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The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach

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Abstract: Litter bags of three mesh sizes (5 × 8 mm, 1 mm, 85 μm) were used to assess the role of faunal components in the breakdown of the kelp *Macrocystis pyrifera* (L.) C. Ag. on a New Zealand sandy beach. The wrack was colonised by the supralittoral fauna in two distinct phases. The macrofauna, including the talitrid amphipod *Talorchestia quoyana* (Milne-Edwards), adult Diptera and Coleoptera, colonised the kelp within 1 day, with highest numbers recorded after 3 days. Following this, their presence in the samples declined and the meiofauna, which consisted of nematodes, enchytraeids, dipteran larvae, and mites, became increasingly abundant. After 18 days in the field, the meiofauna dominated the kelp surface. This faunal succession did not relate directly to the degradation of the algal tissues, which proceeded linearly for the entire study period. Algal material was lost from the bags at a rapid rate, with only 36–59% of the original dry mass remaining after 18 days in the field. Exclusion of the macrofauna from the kelp, using litter bags of finer mesh sizes (< 1 mm), had no appreciable effect on the rate of dry matter loss. Laboratory experiments revealed no effect of different meshes on breakdown rates in the absence of the fauna. The major macrofaunal kelp consumers, including *T. quoyana* and Coleoptera, therefore, did not affect the rate of algal disintegration. The effect of meiofaunal nematodes, enchytraeids and dipteran larvae on kelp breakdown could not be accurately determined. Microbial decay, and abiotic leaching and fragmentation processes were likely to be the major causes of kelp weight loss from the litter bags.

Key words: Decomposition; Litter bag; *Macrocystis pyrifera*; *Talorchestia quoyana*

INTRODUCTION

In many parts of the world, sand beaches receive large inputs of drift algae from offshore kelp beds, e.g., in California (ZoBell, 1959), New Zealand (MacIntyre, 1963), South Africa (Griffiths & Stenton-Dozey, 1981), New England (Behbehani & Croker, 1982) and in Australia (Lenanton et al., 1982). Although much of this organic matter is returned to the surf by successive high tides (Lenanton et al., 1982; Robertson & Hansen, 1982), the remainder forms both a primary food source for the beach's supralittoral fauna (Griffiths et al., 1983) and also may constitute an important source of nutrients for nearshore production. In addition, algal material stranded above the

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extreme high water mark may be partially fragmented and leached, a proportion passing into the beach sediment where it enters the interstitial food chain (McLachlan, 1983).

The processes responsible for the breakdown of coarse particulate matter on sandy beaches have received little investigation. The supralittoral macrofauna of such beaches can reach a considerable biomass (Griffiths & Stenton-Dozey, 1981; Behbehani & Croker, 1982; Griffiths et al., 1983; Stenton-Dozey & Griffiths, 1983) and, in temperate areas, is usually dominated by talitrid amphipods. Although stranded algal material may form a large proportion of the diet of many supralittoral amphipods and isopods (MacIntyre, 1954; Hayes, 1974; Koop & Field, 1980; Behbehani & Croker, 1982), there is little direct evidence showing the contribution of these animals to the breakdown of kelp wrack. To date, most estimates have been based upon laboratory studies and community consumption estimated from standing stock densities (Griffiths & Stenton-Dozey, 1981; Koop & Field, 1980; Koop & Griffiths, 1982; Griffiths et al. 1983; Koop & Lucas, 1983; Stenton-Dozey & Griffiths, 1983). Such studies can seriously over- or underestimate the actual influence that the animals have in fragmenting the kelp on the beach as they neglect the contribution of weathering and biotic interaction to kelp breakdown.

To investigate the processes involved in the degradation of plant material on the beach, experimental manipulations within field conditions are needed.

