

**Stranded *Zostera marina* L.
vs wrack fauna
community interactions
on a Baltic sandy
beach (Hel, Poland):
a short-term pilot study.
Part II. Driftline effects
of succession changes
and colonisation of
beach fauna***

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Abstract

This paper evaluates the second part of a three-year field study to investigate the effects of the beach macro- and meiofauna community structure on the decay of stranded wrack on Hel Beach (see Jędrzejczak 2002), focusing on successional changes and the colonisation of wrack by beach fauna. The investigation enabled the associated faunal assemblages to be characterised. *Zostera marina* tissue was colonised by the supralittoral fauna in two distinct phases. The macrofauna, including the talitrid amphipod *Talitrus saltator*, adult Diptera and Coleoptera, colonised the wrack within a day, with maximum numbers being recorded after 3 days. Thereafter, their numbers in the samples declined and the meiofauna, consisting of nematodes, oligochaetes, turbellarians and dipteran larvae, became

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increasingly abundant. After 18 days, the wrack surface was dominated by meiofauna. This faunal succession was not directly related to the degradation of the seagrass tissue, which proceeded linearly throughout the study period. Exclusion of macrofauna from the wrack by the use of < 1 mm mesh litterbags had no appreciable effect on the rate of dry matter loss. Therefore, the major macrofaunal wrack consumers, including *T. saltator* and Coleoptera, did not affect the rate of seagrass disintegration. The effect of meiofaunal nematodes, oligochaetes, gastrotrichs and turbellarians on wrack breakdown could not be accurately determined. However, the development of the meiofaunal community suggested that changes in the fauna community were linked more closely to successional changes in the chemistry and/or microflora of the beach wrack than to its physical breakdown.

1. Introduction

In many parts of the world, sandy beaches receive large inputs of drift macroalgae, for instance in New Zealand (Inglis 1989), South Africa (Griffiths & Stenton-Dozey 1981), New England (Behbehani & Croker 1982), Australia (Lenanton et al. 1982), and on the Virgin Islands (Williams 1984). However, little is known about the changes in beach wrack quality in relation to the activity of beach organisms on Polish coasts. Stranded debris may provide food and shelter for both aquatic and terrestrial animals. Because of the insects and other organisms that are attached to it, this beach wrack is an important foraging area for shorebirds (Brown & McLachlan 1990). The supralittoral macrofauna 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 (Scapini 1997, Fallaci et al. 1999, Colombini et al. 2000, Nardi et al. 2000, Węśławski et al. 2000a, b, Persson 2001). Although stranded algal material may form a large proportion of the diet of many supralittoral amphipods, isopods and dipteran larvae (Koop & Field 1980, Stenton-Dozey & Griffiths 1980, Behbehani & Croker 1982, Marsden 1991a, b), there is little evidence for the direct contribution of these animals to wrack breakdown. The variations in distribution, composition and structure of sandy beach communities have been related to changes in environmental parameters and to beach morphodynamics. The supralittoral zone, which supports predatory insects, can be readily divided into subzones based on the reach of the tide (Moore & Legner 1976). The subzones fall into three categories: (1) the area wetted by daily tides, (2) the area wetted by only one or two high tides a month, and (3) the berm of the beach, reached only by the highest tides of the year. The insect distribution shows that this subzonation is most apparent on sandy beaches where subzone (1) contains fresh seaweed and nocturnal staphylinids, subzone (2) consists of

decaying seaweed and diurnal species, and subzone (3) has dry seaweed and no staphylinids but other Coleoptera.

Even so, sandy beaches are by no means homogeneous habitats. Not only do they reflect the typical small-scale patchiness of the marine benthos, they also frequently display important shifts in community structure and biodiversity along their slope. Unfortunately, information regarding such shifts on sandy beaches is extremely scanty. To date, most estimates have been based upon laboratory studies and community consumption calculated from standing stock densities (Koop & Field 1980, Griffiths & Stenton-Dozey 1981, Koop & Griffiths 1982, Griffiths et al. 1983, Koop & Lucas 1983, Stenton-Dozey & Griffiths 1983). However, such studies can seriously over- and/or underestimate the actual influence that this fauna has in fragmenting wrack on the beach, neglecting as they do the contribution of weathering and leaching as well as that of biotic interaction to the breakdown of organics (Inglis 1989). Beach community densities too have been analysed in numerous studies; nevertheless, the processes involved in the degradation of organics on the beach need to be investigated by means of experimental manipulation under field conditions. Hence, it is not surprising to find that the links between such diversity patterns and the functioning of sandy beaches remain unknown.

A recent paper motivated by the LITUS Project considered beach wrack breakdown by the fauna associated with this kind of debris in the light of the processes (colonisation, species succession, predation) occurring in these wracks on sandy beaches. The hypothesis is that the rate of seaweed breakdown on the shore is directly related to the successional stages of the different faunal assemblages. Although Haque et al. (1996, 1997a, b), Kotwicki (1997), Kotwicki et al. (1999) and Węśławski et al. (2000a, b) have given brief accounts of the supralittoral fauna at the study site, a full description of the fauna has yet to be written. Its most conspicuous component is the burrowing talitrid amphipod *Talitrus saltator* (Montague), which occurs in all zones of the beach in average densities of 30–60 ind m⁻²; these rise to over 360 ind m⁻² beneath debris and wrack at the strandline (Węśławski et al. 2000a). The aim of the present study was to discover how, when and where wrack is colonised by invertebrates. Successional changes in the wrack fauna were traced using bags of different mesh sizes in order to identify the part played by the various faunal components in the wrack breakdown.

