass decomposition experiments (this study): predried 5–exp. 8; 6–exp. 12, 13; undried 7–exp. 9; 8–exp. 2.

9–17. Terrestrial leaf litter decomposed six months on forest floor: 9–ash; 10–oak; 11–hazel; 12–alder (Bocock 1964); 13–chestnut; 14–beech (Anderson 1973); 15–maple; 16–beech; 17–birch (Gosz et al. 1973).

18–21. Terrestrial leaf litter decomposed in freshwater for 6 months (18) or 50 days (19–21): 18–beech (Iversen 1973); 19–elm; 20–alder; 21–oak (Kaushik and Hynes 1968).

22. Freshwater macrophyte, water milfoil (Nichols and Keeney 1973). Dashed line indicates no change in percent nitrogen.

shown only by the marine detritus, whereas terrestrial and freshwater macrophyte litter decayed with little change in percent nitrogen. In our experiments the total amount of particulate nitrogen in the flasks contain-

Table 8. Processes affecting the nitrogen content (N) of decomposing eelgrass leaf material, and the resultant changes.

Fraction of leaf affected	Processes occurring	Resultant change in: N as % of remaining dry wt.	Resultant change in: Absolute amount of particulate N
Nonnitrogenous	Losses - leaching & decay	increase	no change
Nitrogenous	Losses - leaching & decay	decrease	decrease
Nitrogenous	Gains - bacterial growth	increase	increase

ing predried, dead eelgrass material rose by 12.5–50% during incubation.

Discussion

Leaching from dead eelgrass leaves has, in these experiments, been established as the major process in the decomposition of eelgrass detritus. Of the total loss of organic matter from decomposing eelgrass material, leaching accounted for 73–92% (average 82%) when the leaves were predried and 52–77% (average 65%) when the leaves were not dried. Autolysis may have contributed to the losses, but the sterilization methods used would be expected to inactivate any enzymes still present in the dead leaves (Kretovich 1966). There was some indication that leaching was relatively more important (and microbial decay less so) when the material had been predried, but the high variability of the results with undried leaves and the overlapping ranges of the two sets of data show that the difference was small. Nevertheless, drying did appear to alter the organic matter in such a way that it was less rapidly attacked by microbes whereas the inorganic matter was more easily removed from dried leaves than from fresh leaves (Table 2). This conclusion contradicts that of Zieman (1968) that predrying of turtle grass leaves caused structural and chemical changes in the cells which allowed easier entrance of microbes and a faster rate of decay. Zieman, however, reported only the loss of total dry weight and thus his conclusions cannot be related directly to changes in the organic fraction. Previously microbial decay has been emphasized over leaching in marine detritus studies (Odum and de la Cruz 1967; Burkholder and Doheny 1968) although leaching is known to be an important process in freshwater and terrestrial situations (Krause 1962; Nykvist 1963; Otsuki and Wetzel 1974) and in dying and dead seaweeds (Khailov and Burlakova 1969).

Mechanical reduction in size of leaf material generally increased the rate of decomposition (Fig. 1). As the size of the particles decreased, the total surface would increase with the result that both microbial activity and leaching could occur at greater rates. It has been shown with a variety of types of detritus as well as mud and sand that bacterial activity, as measured by oxygen uptake, is proportional to substrate surface area (Odum and de la Cruz 1967; Hargrave 1972). Leaching, on the other hand, has been thought to occur from whole leaves soon after they die (Oláh 1972), and the effect of fragmentation has been ignored. The particles can lose weight by leaching and saprophytic decay, but they can also be expected to gain weight due to the growth of attached bacteria at the expense, not of the particles, but of soluble material; the latter could also physically adsorb to free surfaces of the particles. Perhaps reasoning of this sort can be used to explain the apparent decrease in rate of decomposition of the very fine particles (Fig. 1). Because of the central role of particle size and surface area in decomposition we

feel that fragmentation should be intensively investigated.

Several processes could have caused the observed changes in the nitrogen content of decomposing eelgrass leaf material (Table 8). Leaching and mineralization through microbial decay affect both nitrogenous and nonnitrogenous components, while growth of bacteria is also accompanied by the immobilization of soluble nitrogen from the medium. Since all of these processes most probably occur in a single sample of detritus, Table 8 can give only a basic analysis of the results.

The increases in percent nitrogen content when dried, dead eelgrass leaf material was decomposed in the laboratory are similar to those reported for a variety of types of macrophyte detritus found in the sea (Fig. 6). The increase in total amount of particulate nitrogen (12.5–50%) was similar to one of 20% we calculated from the data of Fenchel (unpublished) also using eelgrass. These increases were presumably attributable to the uptake of soluble nitrogen from the seawater by microorganisms decaying the structural carbohydrates of the detritus (Newell 1965). That an increased supply of inorganic nitrogen and phosphorus did not increase the rate of decay may indicate the importance of initial levels of nutrients in both the water and the plant debris. Since nitrogen content is a rough index of the protein level in the detritus (Harrison and Mann 1975), and since protein is often a limiting part of an animal's diet, decomposition of eelgrass and other macrophytes in the sea results in an increase in the nutritional value of the plant material.