The present study examined the degradation rate of the kelp *Macrocystis pyrifera* (L.) C. Ag. from litter bags in the supralittoral zone of South Brighton beach, New Zealand. Although a brief account of the supralittoral fauna of this site was given in MacIntyre (1963), the complete fauna was not described. The most conspicuous component is the burrowing talitrid amphipod *Talorchestia quoyana* (Milne-Edwards) which occurs in densities of $>50\ m^{-2}$ beneath debris and wrack at the high tide level. Successional changes were followed in the wrack fauna in bags of different mesh sizes to identify the role of particular faunal components in the breakdown of the kelp. In addition, laboratory experiments were undertaken in the absence of beach animals to follow the rate of algal disintegration in a constant environment.

Materials and Methods

STUDY SITE

Field experiments were undertaken on the ocean beach of South Brighton Spit, at the southern end of Pegasus Bay, Canterbury, New Zealand. This is a moderately exposed sandy beach composed of medium quartz sands of particle diameters 85–300 μm (MacIntyre, 1963). The beach is backed for most of its length by a well developed, stable dune system which forms the upper limit to spring tide wave wash.

Wrack deposits on the beach are almost exclusively composed of the large brown algae *Macrocystis pyrifera* and the bull kelp *Durvillaea antarctica* (Chamisso) Hariot. The input of these algae fluctuates widely but is generally greatest following southeasterly

storms. During January 1986, the standing stock of algal wrack on South Brighton beach ranged between 0.5–4.0 $kg \cdot m^{-1}$ (wet weight).

FIELD STUDIES

Coarse-mesh litter bags, 250 × 200 mm length were constructed of plastic mesh with a 5 × 8-mm aperture. These were designed to allow all of the supralittoral zone fauna access to the enclosed kelp material. Finer mesh sizes were achieved by enclosing a coarse-mesh litter bag, containing the kelp, within a larger nylon bag of either 1-mm or 85-μm aperture width. These bags were designed to exclude the sandy beach macro- and meiofauna, respectively.

Two successive experimental trials were done between March and April 1986. Air temperature during this period ranged from a daytime high of 27 °C to a nighttime low of 2 °C. Each trial ran for 18 days and was set up on the retreating spring tide. In the first trial, loss of kelp dry weight was compared between coarse-mesh bags and 1-mm mesh bags, whilst, in the second trial, coarse-mesh and 85-μm mesh bags were compared.

Fresh *Macrocystis* was collected, blotted dry, and 50-g wet weight portions of laminae and pneumatocysts placed within the coarse-mesh bags. Treatments (i.e., mesh size) were assigned randomly. Five bags of each mesh size were randomly positioned in areas around EHWS from which existing wrack had been removed. Each bag was then lightly covered with sand.

Litter bags were retrieved after 1, 3, 9, and 18 days in the field. The associated fauna was retained by enclosing each bag within a 30 × 30-cm plastic container. Insecticide was then sprayed through a hole into the container and, after ≈ 5 min, the litter bag and any visible fauna transferred to a plastic bag. An area of sand 30 × 30 cm beneath the litter bag was excavated to a depth of 10 cm and sieved through a 1-mm mesh to recover the burrowing elements of the macrofauna.

In the laboratory the content of each litter bag was gently washed onto a 0.25-mm sieve to remove the adhering sediment and surface fauna. The remaining algal material was then dried for 3 days at 60 °C and weighed. Final results were expressed as the percentage of initial kelp dry weight remaining and were analysed using ANOVA. Initial weight values were obtained by drying and weighing five replicates of 50-g portions of fresh *M. pyrifera* tissue.

THE FAUNA

Washings from the kelp surface were retained and concentrated onto an 85-μm mesh net. These samples were then turned onto a glass Petri dish and counts of the animals made under a dissecting microscope.

Macroinvertebrates from the samples were sorted, preserved in 10% formalin in seawater, identified and counted.