2. Materials and methods

The present study was a continuation of the evaluations described in Part I (Jędrzejczak 2002), carried out at the same time and the

same Hel Beach site (54°36'N, 18°49'E). Two parallel experimental trials using litterbags containing *Zostera marina* tissue were carried out in the strandline zone of the beach. 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 c. 5 min, the litterbag and any visible fauna transferred to a plastic bag. An area of sand 30 × 30 cm beneath the litterbag was excavated to a depth of 10 cm. This sand was passed through a 1-mm mesh sieve to recover the burrowing specimens of macrofauna and through a 48- μ m mesh sieve to recover the meiofauna.

In the laboratory the content of each litterbag was gently rinsed onto a 0.25-mm sieve to remove adhering sediment and surface fauna. The washings from the wrack surface were retained and concentrated onto a 48- μ m mesh net. Macroinvertebrates from the samples were sorted, preserved in a 10% solution of formalin in seawater, identified and counted. Meiofaunal assemblages were also processed by the same method using Bengal Rose to stain individual specimens. These samples were then turned onto a glass Petri dish so that the specimens could be counted under a dissecting microscope.

3. Results

The wrack macrofauna, represented by the pooled samples, is set out in Table 1. 30 macrofaunal species were distinguished, 24 of which were identified to the species or generic level. Collectively, 13 species made up > 95% of the individuals in the macrofaunal community. These were: *T. saltator* – a talitrid amphipod, *Fucellia tergina* – a dipteran, *Geophilus* sp. – a centipede, *Stenus biguttatus* and *Paederus litoralis* – staphylinid beetles, *Ptenidium pusillum* – a ptiliid, *Hister quadrinotatus* – a histerid, anthicids, and *Coccinella septempunctata*, *Paramysia oblongoguttata* and *Coccinula quatuordecimpustulata* – coccinellids.

The highest densities of most macrofaunal animals were found within 3 days of the bags being placed on site. Notable exceptions to this pattern were the predatory Coleoptera (above all Coccinellidae) and the centipedes, which were equally abundant on Day 27.

Examination of the wrack tissue suggested that *T. saltator* was likely to be the most important of the macrofaunal consumers. Circular holes with diameters of between 1 and 5 mm were found on leaves recovered from the coarse-mesh bags. In the 0.5-mm and 48- μ m mesh sieves numbers of *Talitrus* were lower (Fig. 1a) and no evidence was found of feeding. Amphipod abundance in the samples of both trials varied throughout the experiment but was greatest within 3 days of the bags being deployed.

Table 1. Percentage composition and total numbers (N) of macroinvertebrates found in the litterbag samples. The figures are the samples pooled over all mesh types and dates from all monthly study periods

	1999		2000		2001	
	N	% of community	N	% of community	N	% of community
Amphipoda						
<i>Talitrus saltator</i> (Montague)	1285	24.87	1309	22.07	1242	23.14
Diptera						
Anthomyiidae						
<i>Fucellia tergina</i> (Zett.)	289	5.59	532	8.97	481	8.96
Coleoptera						
Staphylinidae						
<i>Stenus biguttatus</i> L.	431	8.34	383	6.46	326	6.07
<i>Paederus litoralis</i> (Graw.)	621	12.02	782	13.19	534	9.95
Ptiliidae						
<i>Ptenidium pusillum</i> (Gyll.)	958	18.54	1026	17.30	1048	19.53
Histeridae						
<i>Hister quadrinotatus</i> Scriba	621	12.02	582	9.81	703	13.10
Tenebrionidae						
2 unidentified species	5	0.10	12	0.20	6	0.11
Curculionidae						
<i>Sitonia</i> sp.	21	0.41	53	0.89	38	0.71
Anthicidae						
3 unidentified species	121	2.34	105	1.77	162	3.02
Chrysomelidae						
<i>Leptinotarsa decemlineata</i> (Say.)	62	1.20	31	0.52	58	1.08
Coccinellidae						
<i>Coccinella septempunctata</i> L.	352	6.81	651	10.98	282	5.25

Table 1. (continued)

	1999		2000		2001	
	N	% of community	N	% of community	N	% of community
<i>Coccinula quatuordecimpustulata</i> (L.)	125	2.42	158	2.66	154	2.87
<i>Paramysia oblongoguttata</i> L.	102	1.97	95	1.60	88	1.64
<i>Anatis ocellata</i> (L.)	31	0.60	51	0.86	38	0.71
<i>Adalia bipunctata</i> (L.)	16	0.31	20	0.34	38	0.71
<i>Amphidecta oblitterata</i> (L.)	21	0.41	5	0.08	18	0.34
<i>Adonia variegata</i> (Goeze)	14	0.27	28	0.47	12	0.22
<i>Subcoccinella vigintiquatuorpunctata</i> (L.)	2	0.04	–		4	0.07
<i>Chilocorus bipustulatus</i> (L.)	2	0.04	–		–	
<i>Scymnus frontalis</i> (F.)	–		1	0.02	–	
<i>Exochomus quadripustulatus</i> (L.)	1	0.02	–		2	0.04
Cincindelidae						
<i>Cincindela campestris</i> L.	3	0.06	7	0.12	5	0.09
Carabidae						
Unidentified species	10	0.19	12	0.20	15	0.28
Hemiptera						
Saldidae						
<i>Saldula saltatoria</i> (L.)	10	0.19	16	0.27	12	0.22
Chilopoda						
Geophilidae						
<i>Geophilus</i> sp.	52	1.01	61	1.03	78	1.45
<i>Clinopodes flavidus</i> (Koch)	–		4	0.07	2	0.04
Scolioplanidae						
<i>Scolioplanes</i> sp.	12	0.23	6	0.10	21	0.39
Total	5167		5930		5367	