When undried eelgrass leaves, either aging or dead when collected, were incubated with microorganisms the results were more variable but in general the percent nitrogen content did not increase (Fig. 6). Interestingly, we also found little change in the percent nitrogen level in intact, dead leaves decomposing on the sediment underwater (Harrison and Mann 1975). Other studies of freshwater and terrestrial macrophyte detritus (leaf litter) have shown only slight increases in percent nitrogen (Fig. 6). In the latter studies mesh bags were used to enclose the detritus, and the data can apply only to the large particles (generally greater than 1 mm) remaining in the bags. Nothing can be concluded, therefore, about the nitrogen levels in the small particles that escaped from the bags. In our study, however, it is likely that there was an initial loss of nitrogenous substances from large pieces of leaf, that loss exceeding the gain of nitrogen resulting from colonization by microorganisms. After the soluble and easily decayed nitrogenous materials disappeared, the microorganisms continued to grow.

The increase in potential nutritional value accompanying the eventual rise in percent nitrogen during decomposition was reflected in a drop in the C : N ratio of the detritus (Fig. 5). These results agree with the current understanding of detritus systems, i.e. decay of the plant material (carbon) accompanied by a buildup of microbial protein (Mann 1972). One important detail these experiments revealed is that grazing by protozoa can partly counteract the effect of bacteria, perhaps by excreting some of the ingested bacterial nitrogen as was proposed for phosphorus by Johannes (1968) or by "forcing" the bacteria to maintain a metabolically active population (Fenchel unpublished) which exhibits a faster rate of turnover of nitrogen. Assuming that all nitrogenous materials are equally available to consumers and accepting the value of 17 : 1 as the maximum C : N ratio that gives an adequate diet for animals (Russell-Hunter 1970), then eelgrass detritus with a C : N between 11 : 1 and 17.5 : 1 could provide an animal with a better source of food than intact, dead leaves with C : N between 20 : 1 and 30 : 1.

The available experimental evidence indicates that eelgrass detritus decomposes very slowly. Even when dead leaves were incubated under favorable conditions in the laboratory, 65% of the dry weight remained after 100 days at 20°C. Since the annual primary production of leaves is high, organic detritus should be accumulat-

ing in the eelgrass system. Anecdotal accounts by local fishermen tend to support this idea. If a large pool of detritus exists in the sediments, then even a slow rate of decomposition would be sufficient to support the consumer populations. Following this line of reasoning further, the temporary declines of eelgrass observed at 20- to 40-year intervals in recent history (Cottam 1934) would not be expected to result in an immediate decline in organisms dependent, directly or indirectly, on eelgrass detritus. Only where eelgrass died out and did not repopulate an area, as in some higher salinity regions in Danish waters (Nelson 1947), would the detritus-based system be replaced by one based on, for example, phytoplankton.

Indirect evidence for this pool of detritus is found in the idea of Odum (1969) that detritus-based systems are "mature" and have low production to biomass ratios ($P : B$). The annual accumulation of detritus (P) should be, therefore, only a small proportion of the pool of detritus (B). Also, in the vicinity of the eelgrass bed we studied, the rate of sedimentation of fine particulate organic matter was approximately constant throughout the year (Webster et al. 1975), indicating that the autumn input of dead leaves is converted to particles of detritus over a long period. We have some direct evidence for the pool of detritus in that one can find areas where the subsurface sediment consists wholly of partially decomposed eelgrass leaves. The existence of a large mass of slowly decomposing plant material may thus enable the eelgrass ecosystem to continue functioning even when the main primary producer is temporarily removed.

A simplified model of the eelgrass detritus system is presented in Fig. 7. Each autumn a mass of dead leaves is added to the pool of particulate debris present in the sediment. At the same time, some of the leaf biomass is released as dissolved organic matter, from both dying and dead leaves. The pool of particulate debris is decomposed slowly, mainly by leaching of soluble material but also by direct saprophytic decay. The decay of structural carbohydrates (cellulose) may be the rate limiting step. The pool of dissolved organic matter, on the other hand, is metabolized quickly by microorganisms. Grazing by protozoa on bacteria maintains the latter in an active metabolic state and thus increases the rate of saprophytic decay. Finally, the grinding action of physical forces, as well as animals, fragments the leaves into small particles and increases the rates of leaching and decay. The eelgrass detritus system is complex and although many of the biological and abiological interactions involved need further investigation, it is now clear that the formation of detritus from eelgrass leaves is of fundamental importance in many coastal marine environments.

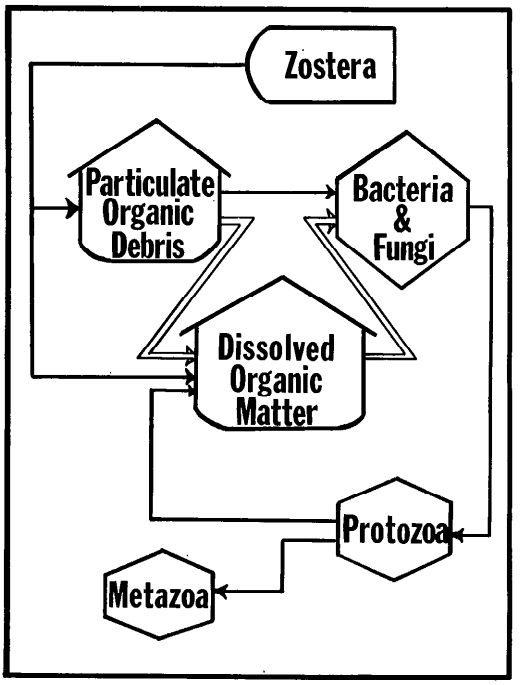

Fig. 7. Model of the eelgrass detritus system showing the major energy flows.

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