LABORATORY EXPERIMENT

The use of litter bags in decomposition studies has a disadvantage in that the bags themselves, particularly the smaller mesh sizes, may provide a more favourable microhabitat for decomposition than is normally experienced by maintaining high internal humidity and temperature. To investigate this effect, a series of litter bags identical to those used in the field were incubated in a constant temperature (20 °C) environment in the absence of any animals. The litter bags were placed within 110 × 35-cm trays in sand from which the interstitial biota had been removed and the trays put in a constant temperature cabinet under a L : D 12 : 12 light regime. After 24 days, the kelp was recovered, dried and weighed. Humidity within the bags was estimated using cobalt thiocyanate papers.

Kelp dry weight loss was expressed as the percentage of initial dry weight remaining at the completion of the experiment and results analysed using ANOVA.

RESULTS

KELP BREAKDOWN

Significant weight loss occurred in bags of all mesh sizes (Table I). The pattern of weight loss was similar in both trials (Fig. 1) and the algae disintegrated in an approximately linear fashion for much of the experimental period. Within 18 days, material within the litter bags had lost between 41–64% of its initial dry weight. Material in the coarse-mesh and 1-mm mesh bags in the first trial fragmented at about the same rate, as did tissue in the coarse- and 85-μm mesh bags in the second trial (Table I). Exclusion of the fauna, therefore, appeared to have had little effect on the rate of kelp breakdown.

TABLE I

Analysis of the proportion (arcsine transformation) of kelp dry weight remaining in the litter bags of different mesh sizes (Mesh) on four sampling occasions (Days): data are for five sites (Sites) on South Brighton Beach.

Sources of variation	Trial 1				Trial 2		
	df	MS(×100)	*F* ratio	*P*	MS(×100)	*F* ratio	*P*
Days	3	30.7	11.0	<0.01	66.7	31.8	<0.01
Mesh size	1	5.7	2.0	>0.05	0.2	0.0	>0.05
Site	4	1.4	0.3	>0.05	1.4	0.1	>0.05
Days × Mesh	3	1.3	0.3	>0.05	2.7	0.2	>0.05
Days × Site	12	2.8	0.6	>0.05	2.1	0.2	>0.05
Mesh × Site	4	2.8	0.6	>0.05	5.1	0.4	>0.05
Days × Mesh × Site							
Nonadditivity	1	1.8	0.6	>0.05	8.1	2.1	>0.05
Balance	11	3.1			3.9		

Arcsine transformation of the data failed to remove significant error variance heterogeneity in the second trial (Cochran's statistic $C = 0.4$, $v = 4$, $k = 8$; $0.01 < P < 0.05$). Toward Day 18, there was a noticeable increase in the variability of material recovered

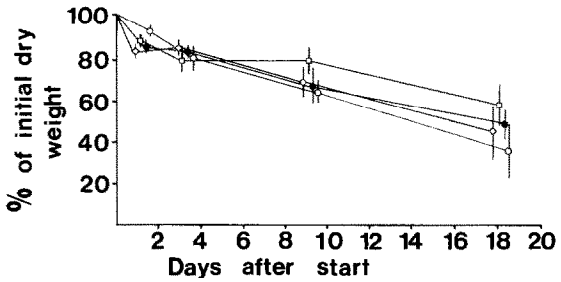

Fig. 1. Changes in the mean dry weight (± 1 SE) of *Macrocystis pyrifera* blades in litter bags secured in the supralittoral zone of South Brighton Beach: ●, coarse mesh bags in the first trial; ◇, coarse mesh bags in the second trial; □, 1-mm mesh bags in the first trial; ○, 85-μm mesh bags in the second trial.

from the litter bags. At this time the *Macrocystis* blades showed a tendency to laminate and, therefore, loss of fine particulate material was likely to be more variable than on earlier sampling dates. Although such heterogeneity of variances can lead to an increased probability of Type I error (Underwood, 1981), it may not have influenced the conclusions of this analysis because the sampling date factor was also significant in the first trial, where treatment variances were deemed to be homogenous ($C = 0.26$, $v = 4$, $k = 8$; $P > 0.05$).