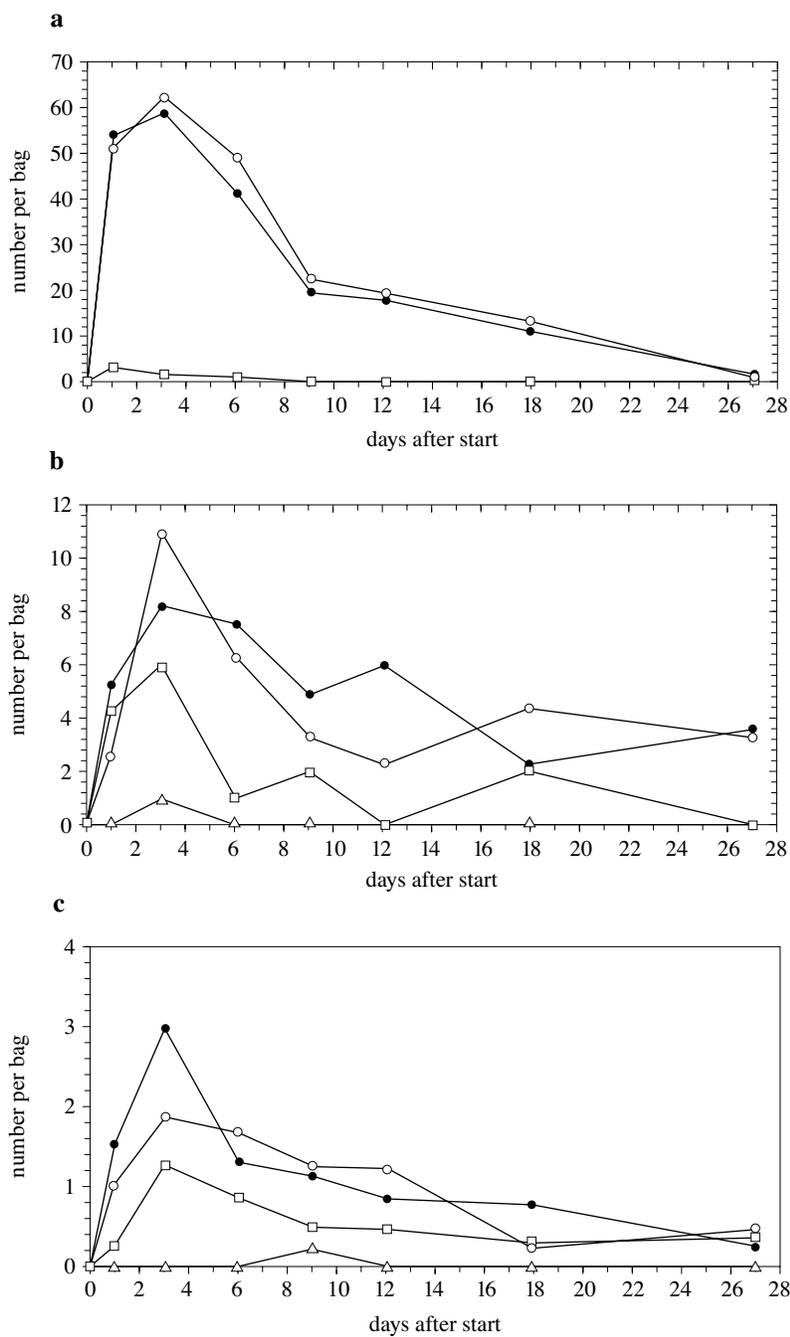


Fig. 1. The mean number of amphipods (a), Coleoptera (b), and centipedes (c) per litterbag sample: coarse mesh bags in the first trial (●-●); coarse mesh bags in the second trial (○-○); 0.5-mm mesh bags in the first trial (□-□); 48-µm mesh bags in the second trial (△-△)

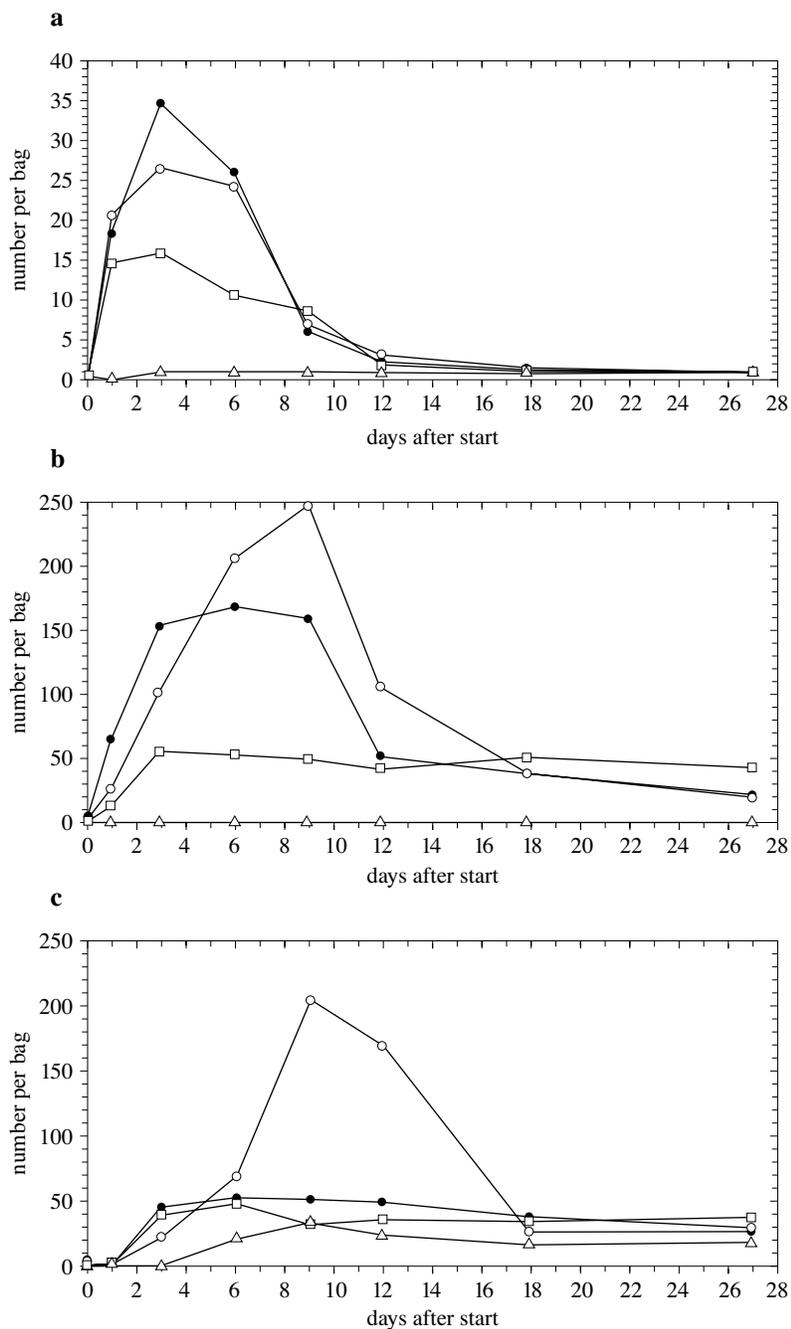


Fig. 2. The mean number of dipteran adults (a), eggs (b), and larvae (c) per litterbag sample: coarse mesh bags in the first trial (●-●); coarse mesh bags in the second trial (○-○); 0.5-mm mesh bags in the first trial (□-□); 48-μm mesh bags in the second trial (Δ-Δ)

The numbers of Coleoptera (Fig. 1b), dipteran adults (Fig. 2a), and dipteran eggs (Fig. 2b) were also consistently highest within 3–6 days of the start of the experiment. However, some members of the Coleoptera, notably the staphylinids, ptiliids and predatory beetles, were found in moderate numbers on Days 18–27. In addition, *H. quadrinotatus* occurred in the wrack during the final days of the experiment.

A large proportion (27.84%) of the coleopteran collection was composed of small staphylinids of the genera *Stenus* and *Paederus*. Their small size enabled them to gain access to the bags through the 0.5-mm mesh. They were, however, excluded by the 48- μ m mesh.

The abundance patterns of the centipedes were similar to those of the talitrids and coleopterans during the sampling period. Encountered frequently (Fig. 1c), they are capable of rapidly colonising recent deposits of wrack.

The Diptera were dominated by the small anthomyiid *F. tergina*, and the variation in numbers in Fig. 2 reflects its abundance. Adult colonisation of the bags was early, peaking on Day 3 and dropping to a mean of between 3 and 9 individuals per bag by Day 9. *F. tergina* adults could enter and oviposit through the coarse-mesh and 0.5-mm mesh bags, but were unable to penetrate the 48- μ m litterbags.

Dipteran eggs and larvae are small and numbers could only be ascertained from the meiofaunal samples. The composition of the meiofaunal community is summarised in Table 2 (wrack surface) and in Table 3 (sand beneath the debris).

Table 2. Percentage composition and total numbers (N) of meiofauna collected from seagrass surfaces inside the litterbags. The figures are the samples pooled over all mesh types and dates from all study periods

	N	% of community
Nematoda	3411070	59.56
Oligochaeta	72576	1.27
Turbellaria	975240	17.03
Gastrotricha	854230	14.91
dipteran larvae	193536	3.38
Acarina	185976	3.25
Collembola	34776	0.61
Total	5727404	