In the laboratory, losses of kelp dry weight were, similarly, unaffected by the mesh size of the litter bags (Table IIa). In the absence of animals and in constant environmen-

TABLE II

(a) Comparison of the proportion of initial kelp dry weight remaining in litter bags of different mesh sizes (Mesh) after 24 days incubation in the laboratory. (b) Humidity readings from within the bags are presented below.

a

Sources of variation	df	MS(× 100)	*F* ratio	*P*
Mesh size	2	12.5	0.52	> 0.05
Error	12	24.0		
Total	14			

b

	Litter-bag treatment		
	CM	1 mm	85 μm
Median relative humidity (%)	95	92.5	95
Range	(95–95)	(85–95)	(85–100)

tal conditions, the algal material lost between 32–41% of its original dry mass in 24 days. Relative humidity was uniform between bags of different mesh types (Table IIb) but may be below that normally experienced in the field, where interstitial moisture retains the moisture in wrack deposits.

THE FAUNA

The wrack community structure, represented by the pooled samples, is given in Table III. 22 macrofaunal species were distinguished, 15 of which were identified to the species or generic level. Collectively, six species made up 93% of the individuals in the macrofaunal community. These were: the talitrid amphipod, *Talorchestia quoyana*; the dipteran, *Leptocera (Limosina) aucklandica* Harrison; the centipede, *Nesogeophilus xylophagus* (Attems); and the beetles, *Lagrioida brouni* Pascoe, *Sitonia humeralis* Stephens, and *Bledius* sp.

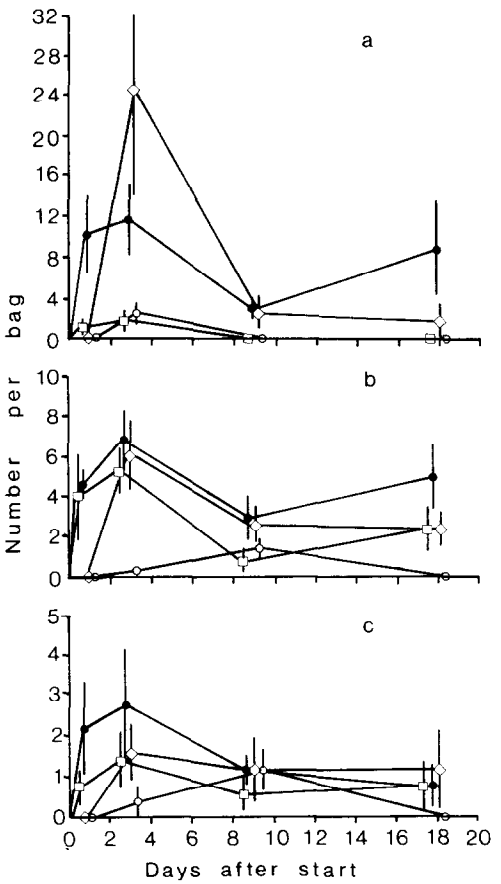

Fig. 2. The mean number (± 1 SE) of (a) amphipods, (b) Coleoptera, and (c) centipedes per litter-bag sample: ●, coarse mesh bags in the first trial; ◇, coarse mesh bags in the second trial; □, 1-mm mesh bags in the first trial; ○, 85-μm mesh bags in the second trial.

TABLE III

Percent composition and total numbers of macroinvertebrate animals found in samples collected with the litter bags. Numbers are the pooled samples over all mesh types and dates.