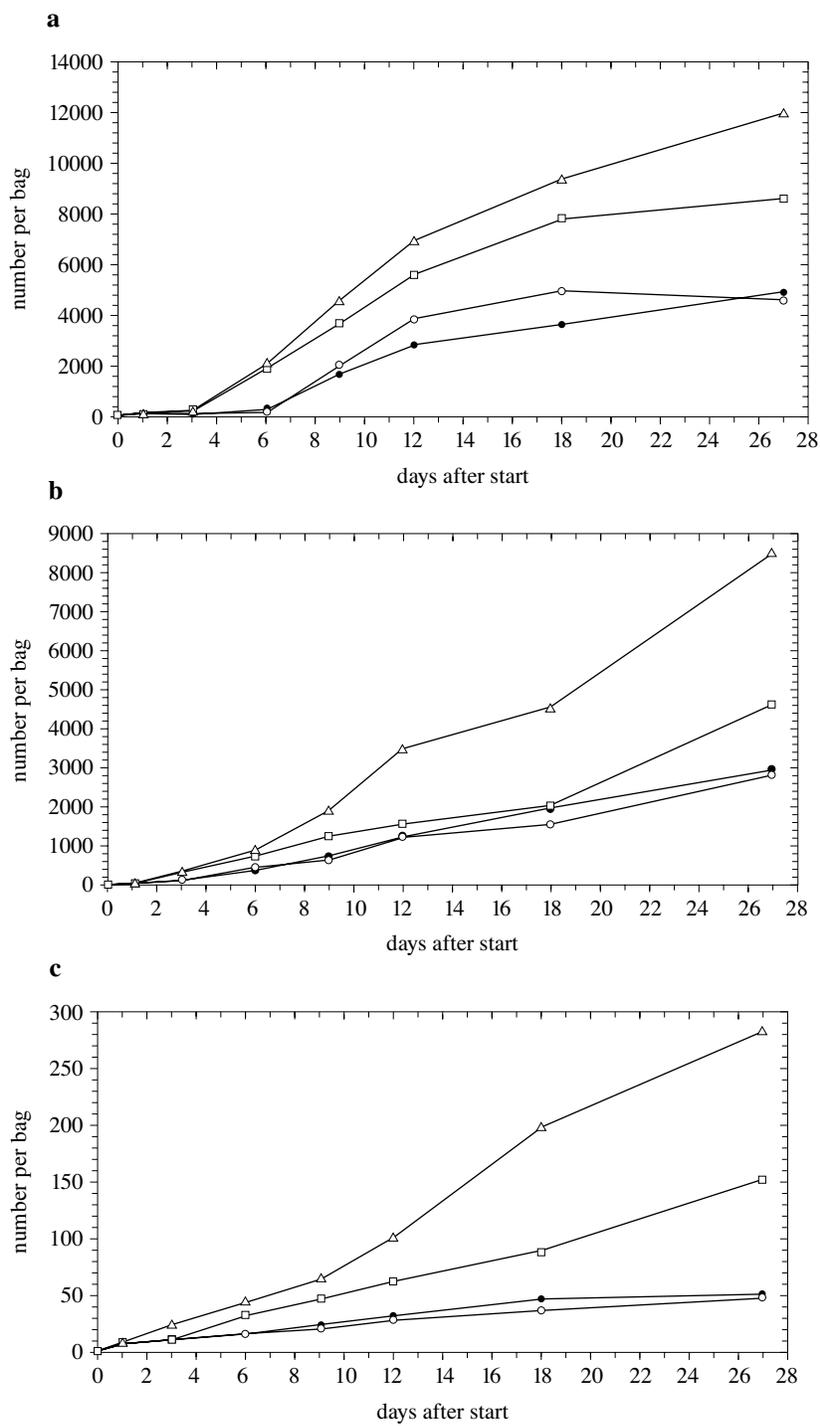
Table 3. Percentage composition and total numbers (N) of meiofauna collected from the beach sand beneath the litterbags. The figures are the samples pooled over all mesh types and dates from all study periods

	N	% of community
Nematoda	2567200	46.60
Oligochaeta	1067500	19.38
Turbellaria	985200	17.89
Gastrotricha	848320	15.40
dipteran larvae	–	0.00
Acarina	40258	0.73
Collembola	–	0.00
Total	5508478	

Dipteran eggs were found on the seagrass leaf surface from Day 1 to 27, but were most abundant within the first 9 days. This corresponds to the peak in adult abundance. Oviposition appears to have been hindered by the 48- μm mesh litterbags, as few eggs were recorded in these samples (Fig. 2b). However, the data shown in Fig. 2c do not corroborate this observation. Indeed, the number of dipteran larvae on the wrack surfaces was not less in the 0.5-mm or the 48- μm mesh bags. The number of larvae found on the eelgrass leaves was highly variable and no clear temporal pattern of colonisation was discernible.

Numerically, nematodes dominated the wrack fauna (Table 2). Their numbers increased dramatically after Day 9 in the coarse bags, and after Day 3 in the 48- μm mesh bags (Fig. 3a). In total, nematodes comprised 60% of the meiofaunal community in the leaf surface and 47% beneath the debris. Their abundance was not reduced by the 48- μm mesh. Indeed, greater densities of nematodes were recorded within this mesh size than in the larger mesh bags. This was also the situation with turbellarians, oligochaetes and gastrotrichs (Fig. 3b, c and d), which were found in greatest numbers after Days 9–27, when they were consistently more abundant within the 48- μm mesh bags. However, oligochaetes were more abundant in the sand beneath the wrack (19.5%), in contrast to the leaf surface, where their numbers were < 1.5%.

Acarina were found on the seagrass leaf surface throughout the sampling period (Fig. 3e) but were characteristically found in greatest numbers when the leaves were in an advanced state of decay. Again, the 48- μm mesh bags

**Fig. 3.**

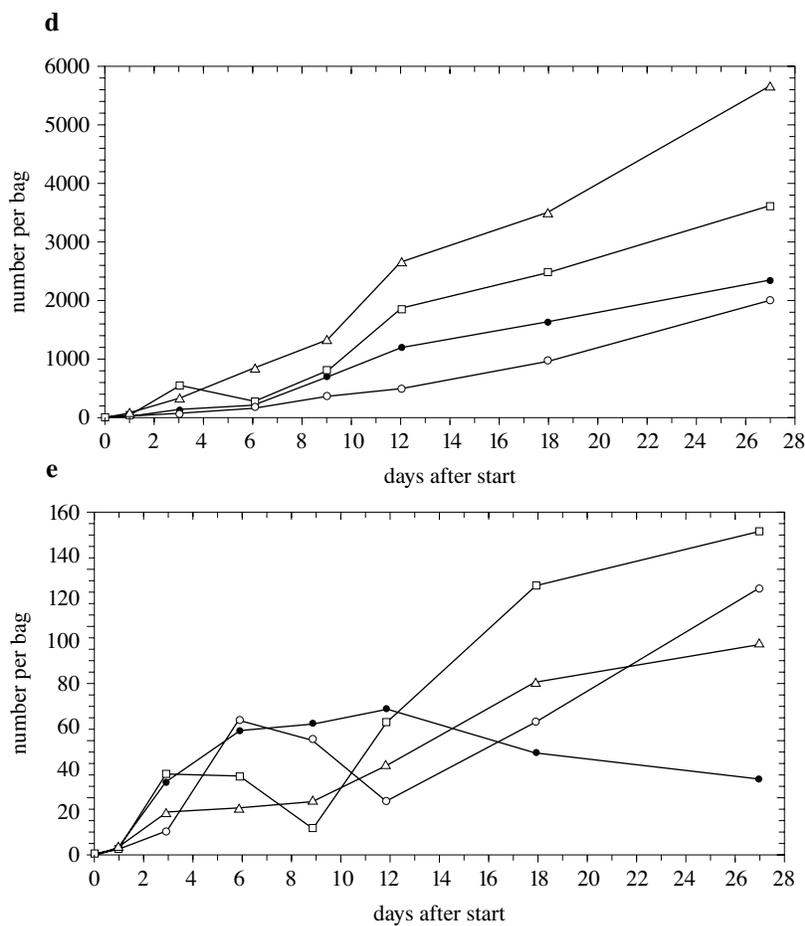


Fig. 3. The mean number of nematodes (a), turbellarians (b), oligochaetes (c), gastrotrichs (d) and mites (e) per litterbag sample: coarse mesh bags in the first trial (●-●); coarse mesh bags in the second trial (○-○); 0.5-mm mesh bags in the first trial (□-□); 48- μ m mesh bags in the second trial (Δ - Δ)

proved ineffective in restricting access of the mites to the leaf surface, so 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.

Collembola constituted only 0.61% of the meiofaunal numbers (Table 2); their presence in the litterbags was sporadic, and only a small number of bags contained them.

4. Discussion

Successional changes in the fauna of wrack litter have also been reported by Griffiths & Stenton-Dozey (1981), Inglis (1989), and Colombini et al.

(2000). Analysis of the species succession in the colonisation of the wrack shows that not all species invade the debris at the same time. Many of the macrofaunal species undergo tidal, wave or beach slope migrations of some kind that allow them to feed on freshly stranded debris. The next step is the migration of predators to the supralittoral zone to prey on the saprophagans (McLachlan 1983, Brown & McLachlan 1990). As a consequence, the population dynamics and migrations of many of the species are directed towards maximising utilisation of food resources (Koop & Field 1980, Behbehani & Croker 1982, Marsden 1991b). Indeed, the observations of Inglis (1989) show that only a small proportion of the material deposited on sandy beaches remains there sufficiently long to reach an advanced state of decay, which agrees with the conclusions of Colombini et al. (2000). In spite of all the local differences, the general trends in the composition of the macrofauna, such as the abundance of talitrids, Diptera and beach beetles Staphylinidae, Ptiliidae, and Histeridae, and the virtual absence of the Tenebrionidae, were also confirmed by Inglis (1989). In this case 28% of the community consisted of the amphipod *Talorchestia quoyana* (Milne-Edwards) and 48% of Diptera, while 5% of the meiofauna were dipteran larvae. Moreover, Stenton-Dozey & Griffiths (1980) reported that the most important herbivores in the degradation of driftline wrack on a South African sandy beach were the amphipod *Talorchestia capensis* Dana and the larvae of the kelp fly *Fucellia capensis*. However, this contrasts with the composition of the surface-active fauna reported by Colombini et al. (1998, 2000).