	Total number	% of community
Amphipoda		
Talorchestia quoyana (Milne-Edwards)	319	27.22
Diptera		
Sphaeroceridae		
Leptocera (Limosina) aucklandica Harrison	533	47.18
Tachinidae		
Mallochomacquartia sp.	2	0.17
Tethinidae		
Tethinosoma fulvifrons (Hutton)	3	0.26
Therevidae		
Anabarynchus bilineatus (Fabricius)	15	1.28
Coleoptera		
Curculionidae		
Sitonia humeralis Stephens	37	3.16
Elateridae		
Two unidentified species	2, 1	0.26
Oedemeridae		
Thelyphassa diaphana Pascoe	1	0.08
Ptiliidae		
Unidentified species	3	0.26
Salpingidae		
Lagrioida brouni Pascoe	59	5.03
Scarabaeidae		
Pericoptus truncatus (Fabricius)	11	0.94
Scydmaenidae		
Unidentified species	2	0.17
Staphylinidae		
Bledius sp.	49	4.18
Cafius littoreus Brown	5	0.43
Tenebrionidae		
Actizeta albata Pascoe	1	0.08
Trogossitidae		
Phycosecis atomaria Pascoe	18	1.54
Hemiptera		
Lygaeidae		
Nysius huttoni Buchanan-White	8	0.68
Hymenoptera		
Formicidae		
Hipoponera eduardi (Forel)	1	0.08
Geophilomorpha		
Geophilidae		
Nesogeophilus xylophagus (Attems)	78	6.66
Juliformia		
Julidae		
Ophyiulus pilosus (Newport)	2	0.10

Highest densities of most macrofaunal animals were found within 3 days of the bags being placed in the field. Notable exceptions to this pattern were the predatory coleoptera and the centipede *Nesogeophilus xylophagus* which were equally as abundant at Day 18.

Examination of the wrack tissue suggested that *Talorchestia quoyana* was likely to be the most important of the macrofaunal consumers. Circular holes, with diameters of between 1 and 5 mm, were found on blades recovered from the coarse-mesh bags. In the 1-mm and 85-μm mesh sizes *Talorchestia* numbers were effectively reduced (Fig. 2a) and no evidence was found of feeding. Amphipod abundance in the samples of both

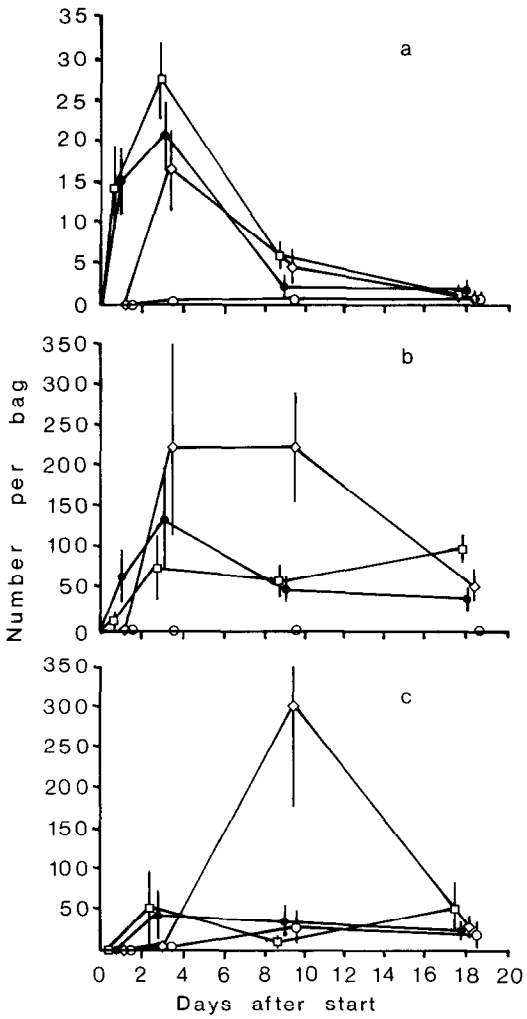

Fig. 3. The mean number ($\pm$ 1 SE) of dipteran (a) adults, (b) eggs, and (c) larvae per litter-bag sample: ●, coarse mesh bags in the first trial; ◇, coarse mesh bags in the second trial; □, 1-mm mesh bags in the first trial; ○, 85-μm mesh bags in the second trial.

trials varied throughout the experiment but was greatest within 3 days of the bags being placed in the field.

The numbers of Coleoptera (Fig. 2b), dipteran adults (Fig. 3a), and dipteran eggs (Fig. 3b) were also consistently greatest within 3 days of the start of the experiment. However, some members of the Coleoptera (notably *Bledius* sp.) were found in reasonable numbers at Day 18.