Talitrid amphipods are generally considered to be primary colonisers of newly stranded wrack (Robertson & Mann 1980, Griffiths & Stenton-Dozey 1981, Inglis 1989, Marsden 1991a, b, Colombini et al. 2000) and, in temperate areas, often dominate the supralittoral fauna of beaches with a moderate macrodebris input (Griffiths & Stenton-Dozey 1981, Behbehani & Croker 1982, Stenton-Dozey & Griffiths 1983, Marsden 1991a, Scapini 1997, Węśławski et al. 2000a, b, Persson 2001). Moreover, Bedford & Moore (1984) have shown that feeding by the amphipod *Gammarus locusta* may even inhibit decomposition by the selective removal of rotting weed. The present studies indicate that during the early colonisation of the deposits at Hel by *T. saltator*, this species also showed a tendency to forage on freshly stranded material. Marsden (1991a) reported that the juveniles of *T. quoyana* occur lower on the shore as compared to adults, and have a stronger association with fresh debris than with old macrophytes. Mediterranean and Atlantic talitrid populations show differences in orientation, zonation and spontaneous migration on the beach, all of which are related to differences in tidal amplitude. In particular, Mediterranean sandhoppers

migrate towards the dune for feeding, whereas Atlantic sandhoppers feed downshore on fresh wrack (Scapini 1997). In microtidal waters, talitrids alter their position as the water level changes (Scapini 1997, Persson 2001). Among other sandhoppers, *T. saltator* tends to occupy coarse sand sites just above the high water mark (Costello et al. 1999). On Polish beaches in summer, densities of sandhoppers are highest between 2 and 4 m from the waterline, in contrast to the colder or stormier periods of spring and autumn, when they retreat dunewards from the shoreline. Węśławski et al. (2000a) reported that Baltic talitrids could be making a significant contribution to organic matter processing at the driftline in summer.

Little is known about the structure of beetle communities on the Polish coast. Sandy beaches are usually inhabited by numerous Coleoptera species with varying degrees of dependence on and adaptation to marine environments (Doyen 1976). Invasion of wrack by predator species more or less coincides with that of amphipods and isopods. Adult cincindelids and some staphylinids are the most obvious beetle inhabitants of the high intertidal. Their larvae normally occur well above the intertidal, and are submerged only during storms, or very briefly during exceptionally high tides. The wrack provides food, probably first in the form of trapped small marine organisms and later in the crustaceans and the fly larvae that soon appear. The wrack deposited by the highest tides or storms remains on the beach longest – up to 15–20 days – and consequently accumulates the largest population of insects. Staphylinids do not breed in the wrack, and few larvae are ever found there (Moore & Legner 1976). In the present study, however, there was a conspicuous abundance of staphylinids during all phases of the experiments.

Also included in this group are numerous other beetle species from such diverse families as the Anthicidae, Chrysomelidae, Curculionidae, Histeridae and Ptiliidae, which frequent the driftline, feeding on decaying wrack. Though characteristic of seashores, these beetles are not aquatic and are very seldom submerged. Changes in microclimatic conditions, particularly relative humidity, may account for their spatial and temporal distribution. Colombini et al. (1998, 2000) reported on the distribution of the ptiliid *Actinopteryx fucicola*, which colonised the wrack soon after it had been deposited. Doyen (1976) also noted that the ptiliid family is not aquatic. While it is possible that Ptiliidae feed on decaying wrack, they are more likely to do so on fungi. The preference of Ptiliidae for wet conditions, however, was also noted in the present study. Anthicidae and Histeridae are certainly predatory, and Chrysomelidae and Curculionidae may drift into the wrack or immigrate from the nearby dune vegetation. The histerid, *H. quadrinotatus*, however, colonised wrack deposits at the end of their

residence period in the high eulitoral, which corresponds well with the findings of Colombini et al. (2000).

Other species, less mobile or occurring lower in the intertidal zone, are probably regularly submerged by high water. This group includes some Carabidae, Coccinellidae, and at least the tenebrionids. The carabids actively move over the sand during low water. There are some carabid beetles that regularly feed on staphylinids, but not on the genera listed here. A food link does exist between the carabid genus *Dyschirius* and the staphylinid genus *Bledius*, but this does not hold for all the relevant species. In turn, the herbivore assemblages on which they prey attract coccinellids into the supralittoral zone. Their abundance varies in relation to the development of the Coccinellidae population in typically inland areas behind the beach. In Poland, the rapid rise in the coccinellid population begins in May and continues until July. Tenebrionids are associated with beached algae or dead fish, and may occur on shingle beaches, but are more prevalent on sandy substrates. Some tenebrionids occupy nearly every sizeable heap of wrack and are restricted to their food substrate, but some are frequently found buried in the sand around their food, sometimes to a depth of 10 cm or more (Aloia et al. 1999). All of these species are common in supratidal sands, where they are usually associated with Staphylinidae, Histeridae, Anthicidae and other Coleoptera, and only marginally occupy the intertidal zone. The virtual absence of tenebrionids in the present study is in good agreement with findings of Colombini et al. (2000).

The adults of sandy beach kelp flies are probably insignificant consumers of wrack (Griffiths & Stenton-Dozey 1981, Szadziewski 1983) because their activities are limited to feeding on substances exuded from rotting seaweed and to laying eggs; they also use the piles of beach wrack for shelter. In temperate areas, they continue to breed even in the hardest winters as they utilise the relatively constant environment deep in the rotting seaweed of wrack patches. Adult Diptera are attracted to the beds of wrack within a few hours of its deposition. The initial decay of the seaweed produces areas where the temperature is higher than in the surroundings, and it is here that the eggs are laid (Colombini et al. 2000). The newly hatched larvae attack the weed for food and so accelerate and spread the decay. This in turn attracts more egg-laying females, and so the cycle continues (Kaczorowska 2001b, c). Provided that there are sufficient numbers of breeding adults, the whole interior of the wrack bed may become a mass of growing larvae in warm decaying seaweed. The larvae, however, may contribute greatly to the breakdown of wrack tissue as a result of their own feeding activity and through the spread of microorganisms (Dobson 1976, Simpson 1976, Stenton-Dozey & Griffiths 1980, Szadziewski 1983, Inglis 1989). *F. tergina*