A large proportion (23.15%) of the coleopteran collection was composed of small staphilinids of the genus *Bledius*. The small size and dorso-ventrally flattened body shape of these beetles enabled them to gain access to the bags through the 1-mm mesh. They were, however, excluded by the 85-μm mesh size.

Nesogeophilus xylophagus showed no definite patterns of abundance during the sampling period. It was frequently encountered (Fig. 2c) and is capable of rapidly colonising recent deposits of wrack.

Dipteran numbers were dominated by the small sphaeroceridoid *Leptocera (Limosina) aucklandica*, and the variation in numbers in Fig. 3 reflects the abundance of this animal. Adult colonisation of the bags was early, peaking on Day 3 and dropping to a mean of between 1–6 individuals per bag at Day 9. *L. aucklandica* adults could enter and oviposit through the coarse-mesh and 1-mm mesh bags, but were restricted from entering the 85-μm litter bags.

Dipteran eggs and larvae, other than those of the robber fly *Anabarynchus bilineatus* (Fabricius), are small and numbers could only be ascertained from the meiofaunal samples. The composition of the meiofaunal community is summarised in Table IV.

Dipteran eggs were found on the kelp lamina surface from Day 1 to 18, but were most abundant within the first 3 days. This corresponds with the peak in adult abundance. Oviposition appears to have been hindered by the 85-μm mesh litter bags, as few eggs were recorded in these samples (Fig. 3b). However, the data shown in Fig. 3c do not corroborate this observation. Indeed, the number of dipteran larvae on the kelp surfaces was not reduced within the 1-mm or the 85-μm mesh sizes. The number of larvae found on the kelp blades was highly variable and no clear temporal pattern of colonisation was discernable.

TABLE IV

Percent composition and total numbers of meiofaunal animals collected from the kelp surface from within the litter bags. Numbers are the pooled samples over all mesh types and dates.

	Total number	% of community
Nematodes	50360	85.33
Enchytraeid oligochaetes	1691	2.86
Dipteran larvae	2805	4.76
Acarina	3360	5.69
Collembola	801	1.36
Total	59017	

Numerically, nematodes dominated the wrack fauna (Table IV). Their numbers increased dramatically after Day 9 in the coarse bags, and after Day 3 in the 85-μm mesh bags (Fig. 4a). In total, nematodes comprised $>85\%$ of the meiofaunal community. Their abundance was not reduced by the 85-μm mesh. Indeed, greater

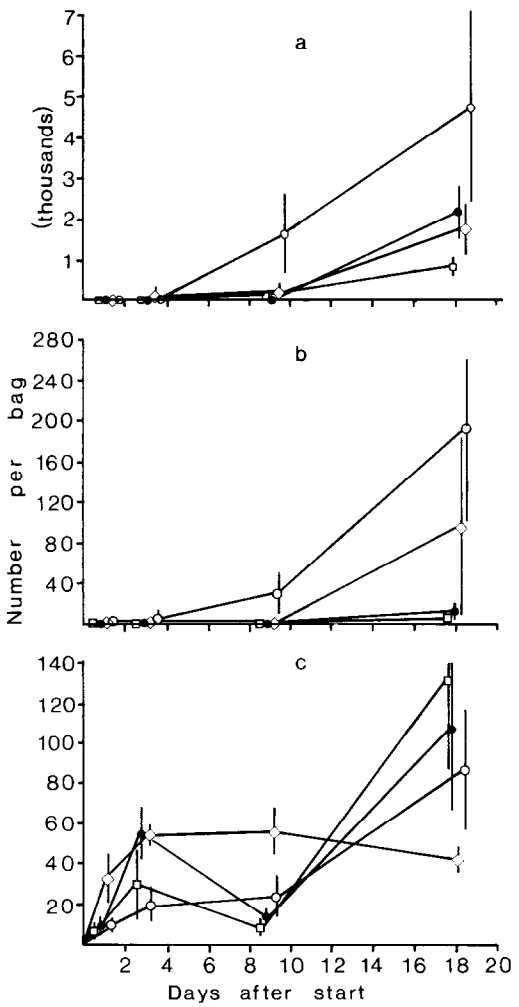

Fig. 4. The mean number ($\pm$ 1 SE) of (a) nematodes, (b) enchytraeid oligochaetes, and (c) mites per litter-bag sample: ●, coarse mesh bags in the first trial; ◇, coarse mesh bags in the second trial; □, 1-mm mesh bags in the first trial; ○, 85-μm mesh bags in the second trial.

densities of nematodes were recorded within this mesh size than in the larger mesh bags. This was also the situation with enchytraeid oligochaetes which were found in greatest numbers after Days 9 and 18 where they were consistently more abundant within the 85-μm mesh bags.

Acarina were found on the kelp surface throughout the sampling period but were characteristically found in greatest numbers when the kelp was in an advanced state of decay. Again, the 85-μm mesh bags proved ineffective in restricting access of the mites to the kelp surface and, therefore, it is inappropriate to draw any conclusions on the role of the meiofauna in the loss of litter from the bags on the basis of the exclusion technique alone.

Although Collembola constituted 1.36% of the meiofaunal numbers (Table IV), their occurrence within the litter bags was sporadic, and was limited to fewer than eight bags in total.

Discussion

The insignificance of macrofaunal involvement in the breakdown of kelp in this study supports the findings of Koop & Lucas (1983) whose calculations from a microcosm involving *Eklonia maxima* suggest that $<9\%$ of the kelp tissue is consumed by grazers, the bulk of the weight loss being attributed to microbial decomposition and abiotic trituration. This contrasts with studies by Griffiths & Stenton-Dozey (1981) who have estimated that supralittoral scavengers removed 60–80% of the organic input to their study site in South Africa.

The breakdown of plant material is heavily influenced by both site- and time-specific environmental conditions (Tenore et al., 1984). These may manifest themselves not only in abiotic fragmentation of the plant material, but also in the structure and function of the local consumer assemblage and in the rate at which the plant material is decomposed by microbial components at a specific site. This spatial and temporal variability in decomposer systems highlights the need for empirical field tests of the importance of consumers in the cycling of organic matter at any given location. Attempts to extrapolate laboratory-derived consumption rates in an effort to explain a field situation are often insufficient to describe the true role of macroconsumers in decomposition processes.

Aside from consumption, the feeding activities of detrital consumers can accelerate the decomposition of plant material through the spread of microorganisms (Frankland, 1974), or by maintaining the surface microbial community in a youthful state (Smith et al., 1982). In addition, sediment-living organisms can make the material more available for decomposition through their burrowing activities. Bedford & Moore (1984) have shown that feeding by the amphipod *Gammarus locusta* may even inhibit algal decomposition by the selective removal of rotting weed. In the laboratory it is often difficult to recreate the variable conditions of temperature, moisture, food availability and biotic interaction that are present in the field and which can all have a potential bearing on the disintegration of plant matter.

With the use of litter bag techniques it may be argued that exclusion of one element of the biota could result in a change in the functional role of a second, nonexcluded assemblage. This is unlikely to have affected the conclusions of this study because the

scavenging macro- and meiofauna inhabited the wrack at different instances and are, therefore, unlikely to have significantly affected each other. Even if the observed increase in meiofaunal numbers in the 85-μm mesh bags resulted from a release in predation pressure by macrofaunal species, this does not appear to have had any affect on the rate of kelp degradation.

In describing the decomposition of salt marsh grasses, Valiela et al. (1985) identified three distinct phases. Initially, organic matter was lost at a fast rate corresponding largely to the leaching of hydrolysed compounds from the plant material. This was then followed by two phases where weight loss became successively slower. Decomposer activity was said to be the major source of weight loss in the second stage, whilst the slower decay of refractory materials characterised the third. Within the course of the present experiment this pattern was not obvious. Loss of algal dry weight from the litter bags was essentially linear, despite distinct temporal changes in the wrack fauna. Tenore et al. (1984) have suggested that algal detritus does have a decay resistant fraction. However, on South Brighton Beach, spring tidal inundation flushes the entire beach face to the level of the shoreward dunes (pers. obs.) so that any such refractory materials are washed back into the surf zone, making them no longer available to the supralittoral community.