is a common species of seaweed fly on the Polish coast (Kaczorowska 2001b, c). These initial investigations suggest that *F. tergina* appears to have a pattern of development similar to that of the South Africa kelp fly, *F. capensis* (Stenton-Dozey & Griffiths 1980), and the New Zealand seaweed fly, *Leptocera (Limosina) aucklandica* (Inglis 1989). Adults lay eggs on material deposited by waves and storms and the larvae mature before the next high-water period. Colombini et al. (2000) noted the absence of larval forms; this is probably related to the short residence time of the beach wrack, which is less than the 28-day reproductive period calculated for *F. capensis* (Stenton-Dozey & Griffiths 1980) and the 27 days for *F. tergina* (Kaczorowska 2001a, d). In the present investigation, this period was long enough for the development of the larval stages.

Numerically, nematodes and turbellarians dominated the wrack fauna in the later stages of decay. However, in the sand beneath the wrack, oligochaetes were the third-largest group. Inglis (1989) recorded a dramatic increase in nematodes and oligochaetes from day 9 to 18 in the coarse-mesh litterbags. By virtue of their numbers alone, all these groups may be of considerable importance in reworking and triturating debris, and their activity can stimulate bacterial metabolism, leading to the rapid decay of plant tissue (Inglis 1989, Jędrzejczak 1999). As a study by Koop et al. (1982) has shown, very steep gradients of dissolved organics occur below drift kelp, and DOM concentrations in such areas are very high. The material released by the decomposing wrack is consumed very rapidly in the sand within distances of 1 m and less. It thus seems likely that the distribution of meiofauna results directly from the high DOM levels in the interstitial water below the decomposing material and the ensuing strong chemical gradients. Gerlach (1977) notes a similar aggregation of meiofauna under decomposing animal matter. It is highly likely that the meiofauna uses the high DOM concentrations in the interstitial water below the debris as a direct food source (Giere 1975). Furthermore, the distribution of oligochaetes in the present study suggests that they feed on the metabolites of the other meiofaunal groups rather than directly on the wrack surface. However, the striking difference with the above-mentioned beaches was the absence of nematodes, oligochaetes and collembolans in the wrack during the study by Colombini et al. (2000), which is probably due to the short residence time of the wrack on the beach (c. 14 days). This may therefore indicate that the meiofaunal forms tend to colonise very old wrack.

However, the possibility cannot be excluded that the initial utilisation of DOM is by bacteria and that these in turn constitute the food source of the meiofauna. In a study on the biodegradation of kelp cast up on beaches, Koop et al. (1982) highlighted the importance of bacteria in the

breakdown of organic material in sandy beaches. They point out that large standing stocks of bacteria may be expected, even if the initial agents of biodegradation are invertebrate macrofauna. Generally, these species then produce smaller particles and faeces, which form a substrate on which bacteria can act. The meiofauna may have an analogous role within the intertidal sediments. Nematodes, turbellarians and oligochaetes were found in greatest numbers when the density of the saprophagous microbial community was greatest (Olańczuk-Neyman & Jankowska 1998), although it is not clear if they were grazing the microbiota directly or if the latter facilitated the phytophagy of the former, which is suggested by Inglis (1989). Thus, despite the rather low contribution to the productivity of the beach as a whole, the macro- and meiofauna may be of disproportionate importance in the initial process of fixing particulate organic material and making it available for mineralisation by bacteria in the interstitial environment.

At the waterline, Olańczuk-Neyman & Jankowska (1998) recorded the largest numbers of saprophytic, mesophytic and faecal coliform bacteria in comparison to other beach zones, where the highest organic content and the highest numbers of meiofauna are to be found. Thus, the waterline and splash zone, where filtration and oxygenation of the water are good, are likely to be a very attractive habitat for interstitial fauna, a fact reflected in the high biotic oxidation rate observed by Urban-Malinga & Opaliński (1999, 2001). Wachendorf et al. (1997) confirm the general trends in the successional progress of lake margin litter decay: the succession moves from the consumption of organic matter by macro- and meiofauna to microbial and physical breakdown.

This paper shows the significance of wrack on a beach where the food is supplied entirely by the sea. On Hel Beach the colonisation of deposits by fauna is influenced largely by the temporary presence of debris on the beach. Only some species are capable of exploiting the wrack, and their successional colonisation is strongly influenced by their physiological needs. There are significant differences in the faunal communities during the decay process. The succession from macro- to meiofauna is the principal feature of the changes in the community. Amphipods, herbivore beetles and seaweed flies are attracted to fresh deposits, on which they feed and lay eggs, and these subsequently attract predatory species (Staphylinidae, Coccinellidae, Carabidae). The grazing of amphipods and other detritivores accelerates the decomposition of vascular plant material by the mechanical action of tissue fragmentation, or alternatively, by the selective grazing of the microbiota, which leads to a general increase in the community metabolism through the excretion of nitrogen-rich materials enhancing microbial growth. Meiofaunal assemblages play an important part in the colonisation of very old wrack.

It is probable 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 in the supralittoral zone of a sandy beach.

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