Grazing of amphipods and other detritivores accelerates the decomposition of vascular plant material not only by the mechanical action of fragmenting tissue (Harrison, 1977; Robertson & Mann, 1980) but, alternatively, by selectively grazing the microbiota, leading to a general increase in the community metabolism (Smith et al., 1982). In marine angiosperms, where structural polysaccharides and a low proportion of available nitrogen make the tissue considerably refractory, such an effect is often detectable. In contrast, algal tissue decomposes rapidly in the absence of animals and its rate of disintegration may even be inhibited by their activities (Bedford & Moore, 1984). When compared with vascular plants, algae are commonly high in nitrogen and other soluble substances, and the leaching of carbohydrates and nonstructural proteins may account for much of their loss in mass following death (Rice & Tenore, 1981; Williams, 1984).

The observed successional changes in the wrack fauna of this study are characteristic of drift line communities. The lack of in situ primary production on sandy beaches means that these consumers must rely on organic inputs that arrive via the surf-zone. Many of the macrofaunal species undergo tidal migrations of some sort that allow them to feed on freshly stranded debris (Benson & Lewis, 1976; Brown, 1983; McLachlan, 1983). As a consequence, the population dynamics (Hayes, 1974; Koop & Field, 1980; Behbehani & Croker, 1982) and daily tidal migrations of many of the species are associated with maximising utilisation of the food resources. Indeed, my observations show that a small proportion of the material deposited on sandy beaches remains for sufficient time for it to reach an advanced state of decay.

Talitrid amphipods are generally considered to be primary wrack colonisers and, in temperate areas, often dominate the supralittoral fauna of beaches with a moderate

macrodebris input (MacIntyre, 1963; Griffiths & Stenton-Dozey, 1981; Behbehani & Croker, 1982; Stenton-Dozey & Griffiths, 1983).

The adults of sandy beach kelp flies are likely to be insignificant consumers of kelp (Griffiths & Stenton-Dozey, 1981) because their activities are limited to feeding on exuded substances and laying eggs. The larvae, however, may contribute greatly to the breakdown of kelp tissue as a result of their own feeding activity and through the spread of microorganisms (Stenton-Dozey & Griffiths, 1980).

From these inital investigations, *Leptocera (Limosina) aucklandica* apparently has a pattern of development similar to that of the South African kelp fly, *Fucellia capensis*. Adults lay ova on material deposited by the spring tide and the larvae mature before the next high-water spring tide (Stenton-Dozey & Griffiths, 1980).

Nematodes and enchytraeids numerically dominated the wrack fauna in the later stages of decay. By virtue of their numbers alone, both nematodes and enchytraeids may be of considerable importance in reworking and triturating kelp debris (Giere & Pfannkuche, 1982) and their activity can stimulate bacterial metabolism leading to the rapid decay of plant tissue (Heip et al., 1982). Both of these groups were found in greatest numbers when the density of the saprophagous microbial community was greatest (pers. observation), although it is not clear if they were directly grazing the microbiota or if the latter facilitated the phytophagy of the former.

Microbial utilisation of carbon and nitrogen from wrack deposits has been estimated at 28 and 94% of the original values, respectively (Koop & Lucas, 1983). The lack of a rigid vascular system and the relatively high proportion of soluble nitrogen in the tissues of brown algae (Albright et al., 1982) means that the material is more readily available to microbial decomposers and does not require the mechanical and enzymatic action of macroconsumers to facilitate saprophytic decay. Microorganisms are thus likely to be of primary importance in the breakdown of seaweeds stranded in the supralittoral zone of sandy beaches.

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